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Diet and Feeding Behavior in Adults of the Apteropanorpidae (Mecoptera)

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The Apteropanorpidae is a small family of scorpionflies endemic to Tasmania. The biology of the family is almost completely unknown. Here we present results of laboratory and field studies of the diet and feeding behavior of adult Apteropanorpidae. We describe the morphology of the alimentary canal and mouthparts and discuss the relationship between diet, feeding behavior and morphology. We compare these results to the feeding ecology of other extant Mecoptera, and speculate on the feeding strategies of fossil Mecoptera, placing all data in a phylogenetic context. Results show that adult Apteropanorpidae are most likely saprophagous in nature, predominantly on dead and decaying invertebrates.

KEY WORDS: Apteropanorpidae; Mecoptera; diet; feeding behavior; related morphology; fossil record.

INTRODUCTION

Apteropanorpa is a small genus of Mecoptera (scorpionflies) endemic to Tasmania, comprising two described species. *Apteropanorpa tasmanica* (Fig. 1) was described from specimens collected from low shrubs on Mt Wellington and on snow from Mt Mawson, southern Tasmania (Carpenter, 1941). Many authors since then have emphasised the presence of this species on snow by omitting mention of its co-occurrence on shrubs

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Fig. 1. Adult male of *Apteropanorpa tasmanica* on kerosine bush (*Ozothamnus ledifolius*, Asteraceae) collected from the summit of Mt Wellington, Tasmania.

(e.g. Riek, 1970; Byers, 1991). A mecopteran larva described from Mt Wellington (Evans, 1942) has been attributed to this species; however, nothing else is known about the immature stages. The second species, *A. evansi*, was described recently from specimens collected on shrubs along the shore of Lake Augusta, Central Plateau Conservation Area, central Tasmania (Byers and Yeates, 1999). *Apteropanorpa* is the only genus in the family Apteropanorpidae. Very little is known of the biology of this intriguing family, and most published reports have been speculative. Unlike most other species of Mecoptera, adult members of the genus are wingless, and unlike most other insects, adults of *Apteropanorpa* can be active in winter.

Diet and feeding behavior is one feature of adult mecopteran biology that has received a high level of attention compared with the relatively low number of species in the order. For example, Mochizuki (1998) examined the characteristics of digestive proteases in the gut of 20 exemplars of 13 insect orders, and discovered the presence of metallo-, serine and cysteine proteases in the gut of an unidentified species of *Panorpa* (Panorpidae). He concluded that these protease identities did not reveal feeding strategy but did have phylogenetic value.

There is a close association of feeding and complicated mating behavior in the Panorpidae and Bittacidae, in which the male provides the female with an arthropod as a nuptial gift (Bornemissza, 1966; Thornhill, 1976). This has probably accelerated the number of field and laboratory studies of feeding in other mecopterans, and the diets of species from several families are now known.

The misconception that Mecoptera are exclusively predacious continues, and members of the order are still cited as a conspicuous example of a predacious feeding strategy in insects. However, the known diets of mecopteran families are varied. Members of the Panorpidae are saprophagous, feeding predominantly on soft-bodied, dead arthropods in nature (Byers, 1963; Thornhill, 1980). They have also been observed to feed on vertebrate carrion (Hetrick, 1935; Thornhill, 1980), and fruit juices and petals (Miyaké, 1912, 1913).

Adult bittacids are the only active predators in the order, preying on a variety of arthropods, mainly insects (e.g. Bornemissza, 1966; Thornhill, 1976, 1977; Alcock, 1979). They also feed on nectar (Bornemissza, 1966). Members of the Boreidae are predominantly phytophagous on bryophytes (Cooper, 1974; Penny, 1977; Russell, 1979, 1982), but are also reported to be saprophagous on dead arthropods (Sukatsheva and Rasnitsyn, 1992). Adults of *Brachypanorpa* (Panorpodidae) are wholly phytophagous, scraping the surface layers of soft leaves from a variety of plant species (Carpenter, 1953; Byers, 1997). The other panorpodid genus, *Panorpodes*, is probably also phytophagous, as it did not feed on animal protein provided as the sole food source in laboratory experiments (Miyaké, 1913). Very little is known of the diets of members of the Eomeropidae, Choristidae, Meropeidae and Nannochoristidae, probably because of their restricted distributions, providing few opportunities for collecting live specimens for study. *Notiothauma*, the only genus in the Eomeropidae, has been collected by baiting with rolled oats (Peña, 1968) and the stomach contents of adults contain compacted fragments of plant material (Hepburn, 1969), indicating saprophagy or phytophagy. Adult choristids fed on dead insects, fresh fruit, carrots and beef in laboratory experiments (Bush, 1967; Byers and Thornhill, 1983). Hepburn (1969, p. 164) speculated that members of the Choristidae and Meropeidae are "probably saprophagous" and the nannochoristids "might be liquid feeders of some kind", on the basis of mouthpart morphology. He also noted that the gut contents of *Apteropanorpa tasmanica* had a texture similar to food fragments in the mesenteron of bittacids and panorpids, and are "very probably of animal origin" (Hepburn, 1969, p. 164). Byers (1971, p. 486) disagreed, stating that although animal matter is the primary diet of the Bittacidae and the Panorpidae, "there is no evidence that food of animal origin enters into the diet of mecopterans of any of the other seven families". He later became less certain, stating that "the gut contents of *A. tasmanica* suggest that it also feeds on plant material; but the shape of the adult mandible is consistent with predatory feeding" (Byers and Yeates, 1999).

