

THE ASSOCIATIONS BETWEEN PTERIDOPHYTES AND ARTHROPODS

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ABSTRACT

Insects belonging to 12 orders, as well as mites, millipedes, woodlice and tardigrades have been collected from Pteridophyta. Primitive and modern, as well as general and specialist arthropods feed on pteridophytes. Insects and mites may cause slight to severe damage, all plant parts being susceptible. Several arthropods are pests of commercial Pteridophyta, their control being difficult due to the plants' sensitivity to pesticides. Efforts are currently underway to employ insects for the biological control of bracken and water ferns. Although Pteridophyta are believed to be relatively resistant to arthropods, the evidence is inconclusive; pteridophyte phytoecdysones do not appear to inhibit insect feeders. Other secondary compounds of pteridophytes, like prunasine, may have a more important role in protecting bracken from herbivores. Several chemicals capable of adversely affecting insects have been extracted from Pteridophyta. The litter of pteridophytes provides a humid habitat for various parasitic arthropods, like the sheep tick. Ants often abound on pteridophytes (especially in the tropics) and may help in protecting these plants while nesting therein. These and other associations are discussed. It is tentatively suggested that there might be a difference in the spectrum of arthropods attacking ancient as compared to modern Pteridophyta. The Osmundales, which, in contrast to other ancient pteridophytes, contain large amounts of phytoecdysones, are more similar to modern Pteridophyta in regard to their arthropod associates. The need for further comparative studies is advocated, with special emphasis on the tropics.

INTRODUCTION

This is the fourth and final installment in a series of review papers intended to explore the relationships between arthropods and the lower green plants. These reviews, while not intended to be comprehensive, are meant to draw attention to some hitherto-neglected areas of arthropod-plant inter-relationships. Former parts dealt with mosses, lichens and algae, respectively (Gerson, 1969; 1973; 1974-76).

The associations between arthropods and pteridophytes have been of some recent interest to entomologists. The continuing weed problem of bracken (*Pteridium aquilinum*) in some parts of the world (Braid, 1959), and the relatively new problem of *Salvinia* as a nuisance in Asian and African waterways (Anders and Bennett, 1975) are being tackled by a biological control approach. Some Pteridophyta, of ornamental interest, are grown commercially; their pests have become of economic importance. Finally, the discovery of insect moulting hormones in many pteridophytes has brought forth a series of biochemical studies and some speculations concerning the role of these and other compounds in regard to insects. Balick, Furth and Cooper-Driver (1978) compiled a fairly comprehensive list of about 420 insects and mites believed to be herbivorous on pteridophytes. The presence of primitive as well as advanced insects among these arthropods suggested to Balick *et al.* (1978) the possibility of co-evolution of arthropods and pteridophytes, both before and after the radiation of angiosperms. The main interest of Balick *et al.* (1978) concerned arthropod feeding on Pteridophyta. This will be the first association to be discussed.

ARTHROPODS FEEDING ON PTERIDOPHYTA

Diverse arthropods, mainly insects and mites, feed on pteridophytes wherever these grow. The insects include representatives of several orders (Table 1). Among the sucking insects, the Hemiptera are dominant. Some examples are the mirid bugs *Bryocoris pteridis* and *Monalocoris filicis*, which feed mainly on sporangia (Southwood and Leston, 1959). The whiteflies *Aleurotulus nephrolepidis* and *Filicaleyrodes williamsi* (Mound, 1966), the mealybugs *Nesopedronia cibotii* (Beardsley, 1971) and *Spilococcus filicicola* (Hussey, Read and Hesling, 1969) and the aphids *Idiopterus nephrolepidis* and *Sitobion ptericolens* (Robinson, 1966) all settle on and suck from the fronds. Among the Thysanoptera (thrips), the fern thrips, *Leucothrips nigripennis* and the gall-making *Pteridothrips pteridicola* will serve as examples. Many fly (Diptera) larvae are found on pteridophytes, the Anthomyiid genus *Chirosia* being restricted to them. Other representatives are the gall midges *Dasineura filicina* and *D. pteridicola*, which form galls on bracken fronds, the Agromyziid *Phytoliriomyza pteridii* which mines in bracken (Spencer, 1973) and the Drosophilid *Drosophila notha* induces multiple galls on bracken in New Guinea (Kirk, 1977). Several beetles (Coleoptera) feed on pteridophytes. These include the notorious fern weevil, *Syagrius fulvitaris* and its relatives (Marshall, 1922), the pteridophyte-specific *Megacolabus* (May, 1973), some Chrysomelids (Kirk, 1977) and *Poecilips pteridophytæ*, a Scolytid from New Guinea (Gray, 1970). Many caterpillars of butterflies and moths (Lepidoptera) were collected from Pteridophyta. The Pyralid *Samea multiplicalis* was tried for the biological control of *Salvinia* in Africa (Bennett, 1972). The leatherleaf fern borer, *Undulambia polystichalis* (Pyraustidae) is a pest of *Rumohra adiantiformis* in Florida (Short, Driggers, Kuitert and Roberts, 1971) as is the Florida fern caterpillar, *Callopietria floridensis*, a Noctuid (Pirone, 1970). *Theichobia verhuellega* induces galls on several pteridophytes (Hering, 1937). The Hymenoptera have many pteridophyte-feeders among members of the Selandriinae, including the *Equisetum*-associated *Loderus* and *Dolerus* (Benson, 1962), *Blasticotoma filiceti* and many *Strongylogaster* spp. (Smith, 1969). Mites reported from Pteridophyta comprise the gall-making Eriophyids

TABLE 1 : THE ORDERS OF INSECTS (BASED ON RICHARDS AND DAVIES, 1977). ORDERS WITH WHICH ARTHROPODS ARE KNOWN TO BE ASSOCIATED ARE MARKED BY AN ASTERISK.

