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Terrestrial Planarians (Platyhelminthes: Tricladaida: Terricola) Predaceous on Terrestrial Gastropods

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Introduction

Triclads, also commonly known as flatworms or planarians, occur in marine, freshwater and terrestrial environments. They form an order within the turbellarian or free-living Platyhelminthes. The Platyhelminthes form a large phylum containing up to 15,000 described species, with many others yet to be described. Platyhelminthes are conventionally divided into the largely free-living ‘Turbellaria’ and the parasitic Neodermata comprising Trematoda, Monogenea, Udonellidea and Cestoda. It has been argued that the Class Turbellaria is paraphyletic (Ehlers, 1985) and that the name Turbellaria can no longer be used in the phylogenetic system of the Platyhelminthes (Ax et al., 1988). Nevertheless the taxon Turbellaria serves as a useful repository in the general sense for free-living and symbiotic planarians (all the non-neodermatans) without implying monophyly of these taxa (Rohde, 1994).

Terrestrial planarians are a relatively species-poor group with only 822 described nominal species worldwide, although some areas such as Australia, New Zealand and Brazil have many additional, as yet undescribed species (Winsor, 1997; Johns, 1998; Sluys, 1999; Leal-Zanchet and Carbayo, 2000; Carbayo et al., 2002). Species diversity is highest in parts of Brazil, Southeast Asia, Indonesia, Australia, New Zealand, Sri Lanka and Madagascar (Sluys, 1999). Some areas of the world are depauperate in terrestrial planarians – Europe for example has only ten extant indigenous species (Jones, 1998).

Given the worldwide distribution and yet very limited dispersal capabilities, Froehlich (1967) suggested the Tricladiida to be a very old
group, probably originating in the Upper Palaeozoic. There has long been interest in triclad organisms by biogeographers (du Bois-Reymond Marcus, 1953; Froehlich, 1967; Ball and Fernando, 1969; Sluys, 1994, 1995; Winsor, 1998c). Freshwater planarians have long been recognized as ‘indicators’ in the assessment of water quality (Kenk, 1974; New, 1995) but recognition of the potential role of terrestrial planarians as biodiversity and environmental indicators has been more recent (Sluys, 1998; Carabayo et al., 2002). The renewed interest in terrestrial planarians has also been stimulated by the adverse impacts on indigenous faunas effected by the predatory activities of invasive species.

**Taxonomy and Systematics of the Tricladida**

Three major groups have long been recognized within the Tricladida, for which Hallez’s (1890) ecological names were applied: Paludicola (freshwater planarians, inclusive of Dugesiidae), Terricola (terrestrial planarians) and Maricola (marine planarians). More recently, Sluys (1990) erected the Infraorder Cavernicola for three species of primarily cavernicolous planarians. The systematic and phylogenetic relationships of these infraorders have been discussed on the basis of morphological and ultrastructural characters by Ball (1977, 1981), Sopott-Ehlers (1985) and Sluys (1989), although the status of the Terricola was recognized as problematic (Ball 1981). The ecological connotation of these infraordinal names generally holds true, and until recently each suborder was thought to represent a monophyletic group.

Monophyly of the Terricola is not strongly supported by recent investigations using 18S rRNA sequences (e.g. Carranza et al., 1998a,b; Baguñà et al., 2001) and its position within the Tricladida needs to be reassessed. These DNA sequence data suggest the terrestrial planarians are derived from freshwater ancestors, and not from marine triclads as had previously been hypothesized (Ball, 1981; Sluys, 1989). These recent analyses support the monophyly of the Maricola, and paraphyly of the Paludicola and Terricola + Dugesiidae. They do not support the monophyly of the Terricola and Dugesiidae. On the basis of their molecular studies Carranza et al. (1998b) suggest that the Infraorder Terricola seems redundant and would be better afforded, like the dugesiids, the status of Family. However, these authors underline the need for more intensive molecular sampling to evaluate better the evolutionary status of the Terricola.

In cytochrome oxidase 1 (CO1) analyses, the Terricola and Dugesiidae cluster together, though the low support does not permit firm conclusions to be drawn regarding the monophyly of each of these clades (Baguñà et al., 2001). However, within the Terricola, the family Bipaliidae and the rhynchodemid subfamily Microplaninae appear highly supported as monophyletic clades (Baguñà et al., 2001).

Carranza (1997), Carranza et al. (1998a,b) and Baguñà et al. (2001) have also shown that, within Terricola, the Geoplanidae is probably
monophyletic. However, molecular analyses of representatives of the Geoplanidae have so far included only members of the Caenoplaninae. More taxon sampling in the molecular analyses of geoplaninids and especially the pelmatoplaninids is required before a firm view of the apparent monophyly of the Geoplanidae emerges. The molecular studies of these authors point to Microplaninae and Rhynchodeminae as independent lineages, in agreement with new analyses of morphological characters (L. Winsor and P.M. Johns, personal communication to Baguñà), thus highlighting the fact that Rhynchodemidae, as currently recognized, is an artificial clade.

The systematics of the terrestrial planarians, as that of the entire Tricladida, presents special difficulties because these animals lack clear external diagnostic characters. Thus, an exhaustive microscopical analysis of the internal anatomy, with emphasis on the copulatory apparatus, is usually needed for identification at the species level. Although almost all of the terrestrial planarians are hermaphroditic, the male and female systems are not necessarily present at the same stage of development in a given individual, and descriptions of protandrous and protogynous individuals have contributed to the present taxonomic confusion (Ball and Sluys, 1990). Moreover, immature animals lack the copulatory apparatus, thus preventing unequivocal identification.

The characters used for systematics and taxonomy of Tricladida have been reviewed most recently by Winsor (1998b) and Winsor et al. (1998). They involve a combination of external morphology and internal micro-anatomical characters. Colour and pattern of markings, number, pattern and distribution of eyes, body shape, specialization of head structures, presence of adhesive suckers, relative positions of body apertures, and width of creeping sole are important external taxonomic characters. Anatomical structures, particularly musculature and copulatory organs, are revealed by histological serial sectioning, staining and reconstruction.

Proper preservation of external and internal characters is essential for planarian identification. Specimens collected for taxonomic purposes are best anaesthetized in 10% aqueous ethanol, then fixed in a straightened body posture and stored in 4% formaldehyde, in 2% aqueous calcium acetate (anhydrous) 2 g, tap water 90 ml), or in modified Tyler’s fixative (Winsor, 1991, 1998a). Fixation in 100% ethanol results in poor material for anatomical investigations but is none the less required for molecular studies.

Despite the long tradition of systematic investigation in the Tricladida, and the recently renewed impetus, the terrestrial planarians remain a poorly known group. Worldwide only some 55% of named species are adequately known histologically, and further comparative anatomical descriptions are essential for advancing their systematics and taxonomy (Winsor et al., 1998). Recent extensive nomenclatural and revisionary changes to the taxonomy of terrestrial planarians have been made by R.E. Ogren and co-authors (Ogren and Kawakatsu, 1987, 1988, 1989, 1990, 1991; Ogren et al., 1992, 1993a,b, 1994, 1995, 1996, 1997a,b).
with a comprehensive coverage of the literature. None the less, consider-
able taxonomic revisionary work remains to be done on species-
and supraspecific-level taxa worldwide, and provision of comparable
descriptions is a priority.

Recently there has been interest in molecular markers as aids to
species identification (e.g. DeSalle and Birstein, 1996) and these method-
ologies are beginning to be applied to Platyhelminthes. Carranza (1997),
for example, has employed molecular markers to differentiate evolution-
ary units within the Dugesia gonocephala (Dugès) species complex
of dugesiid freshwater planarians, and Mateos et al. (1998) employed
sequence differences in the amplified ITS-1 region of ribosomal DNA
for specific differentiation in the Iberian terrestrial planarian genus
Microplana Vej dovský (Rhynchodemidae).

Terrestrial Tricladida

Terrestrial planarians are soft, unsegmented, bilaterally symmetric,
acoelomate, dorsally–ventrally flattened worms, 30–500 mm long. Their
epidermis is cellular, and usually at least partly ciliated. They lack
respiratory and circulatory organs, a skeleton, and an anus. They are
best regarded as muscular hydrocoelomates. The head of many terrestrial
planarians is either expanded and lunate, or tapered to a blunt point. Eyes
may be present on the head and along the lateral margin of the body.
A mouth, which also serves as an anus, is present near the midbody on the
ventral surface. Located within the mouth is a protrusible, posteriorly
directed, muscular pharynx that serves as a feeding organ and is attached
to the intestine. Prey are swallowed whole, or pre-digested before being
ingested by the action of powerful pharyngeal muscles; digestive enzymes
are secreted externally via special glands that empty through the pharyn-
geal lumen or from the tip of the pharynx. The intestine is divided into
one anterior median and two posterior branches, all of which are highly
diverticulate. A cerebral ganglion serves as a brain, innervating a ladd-
er-like, subepidermal nerve plexus and a well-developed submuscular
plexus that is continuous with a ventral nerve plate in the mesenchyme.
Excretion of fluid wastes is accomplished with a primitive proto-
nephridial system. The reproductive system is hermaphroditic. There are
few to many folliculate testes, but a single pair of ovaries, usually lying far
forward in the body. The female system is ectolecithal in that numerous
yolk glands are separate from the ovary, opening via short ducts along
the length of the oviducts. Reproduction is sexual by cross-fertilization,
or asexual by fission; some species can reproduce both sexually and
asexually. The body cavity between the various organs is filled with
parenchyma.

The following synopsis of the families and subfamilies is largely
drawn from Winsor (1998b). A pictorial key to the families is provided
in Fig. 5.1. The terrestrial planarians are presently recognized as
comprising three families: Bipaliidae, Rhynchodemidae (with subfamilies Microplaninae and Rhynchodeminae) and Geoplanidae (Geoplaninae, Caenoplaninae, Pelmatoplaninae).

Bipaliidae

Diagnosis (Kawakatsu et al., 2001): Elongate, flattened body, with semilunate headplate equipped with peripheral sensory pits. Many small marginal eyes occur on or near the headplate. Creeping sole narrow, beginning at the base of head. Reproductive system with simple copulatory organs, with male and female parts separated by a fold of tissue before they enter the common atrium, often with a copulatory bursa or diverticulum, but lacking accessory ducts/glands.

Genera: Bipalium Stimpson; Humbertium Ogren & Sluys, Novibipalium Kawakatsu et al., Diversibipalium Kawakatsu et al.

The family has long been treated as monogeneric, based on Bipalium. However, the genus has been recognized as heterogeneous and several authors point to the probable existence of several monophyletic clades,
some of which may warrant generic status (e.g. Ogren and Sluys, 1998; Winsor, 1998b). The genera Humbertium, Novibipalium and Diversibipalium were recently erected to accommodate some of this phylogenetic diversity. The majority of the 160 bipaliid species occur in the Indonesian archipelago, but the family ranges from Indonesia through Asia to Madagascar.

The best known bipaliid species is the now cosmopolitan Bipalium kewense Moseley, which is native of the highlands of Vietnam but has been transported worldwide together with plant material. The species, reviewed by Winsor (1983a), is frequently selected as a representative of non-parasitic Platyhelminthes in biology texts, and is used in a wide range of biological investigations. Several other Bipalium species have also become invasive outside their native range.

**Rhynchodemidae**

Diagnosis (Ogren and Kawakatsu, 1988): Elongate, cylindrical body form, with two eyes near the simple, tapered anterior end; no tentacles or headplate. Well-defined creeping sole occupying part of the ventral surface. Anterior end may have an adhesive organ on the ventral surface.

Divided into two subfamilies on the basis of cutaneous musculature.

