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THE ECOLOGY OF THE PITCHER PLANT NEPENTHES MIRABILIS AND ITS ASSOCIATED FAUNA IN HONG KONG

by

Barbara Corker

This thesis is submitted to the Botany Department of the University of Hong Kong in fulfillment of the requirements for the degree of Doctor of Philosophy.

JUNE 1984

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Declaration of Authorship

I hereby declare that this thesis represents my own work and that no part of it has been previously included in a thesis, dissertation or report submitted to this university or to any other institution for a degree, diploma or other qualification.

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Abstract

Thesis entitled 'The ecology of the pitcher plant *Nepenthes mirabilis* and its associated fauna in Hong Kong'.
Submitted by Barbara Corker for the degree of Doctor of Philosphy at the University of Hong Kong in June, 1984.

In this study the composition of the *Nepenthes* fauna in Hong Kong was investigated and attempts were made to study the biology of the most common animals and the relationships between community members, as well as the effects of seasonal changes in plant growth on the animal communities.

Large numbers of pitchers were sampled from eleven sites in Hong Kong and Macau; firstly, to identify the local *Nepenthes* pitcher fauna and to determine seasonal population fluctuations of the dominant species; secondly, to examine the effect of pitcher age on the composition of pitcher communities and thirdly, to determine the effects of pitcher size on community composition. Feeding and development of the most common animals was studied in the laboratory and a foodweb was constructed. Results from all pitchers sampled were pooled and observations were made on the effect of geographical location on the pitcher communities. The viability of the plant seeds was determined and flowering and seasonal changes in plant growth were studied in 25 marked plants over a period of 14 months. The development of pitchers, particularly with regard to fluid secretion and pH changes within the fluid, was also investigated.

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Over 60 species of animals were found on the plants but of these only 10 were regular Nepenthes associates. These included the mosquitoes, Armigeres magnus (Theobald) and Culex sumatranus Brug, one phorid (Megaselia corkerae Disney), three anoetid mites (Zwickia sp., Creutzeria sp. and Anoetid A), one oribatid mite (Galumna sp.), one bdellid mite (Bdellodes sp.) and two unidentified lepidoptera. There was a high similarity between the faunas of different areas.

The carrion-feeding Zwickia sp. was the dominant pitcher inhabitant and it occurred most frequently in young pitchers where the proportion of carrion was greatest, while the detritus-feeding Creutzeria and Anoetid A were predominantly found in mature and old pitchers respectively. Zwickia and Anoetid A deutonymphs are capable of active colonization of pitchers and may be able to select pitchers of the correct age, while Creutzeria is totally reliant on insect vectors for dispersal.

Larvae of Culex and Armigeres feed largely on carrion (although they are also facultative predators) and the adults oviposit preferentially in young pitchers. Larval numbers decrease in older pitchers due to a high larval mortality rate and to emergence, while the number of Megaselia larvae increases due to reduced predation by culicine larvae. Species diversity increased in old pitchers both as a result of reduced predation and also because the fluid pH increases and digestive activity of the fluid decreases, allowing animals normally found in other habitats to colonize the pitchers. An increase in species diversity was also noted in the smallest pitchers due to proximity to the ground and to the absence of the highly predacious Armigeres larvae, which were excluded from these pitchers as a result of the large size of the adult females.

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The foodweb in the pitchers is essentially similar to those found in Nepenthes pitchers elsewhere, except that the number of functional components is reduced and each component is composed of fewer species. The culicine larvae have the ability to delay development when food is scarce, and this appears to be a characteristic of Nepenthes animals in general since Zwickia mites were also capable of extending their developmental period under starvation conditions.

Maximum growth of the plants occurred in the summer months when temperatures and rainfall were both high and the majority of flowering also took place at this time. In the winter, when temperatures and rainfall were low, growth was greatly reduced and fewer, smaller pitchers were produced. However this had little effect on the pitcher fauna since the populations of Culex, Armigeres and Zwickia (the dominant inhabitants) fell dramatically during cold periods due to intolerance of low temperatures. Population levels of the more tolerant Megaselia reached their highest level in these periods, in the absence of predation.

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SECTION I

Introduction

Review of the literature

General information on *Nepenthes* in Hong Kong

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Introduction

There are five known genera of pitchered carnivorous plants belonging to the families Sarraceniaceae, Nepenthaceae and Cephalotaceae. The Sarraceniaceae is comprised of three genera, Heliamphora, Sarracenia and Darlingtonia, while the Nepenthaceae and Cephalotaceae each contain a single genus (Nepenthes and Cephalotus respectively). Six species of Heliamphora have been described which occur exclusively in the extreme south of Venezuela, while there are eight generally recognized species of Sarracenia, occurring mostly in the south eastern states of the United States, although the northern subspecies of S. purpurea L. ranges as far north as the arctic regions of Canada (Slack, 1979). Darlingtonia is a monotypic genus which is restricted to the states of Oregon, California and North Carolina in the United States (Lloyd, 1942; Slack, 1979). The Nepenthaceae and the Cephalotaceae each contain a single genus, but over 70 species of Nepenthes have been described, occurring over a wide area including Southeast Asia, New Guinea and Australia, whereas there is only one species of Cephalotus which has a very limited distribution in Western Australia.