APTERYGOTA	
1. Thysanura (Bristle-tails)	14. Isoptera (Termites)
2. Diplura	15. Zoraptera
3. Protura	16. Psocoptera* (Booklice)
4. Collembola* (Spring-tails)	17. Mallophaga (Biting Lice)
	18. Siphunculata (Sucking Lice)
	19. Hemiptera* (Bugs)
	20. Thysanoptera* (Thrips)
PTERYGOTA	
EXOPTERYGOTA	ENDOPTERYGOTA
5. Ephemeroptera (Mayflies)	21. Neuroptera (Lacewings)
6. Odonata* (Dragonflies)	22. Coleoptera* (Beetles)
7. Plecoptera (Stoneflies)	23. Strepsiptera (Stylopids)
8. Grylloblattodea	24. Mecoptera* (Scorpion Flies)
9. Orthoptera* (Grasshoppers and Crickets)	25. Siphonaptera (Fleas)
10. Phasmida (Stick Insects)	26. Diptera* (Flies)
11. Dermaptera (Earwigs)	27. Lepidoptera* (Butterflies and Moths)
12. Embioptera	28. Trichoptera (Caddis Flies)
13. Dictyoptera* (Cockroaches and Mantids)	29. Hymenoptera* (Wasps, Ants)

Phytoptus pteridis (Lawton, 1976) and *Nothopoda paucopus* (Anthony, 1974), the fern mite *Hemitarsonemus tepidariorum* (Cameron, 1925) and several Tenuipalpids, among them *Tenuipalpus lygodii* (DeLeon, 1966). A detailed list of insects and mites reported from Pteridophyta was compiled by Balick *et al.* (1978).

Few other arthropods are known from pteridophytes. Hussey *et al.* (1969) reported that the woodlouse *Porcellio laevis* damages *Adiantum* roots in greenhouses. Kühnelt (1976) cited observations on the Diplopods *Taueriulus* and *Pteridoiulus*, both said to live in pteridophyte rhizomes. Unspecified millipedes (Diplopoda) and sowbugs and pillbugs (Isopoda, woodlice) were reported to feed on the tender new growth of pteridophytes (Hoshizaki, 1975). Horning, Schuster and Grigarick ((1978) collected Tardigrades from Pteridophyta in New Zealand.

Feeding may be on any part of the plants. Roots, rhizomes, stems, fronds and spores are eaten. Members of pteridophyte-feeding genera may utilise different parts of the same plants. Thus *Chirosia parvicornis* mines in bracken frond-tips, *C. crassiseta* mines the stem, and *C. albitarsis* mines in both the stem and leaf stems (Lawton, 1976). Most feeding insects (Coleoptera, Hymenoptera, Lepidoptera) have chewing mouth parts; many of them in fact skeletonise fern fronds (Beer, 1955; Swezey, 1921). Others, such as aphids, whiteflies and scale insects, suck out the contents of pteridophyte tissues. Feeding aphids induced circular, chlorotic areas on pteridophyte fronds, chlorosis extending along the midrib (Severin and Tompkins, 1950). As damage extended to newly developing fronds, it was concluded that the causative agent had a systemic nature. There was no evidence that plant viruses were involved (but see below).

Pteridophyte feeders comprise species confined to one plant alone (monophagous), others which feed on several species of Pteridophyta but on no other plants (oligophagous) and arthropods which attack pteridophytes as well as higher plants (polyphagous). A special, minor group are some aphids which alternate between Pteridophyta and other angiosperm host plants. Examples are *Shinjia pteridifoliae*, alternating between bracken (*Pteridium*) and *Viburnum* (Miyazaki, 1968) and *Aulacorthum pterinigrum*, on *Pteris* and *Vaccinium* (Richards, 1972).

Gall makers are usually monophagous. Several arthropods induce galls on pteridophytes, mites being said to cause more than half of the known galls (Mani, 1964). This author, however, included only mites and Diptera among arthropod gall makers (Mani, 1964; fig. 126), ignoring Hemiptera (Beardsley, 1971), Coleoptera and Thysanoptera (Docters van Leeuwen, 1938), as well as Hymenoptera and Lepidoptera (Buhr, 1964-65). The Pteridophyta appear to have fewer arthropod-incuded galls than other large plant groups (Mani, 1964). Several quite specific insects were found during projects aimed at the biological control of pteridophyte weeds (Bennett, 1966; Wieczorek, 1973). Such specificity is of paramount importance in these projects, the insects therefore undergoing vigorous starvation tests. In other cases, the reported specificity may reflect only lack of knowledge, as most pteridophyte feeders appear to be oligophagous. Feeding on several pteridophyte species has been reported in mites (Beer, 1954; DeLeon, 1966). Thysanoptera (Hussey *et al.*, 1969), Hemiptera (Mound, 1966; Gosh, 1974; McKenzie, 1967; Southwood and Leston, 1959), Diptera (Wieczorek, 1973), Coleoptera (Kirk, 1977; Swezey, 1921), Lepidoptera (Swezey, 1921; Hering, 1937) and Hymenoptera (Benson, 1962; Smith, 1969).

Many of the polyphagous insects which feed on Pteridophyta are pests of agricultural crops (Table 2). While listing these species, it became evident that two superfamilies of plant-feeding Hemiptera, namely the Aphidoidea (aphids) and Coccoidea (scale insects) show a marked difference in specificity to pteridophytes. Among aphids, specificity is the rule, only very few species feeding on other plants also. Pteridophyte-associated scale insects, on the other hand, are by and large not restricted to these plants (see also Eastop, 1973). Even the fern scale, *Pinnaspis aspidistrae*, has many angiosperm host plants (Dekle, 1976).