**Rhynchodeminae**

Generally of elongate, flattened form, with anterior end usually tapered and elongate; eyes conspicuous. Body wall with strong subcutaneous musculature, the longitudinal fibres of which are grouped into large, well-developed bundles. Male and female genital pores separate or united. Penis papilla greatly reduced or absent.

Genera: Cotyloplana Spencer; Digonopyla Fischer; Dolichoplana Moseley; Platydemus von Graff; Rhynchodemus Leidy.

The subfamily occurs worldwide: Europe, eastern USA, central and eastern Africa, Madagascar, India, Southeast Asia, Irian Jaya–Papua New Guinea, New Caledonia, Pacific Islands, eastern Australia, Central America, Colombia, Peru, Brazil, Paraguay and Argentina.

Several rhynchodemines, including Dolichoplana feildeni von Graff, Dolichoplana striata Moseley and Rhynchodemus sylvaticus (Leidy), have been widely dispersed through human activities. The New Guinea species Platydemus manokwari de Beauchamp has been introduced into a number of Pacific countries as a biological control agent of the giant African snail Achatina fulica Bowdich (Achatinidae).

**Microplaninae**

Generally short, plump, cylindrical in form, with the anterior end often blunt; eyes often small or may be regressed. Body with weak subcutaneous musculature in which the longitudinal fibres are poorly developed
and not aggregated into large bundles. Male copulatory organ often complex, with the penis possessing a well-developed papilla. Female copulatory organs simple to complex, often with a genito-intestinal connection; seminal bursa present, with one or more exits, or entirely lacking.

Genera: Amblyplana von Graff; Diporodemus Hyman; Geobenazzia Minelli; Incapora du Bois-Reymond Marcus; Microplana Veidovský; Orthosoma Gray; Pseudartiocotylus Ikeda.

The subfamily is represented in Europe, eastern USA, western central and southern Africa, Madagascar, India, Sri Lanka, Vietnam, Japan, Central America, Peru and Surinam. The European microplaninine Microplana terrestris (Müller) is particularly well known (Ball and Reynolds, 1981).

Geoplanidae

Diagnosis (Ogren and Kawakatsu, 1990): With numerous small eyes concentrated around the anterior and along the sides, sometimes located dorsally, or without eyes; without auricular or tentacular organs, or semilunar headplate.

The family is divided into three subfamilies – the Geoplaninae, Caenoplaninae and Pelmatoplaninae – chiefly on the basis of the width of the creeping sole, the position of the testes and the organization of the cutaneous musculature.

Geoplaninae

Creeping sole 50% or more of body width. Cutaneous musculature in well-developed bundles. Testes dorsal.

Genera: Amaga Ogren & Kawakatsu; Choeradoplana von Graff; Enterosyringia Ogren & Kawakatsu; Geobia Diesing; Geoplana Stimpson (with two subgenera Geoplana s. str. and Barreiana Ogren & Kawakatsu) Gigantea Ogren & Kawakatsu; Gusana Froehlich; Issocca Froehlich; Liana Froehlich; Notogynaphallia Ogren & Kawakatsu; Pasipha Ogren & Kawakatsu; Polycladus Blanchard; Pseudogeoplana Ogren & Kawakatsu; Xerapoa Froehlich.

Geoplanines occur in South and Central America, and the south-eastern USA. Froehlich (1956) provides an interesting account of the biology of Neotropical geoplanids.

Caenoplaninae

With or without a creeping sole. Cutaneous musculature in well-developed bundles. Testes ventral.

Genera: Caenoplana Moseley; Arthurdendyus Jones & Gerard; Artiopathia von Graff; Australoplana Winsor; Australopacifica Ogren & Kawakatsu; Coleocephalus Fyfe; Endeavouria Ogren & Kawakatsu; Fletchamia Winsor; Kontikia Froehlich; Lenkunya Winsor; Newzelandia
Ogren & Kawakatsu; *Pimea* Winsor; *Reomkago* Winsor; *Tasmanoplana* Winsor; *Timyma* Froehlich.

Caenoplanines are mainly found in Australia, New Guinea, New Caledonia, Pacific Islands, New Zealand, Peru, Argentina, Madagascar, India, Sri Lanka, Philippines, Indonesia and Japan.

The best-known species is *Arthurdendyus triangulatus* (Dendy), a predator of earthworms (Annelida, Oligochaeta) native to New Zealand, which has been accidentally introduced into Great Britain, where it is a serious pest species. There is currently intensive research on this species.

**Pelmatoplaninae**

Creeping sole 25% or less of body width. Cutaneous musculature weak, in poorly developed bundles. Testes ventral.

*Genera:* *Beauchampius* Ogren & Kawakatsu; *Pelmatoplana* von Graff.

The pelmatoplanines occur as natives in Madagascar, India, Sri Lanka, Philippines, Thailand, Cambodia, Vietnam, Malaysia, Indonesia and New Caledonia. Several species have been dispersed outside their native range.

**General Biology and Ecology**

Accounts of the biology of the terrestrial planarians are provided by von Graff (1899, 1912–1917), Steel (1901), Bresslau (1927, 1933), Schirch (1929), Goetsch (1933), Pantin (1950), Froehlich (1956), Ball and Reynoldson (1981), Ogren (1995), and in a series of papers in both the *Proceedings of International Symposia on the Biology of the Turbellaria* (Cannon, 1995) and the *OECD Workshop on Terrestrial Flatworms* (Yeates, 1998).

**Physical ecology**

While primarily inhabitants of forests and woodlands, terrestrial planarians occupy a great diversity of ecosystem types. ‘They range in occurrence through mesophile to xerophile habitats; from alpine herbfields to sandy semi-desert, subantarctic rata forest to tropical rainforest’ (Winsor *et al.*, 1998, p. 397). Modern lineages are descendent from planarians that colonized land hundreds of millions of years ago but, despite their long evolutionary history on land, these animals still lack any special physiological or anatomical mechanism for water conservation (Kawaguti, 1932), but may have water-conserving biochemical waste-excretion pathways (L. Winsor, unpublished). They rely strongly on water-conserving behaviours. Most terrestrial planarians are part of the soil fauna, residing primarily in the upper soil layers and under debris and stones on the soil surface. They demand a humid microhabitat but
cannot endure long periods of immersion in water and thus avoid saturated soils. Normally nocturnal in habit, terrestrial planarians remain concealed during the day in humid refuges, and emerge to forage for food on overcast days following rain, and at dusk when the relative humidity of the air is high. These animals cannot endure heat and direct sunlight, as they desiccate quickly (Kawaguti, 1932). They are also strongly seasonal in their activity, probably reflecting seasonal trends in the prevailing habitat moisture conditions – typically, when conditions are too dry, terrestrial planarians retreat into the soil or deep within rotten timber. Some species appear to aestivate within a protective sheath of hardened epidermal secretions.

While primarily members of the soil fauna, some species, under favourable moisture conditions, will seek out prey above the ground. Froehlich (1956) reported the Brazilian Geoplanalivia Froehlich from tree trunks. A number of New Zealand species may be found at night on tree trunks and low foliage (G.M. Barker, personal observation). Where moist humus and leaf litter is suspended above the ground, these microhabitats may also be occupied by terrestrial planarians. Froehlich (1956) noted that bromeliad epiphytes in Brazilian forests were occupied by planarians. This is paralleled in New Zealand with species in the suspended humus in the leaf axils of epiphytic Collospernum hastatum (Colenso) Skottsbd. and Astelia Banks & Sol. ex R. Br. species (Asteliaceae), in the liane Freycinetia baueriana banksii (Cunn.) Stone (Pandanaceae), and in the palm Rhopalostylis sapida Wendl. & Drude (Arecaceae).

Some terrestrial planarians are subterranean and occupy crevices deep within the soil (Percival, 1925). Geobia subterranea (Schlutze & Müller), the sole representative of the Brazilian genus Geobia, is entirely subterranean within the burrows of its earthworm prey, while some species, such as the Brazilian Geoplana goetschi Schirch, Pasipha rosea (Froehlich) and Issoca rezendei (Schirch), are not obligately subterranean but spend a large part of their life within the soil (Froehlich, 1956, 1967). As the planarians have no hard parts to aid penetration of soil, it seems likely that they use existing interstices, including ant and termite tunnels and earthworm burrows. Strong musculature and ability to flatten and mould their bodies undoubtedly helps penetration between yielding soil and litter.

Relatively little is known about the community ecology of terrestrial planarians. Some information has arisen from studies of pestiferous, invasive species (e.g. Boag et al., 1997; Yeates et al., 1997; Jones et al., 1998a; Mather and Christensen, 1998), but there remains a dearth of information relating to species in their natural environment. A number of different planarian species are frequently found associated in the same microhabitat (Bresslau, 1927; Schirch, 1929; Froehlich, 1956; Winsor, 1998c). Froehlich (1956) reported a find of nine species of terrestrial planarians under a single log in forest in São Paulo, Brazil. Winsor (1998c) noted that for eastern Australia, four to five, occasionally up to
nine, species may be found under a single log. A similar situation commonly exists in New Zealand, with Johns (1998) recording 18 species from a single site in Nothafagus (Fagaceae) forest. Winsor (1998c, p. 459) observes, ‘This raises interesting ecological questions regarding food partitioning and species interactions.’ Boag et al. (1998) note that interspecific competition between terrestrial planarians has not been documented. None the less, there is compelling experimental evidence for interspecific competition between aquatic planarians (e.g. Reynoldson and Bellamy, 1973; Lock and Reynoldson, 1976; Reynoldson and Piearce, 1979), and Reynoldson (1966, 1975) suggested that the distribution and abundance of lake-dwelling species of triclad in Britain were mainly determined by interspecific competition for food. Furthermore, recent land-based studies led Boag et al. (1998) to suggest that availability of food and intraspecific competition are key regulatory factors in populations of at least some terrestrial planarians – especially species specializing on particular types of prey.

Reproduction and reproductive ecology

Reproduction in Turbellaria has been reviewed by Gremigni (1983), and in the Terricola by Winsor (1998b). Despite the importance of the reproductive organs in systematics of the group, their function is poorly understood (Winsor, 1998b). As noted earlier, terrestrial planarians reproduce both asexually by fission, and sexually by cross-fertilization. In at least some planarian species, the reproductive strategy varies with prevailing environmental conditions, with asexual reproduction most prevalent in adverse conditions (Barnwell, 1969) where food is limiting (Calow et al. 1979). However, other factors are probably involved, as a Dolichoplana species has been observed to reproduce by fission in commercial earthworm beds where food was abundant (L. Winsor, unpublished). Self-fertilization in the group has not been documented.

Asexual reproduction in the planarians occurs through architomy (fissipary) – transverse splitting in which new organs regenerate only after the fission process has terminated. The mechanism by which this happens is similar for the three species that have been most studied – B. kewense, D. fieldeni and Dolichoplana carvalhoi Corrêa. In B. kewense fission takes place 1–2 days following feeding, and is first manifested by slight pinching of the body 1–2 cm from the tail tip. Severance occurs when the tail adheres to the substratum and the anterior body pulls away. The fragments are immediately motile and develop a head and pharynx within 7–10 days, and within 2–3 weeks is adult in form and behaviour (Connella and Stern, 1969). Mead (1963) noted the propensity for architomy in the Hawaiian Endeavouria septemlineata (Hyman).