Here we present results of laboratory and field studies of the diet and feeding behavior of adult Apteropanorpidae. We describe the morphology of the alimentary canal and relate these data to likely feeding strategies. We compare these results to the feeding ecology and mouthpart morphology of other extant Mecoptera, and speculate on the feeding strategies of fossil Mecoptera, placing all data in a phylogenetic context.

Diets of larval Mecoptera may differ from that of adults; for example, bittacid larvae are saprophagous, and have been maintained in the laboratory on chopped beef, dead moss roots, and fresh grass (Setty, 1931). However, we do not have information on the diet of larval Apteropanorpidae, and so will not comment any further on the diets of mecopteran immatures.

MATERIALS AND METHODS

The systematics of the Apteropanorpidae is currently being studied, and several new species will be described in a forthcoming publication. In this study, new species and populations will be referred to by their locality, while the systematics is being finalised.

Morphology and Light Microscopy

For comparative morphology of the male alimentary canal and adult mouthparts, adults were obtained from several sources. Five well-preserved males and five well-preserved females were selected from pitfall trap samples from Mt Weld, southwest Tasmania (43°00′ S, 146°34′ E) April 2001, altitude 1200 m. Males and females of *Apteropanorpa* were collected from the summit of Mt Wellington, southern Tasmania (42°53′ S, 147°14′ E) on two occasions: 19.vii.2001, C. M. Palmer & D. K. Yeates, and 23.iv.2002, C. M. Palmer. All specimens for dissection were collected and dissected in 80% ethanol. Figures 2 and 3 were prepared with the aid of a camera lucida mounted on a binocular dissecting microscope.

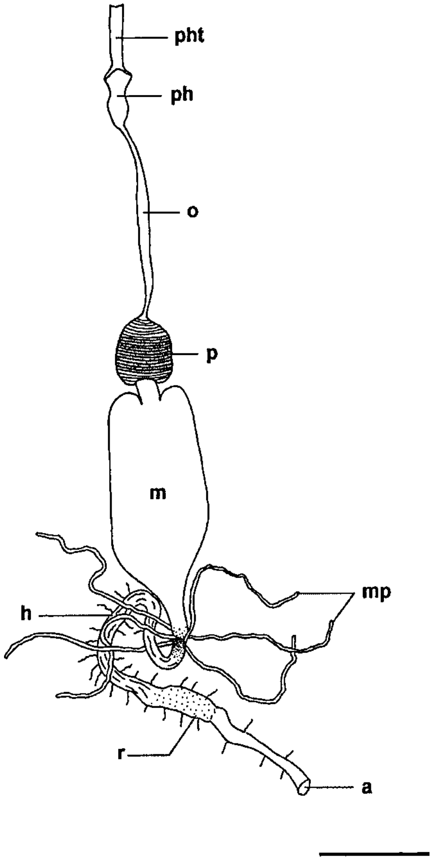

Fig. 2. Male alimentary canal of *Apteropanorpa tasmanica*, ventral view. Abbreviations: a, anus; h, hindgut; m, midgut; mp, malpighian tubules; o, oesophagous; p, proventriculus; ph, pharynx; pht, pharyngeal trough; r, rectum. Scale bar: 1 mm.

Morphology and Histology of Midgut Contents

Adults were collected from a variety of sources for studying the midgut contents: one male and two females of *A. tasmanica* from Mt Wellington summit, 1270 m, 21.vii.2001, C. M. Palmer and O. Seeman; one male of *A. tasmanica*, Mt Wellington summit, 1270 m, 23.v.2002, C. M. Palmer; eighteen males and two females from Mt Weld, pitfall trap, April 2001, 1200 m,

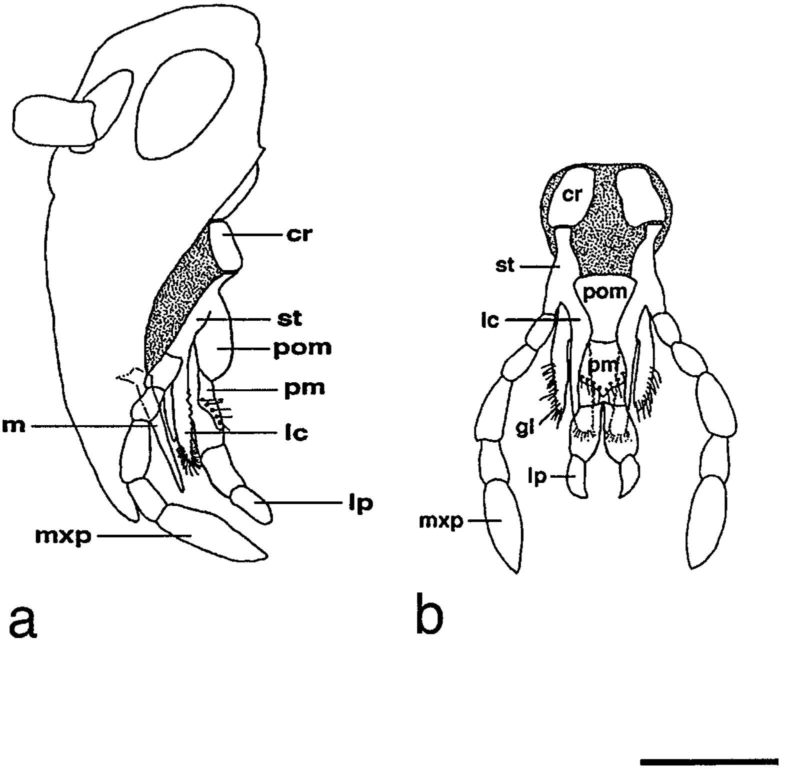

Fig. 3. Male mouthparts of *Apteropanorpa* sp. from Mt Mawson, Tasmania: (a) left lateral view; (b) posterior view (remainder of head removed). Abbreviations: cr, cardo; gl, galea; lc, lacinia; lp, labial palpus; m, mandible; mxp, maxillary palpus; pm, prementum; pom, postmentum; st, stipes. Scale bar: 0.5 mm.