Primitive arthropods are believed to be more closely associated with Pteridophyta than recent ones. Cooper-Driver (1978) has suggested that the more ancient insect orders (except the Orthoptera) are better represented among pteridophyte feeders than would be expected. This was taken to indicate a prolonged association between pteridophytes and these insect orders. Gall makers in particular are said to have been recruited from the older arthropod groups. Mani (1964) who considered the mites to be "undoubtedly" the oldest group of cecidozoa (gall-forming animals), stated that they are responsible for more than half of all known pteridophyte galls. He further wrote that of the Thysanoptera (thrips), only the more general (and thus presumably older) Terebrantia induce pteridophyte galls. The millipedes (Diplopoda) *Taueriulus* and *Pteridoiulus* live in pteridophyte rhizomes; Kühnelt (1976) finds this interesting in view of "the great geological age of ferns and diplopods". Members of the sub-family Selandriinae (Hymenoptera: Tenthredinidae) are regarded as the most generalised in the family, and the genus *Hemitaxonus* as especially primitive (Smith, 1969). Members of this genus feed on Pteridophyta. On the other hand, *Heptamelus*, a related but highly advanced genus, also lives on these plants (Smith, 1969).

As the latter case shows, pteridophytes have also become hosts to arthropods in more recent geological periods. For instance, Docters van Leeuwen (1938) notes that despite the reported antiquity of the Pteridophyta, relatively few galls occur on their older members, most galls being found on what are nowadays called "Polypodiaceous" ferns (Lovis, 1977). Feeding of the Scolytid beetle *Poecilips pteridophytae* on bracken in New Guinea was believed by Gray (1970) to be of recent origin, due to the highly specialised feeding and the relatively recent geological origin of New Guinea. Occurrence of the endemic Hawaiian mealybug *Nesopedronia* on introduced pteridophytes is probably also quite recent (Beardsley, 1971). Hering (1951) concluded that several Dipterous leaf miners have only recently transferred to the Pteridophyta.

A special form of feeding is on the "nectaries" or on sap exudates. Darwin (1877) noted that the secretion of bracken nectaries is attractive to ants. Bees, Elaterid beetles, numerous flies as well as ants were reported by Meikle (1937) to visit these nectaries. Adult sawflies, whose larvae feed on bracken, drink sap exuding from wounded fronds (Beer, 1955). Little is known concerning pteridophyte litter breakdown in the soil through arthropod activity. C. Overgaard Nielsen (in Elton, 1966) reported that the polyphagous millipede *Glomeris marginata* is an important consumer of bracken litter in Denmark. Harding and Stuttard (1974), reporting on former work, found large numbers of the Oribatid mite *Platynothrus peltifer* and the springtail *Onychiurus procampatus* in bracken litter. These authors concluded that . . . "much remains to be investigated concerning the role of microarthropods in the decomposition of litter of pteridophytes and other cryptogams".

ARTHROPODS AS PESTS OF PTERIDOPHYTA

Several pteridophytes (*Asplenium bulbiferum*, *Rumohra adiantiformis* and others) are commercially cultivated; arthropods which damage them are plant pests which require control measures. The fern mite, *Hemitarsonemus tepidarium*, lives in the innermost recesses of unopened frond and pinnae, and feeds there. Damage is manifested as minute brown depressions, leaf deformations and stunted and asymmetric growth, resulting in dwarfed, weak plants (Cameron, 1930). The fern aphid, *Idiopterus nephrolepidis*, is another destructive pest of glasshouse pteridophytes. Infested fronds curl and turn black (Hussey *et al.* 1969). The leatherleaf fern borer, *Undulambia polystichalis*, has recently become a major pest of *Rumohra adiantiformis* in Florida (Short *et al.*, 1971) requiring weekly control measures. Several non-insect arthropods, like Isopoda (sowbugs and pillbugs) and Diplopoda (millipedes) feed on the tender new growth of commercial pteridophytes (Hoshizaki, 1975). Other pteridophyte pests are polyphagous insects which damage many agricultural plants. Some representative, non-specific pteridophyte pests are listed in Table 2.

Many of these pests must be controlled by chemicals, a problem aggravated by pteridophyte sensitivity to certain insecticides. Pirone (1970), for instance, advocated using only pesticides of plant origin (like pyrethrum or nicotine), and warned against organophosphorus compounds. Fluffy ruffle fern, *Nephrolepis exaltata*, was very sensitive to acaricides like Omite and Plictran, Acarol causing leaf deformations and burns (Short and McConnell, 1973). The chemical control of pteridophyte pests thus poses some special problems.

The fern weevil, *Syagrius fulvitaris*, invaded the Hawaiian Islands and became a destructive pest of the large *Sadleria cyatheoides* there in 1919. Pemberton (1948) discovered that the weevil originated from Australia and found an efficient natural enemy (the Hymenopterous Braconid *Ischiogonus syagrii*) in New South Wales. This parasite was introduced to Hawaii and controlled the pest there. Pemberton collected several other pteridophyte-infesting weevils, belonging to the genera *Syagrius* and *Neosyagrius*; these were described by Marshall (1922). The fern weevil also invaded England and Ireland, infesting many Pteridophyta in the Dublin Botanical Gardens (Lloyd, 1944). One way of controlling weevils, as narrated by Lloyd (1944), was by placing infested plants into water, the beetles then floating to the surface. Dozens of weevils and their larvae were thus found to infest single pteridophyte plants.