The majority of terrestrial planarians exhibiting asexual reproduction are tropical species with elongate body form in which the pharynx and reproductive organs are situated in the anterior body third, and the caudal
portion chiefly comprising gut and mesenchymal elements. In these taxa sexual reproduction outside their native habitat is restricted to individuals occupying outdoor situations in tropical or subtropical climates. Elsewhere, such as hothouses and outdoors in temperate regions, they reproduce asexually. The links between sexuality and climate, and switching between fission and egg cocoon production, indicate that several interacting factors are involved, not least the availability of food and climatic variability.

The terrestrial planarians are hermaphroditic. Even though cross-copulation is the rule in sexual reproduction, male and female systems are not necessarily at the same stage of maturation in a given individual. The female gonads are the paired ovaries. These are ectolecithal, with the female germ cells comprising oocytes and vitelline cells. The ovoid-shaped ovaries lie ventrally, above the nerve cords. From each an oviduct runs ventrally caudad to the copulatory apparatus. Numerous vitelline follicles, which are scattered throughout the body, open into the oviduct (thus termed ovovitelline duct). The two ovovitelline ducts, either separately or after their union, open to the female genital canal. The canal receives the secretions of shell glands, and these secretions form the inner cocoon membrane enclosing fertilized oocytes and vitelline cells (Winsor, 1998b). The female genital canal then opens into the female atrium.

In the Terricola there are a number of different types of sperm-resorptive organs. In some species the vitelline follicles may have a sperm-resorptive function, and are then termed resorptive vesicles, of which four types are recognized in terrestrial planarians (L. Winsor, unpublished). In the Terricola the copulatory bursae are all located posterior to the penis and have a demonstrable sperm-resorptive function. They are present in various species in all three families. In some microplanines the copulatory bursae open into the terminal part of the oviduct, whereas in other taxa the bursa opens directly to the ventral surface. It is not uncommon for the bursa, or for the female genital duct if the bursa is absent, to connect with the intestine via a genito-intestinal duct, and in certain species there may be two or three such communications between the reproductive and digestive systems. Other sperm-resorptive bursae may be present adjacent to the ovaries, beside the pharynx and leading from the male atrium. Other female accessory organs include viscid glands (atrial diverticula), the secretions of which are responsible for cocoon adhesion to the substrate, and musculoglandular organs (adenodactyls), which contribute sclerotin substances to cocoon wall formation.

The male gonads are the testes and these take the form of numerous spherical or ovoid follicles that are distributed from the level of the ovaries to the pharynx, to the copulatory apparatus, or to the tail, depending on the species. They may lie ventrally or dorsally to the intestine, or extend dorsoventrally so as to fill the entire intervening space. The copulatory apparatus is situated between the pharynx and the posterior end of the animal. Generally the male and female atria communicate directly with a common atrium, in the floor of which is situated the
The penis occupies the anterior part, the male atrium. There is a muscular hemispherical bulb, embedded in the anterior wall, and the penis papilla, with ejaculatory duct, projects posteriorly into the atrium. In some species the penis papilla is reduced, or absent. Within the penis bulb there may be an enlarged cavity or muscular duct, generally differentiated into a seminal vesicle and prostatic region, which leads into the ejaculatory duct. From the testes the vas deferentia run alongside and behind the pharynx to curve upward and open into the seminal vesicle within the penial bulb.

Fertilization is internal. In broad, flat geoplanids, the copulating individuals come together with ventral surfaces opposed – only the anterior ends remain separated. In slender, more cylindrical species, only the ventral surfaces immediately adjacent to the gonopores come into contact. Terrestrial planarians mate many times during their life. During copulation, the penis of one of the copulating individuals is inserted into the gonopore of the other. Two functional types of penis may be recognized in terrestrial planarians. The protrusible type, common in bipaliiids and microplanine rhynchodemids, bears a permanent papilla that is protruded through the gonopore. The eversible penis, common in many rhynchodemine rhynchodeminids and geoplanids, lacks a permanent papilla and comprises essentially the everted ejaculatory duct, which is ensheathed by the atrium forming a pseudophallus. Spermatophores are apparently not common in terrestrial planarians, having to date only been observed in two species (Winsor, 1998b).

The fertilized ova migrate together along the ovovitelline duct and into the female genital canal. There they are enclosed within a thin membrane (inner cocoon membrane) secreted by the shell glands. The enclosed mass of ova then passes into the female atrium, where it is coated with sclerotin components from secretory cells which condense to form the sclerotinized outer cocoon wall (Winsor, 1998b). The cocoon is generally expelled through the gonopore, together with secretions from special atrial glands that cement the cocoon to the substrate. In some species, such as *Lenkunya munda* (Fletcher & Hamilton) and *A. triangulatus*, the cocoon emerges directly through the dorsal epidermis by means of a rupture. In this situation the number of cocoons laid by an individual is evident as body wall repairs, each a transverse dislocation in the longitudinal dorsal stripes. Sexual *B. kewense* may reproduce asexually prior to and following production of fertile egg cocoons. Fission in this species does not take place during the entire period of oviposition.

In the Brazilian species *Geoplanaburmeisteri* Schulz & Müller mating takes 45–60 min, and egg cocoons are laid between 1 and 117 days after copulation (Rodrigues, 1972). In this species the young can be discerned within the cocoon after 6–17 days, and hatch 9–43 days after cocoon production, with one to 15 individuals per cocoon (Rodrigues, 1972). The cocoons of *B. kewense* are 5–7 mm in diameter, each generally containing only a few young (Connella and Stern, 1969). The cocoons of *R. sylvaticus* are much smaller (in accordance with animal size), being 1.2–1.5 mm in
diameter, and yield four to five young after about 30 days (Ogren, 1957). The cocoons of *Australoplana sanguinea* var. *alba* (Dendy) are 3–4 mm in diameter, and yield one to five juveniles (Terrace and Baker, 1996). In *B. kewense* and *P. manokwari*, the cocoon size and number of young per cocoon declines with each oviposition following a single copulation (L. Winsor, unpublished). Cocoons of *Caenoplana coerulea* Moseley are laid some 9 days following copulation and have an incubation time of 8–9 days. There are five to six young per cocoon (Barnwell, 1978). Egg cocoons are laid in sheltered moist situations and are cemented to the underside of rotting logs, leaf litter, etc., or laid within the soil. When freshly laid, cocoons are pale yellow, undergo progressive darkening with exposure to air, and over the subsequent 24 h change colour from cherry red to tan, brown, and finally black, the colour changes being typical of tanning of the quinonones present in the sclerotin cocoon wall (Winsor, 1998b). The sclerotinized cocoon wall of *P. manokwari* is rich in tryptophane proteins, the hydrophobic nature of which may ensure minimal moisture loss (Winsor, 1990).

Australian and New Zealand terrestrial planarians breed during the winter months (Fletcher and Hamilton, 1887; Dendy, 1892; Steel, 1901), as do Brazilian geoplanids (Froehlich, 1956; Rodrigues, 1972). In the Brazilian *G. burmeisteri*, reproduction appears not to be seasonal under laboratory conditions, suggesting that temporal variability in environmental conditions suited to activity may seasonally constrain reproductive activity. In northern continental areas, terrestrial planarians tend to be inactive during the cold winter months, thus reproductive activity is confined to spring and summer (e.g. Ogren, 1955; Ogren and Sheldon, 1991). *Arthurdendyus triangulatus*, a New Zealand species, is most abundant as sexually mature animals during spring in Northern Ireland, with a peak of oviposition in early summer (Cannon et al., 1999).

Although evidence is largely circumstantial, these triclads are generally regarded as iteroparous. The duration of the life cycle and longevity of terrestrial planarians have been difficult to determine owing to problems in marking individuals and maintenance of disease-free laboratory cultures. In *G. burmeisteri*, the life cycle takes about 1 year and the maximum longevity of laboratory-reared specimens was found to be 390 days. The gonopore is patent at 15–45 days. The onset of size regression in *G. burmeisteri* can begin with egg cocoon production, though senile changes have not been observed in individuals of age less than 200 days. Survival of an individual planarian after the onset of degenerative symptoms never exceeded a quarter of its total life (Rodrigues, 1972).

**Natural enemies**

Terrestrial planarians are commonly found infested with numerous gregarines (von Graff, 1899) which can cause morbidity, and where testes are infected possibly cause sterility (L. Winsor unpublished). Similarly,
phoretic nematode larvae are often observed in the ventral epithelium and cutaneous musculature of sectioned specimens, but generally there is no histological evidence of host tissue damage or reaction. Terrestrial planarians in laboratory cultures may rapidly succumb to fungal and bacterial infections (Barnwell, 1969; Rodrigues, 1972).

The mycetophilid fly Planarivora insignis Hickman represents the only invertebrate known to be a specialist parasitoid of terrestrial planarians. Larvae of this dipteran have been recorded from the Tasmanian species Artioposthia diemenensis (Dendy), Artioposthia mortoni (Dendy) and Tasmanoplana tasmaniana (Darwin) (all Geoplanidae, Caenoplaninae), with approximately 28% parasitism rate ($n = 118$) in the latter species (Hickman, 1964).

There are relatively few records of invertebrates predating on terrestrial planarians, despite the recent interest from the perspective of biological control of pestiferous species. None the less, both laboratory and field studies have confirmed that some Carabidae and Staphylinidae predate on these planarians (Greenwood, 1995; Gibson et al., 1997). There are also observations to suggest that at least some terrestrial planarians are predated by other planarian species (e.g. Boag et al., 1998). It has become well recognized that immunological approaches are needed for proper evaluation of predation on field populations. Cannon et al. (1999) stress the need for fully characterized planarian-specific monoclonal antibodies to avoid the possibility of detecting false positives generated by cross-reactivity with certain invertebrates (e.g. gastropods; Symondson and Liddell, 1996).

It appears that most vertebrates find terrestrial planarians distasteful (Dendy, 1891; Winsor, 1983a; Neck, 1987), and this unpalatability may be related to the production of mucus secretions in disturbed animals (Arndt and Manteufel, 1925; McGee et al., 1996). None the less, terrestrial planarians are predated by some vertebrates (e.g. Cannon et al., 1999). In the USA, Ducey et al. (1999) found that the invasive Bipalium adventitium Hyman was only accepted rarely as prey by salamanders (Plethodon glutinosus (Green) and Desmognathus ochrophaeus Cope (Plethodontidae)) and rejected entirely by other salamanders (Ambystoma maculatum (Shaw), Ambystoma laterale Hallowell -jeffersonianum (Green) complex (Ambystomidae), Desmognathus niger (Green), Plethodon cinereus (Green)) and snakes (Storeria dekayi (Holbrook) and Storeria occipitomaculata (Storer) (Colubridae)).

Winsor (1983b) presented three cases in which cats ((Felis catus Linnaeus) (Felidae)) that had ingested specimens of B. kewense subsequently vomited these worms. Winsor remarked that vomiting was probably induced by the dermal secretions from the ingested planarians. Some planarians have been attributed as having an unpleasant, lasting, astringent taste (Moseley, 1877; Dendy, 1890a), and others implicated in fatal poisoning when ingested by fowls (Gallus gallus (Linnaeus) (Phasianidae)) (Terajima, in Kawakatsu, 1969). In southern Chile, sudden death in cattle ((Bos taurus Linnaeus) (Bovidae)) and horses ((Equus caballus
Linnaeus) (Equidae)) has been attributed to poisoning by Polycladus gayi Blanchard, apparently accidentally ingested with forage (von Graff, 1899).

Arndt (1925) recognized two toxins from B. kewense, namely a cardiotoxin, which was localized in dermal slime, and a haemolytic toxin distributed throughout the body. A paralysing effect has been noted in earthworms touched by B. kewense (Johri, 1952) and strong reactions are provoked in earthworms by contact with A. triangulatus (Blackshaw and Stewart, 1992). Winsor (1998b) notes that certain Australian caenoplanines exhibit autofluorescence when viewed under a Wood’s ultraviolet light, and suggested that this may indicate the presence of a repugnatorial toxin.