R. Bashford and N. Doran; four males and four females from Mt Murchison, 1200 m, 27.iv.2002, C. M. Palmer, O. Seeman, H. Nahrung and S. Baker. These specimens were also used for examination with scanning electron microscopy, and the method used for this is discussed in the next section. Each adult was rehydrated through a graded series of ethanol (95, 80, 50 and 30%, respectively) before being dissected in water. Once specimens were rehydrated, the gut contents of each specimen were removed, spread out on glass slides and allowed to air dry at room temperature. Samples from each specimen were examined unstained under a Zeiss Stemi SV 6 binocular microscope, as well as being examined stained for the presence of the following compounds: cellulose, chitin and fungal material. The presence of cellulose and/or chitin may indicate a phytophagous or mycophagous diet, or may indicate whether *Apteropanorpa* is predacious or saprophagous on insects. The methods used to detect each compound are those described by Post and Laudermilk (1942) for cellulose, Campbell (1929) for chitin, and Gridley (1953) for fungi. Plant and fungal materials, as well as samples of insect exoskeleton, were used as positive and negative controls in each protocol.

Scanning Electron Microscopy (SEM)

For examination with SEM, midgut contents were rehydrated and extracted as for light microscopy. Droplets of water containing gut contents were placed on the surface of an aluminium stub to which carbon tape had been attached. The droplets were then air dried at room temperature before sputter coating with gold. Mandibles were dissected from adult males and females, dehydrated through a graded series of ethanol (30, 50, 80 and 95%, respectively) and then attached to an aluminium stub before drying in air and sputter coating with gold. All SEM images were digitally captured using a Cambridge S360 scanning electron microscope.

Feeding Choice Experiment

Twenty-two females and eleven males were collected over two days, from shrubs on Mt Mawson Plateau (42°41′ S, 146°34′ E), Tasmania, 13–14.iv.2003, C. M. Palmer. Possible food sources were also collected, but only on and around shrubs on which numerous adult scorpionflies were found. Food items selected included: lichen, moss, decaying and fresh leaves from host plants, dead and decaying arthropods, and live arthropods. These were selected as potential food sources based on the known adult diets of other mecopteran families (see Introduction). Each insect was maintained for one week in a small, clean, plastic specimen jar with air holes in the lid, at approximately 10°C, and in 12 h of low light per day to simulate autumnal conditions amongst shrubs at the collection site in Tasmania. The interior of each jar was sprayed lightly with rainwater every 2–3 days to maintain humidity and allow drinking. To prevent feeding the jars did not contain any other items. A circular, clear, plastic container and lid (diameter 12 cm, height 8 cm) was used for observations. A round, laminated cardboard disc covered the bottom of the feeding chamber. On this disc were drawn six, equally spaced 1 cm squares. The middle point between these squares was marked with a smaller square. Each 1 cm square was covered in equal amounts by one of the six potential food items. Each insect was then transferred to the central point between the squares and its behavior was observed for 1 h in low light, at approximately 10°C. A stopwatch was used to time relevant behavioral events over two days.

Field Observations of Feeding

Potential food items were stored separately for later identification whenever adults appeared to be feeding at the time of collection.

Members of the Apteropanorpidae were considered to be potentially predacious or saprophagous on dead animal matter, and in the event of such feeding strategies some shrubs on which adults were collected were also surveyed for abundance and diversity of other invertebrates. Four sites were chosen: the summit of Mt Wellington (42°53′ S, 147°14′ E), the summit of Hartz Peak, Hartz Mountains National Park, southern Tasmania (43°14′ S, 146°46′ E); below the summit of Mt Rufus, Cradle Mountain-Lake St Clair National Park, central Tasmania (42°07′ S, 146°05′ E); and along the shore of Lake Augusta, Central Plateau Conservation Area (41°51′ S, 146°34′ E).

Statistical Analyses

Data were interrogated in spreadsheets created in Microsoft Excel version 5.0 (Microsoft Corporation, Redmond, USA). The statistical program GenStat 7th Edition (VSN International Ltd, Hemel Hempstead, UK) was used to fit linear models and generalised linear mixed models (McCulloch and Searle) to data, and to calculate correlation coefficients.

RESULTS

Morphology of the Alimentary Canal

The alimentary canals of exemplars of several mecopteran families were described by Potter (1938), who examined *Brachypanorpa carolinensis* (Panorpodidae), *Boreus hyemalis* (Boreidae), *Merope tuber* (Meropeidae), *Chorista australis* (Choristidae), *Panorpa communis* (Panorpidae), and *Bittacus pilicornis* (Bittacidae). She showed that the alimentary canals of these species are similar, but there are interfamilial variations. This applies also to the alimentary canal of *Apteropanorpa* (Fig. 2). The epipharynx is a narrow, sclerotised trough. Posteriorly, the pharyngeal trough ends in two short, lateral arms, contiguous with the muscular, membranous pharynx (Fig. 2). The pharynx narrows into the long oesophagous, which expands into the oval proventriculus, the posterior of which connects to the midgut by a short, membranous duct often concealed by the anterior margin of the midgut. The position of the proventriculus varies among individuals, and can occupy the meso- or metathoracic segments or first abdominal segment.