BIOLOGICAL CONTROL OF PTERIDOPHYTA

The tables are turned when pteridophytes become weeds and insects are brought in to control them by feeding on them. The prime example of a pteridophyte weed is bracken, which has long been an agricultural pest in various parts of the world (Rymer, 1976). *Salvinia*, on the other hand, has only become a nuisance in tropical and subtropical waterways in more recent times (Bennett, 1966). While chemical and agrotechnical measures were being taken, biological control by insects was not neglected. The resultant surveys (Bennett, 1966; Kirk, 1977; Simmonds, 1967; Wiczorek, 1973) have materially contributed to general knowledge concerning pteridophyte arthropods. Of the ten phytophagous insects found on *Salvinia* by Bennett (1966), three, namely the Pyralid *Samea multiplicalis*, the weevil *Cyrtobagous singularis* and the Orthopteran *Paulinia acuminata*, were considered most promising. They were subsequently released at various sites in Central Africa, and *P. acuminata* became established there (Anders and Bennett, 1975).

TABLE 2 : SOME POLYPHAGOUS PESTS WHICH ALSO FEED ON CULTIVATED PTERIDOPHYTA.

Thysanoptera	<i>Heliothrips haemorrhoidalis</i> <i>Thrips tabaci</i>	Schneider, 1966 Pirone, 1970
Hemiptera	<i>Trialeurodes vaporariorum</i> <i>Coccus hesperidum</i> <i>Planococcus citri</i> <i>Chrysomphalus aonidum</i>	Schneider, 1966 Pirone, 1970 Hussey <i>et. al.</i> , 1969 Dekle, 1976
Orthoptera	<i>Tachycines asynamorus</i>	Schneider, 1966
Coleoptera	<i>Otiorrhynchus sulcatus</i>	Schneider, 1966
Lepidoptera	<i>Argyrotaenia citrana</i>	Pirone, 1970

Other cases of insect injury to bracken include reduced germination due to spore feeding by deep soil springtails (Collembola) (Conway, 1953), and conspicuous injury to isolated stands by sawflies (Beer, 1955). Balick *et al.* (1978) reported that arthropod damage to wild pteridophytes in tropical Mexico may affect the reproductive capacity of these plants. Invertebrates thus have the potential to affect pteridophyte survival in the field.

PTERIDOPHYTE RESISTANCE TO ARTHROPODS

Notwithstanding all cases of arthropod feeding on Pteridophyta, a concept of intrinsic pteridophyte resistance to insects and mites has found its way into the literature. This concept was formulated in the following quotation: "In spite of the similarity of their foliage to that of the flowering plants, ferns do not commonly serve as food plants for insects. They are, in fact, strikingly immune from insect pests of all sorts. This is hardly what might be expected from the long presence of this group of plants, their enormous development in the past, and their persistence at the present time in quite considerable abundance. Why they should be so sparingly selected as food plants does not seem to have been adequately explained" (Brues, 1920). Although this generalization was already challenged by Swezey (1921), Brues later (1946) reinforced it. This concept was supported by studies in plant galls (Docters van Leeuwen, 1938; Mani, 1964), by Elton's (1966) observations on bracken arthropods and more recently by Cooper-Driver (1978).

Apparent pteridophyte resistance to grazers was subjected to experimental studies. Soo Hoo and Fraenkel (1964) incorporated *Nephrolepis exaltata* frond extracts into a diet for the polyphagous moth *Prodenia (=Spodoptera) eridania*, and reported that this extract contained a water-soluble feeding deterrent. Soon afterwards (Kaplanis, Thompson, Robbins and Bryce, 1967; Takemoto, Ogawa, Nishimoto, Arihara and Bue, 1967) it became known that many Pteridophyta contain ecdysones (insect moulting hormones). These were believed to play a role in pteridophyte defence against herbivorous arthropods (Slama, 1969). Carlisle and Ellis (1968), however, reported that a diet of air-dried bracken fronds did not interfere with the moulting cycle of the desert locust, *Schistocerca gregaria*. Furthermore, there were indications that these insects do not take up ecdysones from the food into their blood. Hikino, Ohizumi, and Takemoto (1975) reviewed and studied the effect of ingested

phytoecdysones on insects. They concluded that the absorption of these compounds by insects is slow and limited, their excretion rapid, and absorbed ecdysterone is rapidly catabolised into compounds with little or no moulting hormone activity. Jones and Firn (1978) showed that amounts of phytoecdysteroids obtained from bracken were considerably below levels which affected several phytophagous insects belonging to three different orders. These authors believed that ecdysteroids might still act as nontoxic feeding deterrents. Hendrix (1977) offered dried bracken-leaf meal to larvae of the polyphagous moth *Trichoplusia ni* and reported some inhibition of feeding, which was not, however, considered to be due to phytoecdysones.

The effect of prunasine, a cyanogenic glycoside present in bracken, on herbivorous insects was studied by Cooper-Driver and Swain (1976). In the south of England bracken was found to be polymorphic in regard to this glycoside, as well as to its hydrolase. Although 96% of individual plants of most populations contained prunasine and its hydrolase (and were thus cyanogenic), there were a few populations in which most individual plants were acyanogenic. Bracken disks from the various populations were offered to *Schistocerca gregaria*. Those originating from cyanogenic plants were hardly touched by the locusts, whereas the others, even though they contained the cyanogenic glycoside itself, were eaten to a large extent. The authors concluded that the production of hydrocyanic acid from prunasine probably has a positive role in protecting bracken against herbivores. In a later study (Cooper-driver, Finch, Swain and Bernays, 1977) they showed that when bracken was periodically collected and offered to the locusts, there were two peaks in inhibition, during late May and in late August. The first period coincided with a maximum of cyanogenesis, the second with a peak in tannin production. The importance of these feeding deterrents for general feeders like locusts was thus demonstrated.

The level of several possible feeding deterrents produced by bracken during its growth cycle was studied by Lawton (1976). He did not exclude any bracken component, including phytoecdysones, from inhibiting arthropod herbivores. As noted, there is no clear evidence that such hormones actually protect ferns, but their occurrence in pteridophytes provides an unexpected link between these two groups. Lists of phytoecdysone-containing Pteridophyta were presented by Hikino, Okuyama, Sin and Takemoto (1973) and by Russell and Fenimore (1971).