As Invasive Species

Some terrestrial planarians are apparently very tolerant of habitat disturbance (Froehlich, 1956; Johns et al., 1998; Cannon et al., 1999; Carbayov et al., 2002) and frequently persist in the vicinity of human dwellings in modified landscapes. The passive dispersal of terricolans by humans is well documented (summarized by Sluys, 1995; Alford et al., 1996). The major factor in the worldwide dispersal of these planarians was probably the invention, in 1833 by Dr Nathaniel Bagshaw Ward of East London, of portable terrariums – Wardian cases – for the transportation of plants (Ward, 1834). Terrariums are also the perfect way to transport planarians. Thus was mediated the initial intercontinental dispersal of planarians, present in the soil or vegetation accompanying the collected plants. Hitherto, the intercontinental transportation by sea of live plants was fraught with difficulties, and only the hardiest plants and associated animals survived. The first test of the Wardian case was the transportation of ferns and grasses from the UK to Sydney in 1833, on the return trip stocked with native Australian ferns – the ferns arrived in perfect condition (Honigsbaum, 2001). Orchid collectors were the first to use the Wardian case to bring plants from India and China (Honigsbaum, 2001). It is no surprise then that Moseley’s B. kewense was collected in 1878 from the orchid house, Kew Gardens. Planarians and their cocoons are frequently associated with rooted/potted plants, rhizomes and certain types of fresh vegetable produce (e.g. Hyman, 1940; Dundee and Dundee, 1963; Winsor, 1983a; Ogren, 1984a,b, 1985; Bloch, 1992; Mather and Christensen, 1992; Hogan and Dunne, 1996). As a consequence, a number of planarian species have established outside their native range as adventives (Table 5.1). In some species, the ability to reproduce asexually is thought to contribute to this invasiveness. Secondary dispersal of planarians occurs with the purchase and exchange of plants between nurseries, botanical institutes and gardeners (Alford et al., 1996).

While the predatory habit has been recognized, the impacts of these introduced planarians on the indigenous invertebrate faunas was long regarded as negligible. However, the realization that A. triangulatus, of
Table 5.1. Checklist of terrestrial planarians recognized as invasive outside their native range, with information on probable origin, countries in which invasion has occurred and ecological impacts.

<table>
<thead>
<tr>
<th>Native region</th>
<th>Introduced range</th>
<th>Environmental impact</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bipalium kewense Moseley Vietnam to Kampuchea, possibly extending to Malaysia</td>
<td>Widespread, including Argentina; Australia; Azores; Barbados; Belgium; Bermuda; Brazil; Canada; Cape Verde Islands; Colombia; Costa Rica; El Salvador; Fiji; France; Germany; Hawaii; Hong Kong; India; Indonesia; Ireland; Israel; Jamaica; Japan; Madagascar; Madeira; Malaysia; Mauritius; Mexico; New Zealand; Panama, Peru; Pitcairn Island; Puerto Rico; Réunion Island; Samoa; South Africa; Spain; St. Helena; Tahiti; Taiwan; Tonga; UK; Uruguay; USA; Zimbabwe</td>
<td>Feeds exclusively on earthworms. Impact as an adventive in the wild is presently unknown. However, recognized as a pest in earthworm farms</td>
</tr>
<tr>
<td><strong>Rhynchodemidae, Rhynchodeminae</strong></td>
<td>Dolichoplana carvalhoi Corrêa Unknown, probably Indo-Malay region</td>
<td>Brazil</td>
<td>Prey unknown</td>
</tr>
<tr>
<td></td>
<td>Dolichoplana fieldeni von Graff Indo-Malay region</td>
<td>Barbados; Guyana; Germany; Ireland</td>
<td>Feeds on earthworms. Impact as an adventive is presently unknown</td>
</tr>
</tbody>
</table>
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Terrestrial Planarians

**Dolichoplana striata** Moseley

Indo-Malay region

Jersey; Germany; Scotland; USA

Feeds on earthworms. Impact as an adventive in the wild is presently unknown. However, recognized as a pest in earthworm farms


**Dolichoplana Moseley** spp.

Indo-Malay region (probably Sri Lanka or Indonesia)

Australia

Prey unknown

Winsor (1998c)

**Platydemus manokwari** de Beauchamp

New Guinea

Australia; Guam, Rota, Saipan (Mariana Islands); Hawaii, Japan; Maldives; Philippines; Samoa

A generalist predator with apparent preference for gastropods. Beneficial impact through control of adventive *Achatina fulica* Bowdich (Achatinidae) populations. However, also suspected of impacting on indigenous gastropod communities


**Rhynchodemus hallezi** von Graff

Philippines

Scotland (single doubtful record from Edinburgh greenhouse)

Prey unknown

Jones (1998), Boag and Yeates (2001)

**Rhynchodemus sylvaticus** (Leidy)

Unknown, probably Europe

Argentina; Azores Islands; Belgium; Brazil; England; Ireland; New Zealand; Peru; USA; Wales

Generalist predator, taking small gastropods and various small arthropods (e.g. Collembola, Diptera). Impact as an adventive is presently unknown


**Rhynchodemidae, Microplaninae**

**Diporodemus indigenus** Hyman

Central or South America

Canada, USA

Prey unknown

Ogren and Kawakatsu (1998)


**Microplana rufocephalata** Hyman

Unknown but probably Europe

USA

Prey unknown


**Microplana scharffi** (von Graff)

Europe

USA

Generalist predator on earthworms and small arthropods. Impact as an adventive is presently unknown


**Microplana terrestris** (Müller)

Europe

Canada, USA

Generalist predator on gastropods, earthworms, and small arthropods. Impact as an adventive is presently unknown

continued
Table 5.1.  Continued.

<table>
<thead>
<tr>
<th>Native region</th>
<th>Introduced range</th>
<th>Environmental impact</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Geoplanidae, Geoplaninae</strong></td>
<td></td>
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<tr>
<td>Geoplaninae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Geoplana arkalabamensis</em> Ogren &amp; Darlington</td>
<td>South America, possibly Brazil</td>
<td>USA</td>
<td>Prey unknown</td>
</tr>
<tr>
<td><strong>Geoplanidae, Caenoplaninae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arthurdendyus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>albidus</em> Jones &amp; Gerard</td>
<td>Unknown, probably New Zealand</td>
<td>England; Northern Ireland; Scotland</td>
<td>Feeds on earthworms. Impact as an adventive in the wild is presently unknown</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Jones and Gerard (1999), Boag and Yeates (2001)</td>
</tr>
<tr>
<td><em>australis</em> (Dendy)</td>
<td>New Zealand</td>
<td>Scotland (single record in 1997; assumed established)</td>
<td>Predator of earthworms. Impact as an adventive in the wild is presently unknown</td>
</tr>
<tr>
<td><em>triangulatus</em> (Dendy)</td>
<td>South Island, New Zealand</td>
<td>England; Faroe Islands; Northern Ireland; Scotland</td>
<td>Feeds on earthworms. As an adventive, demonstrated to effect serious local decline of earthworms in garden and agricultural field situations</td>
</tr>
<tr>
<td>Arthurdendyus Jones &amp; Gerard sp.</td>
<td>New Zealand</td>
<td>Macquarie Island</td>
<td>Suspected predator of earthworms. Impact unknown</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Winsor (2001)</td>
</tr>
<tr>
<td><em>atuettneri</em> (von Graff)</td>
<td>Unknown</td>
<td>Togo, Africa</td>
<td>Prey unknown</td>
</tr>
<tr>
<td><em>purpurea</em> (Dendy)</td>
<td>New Zealand</td>
<td>UK</td>
<td>Prey unknown</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Ogren and Kawakatsu (1991)</td>
</tr>
<tr>
<td><em>sanguinea</em> (Moseley)</td>
<td>Australia</td>
<td>New Zealand</td>
<td>Feeds on earthworms. Impact as an adventive in the wild is presently unknown</td>
</tr>
</tbody>
</table>
**Australoplana sanguinea** (Moseley) var. *alba* (Dendy)

*Australia*

Feeds on earthworms. Impact as an adventive in the wild is presently unknown.  

**Caenoplana coerulea** Moseley

*Eastern Australia*

Generalist predator, attacking gastropods, arthropods, diplopods and earthworms. Impact as an adventive in the wild is presently unknown.  

**Caenoplana sulphurea** Fletcher & Hamilton

*Australia*

Prey unknown.  

**Fletchamia quinquelineata** (Fletcher & Hamilton)

*Australia*

Prey unknown.  

**Kontikia andersoni** Jones

*New Zealand*

Prey unknown.  

**Kontikia bulbosa** Sluys

*Madeira; Canary Islands*

Prey unknown.  

**Kontikia orana** Froehlich

*Australia; Brazil; Trinidad; Uganda (Type locality São Paulo, Brazil, but considered introduced there)*

Prey unknown.  

**continued**
Table 5.1. *Continued.*

<table>
<thead>
<tr>
<th>Native region</th>
<th>Introduced range</th>
<th>Environmental impact</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parakontia coxi (Fletcher &amp; Hamilton)</td>
<td>Australia</td>
<td>UK</td>
<td>Predator of earthworms. Impact as an adventive in the wild is presently unknown. However, recognized as a pest in earthworm farms</td>
</tr>
<tr>
<td>Geoplanidae, Pelmatoplaninae</td>
<td>Pelmatoplana graffi Fuhrmann</td>
<td>Unknown</td>
<td>Colombia</td>
</tr>
</tbody>
</table>
New Zealand origin, poses a significant threat to elements of the European earthworm fauna has stimulated renewed interest in the ecological role of the introduced species, in both natural and modified landscapes. Several of these invasive terrestrial planarians predate on gastropods (Tables 5.1 and 5.2).

**Feeding and Prey-handling Strategies**

As remarked upon by Jennings (1997), an outstanding feature of the free-living Turbellaria is the enormous range of prey exploited by such relatively simple animals, which lack any of the segmental appendages or buccal armatures used by higher invertebrates for seizing, handling and disintegrating food materials. Prey utilized extend from bacteria and unicellular algae through protozoa and virtually all types of invertebrates, to the eggs and young stages of fishes and amphibians. The ability to attack this range of prey resides in the elaboration of the embryonic stomodaeal invagination, in the great majority of species, into a muscular suctorial pharynx. This is variously capable of protrusion, extension or eversion and can be inserted into, applied to or extended over soft- or hard-bodied organisms either to swallow them whole or to withdraw body contents for subsequent extra- and intracellular digestion in the turbellarian’s gut. Amongst the predominantly free-living Turbellaria, almost 200 species from 35 families have evolved life strategies that involve permanent associations with other animals (Jennings, 1997). In the simplest turbellarian symbioses, ectosymbiotes such as the Temnocephalida, some Rhabdocoela and a few Tricladiida live on the body surfaces or in the branchial chambers of their mainly arthropodan or chelonian hosts. They feed on the same types of prey as their free-living relatives but supplement their diet by opportunistic commensalism. Their digestive physiology is the same as in free-living species. The endosymbiotic Acholadidae, Fecampiidae, Graffillidae, Pterastericolidae and Umagillidae live in internal body cavities or body wall derivates of echinoderms, molluscs or arthropods and exhibit a range of metabolic dependence on their hosts. Patterns of digestive physiology generally differ markedly from those of ectosymbiotic and free-living species. Many freshwater planarian species are known to feed on gastropods (e.g. Pickavance, 1971; Reynoldson and Piearce, 1979; Young, 1981; Seaby et al., 1996). Furthermore, some marine Turbellarians of the genus *Stylochus* Ehrenberg (Stylochidae) are important predators of marine bivalves and barnacles (Murina and Grintsov, 1998, and references therein).