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All five genera have leaves which are modified to form pitchers which act as pitfall traps. In Heliamphora, Darlingtonia and Sarracenia the whole leaf is modified to form a hollow, tube-like pitcher, while in Nepenthes the terminal part of the leaf is modified to form a pitcher which is attached to the rest of the leaf by a tendril. In Cephalotus, two types of leaves occur, the normal foliage leaves, and the pitchered leaves which are formed from the entire leaf as in the Sarraceniaceae.

The traps of all five genera function in much the same way. Nectar is secreted on the pitcher body and lid and under the rim of the pitcher mouth and this attracts small animals (usually insects) which crawl around on the pitchers, occasionally entering them in search of the nectar secreted under the rim of the pitcher mouth. The interior walls of the pitchers are very smooth and offer no foothold for animals attempting to walk on them, so that the animals lose their footing and fall into the fluid accumulated in the base of the pitcher. Most animals drown when they enter the fluid since sharp, downward-pointing hairs on the lower part of the walls prevent escape from pitchers of the Sarraceniaceae, while in Nepenthes and Cephalotus the pitcher walls are smooth and impossible to scale. The trapped animals are gradually digested in the fluid, which is a product of plant secretions and rainwater, and the

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resulting nutrients are absorbed by the pitchers and utilized by the plants.

It is less well known that besides the animals trapped by the pitchers there is also a wide range of aquatic and terrestrial animals which live in the pitchers and which are apparently immune to the digestive enzymes in the fluid. These animals usually occur exclusively in the pitchers and are specifically adapted to the pitcher environment, although species which normally live in other habitats are sometimes also found. Sarracenia, Darlingtonia, Nepenthes and Cephalotus all possess living pitcher inhabitants and, although they have never been found in the pitchers of Heliamphora, it is probable that this genus also possesses animal associates which have simply never been recorded due to the rarity of the plants and the difficulty of obtaining material for study.

Most of the pitcher inhabitants are insects and arachnids and the pitcher fauna is normally dominated by diptera. Little is known about the fauna of Cephalotus and Darlingtonia, but the fauna of Sarracenia has been fairly extensively studied in terms of both taxonomic composition and ecology. Extensive literature also exists on Nepenthes pitcher inhabitants but studies have so far tended to deal only with the taxonomic composition of the fauna in different areas. Ecological and community studies have been largely neglected apart from the work

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of Beaver (1979a; b; 1983), while studies on the growth of the plants have never been carried out.

Hong Kong represents virtually the northernmost point at which Nepenthes occurs and only one species, N. mirabilis Druce, is found in the region, whereas in Borneo (which is close to the centre of origin of the genus) numerous species occur. In contrast to most other areas where Nepenthes occurs, Hong Kong has a subtropical climate with definite seasonal variations in temperature and rainfall. This may be the reason why N. mirabilis is the only species to occur in Hong Kong, because whereas most species of Nepenthes have a limited distribution in tropical regions (presumably due to specific climatic requirements), N. mirabilis is a very widespread species which must tolerate a wide range of climatic conditions. In most other areas, climatic conditions vary little seasonally and it is therefore almost impossible to isolate which factors are most important in controlling growth and reproduction in the plants. However, the seasonal nature of the climate in Hong Kong leads to marked seasonal variation in growth of the plants and as a result it was possible to measure the effect of different climatic factors on growth and reproduction in Nepenthes. Towards the edge of the range of Nepenthes, fewer animal species tend to be associated with individual Nepenthes species (Beaver, 1983) and this

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proved to be the case in Hong Kong. The pitcher communities were therefore simple in comparison to those of Nepenthes species closer to the centre of origin of the genus, so that the ecology and community interactions of the Nepenthes fauna in Hong Kong could also be studied with relative ease.

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Review of the Literature

Although the present study is confined to Nepenthes, literature dealing with other genera of carnivorous plants will also be reviewed where applicable, since in many cases research on other carnivorous plants may be applied equally well to Nepenthes in the absence of specific research on Nepenthes itself. Topics which are already well documented and which therefore have not been investigated in the course of this research are also included in order to give a broader understanding of the problems which have been studied.