As recent studies on pteridophyte-associated arthropods show, these plants actually have a considerable number of herbivores. Lawton (1976) compared the bracken fauna to that of other English plants and showed that the *Pteridium*-supported fauna is not an improvised one. (See also Lawton and Schroder (1977) in regard to *Dryopteris villarii*). Further studies will likely provide similar results in regard to other Pteridophyta. Although, as noted, pteridophytes are supposed to deter the feeding of arthropods, Milne (1968) obtained complete development of several springtail species which were given bracken spores as their only nutrient. Balick *et al.* (1978) reported that insects appeared to prefer pteridophytes over angiosperms as a food source in tropical Mexico.

Another kind of defence mechanism was called the "set a thief to catch a thief" principle (Lawton, 1976). Ants which visit pteridophyte nectaries may repel other insects, coming for that or other purposes. Little is known about this mechanism at present, but Bentley (1977) believes that most plants gain some protection from herbivore damage by the ants which visit their nectaries.

TABLE 3 : TOXICITY OF SOME PTERIDOPHYTE EXTRACTS TO THREE SPECIES OF INSECTS.

(A: Effect of injecting pteridophyte extracts into American cockroaches, *Periplaneta americana*; 1 = 100% paralysis at 1 day, without recovery; 2 = 100% paralysis at 2 days, without recovery; 3 = 50% mortality at 3 days; 4 = less than 50% mortality at 3 days. B and C: Effect of immersion of German cockroaches, *Blattella germanica*, and milkweed bugs, *Oncopeltus fasciatus*, respectively, into aqueous fern extracts for one minute; N = less than 20% average mortality in 4 days). (From Table 1 in Heal *et al.*, 1950).

Pteridophyte	Part of Plant	A	B	C
<i>Adiantum</i> sp.	Entire	3	N	—
<i>Anemia mexicana</i>	Entire	2	N	—
<i>Cheilanthes microphyllus</i>	Entire	3	N	N
<i>Dryopteris filix-mas</i>	Leaves	3	N	N
<i>D. marginalis</i>	Rootstocks	3	—	—
<i>Equisetum arvense</i>	Entire (fresh)	1	—	—
<i>E. arvense</i>	Entire (dry)	2	—	—
<i>E. bogotense</i>	Entire	3	N	N
<i>E. hyemale</i> var. <i>californicum</i>	Stems	4	N	N
<i>E. robustum</i>	Stems	3	N	N
<i>Isoetes dodgei</i>	Entire	2	N	N
<i>Lycopodium clavatum</i>	Entire	4	N	N
<i>L. complanatum</i> var. <i>flabelliforme</i>	Fronds	4	N	—
<i>Marsilea vestita</i>	Entire	1	N	—
<i>Notholaena sinuata</i>	Entire	3	—	—
<i>Osmunda claytoniana</i>	Rhizomes	3	N	N
<i>Pellaea ornithopus</i>	Entire	4	N	N
<i>Polypodium angustifolium</i>	Entire	2	N	N
<i>P. neriifolium</i>	Entire	2	N	N
<i>Polypodium</i> sp.	Rhizomes	4	N	N
<i>Pteridium aquilinum</i>	Leaves	2	N	—
<i>P. aquilinum</i>	Stems	3	N	—
<i>P. caudatum</i>	Leaves	3	N	N
<i>P. caudatum</i>	Stalks	4	N	N
<i>Selaginella myosurus</i>	Entire	2	N	N

ANTI-ARTHROPOD SUBSTANCES FROM PTERIDOPHYTA

Heal, Rogers, Wallace and Starnes (1950) assayed extracts from many plants for insecticidal properties. Some of their results, in regard to pteridophyte extracts, are presented in Table 3. It is noteworthy that bracken was not among the most toxic. In a further set of tests, extracts of fewer Pteridophyta were assayed against more insect species. Extracts of *Lycopodium annotinum*, *L. clavatum*, *L. complanatum* var. *flabelliforme* and *L. quadrangulare*, as well as *Anemia mexicana*, *Dryopteris marginalis* and *Marsilea vestita* were used. Of several household pests, only the black carpet beetle, *Attagenus piceus*, was consistently affected. Woollen fabric impregnated with extracts of all *Lycopodium* spp., *Anemia mexicana*, and *Dryopteris marginalis* reduced feeding injury of this pest by 90% or more. Filicin, a drug originating from *Dryopteris*, gave 90% kill of the aphid *Aphis rumicis* (Hartzell and Wilcoxon, 1941). Additional information on the insecticidal activity of *Dryopteris* and other Polypodiaceae was provided by Jacobson (1958). Seaward (1976) suggested that bracken layers placed in Roman dwellings at Vindolanda (north England) produced an insecticidal exudate which adversely affected stable flies. A liquid from boiled bracken fronds was reported to be very effective against rose aphids (Long and Fenton, 1938). Botanists at a European meeting were seen by Rymer (1976) to burn bracken in order to repel nuisance midges. Rhizomes of *Pellaea involuta* (crushed in milk) are being applied by

Southern Sotho (Africa) tribesmen to counteract spider bites. They also use a decoction from rhizomes of *Polystichum pungens* as an enema for horse bots (Watt and Breyer-Brandwijk, 1962).

ARTHROPOD-TRANSMITTED VIRUSES IN PTERIDOPHYTA

Feeding by sucking insects (especially Hemiptera) is often accompanied by transmission of plant viruses. Eastop (1977, appendix 1-11-2) maintains that no aphid-transmitted viruses occur in the Pteridophyta. Nienhaus, Mack and Schinzer (1974), however, suggested that a viral disease of *Polypodium vulgare* and *Dryopteris filix-mas* may be vectored by aphids. They inoculated the angiosperm test plant, *Nicotiana glutinosa*, with this virus. Aphids (*Myzus persicae*, a vector of many plant viruses) were allowed to feed on *N. glutinosa* for one minute, and then placed onto healthy test plants. These *N. glutinosa* later showed symptoms of the same fern virus. The disease may therefore be transmitted by aphids.