Originally considered by Charles Darwin to be vegetarians, terrestrial planarians were subsequently found to be carnivorous. Most are predators, though some species are necrophagic (Winsor, 1977). The food of terrestrial planarians includes Isopoda (woodlice) (Brittlebank, 1888; Froehlich, 1956; Barker, 1989; Terrace and Baker, 1994; Carbayo et al., 2002), Onychophora (peripatus) (Steel, 1901), small Arachnida (spiders)
Table 5.2. A checklist of terrestrial planarians with known malacophagous habit, with lists of terrestrial gastropods reported as prey (see text for further information on prey preferences).

<table>
<thead>
<tr>
<th>Planarian species</th>
<th>Location</th>
<th>Gastropod prey</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bipalium adventitium Hyman</td>
<td>Massachusetts, USA</td>
<td>'Slugs' Achatina fulica Bowdich</td>
<td>Klots (1960)</td>
</tr>
<tr>
<td>Bipalium pennsylvanicum Ogren</td>
<td>Pennsylvania, USA</td>
<td>'Mashed slugs' (An earthworm predator. Rejected live gastropod slugs (Agriolimacidae: Deroceras reticulatum (Müller); Arionidae: Arion subfuscus (Draparnaud); Limacidae: Limax maximus Linnaeus) and snails (Helicidae: Helix Linnaeus sp.; Zonitidae: Zonitoides arborescens (Say)))</td>
<td>Ogren and Sheldon (1991)</td>
</tr>
<tr>
<td>Bipalium penzigi Müller</td>
<td>Java, Indonesia</td>
<td>Cyclophoridae: Cyclophorus rafflesi (Broderip &amp; Sowerby)</td>
<td>van Benthem Jutting (1932, 1948)</td>
</tr>
<tr>
<td>Bipalium Stimpson sp.</td>
<td>Ogasawara, Japan</td>
<td>Achatinidae: Achatina fulica Bowdich</td>
<td>K. Takeuchi, personal communication</td>
</tr>
<tr>
<td>Bipalium Stimpson sp.</td>
<td>Japan</td>
<td>'Snails'</td>
<td>Miyoshi (1955)</td>
</tr>
<tr>
<td>Rhynchodemidae, Rhynchodeminae Platydemus manokwari de Beauchamp</td>
<td>Queensland, Northern Territory, Australia; Hawaii; Guam; Japan; Saipan; Mariana Islands; Maldives; New Guinea; Palau; Philippines; Samoa</td>
<td>Achatinidae: Achatina fulica Bowdich; Bradybaenidae: Acusta despects sieboldiana (Pfeiffer), Bradybaena similis (de Férussac)<em>, Euhadra amalii cauza (Crosse), Euhadra peliomphala (Pfeiffer)</em>, Euhadra quaesita (Deshayes)<em>, Trispipila consopra (Pfeiffer)</em>; Camaenidae: Satsuma japonica (Pfeiffer)<em>; Clausiliidae: Euphaedusa tau (Boettger)</em>, Pinguiphaedusa hakonensis (Pilsbry)<em>, Zaptychoplos buschi (Pfeiffer)</em>, Discidae: Discus pauper (Gould)<em>; Helicarionidae: Helicarion de Férussac sp.; Limacidae: Lehmannia marginata (Müller)</em>, Partulidae: Partula radiolata (Pfeiffer); Ellobiidae: Pythia scarabaeus Linnaeus; Streptaxidae: Gonaxis quadrilateralis (Preston); Zonitidae: Zonitoides arborescens (Say)*</td>
<td>Mead (1963, 1979), Schreurs (1963), van Driest (1968), Munippan (1983, 1987, 1990), Munippan et al. (1986), Waterhouse and Norris (1987), Kaneda et al. (1990, 1992), Hopper and Smith (1992), Kawakatsu et al. (1992, 1993), Winsor (1999); Raut and Barker (2002)</td>
</tr>
<tr>
<td>Rhynchodemus sylvaticus (Leidy)</td>
<td>Illinois, Wisconsin and New York, USA</td>
<td>'Crushed snails'</td>
<td>Ogren (1955)</td>
</tr>
<tr>
<td>Rhynchodemidae, Microplaninae Microplanus schafti (von Graf)</td>
<td>Britain</td>
<td>'Slugs' Agriolimacidae: Deroceras agrestes (Linnaeus); Arionidae: Arion de Férussac species, including Arion hortensis de Férussac; Helicidae: Cepaea nemoralis (Linnaeus); Zonitidae: Oxylus collaris (Müller)</td>
<td>Gunn (1944), Jennings (1959), Gunn (1992)</td>
</tr>
<tr>
<td>Microplanus terrestris (Müller)</td>
<td>Britain</td>
<td>'Slugs' Agriolimacidae: Deroceras agrestes (Linnaeus); Arionidae: Arion de Férussac species, including Arion hortensis de Férussac; Helicidae: Cepaea nemoralis (Linnaeus); Zonitidae: Oxylus collaris (Müller)</td>
<td>Gunn (1944), Jennings (1959), Gunn (1992)</td>
</tr>
<tr>
<td>Geoplanidae, Geoplaninae</td>
<td>Brazil</td>
<td>‘Snails, agriolimacid slugs’; Bradybaenidae: Bradybaena similars (de Férussac)</td>
<td>Froehlich (1956), Rodrigues (1972)</td>
</tr>
<tr>
<td>--------------------------------</td>
<td>--------------------------------------------</td>
<td>-------------------------------------------------------------------------------</td>
<td>----------------------------------</td>
</tr>
<tr>
<td>Geoplanina burmeisteri Schulz &amp; Müller</td>
<td>Brazil</td>
<td>‘Snails, agriolimacid slugs’</td>
<td>Froehlich (1956)</td>
</tr>
<tr>
<td>Geoplanina carinata Riester</td>
<td>Brazil</td>
<td>‘Snails’</td>
<td>Froehlich (1956)</td>
</tr>
<tr>
<td>Geoplanina chiuna Froehlich</td>
<td>Brazil</td>
<td>‘Snails’</td>
<td>Froehlich (1956)</td>
</tr>
<tr>
<td>Geoplanina multicolour von Graff</td>
<td>Brazil</td>
<td>‘Snails’</td>
<td>Froehlich (1956)</td>
</tr>
<tr>
<td>Geoplanina pavani du Bois-Reymond Marcus</td>
<td>Brazil</td>
<td>‘Snails’</td>
<td>Froehlich (1956)</td>
</tr>
<tr>
<td>Unidentified geoplanid, probably Notogynaphallia meinieri (Reister)</td>
<td>Trinidad</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geoplanidae, Caenoplaninae</td>
<td>Victoria, Australia; San Antonio and Florida, USA</td>
<td>Helicidae: Cantareus aspersus (Müller)</td>
<td>Smith (1979)</td>
</tr>
<tr>
<td>Endeavouria septemlineata (Hyman)</td>
<td>Hawaii, USA</td>
<td>Achatinellidae: Achatinella Swainson spp.; Achatinidae: Achatina fulica Bowdich</td>
<td>Mead (1973), Barnwell (1978)</td>
</tr>
<tr>
<td>Kontikia forsterorum (Schröder)</td>
<td>New Caledonia</td>
<td>‘Snails and slugs’, inclusive of one or more of the following – Agriolimacidae: Deroceras laeve (Müller); Bradybaenidae: Bradybaena similars (de Férussac); Helicidae: Cantareus aspersus (Müller); Sululiniidae: Subulina octona (Bruguière), Opeas Albers sp.; and other gastropods</td>
<td>Ash (1976)</td>
</tr>
<tr>
<td>Parakontikia ventrolineata (Dendy)</td>
<td>Victoria, Australia; Waikato, New Zealand</td>
<td>Agriolimacidae: Deroceras panormitanum (Lessona &amp; Pollonera); Athetaophorophoridae: Athetaophorus bitenaculatus (Quoy &amp; Gaimard); Helicidae: Cantareus aspersus (Müller)</td>
<td>Smith (1979), Barker (1989)</td>
</tr>
<tr>
<td>Newzealandia nr. graffii</td>
<td>Waikato, New Zealand</td>
<td>Agriolimacidae: Deroceras panormitanum (Lessona &amp; Pollonera); Athetaophorophoridae: Athetaophorus bitenaculatus (Quoy &amp; Gaimard); Helicidae: Cantareus aspersus (Müller)</td>
<td>Smith (1979), Barker (1989)</td>
</tr>
<tr>
<td>occidentalis (Dendy)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Newzealandia Ogren &amp; Kawakatsu sp</td>
<td>Fiordland, New Zealand</td>
<td>Athetaophorophoridae: Athetaophorus Fischer sp.</td>
<td>G.M. Barker, personal observation (2001)</td>
</tr>
<tr>
<td>Anticostha gramnicola (Steel)</td>
<td>New South Wales, Australia</td>
<td>‘Dead slugs’</td>
<td>G.M. Barker, personal observation (2001)</td>
</tr>
<tr>
<td>Unidentified Geoplanidae species</td>
<td>Ogasawara, Japan</td>
<td>Achatinellidae: Achatina fulica Bowdich</td>
<td>G.M. Barker, personal observation (2001)</td>
</tr>
</tbody>
</table>

*Species known as prey only under laboratory conditions.
and Acari (mites) (du Bois-Reymond Marcus, 1951), Isoptera (termites) and various insect larvae (Brittlebank, 1888; Froehlich, 1956; Sheppe, 1970; Jones et al., 1990, 1995; Cumming, 1995; Jones and Cumming, 1998), other small cryptozoic arthropods (e.g. Collembola) (Froehlich, 1956; Carbaya et al., 2002), Diplopoda (millipedes) (Jennings, 1959; Terrace and Baker, 1994), Dermaptera (earwigs) (Terrace and Baker, 1994), oligochaete Annelida (earthworms) and Hirundinea (leeches) (e.g. Steel, 1901; du Bois-Reymond Marcus, 1951; Blackshaw, 1990, 1995; Blackshaw and Stewart, 1992; Christensen and Mather, 1995; Terrace and Baker, 1996; Yeates et al., 1997; Winsor, 1998d; Carbaya et al., 2002), other planarians (Froehlich, 1956; Winsor, 1977; L. Winsor in Waterhouse and Norris, 1987), and terrestrial gastropods (Table 5.2). Cannibalism has only been observed under laboratory conditions (Froehlich, 1956; L. Winsor, personal observation). As noted by Ogren (1995) and Jones and Cumming (1998), relatively few published observations exist describing the predatory behaviour of terrestrial planarians and the prey type is unknown for most terrestrial planarian species.

Predation behaviour of land planarians has been reviewed by Barker (1989), Ogren (1995) and Lillico et al. (1996).

**Search behaviour**

Terrestrial planarians can apparently find food by waiting for prey to make physical contact (‘ambush’ strategy), by chance encounter during random locomotion (‘random search’ strategy) and by oriented behaviour tracking the prey by sensory cues (‘hunting’ strategy). Evidently most species have adopted the ‘ambush’ and ‘random search’ strategies (Ogren, 1995, and references therein). Jennings (1959, p. 120) notes in *M. terrestris*, a predator of gastropods, earthworms and various arthropods, that ‘The prey appears to be found by chance and starved individuals show no awareness of the proximity of either damaged or intact animals until random movements bring them into direct contact.’ Planarians are often to be found beneath stones or logs, or in soil, presumably quiescent between meals, with live prey species nearby. If contact with prey is made, and the planarian is ready to feed, arousal and predatory behaviour will occur (Neck, 1987; Blackshaw and Stewart, 1992).