Section A. Plant Structure, Physiology and Ecology

1. Historical Background

Nepenthes was first recorded under the name of Amramitico by E. de Flacourt, a colonial governor of French Madagascar in 1658 (Kurata, 1976). In 1682, H.N. Grimm named pitcher plants from Ceylon, Planta mirabilis distillatoria, due to the secretion he observed in the pitchers and this same species was later described by J.P. Breyne in 1689 under the name of Nepenthes zeylanicum flore minore (Kurata, 1976). This was the first time that the generic name Nepenthes had been used and it was later adopted by Linnaeus who renamed the species N. distillatoria L. (Kurata, 1976).

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For a long time the carnivorous nature of pitcher plants went totally unsuspected as it never occurred to anyone that plants might trap and digest prey in the same way as animals. The earliest known reference to the possibility of carnivory in a plant was made by Ellis in 1770 with regard to the Venus fly trap, Dionaea musculipa Ellis, of which he says; "it is as if the great authority Nature intended the plant to receive some nourishment from the animals it seizes" (Hooker, 1874). When Sarracenia was first grown in cultivation it was noted that the pitchers contained water and consequently the idea arose that the function of the pitchers was to collect and hold water to tide the plants over periods of dry weather. Linnaeus and others thought that the lid, which Morison described erroneously as being hinged, closed over the pitcher to conserve the water inside (Lloyd, 1942). Collinson noted that many insects drowned in the pitchers (Hooker, 1874) but it was probably William Bartram who first recognized that the pitchers of Sarracenia were constructed for the specific purpose of catching insects, even surmising (correctly, as we know today) that the short, stiff, downward-pointing hairs inside the pitchers served to prevent the victims escaping (Slack, 1979). Despite these observations he doubted that the insects were actually utilized by the plant, but thought like Linnaeus, that the fluid in the pitchers was a provision against drought (Slack, 1979).

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In 1875, Mellichamp demonstrated that the pitcher fluid of Sarracenia was a secretion of the plant rather than captured water and he tested the digestive activity of the fluid by comparing the rate of digestion of pieces of meat placed in pitcher fluid and in distilled water. He found that the meat dissolved more readily in pitcher fluid than in distilled water and therefore concluded that the pitcher fluid accelerated decomposition. However, Schimper (1882) found that meat dissolved at the same rate, irrespective of whether it was placed in pitcher fluid or in distilled water and he concluded that the plants did not secrete digestive enzymes and that any digestion which took place in the pitchers was purely bacterial. The problem of whether the plants actually secreted digestive enzymes into the pitchers or not was finally resolved by Hepburn, St. John and Jones (1927). They tested the digestive action of pitcher fluid from Darlingtonia californica and from most species of Sarracenia on a variety of substrates, using trikresol as a bactericide and replicating the experiments many times. The results of these experiments demonstrated conclusively that in all the species of Sarracenia studied, the pitcher fluid contained a native protease which in most cases worked best in an alkaline environment, and they also confirmed the earlier findings of Edwards and Goebel (cited by Lloyd, 1942), that pitchers of D. californica did not contain a native protease, digestion

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in this case being effected by bacterial action alone. Hepburn et al (1927) also showed that water, nitrogenous substances and phosphate were absorbed by the pitchers in substantial amounts, demonstrating that it was possible for the plants to benefit directly from the digestion of trapped insects and hence it became widely accepted that the plants were truly carnivorous.

Experiments being carried out on digestion in Sarracenia in the late nineteenth century stimulated interest in Nepenthes and a number of people began similar investigations on digestion in Nepenthes pitchers. The pitcher fluid was found to have a marked digestive action, dissolving shreds of fibrin within one hour at a temperature of 40°C (Gorup-Besanez, cited by Lloyd, 1942), but in contrast to Sarracenia, an acid environment was necessary for digestion to take place. To eliminate the problem of contamination of the pitcher fluid with bacterial and insect enzymes, Vines (1876; 1877) attempted to obtain an active extract from the pitcher glands using similar methods to those used to obtain enzymatic extracts from animal tissues. He succeeded in obtaining a glycerine extract from the pitcher wall which showed digestive activity (although only when acidified) the rate of digestion being much slower than that noted by Gorup-Besanez for the pitcher fluid itself. Vines (1877) explained this by assuming that in the fluid the proteolytic enzyme was in a free state while in the extract it was in the form

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of a zymogen which was split by acid to release the free enzyme. Pretreatment of pitchers with acid resulted in a more active extract, a fact which seemed to support his assumption.