PTERIDOPHYTES AND THEIR LITTER AS SHELTER FOR ARTHROPODS

Old or dying pteridophytes are inhabited by various non-specific insects in Hawaii (Swezey, 1921). Many beetles, belonging to the families Nitidulidae, Staphylinidae and Curculionidae were reported from insect-damaged pteridophytes by Gray (1970, 1972), none of these beetles apparently feeding on Pteridophyta. Roaches deposit and live in older tuber ferns (Gómez, 1974; Yapp, 1902); the latter author also found a centipede in that habitat. Bracken litter maintains a considerable dampness, allowing arthropods to flourish there (Elton, 1966). Though none of these arthropods appear to be specific to bracken, their numbers may exceed those found in oak litter (Elton, 1966). Certain members of the bracken litter, like the pill millipede, *Glomeris marginata*, are important consumers of bracken litter (Elton, 1966). Frankland (1966), in her study of bracken breakdown in the soil, noted some mites and Collembola in decaying petioles, but found no evidence that they were actually feeding on bracken. She considered them to be mycophagous, and even to aid in fungal dispersal. Bracken litter arthropods may occur on the plant above ground; the mite *Chamobates* is one example (Lawton, 1976).

The bracken litter fauna may have some value as prey for small vertebrates, like the bank vole, which uses bracken as cover (Elton, 1966). Other small vertebrates also shelter there, and their parasites and inquilines possibly find the litter suitable for host finding and resting. An example is the sheep tick, *Ixodes ricinus*, which completes its life cycle in the humid bracken litter (Nicholson and Patterson, 1976).

ANTS AND PTERIDOPHYTA

Ants are often associated with pteridophytes. At least two species visit bracken nectaries, where they suck up the abundant secretion and possibly also gnaw shallow excavations (Darwin, 1877). In the tropics many ants nest fortuitously in pteridophytes (Yapp, 1902), but many more constant associations have also been reported. *Camponotus* sp., for instance, regularly visits the Neotropical potato fern, *Solanopteris brunei*, although it was never observed to breed there (Gómez, 1974). At a more advanced level, the ants consistently nest within a certain pteridophyte species; this relationship is regarded as symbiotic. *Azteca* sp. regularly built its nest on and in touch with the potato fern (Gómez, 1974). The tubers served queen ants to start new colonies, and were also used as brooding chambers, in which eggs were deposited and larvae tended by worker ants.

Two Malaysian "myrmecophilous" Pteridophyta and their ant associates were reported by Yapp (1902). *Polypodium (=Lecanopteris) carnosa* was associated with the ant *Crematogaster yappi*, and *Polypodium (=Lecanopteris) sinuosum* with *Technomyrmex albipes*. Ants entered both plants through openings excavated in large-celled, thin-walled tissue (with apparent water-storing functions), which, upon breaking down, gives rise to the galleries that run throughout the plant. These and other Malaysian *Lecanopteris* and their ant associates were also discussed by Holttum (1954). *Lecanopteris* was recently revised by Jermy and Walker (1975), who provided additional data on the accompanying ants, like a *Camponotus* sp. on *L. spinosa*. Daniels (1974) briefly referred to *Iridomyrmex cordatus*, an ant living in the rhizome galleries of *Drynaria quercifolia* in Australia. Advantages accruing to ants from this relationship are shelter, moisture and carbohydrates present in the plants' "ripe" parenchymatous cells (Gómez, 1974). Pteridophyta appear to have evolved towards mutualism with ants, as suggested by various anatomical modifications; thin-walled points of entry, ready-made galleries and carbohydrate-containing tissues. *Solanopteris brunei* produces an aldehyde-like substance which attracts the ant *Azteca* and may serve as an allomone, restricting these ants to the plant. What the pteridophytes gain from this association is not clear. Darwin (1877) rejected the possibility of defence against herbivores, a possibility which Lawton (1976) termed the "set a thief to catch a thief" principle. Such protection is usually ruled out in regard to tropical ant ferns (Gómez, 1974; Jermy and Walker, 1975; but see Bentley, 1977 for a divergent view). Other postulated advantages include imported minerals and nitrogen from ants' excreta (Holttum, 1954), and CO₂ provided by actively respiring ants in the green rhizomes of *Lecanopteris spinosa* (Jermy and Walker, 1975).

Janzen (1974) conducted a comparative study of the relationships between several epiphytes (including *Phymatodes (=Lecanopteris) sinuosum*) and their associated ant, *Iridomyrmex myrmecodiae*. He thought that ants may prefer epiphytes for nesting as they provide relatively dry cavities of long duration (in the tropics). He also pointed out that epiphyte-ant associations often occur when epiphytes develop on slow-growing vegetation with an insufficient supply of nutrients. Without the ants, which supply their remnants as well as CO₂, the epiphytes, including Pteridophyta, may not have been able to survive in low productivity habitats. One such association appears to have implications for a Lepidopteran herbivore, the Lycaneid *Hypochrysops theon medocus*, whose larvae feed on *Drynaria quercifolia*. Ovipositing Lycaneid females alight on the undersurface of the fronds and walk about. Eggs are laid only if ants are encountered; otherwise females search other fronds. Larvae feed within rhizome galleries, where they coexist with the attendant ant, *Iridomyrmex cordatus*, which apparently never molests the larvae (Daniels, 1974). This appears to be another case of Lycaneid-ant symbiosis, a little understood series of associations (Owen, 1971).