In freshwater planarians, Calow and Woollhead (1977) found the locomotory strategies of two species were related to the activity of their prey. The species that fed on live mobile prey, *Dendrocoelum lacteum* (Müller) (Dendrocoelidae), adopted a ‘sit and wait’ strategy upon starvation, whilst the species which fed on dead or dying carrion, *Polycelis tenuis* Ijima (Planariidae), adopted a ‘search out’ strategy, becoming more active when starved.

At least some terrestrial species exhibit oriented, chemotactic predatory activity. Prey may be tracked by chemical signals, e.g. from mucus trails of gastropods and annelids (Ogren, 1995). Once the prey signal is
sensed, the planarian moves towards the source. Some species will orientate to tissue exudates from injured prey – *Bipalium pennsylvanicum* Ogren, a species that predominately predates earthworms, stopped to feed on mashed and torn gastropod slugs (Ogren and Sheldon, 1991). *Parakontikia ventrolineata* (Dendy), *E. septemlineata* and *P. manokwari* show very aggressive orientation behaviour towards their gastropod prey (Mead, 1963; Barker, 1989; Kaneda *et al.*, 1990). Mead’s description (1963, p. 306) of *E. septemlineata* pursuit and capture of *A. fulica* is illustrative:

> Very frequently their anterior end is attenuated, elevated, and flailed about in an apparent effort to locate prey. Both in the field and in the laboratory they seem sensitive to the slime trail of a snail; and, in the vicinity of these worms, a snail is soon seen with a number of worms crawling almost frantically in its wake. The directive motion of the worms permits them soon to overtake the snail with its hesitant, probing locomotion.

Mead (1979) recorded as many as 50–100 *E. septemlineata* on a single specimen of *A. fulica*, while Barker (1989) observed as many as seven *P. ventrolineata* attacking specimens of *Deroceras panormitanum* (Lessona & Pollonera) (Agriolimacidae). The Australian species *L. munda* emerges at dusk from soil cracks in the banks of watercourses to feed on carrion stranded at the water’s edge, the species forming large feeding aggregations similar to those observed in freshwater planarians (Winsor, 1977), probably through chemotaxis. In the Paludicola, such aggregations are mediated by the joint effects of chemotaxis, distinctive morphology and photokinesis (Reynierse *et al.*, 1969).

**Capture**

Physical holding or immobilization is a common prey-handling strategy (Schremmer, 1955; Dindal, 1970; Neck, 1987; Ogren and Sheldon, 1991; Jones, 1996; Jones and Cumming, 1998). The capture of gastropod snails by geoplanid species is described by Froehlich (1956), in which the planarian adheres to the snail’s shell by its anterior end, eventually surrounding the prey, then extending the pharynx through the shell aperture to begin feeding. The head is used as a grasping organ in a number of species, as the ventral surface is adhesive and can strongly attach to the prey or substrate or both. Very similar behaviour involving the enclosure of the gastropod snail prey has been described for a *Bipalium* sp. by Miyoshi (1955). Jennings (1959) described how the prey is held down by *M. terrestris*, where the body is arched over the gastropod or earthworm prey and the foot is attached to the substrate on either side by mucus. Raut and Ghose (1979) found that *Bipalium indicum* Whitehouse predation on *A. fulica* involved the planarian crawling on to a moving snail and, anchoring either the anterior or posterior end of the body on the soil substrate, turns the snail upside down. The planarian then advances over the shell to reach the upwardly directed shell aperture and secretes digestive
fluid over the exposed part of the snail to immobilize the prey. The planarian then enters the shell aperture to feed.

In some aquatic triclads the mucus produced during locomotion persists as sticky strands and plays a role in entanglement of insect larvae and crustacean prey. Entrapment in sticky mucus is also an important component of prey holding in many terrestrial planarians, or as a prey-capture mechanism independent of holding by the planarian’s body (Brittlebank, 1888; Dendy, 1890a,b; Spencer, 1891; Steel, 1901; Arndt, 1938; Schremmer, 1955). Observations by Steel (1901) on Australian terrestrial planarians indicate they are effective predators, capturing annelids, gastropods and arthropods by crawling over the body, which then becomes entangled in mucus.

A number of terrestrial planarians possess a cephalic specialization, often in the form of a hood or headplate equipped with sensory structures (Fernandes et al., 2001), and may be expansive and/or incorporate adhesive musculoglandular structures. In a number of terrestrial planarians the functional role of the cephalic specialization in prey capture is suspected or indeed has been confirmed. The broad, semilunar head in Bipalium is encircled by a sensory tract that serves for detection of prey, and its ventral surface for adhesive attachment. On coming into contact, the planarian usually adheres to the earthworm prey, and then moves on to the prey to position the pharynx. In examining the predation behaviour of B. kewense, Barnwell (1966) was able to demonstrate that the head is important for detection of prey, but is not obligatory for prey capture. In this context it is notable that other earthworm predators in the genera Arthurdendyus, Dolichoplana and Australoplana, which lack cephalic specialization, exhibit similar prey-capture behaviour to that in Bipalium. E.M. Froehlich in Ogren (1995) mentions that the geoplanid Pasipha pasipha (du Bois-Reymond Marcus) captures isopods with its cephalic musculo-glandular organ. In Rhynchodemus species, Wallner (1937), Froehlich (1956) and Ogren (1995) observed that the expansive cephalic hood is utilized in capture of collembolan prey. The cephalic hood adheres to the victim and is usually lifted above the ground, thus preventing prey escape. The prey is then transferred to the mucus trail, and the planarian advances forward and over the prey until the pharynx can be applied.

Anteroventral adhesive organs are present as concave adhesive cups in the rhynchodemid Cotyloplana, and in two species of the peltmato-planine Beauchampius, and as an adhesive pad in the geoplaninids Choeradoplana, Isocca, Pimea and an undescribed Australian species (Winsor, unpub.). Epidermal adhesive elements are involved in all these taxa except Pimea, which shares with the marine triclads specialized adhesive structures termed haftpapillen. Anterior adhesive organs require a temporary adhesion system for the capture of the prey, followed by release of the prey to pass it into the pharynx. It is uncertain whether a duo-gland adhesive system operates in the adhesive organs and adhesive margins in all Terricola. True suckers, in which adhesion is obtained from
a vacuum principle rather than by adhesive secretions, are found only in some species of paludicoles from Lake Baikal (Hyman, 1951).

Prey-capture behaviour in the termite-eating specialist *Microplana termitophaga* Jones, Darlington & Newson combines anterior adhesive attachment, despite absence of any apparent cephalic specialization, with entrapment in sticky mucus (Jones and Cumming, 1998). Siting itself at the entrance to an airshaft of the termite mound, *M. termitophaga* actively captures worker termites by extending its head, touching the dorsum of the prey to effect attachment, quickly withdrawing the extended anterior, and then crawling over the termite so that it becomes entrapped in mucus.

In addition to physical restraint, immobilization of prey may involve induced paralysis. Johri (1952) observed that earthworm prey of *B. kewense* initially reacted violently but was soon paralysed. The abundant sticky mucus was presumed by Johri to be an important factor in prey immobilization. Toxicity of terrestrial planarian mucus to prey remains unconfirmed and is probably not an important factor (Hyman, 1951; Ogren, 1995). None the less, the mucus of *A. triangulatus* contains at least 40 polypeptides, including a chymotrypsin-like serine protease (McGee et al., 1998). It is more probable that immobilization is brought about by the action of digestive fluids, which contain proteolytic enzymes and other biochemicals and are released on to or within the prey via the pharynx. This has been studied in depth by Jennings (1959, 1962) for *M. terrestris*, a species in which the cylindrical pharynx is thrust into the body of the prey and digestive fluids released to digest the tissues.

In most species the pharynx is not thrust through the body wall of the prey but is applied to the exterior surface. Prey immobilization is effected by release of copious digestive fluids on to the prey’s exterior. This is well illustrated by Dindal (1970) and Ducey et al. (1999), reporting on earthworm predation by *B. adventitium*. With respect to predation on gastropods, Mead (1963, p. 306) observed that *A. fulica*, attacked by *E. septemlineata*, ‘is unduly sensitive to physical contact with these worms since it elaborates a considerable amount of heavy, greenish, frothy mucus. This discharge does not discourage the worms.’ These observations are consistent with those of Raut and Ghose (1979) on *A. fulica* predation by *B. indicum*. The withdrawal of snails into their shell in response to the planarian digestive fluids is clearly counter productive, as the snails forsake an escape opportunity and yet expose their soft tissues to further attention by the predator. In a description of malacophagy in Brazilian geoplanids, Froehlich (1956, p. 268) noted that ‘Some snails, when attacked, produce masses of froth, succeeding often, in this way, to ward off the land planarian.’

For gastropod slugs, retreat within a shell is not possible and the only options available are secretion of copious mucus and/or rapid locomotor activity. Froehlich (1956, p. 268) observes:

When a slug-preying land planarian touches the body of a slug with its anterior end, it adheres to the prey and extends the body forwards, trying to get hold of the head of the slug, preventing the slug’s escape. The slug,
on the other hand, secretes on the whole surface fluid mucus to counteract
the adhesive glands of the planarian, and also begins to creep at full speed.
Sometimes it manages to escape, but often the planarian succeeds in
encircling its head and cutting off the retreat. The land planarian then
creeps over the slug, keeping the body broadened and the margins closely
adhered to the substrate... 

Ingestion and digestion

The pharynx is protruded from the mouth, in response to chemical cues
associated with prey (Ogren, 1956). This protrusion is effected by con-
traction of a thick circular muscle layer. The inner and outer wall of the
pharynx is covered by an epithelium, much of which liberates lubricating
and digestive fluids. The pharynx functions as a suctorial organ, pumping
prey fluid and tissues into the gut in a triturating action so that only small
pieces of tissue are ingested. Winsor et al. (1998) noted that the relation-
ship between pharynx structure and feeding behaviour has not been
adequately examined in terrestrial planarians. None the less, three
principal types of pharynx can be recognized (Winsor et al., 1998):
(i) cylindrical pharynx – to feed the planarian inserts the pharynx into the
prey; (ii) bell-form pharynx – to feed the planarian extends the pharynx,
as a wide-mouthed funnel, over all or part of the prey; (iii) plicate
pharynx – to feed the planarian extends the pharynx, in a translucent
veil, over all or part of the prey.

Jennings (1959) noted that on capture of a gastropod or earthworm,
M. terrestris protruded its pharynx, which after moving rapidly over the
surface of the prey is thrust through the body wall. Penetration through
the body wall appeared to be purely mechanical, as there was no evidence
of prior release of digestive fluids. Once within the body cavity the
pharynx moves around disorganizing the softer tissues to pass them back
in a finely divided condition into the gut. This disruption of the tissues
was rapid and mechanical, with the pharynx acting as a simple suctorial
tube extracting tissue fragments and body fluids. Ingestion of the
body contents continues until either the food source is depleted or the
planarian is replete, when the pharynx is retracted and the remnants
of the prey are abandoned. Feeding lasts 10–20 min. Jennings (1959)
remarked that the mode of feeding in M. terrestris differs little from that
described in aquatic triclads by Willier et al. (1925), Kelley (1931) and
Jennings (1957, p. 123), and concluded, ‘The typical triclad feeding
mechanism, with the pharynx functioning as a suctorial tube which
penetrates the prey to withdraw the body contents piecemeal, has appar-
ently proved adequate to the needs of a terrestrial life and is retained
unmodified.’ In a subsequent publication, Jennings (1963) generalizes
these and other observations to state that the simple cylindrical pharynx
of the triclad is thrust into the body of the prey, where fragmentation
occurs.
However, the penetration of the pharynx is not at all typical of the mode of food ingestion in terrestrial planarians. For most species in which feeding has been observed, the pharynx is extended over part of the prey, without any penetration through the body wall. Froehlich (1956) states that some South American geoplanids swallow their gastropod, planarian or arthropod prey whole. Little prior digestion is implied, but Froehlich provided little detail and it remains uncertain to what degree the prey tissues are modified by digestive fluids before being ingested. South American geoplanids generally possess a bell-form type of pharynx. Swallowing of whole prey has been observed in some caenoplanines that possess broad cylindrical or bell pharynges, with no microscopical evidence of extra-intestinal digestion (L. Winsor, unpublished).