The proventricular wall is endowed with circular and longitudinal muscles, and small, dark, finger-like acanthae, which project into the lumen. The midgut is short, narrowing posteriorly to form a conical tube, which narrows further still at the points of origin of the malpighian tubules. There are six malpighian tubules, in two groups of three, each group located laterally on the gut wall. That portion of the hindgut immediately behind the base of the tubules is dark, rapidly becoming pale. The hindgut is initially narrow, then widens slightly and remains so for the length of the rectum. The hindgut walls are endowed with longitudinal muscles, projecting into the lumen of the canal, forming internal folds. The hindgut and rectum walls are endowed with numerous, very small, translucent tracheae, which project into the body cavity. Rectal glands are apparently absent. The alimentary canal posterior of the rectum narrows before opening to the anus.

Morphology of Mouthparts

Each mandible is elongate, light yellowish brown, with a single acuminate tooth shortly before its inwardly curved apex (Fig. 4e and f). Each mandible possesses a narrow groove on its anterior surface, close to the inner margin, reaching the mandible’s edge at the tooth (Fig. 4f). The mandibular bases articulate anteriorly with the clypeus, and posteriorly by a condyle connecting to a process of the gena. The mandibles are largely obscured by the other mouthparts—in anterior view by the rostrum, and in posterior view by the maxillae (Fig. 3a and b). The basal cardo is subrectangular, distinctly wider than the stipes, the inner margin of the latter being prolonged, giving rise to the lacinia (Fig. 3a and b). The galea arises from a lateral articulation with the lacinia, and both sclerites are joined by membrane. The lacinia is toothed mesally and very setose distally. The maxillary palps are five-segmented, segment 3 is longer than 1, 2 or 4, segment 5 is thick at its base, with a narrowed, nearly acute apex; all segments are setose. Each of segments 1 and 2 possesses one long, dark bristle (as long as or longer than the maxillary segment), directed anteriorly. The mentum is hourglass-shaped and divided into subequal post- and prementum. Labial palps are two-segmented; the apical segment of each is narrowed toward the tip and is curved mesad.

Morphology and Histology of Midgut Contents

The unstained midgut contents of the Apteropanorpidae were mainly a homogeneous, brown, particulate mass under the light microscope. However, some small fragments contained fungal hyphae and fungal spores,

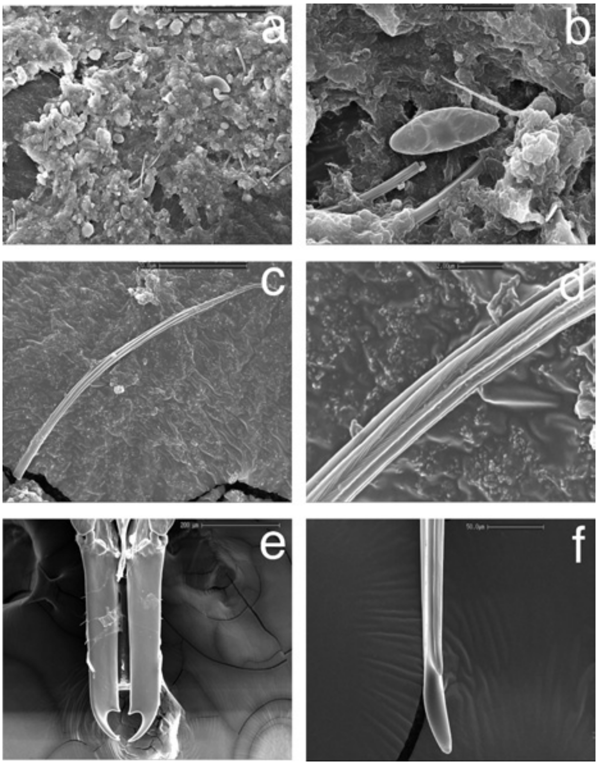

Fig. 4. (a–d) Midgut contents of *Apteropanorpa* spp. Round and fusiform objects in (a) and (b) are probably fungal spores. Long, striate structure in (c) and (d) is a hair or seta, (e) mandibles of male *Apteropanorpa* sp. from Mt Weld, Tasmania, anterior view (remainder of mouthparts removed); (f) right mandible of male *Apteropanorpa* sp. from Mt Weld, Tasmania, left lateral view (remainder of mouthparts removed).

some of which were identified as ascospores belonging to the genus *Podospora*. Other palynological material discovered comprised one pollen grain belonging to the coniferous genus *Podocarpus* (Podocarpaceae), and a single polyad belonging to the angiosperm *Acacia* (Mimosaceae). Midgut contents showed a weakly positive result for the presence of chitin and a positive result for the presence of fungal material. Siliceous mineral particles characteristic of plant tissue (phytoliths) were not detected. A negative result was obtained for the presence of cellulose.

The SEM yielded results similar to those produced by light microscopy. Identifiable fragments were occasionally found, such as hairs or setae

(Fig. 4c and d), and distinctively shaped structures which most likely were also fungal spores (Fig. 4a and b).

Feeding Choice Experiment

Of 33 adults (12 males, 21 females) included in the feeding experiments, 10 males (83%) and 15 females (71%) were observed to contact the selected food items with their mouthparts. Feeding began at any time between 2 s and 57 min from the commencement of observations. Forty-six mouthpart contacts occurred on dead invertebrates, four occurred on moss, and three on live invertebrates (Fig. 5). In most cases contact by mouthparts on invertebrates clearly indicated feeding. There were no such contacts on lichen, fresh leaves or decaying leaves and fungi. Contacts by adults other than with their mouthparts involved antennating or tarsal contact (e.g. when walking on or beside each potential food item). Numerous non-mouthpart contacts occurred on all potential food items, and most of these also occurred on dead invertebrates (Fig. 5). The higher number of non-mouthpart contacts on dead arthropods is due mainly to fifteen such contacts by one female. Figure 5 shows that adults visited dead arthropods approximately five times as often as any of the other potential food items. The cumulated time across the whole experiment during which the mouthparts of all adults were in continuous contact with dead arthropods is 13 h and 49 min (mean = 18 min and 1.3 s for each contact). The total time in contact with live arthropods was 2 h, 12 min and 56 s (mean = 44 min and 18 s), and with moss 2 min and 55 s (mean = 44 s). The average length of time each female fed on dead or live invertebrates (46 min and 7 s; $n = 15$) was longer than each male (32 min and 27 s; $n = 10$).