Pitcher fluid was found to be much more effective in digesting egg white, fibrin, cartilage and meat when it was contained in the pitchers rather than *in vitro* (Hooker, 1874) and it was also found that while albumen was vigorously digested when placed in fluid *in situ*, similar experiments with albumen placed in pitcher fluid in glass tubes left next to the plants in the natural habitat, had negative results (Clautriau, 1900). Gorup-Besanez and Will (1876) found that fluid from pitchers which had not trapped insects (unstimulated pitchers) required the addition of acid before it had any digestive activity, while fluid from pitchers containing insects (stimulated pitchers) showed digestive activity with or without the addition of acid. Hepburn (1918) obtained similar results by artificially stimulating the pitchers, both mechanically, by shaking glass beads around inside the pitchers, and chemically, by adding organic substances to the fluid. As Zeeuw (1934) found that the addition of fibrin and egg white to the pitchers stimulated the production of acid, the function of the pitchers may therefore be to regulate the pH within the fluid in order to maintain an environment favourable for an enzyme already present, or to activate a zymogen.

For many years investigators of digestion in *Nepenthes* were firmly polarized into two camps: those who believed that digestion

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in the pitchers was due to enzymes secreted by the plant, and those who were convinced that digestion relied on bacteria introduced into the pitchers after opening. The main proponents of the latter theory were Dubois (1890) and Tischutkin (1891), neither of whom could find any evidence of digestion in pitchers other than that attributable to bacterial action. Vines (1897) took issue with the conclusions of Dubois and Tischutkin and as a result carried out a number of experiments which demonstrated that digestion of protein by native plant enzymes did occur. He found that pitcher fluid would digest fibrin even in the presence of hydrocyanic acid and added these words in his conclusion: "Those who support bacterial digestion only, must first produce an organism which will digest fibrin in the presence of 1% hydrocyanic acid and which will retain its digestive activity for several weeks in pure glycerine." Couvreur (cited by Lloyd, 1942) argued that Vines' results were due to the interaction of reagents on one another, but since Goebel (cited by Lloyd, 1942) found that neutral fluid from a closed pitcher would digest fibrin on the addition of formic acid when no trace of bacteria could be detected, it seems indisputable that the plants do secrete proteolytic enzymes into the fluid.

In his work of 1897 and further in 1898, Vines investigated the properties of the plant protease which he called nepenthin and he found that it was very stable to heat and alkalis and appeared to be essentially tryptic in character. Abderhalden and

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Teruuchi (1906) disputed the tryptic nature of the enzyme, while Clautriau (1900) suggested that it was instead a pepsin as it acted only in acid medium, producing peptones as a result. Kramer (cited by Lloyd, 1942), Stern and Stern (1932) and Zeeuw (1934) all detected tryptic action in pitcher fluid, but Kramer and Zeeuw considered that the tryptic action was bacterial in origin while Stern and Stern thought that the tryptic enzyme was secreted by the plants. The nature of the plant enzymes remained in doubt until many years later, when, with the advent of more sophisticated techniques for the isolation and characterization of enzymes, it was shown that at least two proteases were secreted by the plant, the major enzyme being pepsin-like in its mode of action (Tokes, Woon and Chambers, 1974).

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II. Geographical distribution

Fig. 1 Geographical distribution of *Nepenthes*; Black areas indicate regions where *Nepenthes* occurs. The broken line defines the limits of the genus in the Southeast Asian region, the closed line defines the limits of *N. mirabilis*. (redrawn from Danser, 1928)

The total area of distribution of *Nepenthes* is shown in Fig. 1 The genus extends westwards to Madagascar, eastwards to New Caledonia, northwards to the Khasi Highlands in India and to Southern China, and southwards to the York Peninsula in Australia (Danser, 1928). It does not occur in Africa although it is found on the island of Madagascar close to the African coastline. Most *Nepenthes* species are concentrated in Southeast Asia, particularly on the islands of Borneo (30 species) and Sumatra (21 species) and because of this the Malay Archipelago is presently considered to

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be the centre of evolution of the genus (Kurata, 1976).

The first monograph of the genus was published by Hooker in 1873 (Kurata, 1976) although the number of species has since been revised many times. Macfarlane (1908) recognized 58 species, which Danser (1928) reduced to 48, while at the same time adding 17 new species of his own to bring the total to 65 species. A number of these were modified by Harms (1936) and since then 8 new species have been described to give a final total of 71 species (Kurata, 1976). Many of these species have a very restricted geographical distribution, thus four species: N. madagascariensis Poir., N. pervillei Blume, N. distillatoria L. and N. khasiana Hook.f. (found respectively in Madagascar, the Seychelles, Sri Lanka and India) are isolated in the western end of the generic range, each species occuring on its own, while many of the species in Borneo are restricted to one particular mountain top where they probably originated (Danser, 1928). A few species cover wide areas within the geographical range of the genus, of which N. mirabilis is the most widespread (Fig. 1).