Many terrestrial planarians prepare their food for ingestion by subjecting prey to extra-cellular digestion by the action of enzymes released from the pharynx. In some cases the quantities of digestive enzymes released on to the surface of the prey are apparently restricted, resulting in localized tissue digestion. In *E. septemlineata* attacking *A. fulica*, for example, Mead (1963, p. 306) noted that the translucent pharynx acts in carpet sweeper fashion, sucking in fluids and mucus, and ‘many deep holes (c. 0.75 mm in diameter) and grooves appear at the site of attack’. Death was observed to be effected rather rapidly in hatching snails, and the tissues were often completed removed from the shell. In larger *A. fulica*, however, attacks by one or two *E. septemlineata* generally did not result in death, and damage was limited to the removal of tissue from the exposed mantle and the posterior margins of the foot – parts that are vulnerably exposed to the planarian when the snail is in a resting position on the ground. Mead’s description clearly indicates that in the larger snails the likelihood of death, and the speed at which it occurred, was related to the numbers of *E. septemlineata* attacking and the tissues on which they fed. Barker (1989) observed that *P. ventrolineata* attacking *Atheta* *bitentaculatus* (Quoy & Gaimard) (Athetacephoridae) and *D. panormitanum* similarly inflicted localized wounds to the body surface of the prey. *E. septemlineata* and *P. ventrolineata* possess the cylindrical type of pharynx.

In *Bipalium* the pharynx is of the plicate type and spreads out over the surface forming a strong attachment. Dindal (1970) showed that in *B. adventitium*, the released digestive fluids quickly liquefied portions of the earthworm prey surface. With progressive movement of the pharynx over the body, a large body of prey tissue can be pre-digested and ingested. Terrestrial planarians feeding in this way are able to not only capture prey much larger than themselves (Zaborski, 2002), but also may ingest considerable quantities of food in a single meal. Dindal (1970) recorded an average weight gain of 89 ± 12 mg or 82% of initial body weight in *B. adventitium* feeding on earthworms, while Zaborski (2002) recorded an average gain representing 52% of initial body weight in this species feeding on earthworm prey.
A collagenase, particularly active against earthworm cuticle, has been isolated from *B. kewense* and characterized (Phillips and Dresden, 1973; Dresden and Landsperger, 1977; Landsperger *et al.*, 1981). This collagenase is primarily located in the pharyngeal region and may be a component of the pharyngeal acidophil secretions.

After feeding, the terrestrial planarians typically move away from the remains of the victim (if any) and retreat to a moist, sheltered site and remain somewhat motionless for several days. While food is generally reduced to small particles prior to entering the gastrovascular cavity, most of the digestion is intracellular, in food vacuoles, following phagocytosis by the gastrodermis. A certain amount of intraluminal digestion of proteins also occurs (Jennings, 1974). In the absence of a blood transport system, nourishment reaches the different parts of the planarian body via the ramifying intestinal tract and transport by mesenchyme cells.

Planaria store food in their gastrodermis, with emphasis on lipid storage as opposed to glycogen storage (Jennings, 1997, references therein). They can survive many weeks without feeding, shrinking slowly in size as the food reserves are called upon (e.g. Calow, 1977; Blackshaw, 1992). Furthermore, they are capable of utilizing their own tissues, such as reproductive organs, for food when reserves are exhausted.

**Pseudoparasitism or symbiosis**

As noted earlier, many Platyhelminthes are ecto- or endosymbionts or parasites on various invertebrate and vertebrate hosts. Amongst Turbellaria symbiotic or parasitic associations are largely confined to marine species (Ball and Khan, 1976). However, van Benthem Jutting (1932, 1948) records *Bipalium penzigi* Müller occurring as a symbiont in the pallial cavity of the terrestrial prosobranch gastropod *Cyclophorus rafflesii* (Broderip & Sowerby) (Cyclophoridae) in Java.

**Prey preferences**

The majority of terrestrial planarians are evidently generalist opportunists, predating upon a range of organisms that occur within their habitat. They can also be cannibalistic and necrophagic.

Amongst the better-known generalist species with malacoephagous habits (Table 5.2), we note that, in addition to gastropod prey, *R. sylvaticus*, a rhynchodemid Rhynchodeminae, feeds on small arthropods (Wallner, 1937; Arndt, 1938; Schremmer, 1955) and earthworms (Lehnert, 1891); *M. terrestris* in rhynchodemid Microplaninae feeds on small earthworms and a range of small arthropods, which includes collembola, isopods and myriapods (Jennings, 1957, 1959); *Caenoplanca coerulae* Moseley in geoplanid Caenoplaninae feeds on isopods, diplopods and earwigs (Dermaptera) (Olewine, 1972; Terrace and Baker, 1994);
Parakontikia ventrolineata, also a Caenoplaninae, feeds on isopods (Barker, 1989). These planarians range in size from 10 mm in R. sylvaticus to 100–120 mm in C. coerulea.

The generalist, opportunistic strategy is seen in a number of species that are recognized as very effective predators of one particular prey type. *P. manokwari* is best known for its role as a biological control agent of *A. fulica* in New Guinea and various island territories in the Western Pacific, and its associated adverse effects on the native gastropod faunas of those territories (see Table 5.2 for details and references). In Queensland, Australia, *P. manokwari* has been observed feeding, often communally, on *Pheretima* Kinberg sp. earthworms (Annelida, Oligochaeta, Megascolecidae), various vertebrate and invertebrate carrion, and, in captivity, on native geoplanid land planarians and native gastropods of the genera *Helicarion* de Férussac sp. (Helicarionidae) and *Physastra* Tapparone-Canefri sp. (Planorbidae) (L. Winsor in Waterhouse and Norris, 1987). *P. manokwari* grows to in excess of 80 mm in length, and is able to utilize quite large prey.

*E. septemlineata* is well known as a predator of *A. fulica* in Hawaii. In its unaltered Hawaiian endemic state, *E. septemlineata* was apparently not a common animal. It has been seen feeding on earthworms and small insects. Gastropods originally may not have figured importantly in the diet of this ground-dwelling planarian as approximately half of the Hawaiian indigenous snails were tree dwellers. Mead (1963) argues that with the arrival of *A. fulica*, and then the purposeful introduction of the predatory gastropods *Gonaxis quadrilateralis* (Preston), *Gonaxis kibweiensis* (Smith) (Streptaxidae) and *Euglandina rosea* (de Férussac) (Oleacinidae), an abundant supply of acceptable food became available. *E. septemlineata* was observed predateing on the introduced agriolimaxid *Derooceras reticulatum* (Müller), and was suspected of predateing on other introduced, pestiferous gastropods. The population of *E. septemlineata* unquestionably increased as a result of opportunistic use of this unnaturally abundant ground-dwelling gastropod prey resource.

*E. septemlineata* usually measures about 40 mm long by 2 mm wide in the extended state, although Mead (1963) indicated that specimens up to 60 mm were not infrequently encountered. While *E. septemlineata* will attack even the largest of *A. fulica*, Mead (1963, p. 307) records that the planarian exhibits a strong preference for the newly hatched *A. fulica*:

...it has been observed both in the field and in experimental cages that these worms will congregate in great numbers in the egg masses. In fact, they are found laced all through the eggs and adjacent debris; and even the intact soil around the ‘nest’ invariably contains a few more specimens. In attacking the newly hatched snail, the worm either embraces it in its folds so that the proboscis can enter the aperture of the shell, or it crawls into the shell and out again, forming a U-shaped fold that carriers the proboscis deeply into the body whorl. The small shell characteristically is left intact and completely clean of any flesh.
That prey specialization does occur in geoplanids and rhynchodemids is clearly demonstrated by obligate earthworm predation in the Austral geoplanid species *A. triangulatus*, *Arthurdendyus australis* (Dendy), *Parakontikia coxii* (Fletcher & Hamilton), *Australoplana sanguinea* (Moseley) var. *alba* (Dendy) and the Indo-Malayan rhynchodemids *D. fieldeni* and *D. striata* (see Table 5.1 for references). Perhaps the most extreme specializations in Microplaninae occur in *M. termitophaga* that feeds on African termites (Isoptera) (Jones et al., 1990, 1995; Cumming, 1995; Jones and Cumming, 1998). Studies by Terrace and Baker (1996) indicate that geoplanids and rhynchodemids do not exhibit preferences among earthworm species as prey, although spatial dispersion within the habitat (Blackshaw, 1990; Lillico et al., 1996) can influence relative vulnerability of earthworms to predation. *M. termitophaga* is not species-specific but to date has only been recorded feeding on termites of the genus *Odontotermes* Holmgren (Termitidae, Macrotermiteinae) (Sheppe, 1970; Jones et al., 1990; Cumming, 1995; Jones and Cumming, 1998).

Amongst South American geoplanids a number of *Geoplana* species apparently specialize on gastropod prey and are readily maintained in captivity on a diet of ‘slugs and snails’ (Froehlich, 1956) (see Table 5.2 for a list). A number of additional cases of malacophagy in geoplanids are available from other parts of the world. Thus, Ash (1976) reported predation on *Deroceras laeve* (Müller) and other gastropods by the New Caledonian species *Kontikia forsterorum* (Schröder); Smith (1979) reported cases of suspected malacophagy in Australian *Parakontikia atrata* (Steel); K. Takeuchi (personal communication) has observed an unidentified geoplanid attacking *A. fulica* in Ogasawara, Japan; and G.M. Barker (personal observation) has witnessed several cases of predation by *Newzealandia* on agriolimacid and athoracophorid slugs in New Zealand (Table 5.2). In many of these cases the observations on feeding behaviour are rather limited and it is not presently possible to determine the breadth of prey types and the degree of specialization.

While only a small number of species have been studied, it is evident that the full spectrum of prey associations from generalist to specialist occurs with the Indo-Asian bipaliiid genus *Bipalium*. *B. adventitium* feeds primarily on earthworms (Dindal, 1970; Ogren, 1984a; Ducey and Noce, 1998; Ducey et al., 1999; Zaborski, 2002) but will also utilize gastropods (Klots, 1960). In feeding trials, Ogren and Sheldon (1991) found that *Bipalium pennsylvanicum* Ogren readily fed on macerated slugs (*Arion subfuscus* (Draparnaud) (Arionidae); *Limax maximus* Linnaeus (Limacidae); *D. reticulatum*) but rejected live animals of these species as prey. The preferred prey of *B. pennsylvanicum* is earthworms. Both *B. adventitium* and *B. pennsylvanicum* exhibit little preference among earthworm species as prey (Ogren and Sheldon, 1991; Ducey et al., 1999; Zaborski, 2002). *B. kewense* feeds exclusively upon earthworms (Barnwell, 1966). Raut and Ghose (1979) found that *B. indicum* was an effective predator of juvenile *A. fulica* in India, but the breadth of prey in this species has not
been studied. A malacophagous specialization is, however, more clearly evident for *B. penzigi*, an endosymbiont living in the pallial cavity of the Javanese cyclophorid *C. rafflesi* (van Benthem Jutting, 1932, 1948).