EPIZOIC SYMBIOSIS

A different form of pteridophyte-arthropod mutualism was reported by Gressitt (1969) within the context of "epizoic symbiosis". This involves weevils which support extensive plant growths on their backs. The beetles — mostly belonging to the subgenus *Symbiopholus* in the genus *Gymnopholus* — are structurally modified to accommodate the plants growing on them. These modifications include dorsal depressions surrounded by ridges, as well as various adapted setae and scales. A sticky secretion, which may promote propagule germination and subsequent growth, is also produced. Most plants found were fungi, algae, lichens and mosses; but a specimen of

Gymnopholus (*Symbiopholus*) *lichenifer* had an unidentified pteridophyte gametophyte growing on it. The association was believed to be mutualistic; the weevils providing a favourable environment for the plants, the latter serving as protective covering for the beetles (Gressitt, Samuelson and Vitt, 1968).

DISPERSAL AND AN ETYMOLOGICAL ASSOCIATION

Some herbivores of Pteridophyta, especially those which attain pest status, were probably inadvertently brought to various parts of the world with their host plants by humans. The aforementioned fern weevil, of Australian origin, is one example. Arthropod dispersal of pteridophytes appears to be of minor importance. Ants were seen to carry spores on their bodies, thus transferring them from tree to tree. Such spore transport was considered by Holtum (1954) to be "hardly necessary" as wind dispersal of spores was very effective. Thompson (1977) observed that *Apirocalus*, a New Guinean weevil, sometimes has pteridophyte sporangia attached to it, although the beetles were never collected on cryptogamic plants. Many spore feeders possibly void some viable spores away from the feeding site and thus disseminate them.

Finally, on a whimsical note, it might be mentioned that the scientific name for pteridophytes, and the names of the insect subclasses (as well as many orders) (Table 1) have a common root, the Greek word *Pteron*, a wing. Thus the names Pteridophyta, Apterygota, Pterygota, Diptera, Lepidoptera *etc.*, have all originated from the same word.

DISCUSSION

The most interesting current problem in regard to pteridophyte-associated arthropods is the extent to which the plants' defences deter or inhibit insect feeders. The opinions of Brues (1920, 1946), Elton (1966) and more recently Cooper-Driver (1978), were that Pteridophyta have far less than their share of herbivores. The discovery of phytoecdysones in pteridophytes (Kaplanis *et al.*, 1967), as well as other feeding deterrents (Lawton, 1976; Cooper-driver, 1978) tended to support the hypothesis that Pteridophyta are highly resistant to insect attack (Hendrix 1977; Slama, 1969). However, other, contradictory data were concurrently becoming available. The search for natural enemies of bracken and water pteridophytes disclosed that these plants were actually being attacked by a large and diverse arthropod fauna (Bennett, 1966; Kirk, 1977; Simmonds, 1967; Wieczorek, 1973). An analysis of the structure of an arthropod community on bracken (Lawton, 1976) showed that the size of this fauna fits well within the range of comparative angiosperm-associated faunas. Working in tropical Mexico, Balick *et al.* (1978) reported that pteridophytes were apparently preferred over angiosperms as food for insects.

On theoretical grounds, there is no reason why the pteridophyte fauna should be depauperated. Strong, McCoy and Rey (1977, and former papers) strongly argue that host-plant range is the most important factor determining the species-richness of its herbivores. Age of a host within a given region was considered to be of minor importance. Smith (1972) concluded that the number of endemic pteridophyte genera is less than half that of the flowering plants and that pteridophyte genera and species, on the whole, are more widely distributed than angiosperms. Upon applying the concept stated by Strong *et al.*, (1977) to Pteridophyta, it becomes reasonable to expect that these plants may actually have as many, or more, arthropods associated with them as the angiosperms. As to the role of pteridophyte chemical defences, the secondary substances, there is no doubt that they confer some protection upon the Pteridophyta (Cooper-Driver *et al.*, 1977). However, this by itself does not mean that

TABLE 4 : SOME ANCIENT PTERIDOPHYTA AND THE SPECIFICITY OF THEIR HERBIVORES.

(Monophagous: feeding only on one genus; oligophagous: feeding on ancient as well as modern ferns; polyphagous: feeding on ferns and on flowering plants).

Pteridophyte	Arthropod taxon	Monophagous	Oligophagous	Polyphagous	Source
<i>Equisetum</i>	<i>Dolerini</i> (Hymenoptera: Tenthredinidae)	+			Benson, 1962
	<i>Liriomyza</i> spp. (Diptera: Agromyzidae)	+			Spencer, 1972
	<i>Sitobion equiseti</i> (Hemiptera: Aphidoidea)	+			Ossiannillson, 1964
	<i>Aphis equiseticola</i> (Hemiptera: Aphidoidea)	+			Ossiannillson, 1964
<i>Selaginella</i>	<i>Phenacoccus solani</i> (Hemiptera: Pseudococcidae)			+	McKenzie, 1967
	Cecidomyiidae (Diptera)	+			Docters van Leeuwen, 1938
	<i>Euptychia westwoodi</i> (Lepidoptera: Nymphalidae)	+			Singer, Ehrlich & Gilbert, 1971
	<i>Boreus reductus</i> (Mecoptera: Boreidae)	+			Penny, 1977
<i>Dicranopteris</i>	<i>Nesopedronia</i> spp. (Hemiptera: Pseudococcidae)	+			Beardsley, 1971
<i>Lygodium</i>	<i>Saissetia coffeae</i> (Hemiptera: Coccidae)			+	Hussey, Read & Hesling, 1969
	<i>Tenuipalpus lygodii</i> (Acari: Tenuipalpidae)	+			DeLeon, 1966
<i>Marattia</i>	<i>Agromyza</i> sp. (Diptera: Agromyzidae)	+			Swezey, 1921
<i>Osmunda</i>	<i>Micromyzus osmundae</i> (Hemiptera: Aphididae)	+			Miyazaki, 1968
	<i>Utamphorophora filicis</i> (Hemiptera: Aphididae)		+		Miyazaki, 1968
	<i>Chirosia hystricina</i> (Diptera: Anthomyiidae)		+		Hering, 1937
	<i>Phytoliriomyza hilarella</i> (Diptera: Agromyzidae)		+		Hering, 1951
	<i>Hemitaxonus dubitatus</i> (Hymenoptera: Tenthredinidae)		+		Smith, 1966
	<i>Hemitaxonus albidoptictus</i> (Hymenoptera: Tenthredinidae)			+	Smith, 1969
	<i>Strongylogaster osmundae</i> (Hymenoptera: Tenthredinidae)	+			Okutani, 1967
	<i>Strongylogaster secundus</i> (Hymenoptera: Tenthredinidae)	+			Okutani, 1967
	<i>Euplexia lucipara</i> (Lepidoptera: Noctuidae)			+	Heslop-Harrison, 1944
<i>Polia assimiles</i> (Lepidoptera: Noctuidae)			+	Godfrey, 1972	
<i>Todea</i>	<i>Syagrius intrudens</i> (Coleoptera: Curculionidae)		+		Lloyd, 1944