III. Habitat

Nepenthes plants are generally supposed to be plants of damp, humid jungles (Lloyd, 1942; Slack, 1979) but according to Kurata (1976) most species of Nepenthes exhibit a preference for more exposed places such as mountain ridges, forest edges, rock faces, swamps and the crowns of tall trees. A number of species of

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Nepenthes occupy fairly specialized habitats, thus N. northiana Hook.f. (Sarawak), N. clipeata Dans. (Central Borneo) and N. campanulata Kurata (East Borneo) grow on the vertical walls of limestone cliffs, with their roots fixed into indentations in the rock and their stems climbing up and along fissures in the rock face (Kurata, 1976). N. thorelii LeCompte grows in sandfields of the Lower Mekong and has a stem which is strongly expanded at the base, which acts as a water tank allowing the plants to withstand long periods of drought in between monsoons (Kurata, 1976). In contrast to this, N. mirabilis grows preferably in swamps and along the banks of streams where the plants may be semi-submerged (Kurata, 1976), and N. gracilis Korth. is common in peat swamps, with small plants growing on detritus floating on the water and larger ones growing on islands formed around the base of trees (Green, 1967). N. albo-marginata Lobb has been collected on maritime rocks and in coastal regions and N. reinwardtiana Miq. has been collected on the coast near Sumatra, so these species may be classified as seaside plants (Kurata, 1976).

In terms of vertical distribution, Nepenthes grows at altitudes from sea level to approximately 3000m (Lloyd, 1942). Most species can be classified into either lowland types, which grow below 1000m, or highland types, which grow above 1000m (Kurata, 1976). Lowland species such as N. mirabilis and N. ampullaria Jack prefer high temperatures and high humidity daylong, while the highland type (which includes 68% of all species of Nepenthes) prefer a cooler,

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wetter climate at night (Kurata, 1976). Some species such as N. tentaculata Hook. f. have a wide range of vertical distribution, while others such as N. villosa Hook. f. are more limited (Kurata, 1976). N. villosa grows only at high altitudes (2400-3200m) and is therefore classified as an alpine plant, since the temperature at this altitude falls to $5^{o}C$ in the early morning (Kurata, 1976). The highest place where Nepenthes has been recorded is a swamp in Central New Guinea at 3520m altitude, where N. vieillardii Hook. f. was collected and it was noted here that the temperature fell below freezing point in the early morning (Kurata, 1976).

IV. Morphology

In general structure most species of Nepenthes are fairly uniform, the most striking differences being found in the size and shape of the pitchers (Lloyd, 1942). The plants are dioecious undershrubs or lianas with stems which are usually long and climbing, although they may be prostrate or short and erect (Danser, 1928). Young plants are rosette-shaped, while older plants are always elongated, often bearing short, non-climbing stems (short shoots) on the main climbing stem (Danser, 1928), which arises from a creeping rhizome (Lloyd, 1942). The leaves may be sessile or petiolate and they consist of a leaf blade, a tendril and a pitcher with a lid. The leaf blade varies in shape from linear-lanceolate, to spathulate or elliptic and is 10-45cm long and 1-15cm broad, with a well-developed midrib which gradually merges into the tendril (Kurata, 1976). The tendrils of the leaves borne on the elongated stems are usually one and a half times as long as the leaf blade, with two or three spirals midway along their length, while those of the short shoots and lower leaves are

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normally shorter than this, with or without spiralling (Danser, 1928). The tendrils of rosette leaves are shorter and never spiral (Danser, 1928). The end of the tendril merges gradually into the base of the pitcher and the pitcher is supported in an upright position by the twining of the pitcher tendril around adjacent vegetation. The pitchers must remain in an upright position in order to function and this is accomplished by tropisms in the region of the pitcher base and the end of the tendril (Lloyd, 1942).

Most species have pitchers which range in size from 5-15cm in length (Lloyd, 1942), although the pitchers of species such as N. rafflesiana Jack and N. edwardsiana Hook. f. may reach lengths of up to thirty or even thirty five centimetres (Kurata, 1976). In shape, pitchers may be cylindrical, funnel-shaped or sac-like (Lloyd. 1942) with many gradations of form between these broad categories. Pitchers produced on a individual plant may also be mono-. di-, or trimorphic (Macfarlane, 1908), thus the rosette pitchers in contact with the ground may differ from those of the climbing stems and the uppermost pitchers may be different again to those midway up the stem. The rosette pitchers are usually small, urceolate to ovate with two broad, well-developed, fringed wings running from the base of the pitcher to the mouth, while pitchers of the short shoots and of the lower parts of the climbing stem are similar in shape, although larger, and they lack the fringed edges to the wings, which are sometimes reduced to prominent ribs (Danser, 1928). In some cases, leaves of the climbing stems do not develop pitchers, but when they are present they are tubulose to infundibuliform, are

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smaller than the pitchers carried on the lower parts of the stem and lack the two wings which are reduced to prominent ribs (Danser, 1928). The orientation of the pitchers also changes with the position of the pitchers on the plant; thus the mouths of pitchers borne on the lower parts of the plant open inwards towards the stem, while those of the upper pitchers open outwards. In simpler species such as N. gracilis, this twisting round of the upper pitchers is a gradual process with intermediate stages which involve little change in the shape of the pitchers, but in more specialized species, the change in direction of the pitcher opening may be quite sudden between one leaf and the next and it may be accompanied by a dramatic change in shape (Green, 1967).