In an analysis of the proportions of feeding that included all potential food items, males (0.65) were shown to be twice as likely to feed as females (0.32). Across both sexes there was a 0.78 probability that contact with mouthparts would occur on dead arthropods, and a 0.20 probability that such contact would occur on any of the other five potential food items. Wald tests for fixed effects (GenStat 7th Edition) also showed that males were more likely to feed than females ($P = 0.039$), and showed that both sexes exhibited a preference for dead arthropods ($P \leq 0.001$).

Although feeding on live invertebrates was observed with three adults, there were fifteen contacts with live invertebrates that did not result in feeding. In the case of each non-feeding contact, the adult antennated on the invertebrate, which responded by moving. This movement startled the mecopteran, causing it to move quickly away.

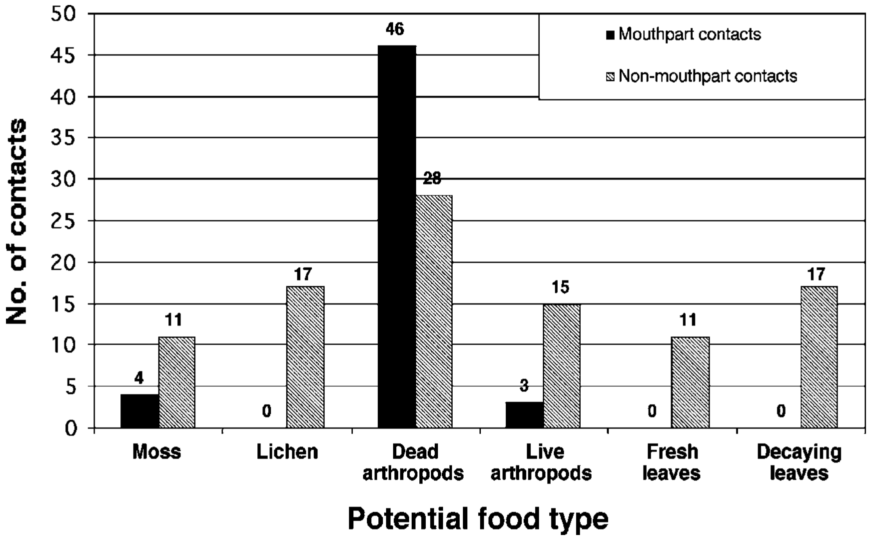

Fig. 5. Contacts by adult *Apteropanorpa* sp. ($n = 33$) from Mt Mawson, Tasmania, with potential food items in a feeding choice experiment (see text for details).

Feeding Behavior

Twenty-two adults (9 males and 13 females) were observed to feed on dead invertebrates. Two of these adults also fed on live invertebrates. An additional adult male fed exclusively on live invertebrates. Some aspects of feeding behavior were common to all 23 adults that fed on invertebrates, and varying numbers of these adults exhibited other aspects of feeding behavior (Fig. 6). There was no difference in behavior between males and females. In all cases of initial contact, *Apteropanorpa* antennated on food items and then slowly walked up to them, antennating continually until contact was made with the mouthparts. *Apteropanorpa* then fed by inserting its head into the body cavity of the invertebrate, selecting areas where the integument was already broken. These existing holes in the exoskeleton were then used as entry points into the rest of the body, and the soft internal organs were consumed. Cessation of feeding almost always occurred once the internal organs were consumed, and an empty ‘shell’ was all that remained. Occasionally an adult consumed the entire invertebrate, including the exoskeleton, but such behavior was unusual in this experiment ($n = 3$). Individual feeding episodes lasted between 3 s and 1 h, 27 min and 50 s.

Ten adults were observed to impale a dead invertebrate on the end of the rostrum and move the carcass to another part of the observation

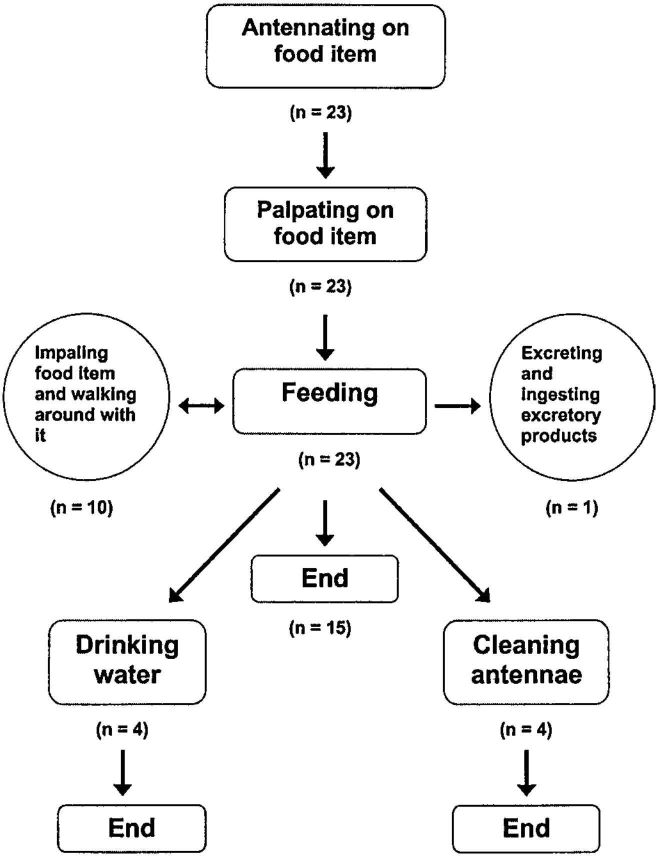

Fig. 6. Sequence diagram of feeding behavior in *Apteropanorpa* sp. from Mt Mawson, Tasmania ($n = 23$) (see text for details).

chamber to continue feeding (Fig. 6). At the cessation of feeding, fifteen adults were stationary or walked around the observation chamber, four adults drank water on the side of the container, and four different adults cleaned their antennae.