the protection afforded to pteridophytes is much more efficient than that given to angiosperms. The latter are extremely diverse from the chemical point of view, and lumping all flowering plants together in order to compare them with pteridophytes, in regard to number of associated arthropods (Brues, 1920), is not convincing. What may be needed is a comparative study on one or two angiosperm groups with similar numbers of species, distribution and apparency (*sensu* Feeny, 1976). Plant chemistry alone possibly makes little difference to the total number of insect species which eventually evolve to exploit a given plant (Lawton, in press); or, as stated by Levin (1976), "no defence is sacrosanct". The considerable insect and mite guilds which live on bracken and *Salvinia* suggest that arthropods have indeed evolved mechanisms to circumvent the plants' protective chemicals. Other often ignored factors in host-plant selection are temperatures and specific habitats (especially in the tropics), as shown by Eastop (1973) in regard to aphids, and the non-chemical (i.e., plant architecture, abundance, seasonality) components of apparency. There is no cause to exclude the Pteridophyta from such considerations.

And yet, some of the available literature tentatively suggests that a distinction could perhaps be made between the ancient Pteridophyta (including *Selaginella* and *Equisetum*) and the modern ones. Although records of ancient pteridophyte-associated arthropods are meagre, the pattern of these associations appears to differ from those of modern Pteridophyta.

A difference between the number of animal-induced galls formed on ancient and modern Pteridophyta was noted by Docters van Leeuwen (1938). A listing of arthropods currently known to feed on and live on ancient pteridophytes suggests that most insects and mites which feed on them are either monophagous (restricted to one pteridophyte species or genus), or else polyphagous (subsisting on Pteridophyta as well as flowering plants). Aside from two exceptions (see below), ancient Pteridophyta are only very rarely attacked by arthropods which also feed on modern pteridophytes (Table 4).

The exceptions are *Osmunda* and *Todea*, both members of the order Osmundales. They are attacked by aphids, sawflies, leaf-mining fly maggots and a weevil (Table 4), all of which also occur on one or more modern Pteridophyta. In so far as further collections confirm these observations, it could be argued that from the herbivore point of view, *Osmunda* and *Todea* are more similar to modern pteridophytes than to the ancient ones. According to current ecological concepts, the similarity is probably biochemical in nature. Hikino *et al.* (1973), while assaying Japanese Pteridophyta for phytoecdysones, found no activity in most ancient pteridophytes. These included Equisetaceae, Lycopodiaceae, Selaginellaceae, Ophioglossaceae, Marattiaceae, Schizaeaceae and Hymenophyllaceae. Only in *Hicriopteris glauca* (Gleicheniaceae) and in six members of *Osmunda* (Osmundales) were phytoecdysones found. The related *Todea* also showed insect moulting hormone activity (Russell and Fenemore, 1971). Nothing is known about arthropods of *H. glauca*, so it will not be further discussed. The Osmundales remain as almost the only group of ancient Pteridophyta with high phytoecdysone activity, and the only group which has herbivores in common with modern pteridophytes. It is tempting to postulate that these phenomena are related.

As already noted, available experimental data do not confirm that phytoecdysones act as feeding deterrents in Pteridophyta. This does not imply that they did not affect herbivores in the past; the phytoecdysones may have played an important role in the co-evolution of Pteridophyta and their associated herbivores, but have now become a "redundant defence mechanism" (Jones and Firn, 1978). The associations between arthropods and the ancient Osmundales may well have initiated

later co-evolutionary processes with modern pteridophytes. A relatively advanced state of Osmundales-arthropod co-evolution is also suggested by the disproportionately high number of insects found on the few extant species of Osmundales, as pointed out by G. Cooper-Driver (in lit.).

The comparative studies of Lawton (1976) and Kirk (1977) on bracken arthropods in England and Papua New Guinea, respectively, emphasize the differences in these faunas between temperate and tropical regions. Britten (1881), and Cooper-Driver (1978), among others, noted dissimilarities in the extent of pteridophyte susceptibility to insect attack between temperate and tropical regions, but quantitative data are scarce. And yet over 90% of all extant Pteridophyta grow in the tropics (Manton, 1973) and evolution in tropical regions operates in fundamentally different ways than in temperate zones (Dobzhansky, 1950). Tropical Pteridophyta doubtless carry a multitude of unstudied arthropods (Balick *et al.*, 1978); relevant studies thus promise to enrich and modify our concepts about pteridophyte-arthropod associations.

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