During development of a pitcher the mouth is hermetically sealed by the lid which opens only when the pitcher has reached its definitive size and shape (Lloyd, 1942). The positioning of the lid of pitchers of different species often differs in the degree to which it overhangs the pitcher mouth once the pitchers have opened. In its final position when growth has ceased, it may overhang the pitcher mouth forming a more or less effective barrier to the entrance of rainwater, particularly in forms such as N. rajah Hook. f. where the lid grows and reaches a sufficiently large size to overshade the mouth completely, while in other species such as N. ampullaria and N. dubia Dans. it remains small and narrow and turns completely back, fully exposing the mouth of the pitcher (Lloyd, 1942). Numerous nectar glands occur on the undersurface of the lid and are also found on other parts of the plant such as the leaf mid-

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ribs and tendrils, where they serve to attract a wandering population of ants and other insects which sooner or later find their way to the pitcher mouths (Lloyd, 1942).

The pitcher mouth has a rim or collar termed the peristome which is hard, glossy and rounded (Lloyd, 1942) and regularly corrugated with parallel ribs which are often made conspicuous by contrasting red, green and occasionally white variegation (Slack, 1979). Each rib terminates within the pitcher in a sharp, downward-pointing tooth and between the angles of each pair of teeth are single nectar-secreting glands (Slack, 1979). The nectar from these glands and those on the pitcher lid acts as a lure enticing insects to enter the pitchers (Lloyd, 1942).

The internal surface of the pitchers is always glandular, but the relative amount of glandular tissue contained in the pitchers differs in different species of Nepenthes. In most species, just beneath the rim of the pitcher mouth there is a broad zone with a glaucous, opalescent appearance which is due to an ample waxy secretion (Lloyd, 1942). This whole waxy zone is a conducting, slippery surface which insects are unable to walk on (Lloyd, 1942), so that they fall into the fluid below and drown. The extent of the conducting zone varies, so that in species such as N. ampullaria, N. rafflesiana and N. rajah it is entirely lacking and the whole internal surface is glandular, while in species such as N. mirabilis and N. gracilis it occupies approximately the upper half of the pitcher, the lower half being glandular (Kurata, 1976). The

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surface of this glandular zone is richly supplied with digestive glands, each standing in a slight depression, with the upper edge projecting and overhanging the gland like an eave (Lloyd, 1942). In the depths of the pitcher the glands become more or less irregular in shape and are devoid of any overhang (Macfarlane; Stern - cited by Lloyd, 1942). Danser (1928) notes that in pitchers of N. stenophylla Mast. there are as many of 6000 glands per cm^2, while in N. gracillima Ridl. there are only 100 per cm^2.

V. Physiology

a) Fluid Secretion

The glands on the inner surface of the pitchers secrete a fluid which Voelcker (1849) described as being limpid and colourless with a slight agreeable odour and taste. This fluid is secreted during development of the pitchers and a substantial amount is formed long before the pitchers mature and open, for example, Heslop-Harrison (1975) found that up to 20mL of pitcher fluid was present in pitchers of N. chelsonii before opening. In mature plants the pitcher capacity varies with the species and the conditions, in which it is growing, from about 20mL up to 1000mL in N. rajah in Borneo (Beaver, 1983). Young plants have small pitchers with a capacity of only 2-5mL (Beaver, 1983).

Although most of the pitcher fluid is secreted during pitcher development, a certain amount of secretion also takes place after opening of the pitcher. Hooker (1874) observed that if the fluid was removed from a fully formed pitcher which had not received any

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animal matter, a comparatively small quantity was reformed over a period of several days and to some extent even after the pitcher had been removed from the plant. He also observed on two occasions that when animal matter was placed in pitcher fluid in situ there was a considerable increase in the amount of fluid held by the pitcher. Inorganic substances introduced into the pitchers had no effect on fluid volume.