The three adults that fed on live invertebrates varied in their response to the invertebrates' movement. The adult male that fed exclusively on a live arthropod was undeterred by its movement and persisted in feeding on it for 1 h, 23 min and 21 s, until the whole animal was consumed. Two adults fed on both live and dead arthropods, and one of these mecopterans (a female) also continued feeding on the live arthropod for 49 min and 10 s, until all the internal organs were consumed. The third adult, a male, was startled by the invertebrate's movement during feeding, and ran away after 25 s.

Four adults contacted moss with their mouthparts, and each adult was either stationary or slowly moved its mouthparts along the moss surface. There was no insertion of the beak. The longest time that an adult was in contact with moss was 1 min and 25 s.

Field Observations of Feeding

Hundreds of adults have been collected from alpine shrubs all over Tasmania, and of these, only one male of *Apteropanorpa* sp. was observed to be carrying an item by its mouthparts. This male was collected in a beating tray from a sheltered depression approximately 5 m below the Mawson Plateau, at approximately 1260 m, approximately 300 m NW of Mt Mawson summit, Mt Field National Park, Tasmania, on 18 April 2002 (42°41′ S, 146°34′ E). At the time of collection this male possessed a small (1.9 mm long), decaying early instar nymph of a fulgoroid hemipteran in its mouthparts. Although it was not possible to observe whether the adult was feeding at the time of collection, it dropped the dead insect after approximately 2 min of walking around the collecting tray, indicating a reluctance to release it.

Invertebrates Associated with Members of the Apteropanorpidac

Invertebrates found in association with *Apteropanorpa* were both taxonomically diverse and very abundant. Non-insect invertebrates found included members of several families in the orders Araneae, Acari, and Isopoda. Flatworms (phylum Platyhelminthes) were also occasionally found. Adult and immature insects from the following orders were also very abundant: Collembola, Blattodea, Hemiptera, Diptera, Coleoptera, Lepidoptera and Hymenoptera.

DISCUSSION

Evidence for Saprophagy in *Apteropanorpa*

All the data presented here collectively suggest that members of the Apteropanorpidae have a scavenging and saprophagous feeding strategy. They most likely feed primarily on dead arthropods in nature, but may also feed on moribund invertebrates if that is the only food source available.

Apteropanorpids are unlikely to be predacious in normal circumstances. They do not possess conspicuous adaptations for a predacious feeding strategy, such as the large eyes and single-clawed raptorial tarsi present in the Bittacidae. The Apteropanorpidae antennate and palpate food before feeding, suggesting that sight is probably less important than olfaction in locating food, as is also the case in the Panorpidae (Thornhill, 1979), which employ the same feeding strategy. The Apteropanorpidae possess distinctive structures for implementing their feeding strategy. The long rostrum and mobile head allow the mouthparts to be inserted deeply into the arthropod body cavity, and the long hind legs facilitate access into the body cavity of the dead invertebrate.

Males were twice as likely to feed as females, which may occur because males are probably more active than females in searching for mates. Females may depend on males to provision at least some of their food, as is the case in *Harpobittacus*, in which females do not catch their own prey but are provided with nuptial prey to induce copulation (Bornemissza, 1966; Thornhill, 1977). Mating in Apteropanorpidae may also be preceded by males offering females a nuptial gift.

There is a large variety and abundance of invertebrates associated with the Apteropanorpidae on shrubs in the alpine zone. This association is so pronounced that it is possible to predict the presence of mecopterans by the abundance of associated arthropods. The co-occurrence is probably based partly on a potential food source for the Apteropanorpidae because, like the Panorpidae (Thornhill, 1980) and the Bittacidae (Thornhill, 1977), apteropanorpids do not discriminate between the taxa of invertebrates preferred as food. However, the association is probably also one of shared favourable microhabitat, because even when the Apteropanorpidae are absent in a particular locality, other arthropods are usually found aggregating on particular alpine shrubs (C. Palmer, personal observations). Ecological interactions were not apparent between *Apteropanorpa* and associated invertebrates collected as part of this study, although a parasitic association between *Apteropanorpa* and two undescribed species of mites has been observed on one occasion during other field studies, and this will be described in a forthcoming publication.

The much shorter periods of time that the mouthparts of four adults were in contact with moss could indicate that apteropanorpids will ingest some vegetable matter or, alternatively, moss may be a source of water. The only identifiable plant matter present in the midguts of 32 adults comprised one pollen grain belonging to *Podocarpus*, and one polyad from *Acacia*. *Podocarpus* is widespread throughout the alpine zone in Tasmania (Curtis, 1956; Kirkpatrick, 1997), and adult Apteropanorpidae have been collected from *Podocarpus lawrenceii* on mountains throughout western Tasmania. The presence of pollen grains from plants of this genus in the midgut is expected. *Acacia* is another genus which may be found in alpine areas

(Curtis, 1956); however, scorpionflies have not been collected from these shrubs. The very low incidence of pollen, the absence of plant phytoliths, and the negative result obtained in the test for cellulose indicate that the Apteropanorpidae are not phytophagous. Pollen is probably ingested incidentally when *Apteropanorpa* feed on invertebrates.