Within the terrestrial planarians we can thus recognize a spectrum of predation specialization, from generalists that take a range of prey types, through intermediates with broad prey choices but with preference for a particular prey type, to specialists taking a single prey type. While a general lack of data has prevented an empirical synthesis, it is apparent that ‘ambush’, ‘random search’ and ‘hunting’ strategies for prey location are represented across the full generalist–specialist spectrum. Furthermore, there is no clear trend across this generalist–specialist spectrum in behavioural or structural traits associated with handling prey. These conclusions are compelling when it is considered that generalist and specialist predators are represented in each of the family and subfamily taxa currently recognized, which points to repeated emergence of specialization in the terrestrial planarians. While some planarians evidently specialize on predation of gastropods, there is no compelling evidence for prey specialization down to species level. Even in the case of endosymbiont *B. penzigi* there is presently insufficient information to determine if the species is confined to a single host species.

The soil and litter microhabitat and diurnal predatory activity does not provide for easy observation of feeding and prey preferences in terrestrial planarians. Most prey records in the literature are the result of chance observations of planarians in the act of predation or feeding, and collectively may not provide an accurate summation of prey breadth nor preferences. Given that planarians generally feed on the digested soft tissue and fluids of their prey, there is little material held in their gut that may be used to identify recently ingested prey. Therefore the most satisfactory approach for determining their natural food is the use of a serological technique. Such serological techniques have been widely employed in the study of food and feeding in freshwater planarians (e.g. Pickavance, 1971; Young, 1981, and references therein), but are not yet routinely employed in the study of the diet in terrestrial planarians. Perhaps the absence of quantitative diet studies reflects the present pre-occupation with a narrow range of invasive, diet-specialist species and the general absence of interest in community and population ecology under natural conditions. The serological techniques may be usefully complemented by controlled feeding experiments in the laboratory, where prey preferences are determined under choice and non-choice conditions.

**Role in Biological Control**

The role of terrestrial planarians in population regulation of their natural prey in undisturbed habitat has not been demonstrated, and indeed most studies on feeding ecology have concerned invasive species. The potential role of terrestrial planarians in biological control programmes is...
clearly indicated, however, by the ability of a range of species to tolerate habitat disturbance, to readily establish as aliens outside their native range and to effect population decline in their prey under these conditions, or, in other cases, to effect control of prey introduced into the planarian’s native range.

The invasiveness of terrestrial planarians has been addressed in an earlier section of this chapter. That invasive planarians can be effective predators in their new geographic range is amply illustrated by those species that utilize earthworm prey, with Austral species in the genera *Arthurdendyus* and *Australoplana* effecting serious local depletion of earthworm populations and diversity in garden and agricultural field situations in Europe (e.g. Blackshaw, 1989, 1990, 1995; Mather and Christensen, 1992; Christensen and Mather, 1995; Jones and Boag, 1996; Lillico *et al*., 1996), and Indo-Malayan *Dolichoplana* and *Bipalium* species adversely impacting on commercial earthworm beds in parts of North America (Dindal, 1970). A native *Dolichoplana* sp. is recognized as a major pest of commercial earthworm beds in Australia where European lumbricid species are farmed (Winsor, 1998d). Most of these examples involve obligate predators of earthworms, but the inclusion of *B. adventitiium*, a species that utilizes both earthworms and gastropods, indicates more generalist planarians may also be useful biological control agents.

Despite this apparent potential, there are only two examples of planarian species being implicated in or associated with the effective control of an invertebrate pest. Both involve control of *A. fulica*, of African origin (Raut and Barker, 2002), in the Pacific region.

The establishment of *A. fulica* on the islands of Hawaii in the 1950s and its rapid emergence as a significant pest led to considerable interest and activity in biological control (summarized by Mead, 1979; Raut and Barker, 2002). Early in the history of *A. fulica* infestation in the Hawaiian Islands, at about the time of peak abundance of the pest snail, *E. septemlineata* emerged as an important predator (Mead, 1963, 1979). The opportunistic utilization of *A. fulica*, and other introduced gastropods, led to markedly increased abundance in this Hawaiian endemic planarian, particularly in the more moist sections of the islands of Oahu and Kauai. Attacking en masse, *E. septemlineata* was shown to be able to kill even the largest specimens of *A. fulica*, with removal of flesh from the exposed parts, stimulation of excessive production of mucus and invasion of the pallial cavity with associated damage to vital pallial organs. When only one or two planarians attacked a snail, the damage was observed to be limited to the removal of tissue from the mantle and foot, and the prey usually survived. The strongest preference was found to be the newly hatched achatines, and Mead (1963, p. 307) concluded that *E. septemlineata* ‘undoubtedly is having its greatest effect in biological control by destroying the juveniles’. The tenor of Mead’s (1963) account of *E. septemlineata* indicated a belief that this predator was to play a major role in regulation of *A. fulica* in Hawaii, although Mead stops short of specifically making a prediction. Mead (1979, p. 73) mentions that the
initial opinions of the possible biological control value of *E. septemlineata* in Hawaii were ‘both cautious and sceptical (Davis and Butler, 1964; Davis and Krauss, 1964; Davis and Chong, 1969; Davis, 1971). The principal basis for judgement was the infrequency with which the worms were encountered in the field, particularly in the act of attacking a snail.’ Mead points out, however, that *E. septemlineata* are strongly nocturnal and provocatively elusive. Diligent searching through a likely site in the day has not revealed a single specimen, yet well after dark in the same area, when the environmental moisture is high, these jet black, leech-like worms have been seen emerging from the leaf litter in surprising numbers – 10–15 per square foot (c. 110–170 m\(^{-2}\)), and 50–100 or more on a single giant snail specimen.

None the less, the ecology of decline in *A. fulica* populations observed in Hawaii is clearly complex (Mead, 1979; Raut and Barker, 2002). The level of contribution of *E. septemlineata* to the decline of *A. fulica* in Hawaii remains uncertain. Although Mead assumed *E. septemlineata* to be endemic to Hawaii, the possibility that this species is in fact an introduction has been raised by Gagne and Christensen (1985) and Hadfield (1986).

Perhaps a more compelling example of successful biological control by a terrestrial planarian is that of *P. manokwari*. Schreurs (1963) reported observation of predation on the invasive *A. fulica* by *P. manokwari* at Manokwari in Irian Jaya. The planarian was thought to have been responsible for the apparent local extinction of *A. fulica* in some parts of the region (Schreurs, 1963; Muniappan, 1983). In the late 1970s and early 1980s, *P. manokwari* was accidentally introduced to Guam and the northern Mariana Islands (Muniappan, 1983; Eldredge, 1988), where it reduced *A. fulica* to the status of a minor pest with considerable financial saving in crops and non-purchase of molluscicides (Muniappan, 1983; Waterhouse and Norris, 1987; Eldredge, 1988). Subsequently, *P. manokwari* was purposefully introduced to the Philippines (Muniappan et al., 1986) and the Maldives (Muniappan, 1987) for *A. fulica* control, with similar success. *P. manokwari* continues to be dispersed in the Pacific region through both accidental and purposeful introductions.

Both *P. manokwari* and *E. septemlineata* are unselective in their prey and there are serious reservations about the use of these species for biological control purposes as they may not only predate upon *A. fulica*, but also upon native gastropods and other fauna. Mead (1963) noted that *E. septemlineata* predated on the predatory snails, especially *E. rosea* and *G. quadrilateralis*, introduced into Hawaii for biological control of *A. fulica*, but offered no opinion on whether control outcomes were compromised.

Schreurs (1963) mentions the predation of *P. manokwari* on predatory snails introduced into New Guinea for biological control of *A. fulica*. Furthermore, Hopper and Smith (1992) noted that while *P. manokwari* is largely a ground-dwelling species, it will climb trees. At one location in Guam this planarian was observed feeding on a partulid (Hopper
and Smith, 1992). In captivity *P. manokwari* was found to feed on *Partula radiolata* (Pfeiffer) (Partulidae) and *Pythia scarabaeus* Linnaeus (Ellobiidae) (D.R. Hopper in Hopper and Smith, 1992). In the field this planarian has been noted in great abundance in areas where partulids are declining rapidly, as evidenced by the presence of large numbers of shells from recently deceased snails. Hopper and Smith (1992) concluded that *P. manokwari* is probably the major threat to the continued existence of Partulidae on Guam, other Mariana Islands and possibly Oceania as a whole.

*P. manokwari* has established in northeast Queensland and other areas in northern Australia (L. Winsor in Waterhouse and Norris, 1987), and was recently found in Darwin, in the Northern Territory (L. Winsor, unpublished) and Samoa (Cowie and Robinson, 2003).

K. Takeuchi (personal communication) noted predation on *A. fulica* in Ogasawara by *Bipalium* sp. and an unidentified geoplanid. However, the importance of these predators in effecting decline of *A. fulica* was considered negligible.

*B. indica* is reported as an effective predator of *A. fulica* in India but Raut and Ghose (1979) considered such predation not significant because of the relatively low numbers of the planarian.

Classical biological control theory, developed primarily from predictions of the discrete-time Nicholson–Bailey models, emphasizes attributes of enemy biology that result in low, stable equilibrium prey abundances (Hassell, 1978). The theory assumes that enemies are monophagous and that they display synchronous development with their prey, exhibit a rapid numerical response to shifts in prey densities, require few prey to complete their life cycles, and possess a high search ability (Beddington et al., 1978; Horn, 1988). In re-evaluating the characteristics of enemies best suited for biological control, Murdoch and Bence (1987) suggested that a stable prey equilibrium may not be the only means to achieve successful prey control. Indeed, effective control can result from the local extinction of the prey caused by a polyphagous enemy that is resistant to starvation and displays a high efficacy for the prey upon re-invasion or density increase (Washburn and Cornell, 1981; Murdoch and McCauley, 1985; Chesson and Murdoch, 1986; Murdoch and Bence, 1987). Extended control results when the enemy persists in the habitat by exploiting alternative prey species, thus enabling it to switch to the target prey when it recovers or recolonizes.

Thus, terrestrial planarians display a number of characteristics that suggest they may be useful in biological control. Many species are polyphagous predators with a high resistance to starvation, can survive and reproduce on alternative prey, have the potential for a rapid numerical response and develop relative synchrony with prey populations. These traits clearly have, for example, contributed to the successful utilization of *A. fulica* by *P. manokwari* and *E. septemlineata*, but also bring the threat of impacts on other fauna when these planarians are introduced to new areas. Inter- and intraspecific competition for food is important in
regulating populations of freshwater planarians (Reynoldson, 1977), and as a consequence of the over-exploitation of prey species, starvation probably appears quite frequently in naturally occurring triclad populations (Calow, 1977). Blackshaw (1995) considered that *A. triangulatus* behaved in a typical planarian manner in over-exploiting its food supply. Christensen and Mather (1998a) concluded that prey availability was the main factor regulating *A. triangulatus* population density. Shrinkage, or degrowth, occurs as a result of planarians metabolizing their own tissues during periods of starvation; the rate of this degrowth process varies with both species and prevailing environmental conditions. Christensen and Mather (1995) found that *A. triangulatus* maintained without prey, in a soil medium at 12°C, were still surviving after 15 months.

Species that have established by accidental introductions or through biocontrol programmes, and deemed unwanted organisms because of adverse impacts on other biota, are likely to be extremely difficult to manage or eradicate. Blackshaw (1996) presented a synopsis of potential control options for *A. triangulatus*.

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