Several authors have noted that stimulation of pitchers causes a secretion of acid, thus Clautriau (1900) found that the fluid in unstimulated pitchers was neutral in reaction but that it became acidic on the introduction of foreign bodies to the pitcher, or on shaking, while Zeeuw (1934) found that acid was secreted by the glands when they were stimulated by chemical means. There is some disagreement over the method of stimulation of the pitchers, as both Clautriau (1900) and Hepburn (1918) were able to mechanically stimulate the pitchers to produce acid, while Zeeuw was only able to stimulate the pitchers by chemical means. It is possible that the acid secreted is formic acid, since Goebel (cited by Lloyd, 1942) found that formic acid was secreted by normal pitchers when they were stimulated by the presence of an insect.

Fluid from stimulated pitchers exerts a digestive action in both the presence and the absence of acid, while fluid from unstimulated pitchers is only active when acidified (Gorup-Besanez and Will, 1876; Hepburn, 1918). The prime function of stimulation may therefore be to produce a change in the hydrogen ion conentration, so that the pH becomes favourable for the activity of a

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protease already present in the pitcher fluid (Hepburn, 1918). Alternatively, stimulation may activate a zymogen already present, or it may give rise to an increased secretion of protease by the plant (Hepburn, 1918).

b) Fluid pH

The pH of pitcher fluid varies considerably, ranging from extremely acidic to weakly alkaline. Unopened pitchers have been reported to have pH values in the range of 4.5-6.6 (Zeeuw, 1934), 4.2-6.6 (Morrissey, 1955), 7.0 (Nakayama and Amagase, 1968) and 2.8-3.6 (Tokes et al, 1974); the range in pH quoted is thus 2.8-7.0. Heslop-Harrison (1975) showed that in developing pitchers of N. chelsonii, the pitcher fluid first secreted had a pH of 7.0-7.5 and that this gradually decreased to 2.5 just before the pitcher opened. The fluid pH recorded for a closed pitcher could therefore be anywhere within the range of 2.5-7.5 depending on the developmental state of the pitcher, which agrees fairly well with the range of values quoted above.

The fluid pH in open pitchers ranges from 2.1-7.2. depending on pitcher age and possibly also on the species of Nepenthes. The fluid in newly opened pitchers is very acid, thus values of 2.3-4.6 (Morrissey, 1955) and 2.5 (Nakayama and Amagase, 1968) have been recorded in newly opened pitchers. There is some suggestion that the fluid pH varies slightly in different species of Nepenthes, as Tokes et al (1974) found that the pH in newly opened pitchers of N. macferlanei Hemsl. was much lower (2.1-2.8) than the secretions of most other species, which usually had a pH of

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3.0-4.5. The fluid pH of closed pitchers of this species (2.8-3.6) was also lower than that recorded for N. gracilis and N. albo-marginata, which had pH values of 5.0 and 6.0 respectively (Tokes et al, 1974), although this may have been due to the fact that the pitchers were at different developmental stages. The fluid in the pitchers remains acid in the early stages of digestion, but when completely digested insect cadavers are present, the fluid pH is usually neutral or weakly basic (Lloyd, 1942). The maximum pH value recorded for an open pitcher is 7.2 (Zeeuw, 1934).

c) Chemical constituents of the pitcher fluid

The accurate detection of plant-secreted substances in the pitcher fluid poses many problems, perhaps the greatest being that once the pitcher has opened, the fluid becomes heavily contaminated with micro-organisms and captured insects in varying stages of decay. As a result it becomes extremely difficult to separate the substances actually secreted by the plant from those which have been introduced into the pitchers. For this reason much of the work done on the chemical constituents of the fluid is of very dubious value, since it was carried out on fluid from open pitchers contaminated by bacteria and insect remains.

Voelcker (1849) analysed the fluid of unopened pitchers of Nepenthes and found that on evaporation, it yielded a dry residue which contained potassium, sodium, magnesium, calcium, chloride (as hydrochloric acid) and organic acids (chiefly malic and citric). Morrissey (1955) found that the secretions of freshly opened pitchers

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did not contain any significant amounts of the commonly occurring organic acids, but tests with silver nitrate revealed that all pitchers contained chloride. The chloride concentration was low in immature pitchers, but in newly opened pitchers the chloride concentration was in the range of 600-900mg per litre and there appeared to be a definite quantitative correlation between hydrogen ions and chloride ions. As it was well known that the pitcher protease worked best in an acid medium, Morrissey drew the conclusion that the proteolytic action in the pitchers was established, as in the mammalian stomach, by concomitant secretions of a protease and hydrogen ions, the latter being balanced by a simultaneous secretion of chloride ions. More recent research however, indicates that the ionic balance in the pitchers is probably far more complex than this. Nemcek, Sigler and Kleinzeller (1966) discovered what appeared to be separate active pumps transporting sodium and chloride ions into the pitcher tissue from the fluid, against their electrochemical gradients, as well as an active pump transporting potassium ions in the opposite direction, while Luttge (1966) obtained somewhat conflicting results as he found that there was active transport of chloride ions into the pitcher fluid. This took place *in vitro* even when a high gradient of chloride concentration had been set up between the pitcher tissue and the solution in contact with the glands. *In vivo*, the chloride concentration of the pitcher fluid and the amount of chloride per gram of tissue water were almost equal (Luttge, 1966). Although the results obtained by Nemcek *et al* (1966) and Luttge (1966) appear to contradict each other, it must be noted that in both cases, whole tissue concentrations of ions were determined which may not accurately reflect the