Light microscopy and histology showed that fungal material was more common than plant matter in the midgut. Several ascospores belonging to the coprophilous fungal genus *Podospora* were identified in the midguts of Apteropanorpidae. *Podospora* is an ascomycete fungus associated with humans or cattle (Van Geel, 2001) and requires dung as a substrate. How such spores could be present in the midgut is unknown, but ingestion was probably inadvertent. Midgut contents showed a weakly positive result for the presence of chitin. Chitin is present in the exoskeleton of insects, and the cell walls of fungal hyphae, supporting the notion that apteropanorpids include fungi in their diet. However, adults were not observed to feed on fungi offered in the feeding choice experiment, and as two-thirds of adults were observed to feed on dead and decaying arthropods it is more likely that most of the chitin ingested was of animal origin, and that fungal material was ingested inadvertently with carrion.

The type specimens of *Apteropanorpa tasmanica* were collected on snow from Mt Mawson, and from low shrubs on the summit of Mt Wellington (Carpenter, 1941). Carpenter's species description implied an ecology that is more similar to some members of the Boreidae, the snow scorpionflies of the Northern Hemisphere. However, extensive field collecting during this study has shown that *Apteropanorpa* is found on and beneath alpine shrubs, which provide shelter and food as other invertebrates die and fall to the ground. We have not collected any adults on snow, the color of which would contrast strongly with dark scorpionflies, possibly exposing them to predation during the day. Laboratory experiments showed that Apteropanorpidae are not adapted to survive temperatures much below 0°C (Palmer *et al.*, 2004), limiting their ability to survive for long periods on the snow surface. Based on this evidence the type specimens collected on snow in 1939 and 1940 are probably aberrant records.

Inferences About Diet from Comparative Morphology

Structure of the alimentary canal and mouthparts can be a morphological expression of the feeding strategy of a particular insect taxon. Examples are fluid-feeding Diptera, which possess sponging mouthparts and a large crop, the greatly elongate, siphonate proboscis of Lepidoptera, which feed largely on nectar, and the mandibulate mouthparts of Coleoptera, which are mainly phytophagous. Inferences of a particular feeding strategy based on comparative morphological studies are most useful in the absence of other data, a strategy that has been applied extensively to fossil taxa (e.g. Labandeira, 1997). This strategy can also be applied to extant taxa to support conclusions based on other evidence.

The alimentary canal of the Apteropanorpidae most resembles that of the Boreidae and Meropeidae: in all three families the combined length of the oesophagous, pharynx, and pharyngeal trough is longer than the midgut. In the Choristidae, Panorpidae and Bittacidae this combined length is much shorter than the length of the midgut. In *Bittacus pilicornis* the midgut is approximately ten times as long as the combined length of these three organs (Potter, 1938), and across the whole family typically constitutes about two-thirds the length of the entire alimentary canal (Byers, 1991). The midgut constitutes approximately one quarter the length of the alimentary canal in Choristidae and Meropeidae (Byers, 1991), and in Apteropanorpidae (see Fig. 2).

Adult body size varies markedly between families and this may partially explain size differences of various components of the alimentary canal. However, in Panorpidae (forewing length 9–20 mm) (Kaltenbach, 1978), and Apteropanorpidae (body length 5–10 mm) the midgut is much shorter compared to the remainder of the alimentary canal, and members of both families have a largely carnivorous diet. In the Apteropanorpidae, Choristidae, and Bittacidae the malpighian tubules are arranged in two groups of three around the alimentary canal, immediately posterior of the midgut. In the Meropeidae and Boreidae the malpighian tubules are equally spaced around the alimentary canal (Meropeidae) or arranged on the ventral and lateral planes (Boreidae). Potter (1938) did not specify the positions of the malpighian tubules in *Brachypanorpa*. The rectum bears six rectal glands in members of the Choristidae, Panorpodidae, Meropeidae, Panorpidae, and Bittacidae, but they are absent in both the Boreidae (Potter, 1938), and in the Apteropanorpidae. Rectal glands are involved in the reabsorption of water (Wigglesworth, 1972), a function which may be unnecessary in the environments in which apteropanorpids and boreids occur. The absence of rectal glands is reflected in the nature of the pellet excreted by the Apteropanorpidae, which takes the form of a droplet. During the feeding choice experiment one adult was observed to ingest the liquid droplet immediately after it was excreted, suggesting an alternative means of water reabsorption. Comparative morphology of the alimentary canal in the families examined does not provide information on adult mecopteran diets, and indicates that the various structures of the alimentary canal have a conservative evolutionary history.

Kaltenbach (1978) examined the mouthparts of exemplars from all mecopteran families except the Nannochoristidae. Mandibles are illustrated for the following taxa: *Merope tuber* (Meropeidae), *Notiothauma reedi* (Eomeropidae), *Chorista australis* (Choristidae), *Brachypanorpa carolinensis* (Panorpodidae), *Panorpa bicornuta* (Panorpidae), *Apteropanorpa tasmanica* (Apteropanorpidae), *Bittacus strigosus* (Bittacidae), and *Boreus nivoriundus* (Boreidae). The mandibles of *Apteropanorpa* are relatively long and narrow, and possess one subapical tooth. They are almost identical to the mandibles of bittacids, which also feed on arthropods. The mandibles of panorpids (saprophagous on dead arthropods) and the panorpodid *Brachypanorpa* (phytophagous on soft leaves) possess two subapical teeth. Based on the presence of these subapical teeth, one may conclude that panorpodids and panorpids share the same feeding strategy. However, panorpodids also bear numerous very small teeth near the base of each mandible (Kaltenbach, 1978). The mandibles of boreids, the only other family for which a phytophagous diet is known, possess four subapical teeth. Presence of small subapical teeth in phytophagous taxa implies they function in chewing plant matter. The eomeropid *Notiothauma* also has several subapical teeth, indicating a primarily phytophagous diet. The mandibles of choristids do not bear subapical teeth, and those of the Meropeidae bear two subapical teeth. Mandibles of the predacious Bittacidae are very long and narrow, while those of the phytophagous/saprophagous Boreidae and phytophagous Panorpodidae are short and stout. The mandibles of saprophagous Apteropanorpidae and Panorpidae, as well as the Choristidae, Meropeidae and Eomeropidae, are intermediate in length.

The function of the groove on the anterior surface of each of the apteropanorpid mandibles is unknown. It is possible that each groove is a channel along which fluid food is delivered to the pharynx, and that uptake of food is more efficient when the mandibles are occluded.

Head morphology of several families of Mecoptera is illustrated in Kaltenbach (1978). Excluding the mandibles, the remaining mouthparts also possess structural modifications, but these alone cannot be related to a specific diet. However, there is considerable familial variation in head shape with consequent changes in mouthpart morphology, some of which can be related to a particular feeding strategy. The front of the head in the Apteropanorpidae, Panorpidae, Bittacidae and two of the three boreid genera forms a distinct rostrum, traditionally the most recognisable synapomorphy of the order. In these families, some components of the mouthparts are elongated to accommodate this extension of the head; for example, the stipes of Panorpidae, and the strikingly elongated mandibles and maxillae of Bittacidae. Apart from the stipes, the remaining mouthparts in the Panorpidae constitute a small proportion of the length of the head. In Apteropanorpidae, the maxillary palps are relatively long, and this would help with tactility and probably olfaction of food items. During the feeding experiment adults were observed to move the maxillary palps over dead arthropods, after the food item had been located with the antennae, immediately prior to the commencement of feeding. The rostrum of Apteropanorpidae, Bittacidae, Panorpidae and Boreidae is probably an adaptation for allowing the head to be inserted deep into the body cavity of invertebrates. The rostrum is shorter and of variable shape in the remaining mecopteran families (Kaltenbach, 1978), with consequent shortening of the mouthparts. A prolonged rostrum is scarcely evident in the phytophagous *Brachypanorpa*, and the rostrum is short and very slender in the Nannochoristidae, so that adults superficially resemble nasute termites.

Mecopteran Diets and the Fossil Record

The Mecoptera have an ancient fossil record, dating back to the Permian (Carpenter, 1930; Riek, 1953; Pinto, 1972), and arose well before the evolution of angiosperms (Crane *et al.*, 1995). The origin of Mecoptera coincided with the Permian evolutionary radiation of many other insect orders, especially basal clades of the Hemipteroidea and Holometabola (Kukalová-Peck, 1991; Labandeira and Sepkoski, 1993). The wings of Permian mecopterans are almost always the only bodyparts preserved; however, a specimen of one species belonging to the Permopanorpidae is more complete. Most of the mouthparts in this specimen are not preserved, but the head possesses a short rostrum and relatively long maxillary palps and large compound eyes (Carpenter, 1930). From the more recent mid-Mesozoic, one genus comprising two species of fossil mecopterans dating from the Upper Jurassic and Lower Cretaceous has been placed in the Boreidae (Sukatsheva and Rasnitsyn, 1992), and these fossils are more complete. Their mouthparts are not preserved, but both species also possessed a shorter rostrum, characteristic of the extant phytophagous boreid genus *Caurinus*. The remaining extant boreid genera, *Boreus* and *Hesperoboreus*, possess the longer rostrum of saprophagous Panorpidae and Apteropanorpidae.

Fossil orthophlebiid scorpion flies and other species placed as *incertae sedis* in the Panorpidae, with long rostrum and hypognathous mouthparts, date from the Jurassic (Willmann, 1989; Sukatsheva, 1990; Labandeira, 1997). The heads of these species are morphologically very similar to those of the extant *Boreus*, *Hesperoboreus*, Apteropanorpidae, and Panorpidae, indicating that carrion has been a significant component of mecopteran diets for at least the last 150 million years. However, this has likely been the case for a much longer period of time, considering that the oldest fossil hexapods (Archaeognatha and Collembola) date from the Lower Devonian (e.g. Labandeira *et al.*, 1988), 100 million years before the oldest known fossil Mecoptera. A combination of saprophagy and phytophagy may also have been present in the Boreidae since at least the mid-Mesozoic.

Phylogenetic Implications in Extant Taxa

A recent (Whiting, 2002) molecular phytogeny of the Mecoptera and Siphonaptera based on combined evidence from 18S, 28S, EF-1α and COII genes, supports a paraphyletic Mecoptera with two major lineages: Nannochoristidae + (Siphonaptera + Boreidae) and Meropeidae + ((Choristidae + Apteropanorpidae) (Panorpodidae + (Panorpidae + Bittacidae))). The Eomeropidae were not included in this analysis. Mapping known mecopteran diets onto this phylogeny suggests that phytophagy has evolved independently in the Boreidae and Panorpodidae, and that the predacious feeding strategy of the bittacids has evolved from a saprophagous ancestor. Saprophagy in the Panorpidae and Apteropanorpidae has also evolved independently based on Whiting's hypothesised phylogenetic relationships. *Apteropanorpa* is one of the most basal taxa of the Mecoptera *sensu stricto*. Saprophagy may be the oldest feeding strategy of the order, however, the diet of the most basal taxon, *Merope*, is unknown.

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