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concentrations of ions in the tissue cells adjacent to the fluid, and this may account for the discrepancy in the results. The actual function of chloride in the fluid is still uncertain, but Luttge (1966) noted that there was a definite correlation between the chloride content of the fluid and its enzymatic activity.

It is indisputable that the proteolytic activity of the pitcher fluid in Nepenthes is largely due to the secretion of one or more proteases by the pitcher glands, since proteases isolated from both open and closed pitchers are electrophoretically constant (Amagase, 1972) and have identical patterns of activity (Tokes et al, 1974). This not only demonstrates that they cannot be derived from bacterial or insect contamination but also indicates that no new proteases are secreted after opening of the pitchers. Proteases from different species of Nepenthes appear to be very similar as they have identical pH (2.2) and temperature (40-50°C) optima (Steckelburg, Luttge and Weigl, 1967). The activity of the enzymes is markedly affected by pH with only 10% of the maximum proteolytic activity being detectable at a pH of 4.0 (Tokes et al, 1974). The protease, named nepenthesin (Nakayama and Amagase, 1968), is an endopeptidase with an apparently specific action on aspartic acid residues in peptide chains (Amagase, Nakayama and Tsugita, 1969). Amagase et al (1969) reported that the specificity of nepenthesin was different to that of pepsin to which it is often likened due to its similar pH range, but there is some disagreement over this as the major of two enzyme fractions (nepenthesin) isolated

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by Tokes et al (1974) had a broader specificity than that reported by Amagase et al (1969), as well as a striking similarity to the action of pepsin. Both enzyme fractions isolated by Tokes et al were active independent of one another and the minor fraction did not activate the major one, thus disproving Vines' theory (1877) that the proteolytic enzyme in the fluid was secreted as a zymogen.

Other enzymes besides proteases have also been detected in Nepenthes pitcher fluid. Amagase, Mori and Nakayama (1972) demonstrated that the fluid had chitinolytic activity while Matthews (1960) found substantial ribonuclease and phosphatase activity in the pitcher fluid. However, as the pitcher fluid in both cases contained bacterial and insect contamination, the origin of the enzyme activity is in doubt, although the phosphatase detected by Matthews may have been plant-secreted, since Heslop-Harrison (1975) isolated both acid phosphatase and esterase from the secretion of unopened pitchers. Clautriau (1900) and Robinson (1908) could not detect any amylase activity in Nepenthes pitcher fluid, but more recent studies by Tokes et al (1974) on fluid from unopened pitchers demonstrated that there was some amylase activity at a pH of 6.0, although none at pH values of 2.0 or 4.0. Since the latter pH values are within the normal range of an actively digesting pitcher, they concluded that amylase activity was relatively unimportant in digestion. Tokes et al (1974) also detected definite lipase activity which might play an important role in disrupting cell membranes to make proteins available for breakdown.

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d) Microbial contents of the fluid

The fluid from unopened pitchers is sterile (Hepburn, 1918; Okahara, 1932; Lloyd, 1942), but on opening the pitcher fluid is rapidly invaded by bacteria and 7-10 days after opening there may be as many as 3-37 million bacteria per mL of fluid (Okahara, 1932). Hepburn (1918) found that the bacteria in pitcher fluid were able to liquefy gelatine and could utilize proteins or simple organic compounds as the sole source of carbon and nitrogen. They decomposed simple nitrogenous compounds (glycocoll, acetamide, asparagin and ammonium lactate) frequently producing an odour of ammonia and always imparting an alkaline reaction to the medium, and they usually digested protein, but at an extremely slow rate. Hepburn therefore concluded that the bacteria played only a minor role in the digestion of protein. In addition to bacteria, Okahara (1932) also isolated a number of fungi (*Mucor mucedo*, *M. racemosus*, *Rhizopus nigricans*, *Aspergillus glaucus* and *Penicillium glaucum*) from *Nepenthes* pitcher fluid. These micro-organisms fell into two groups in terms of digestion, one group attacking peptones and glycocoll and the other, various nitrogenous compounds such as peptone, glycylglycine, glycocoll and alanine, with both groups cooperating to reduce these substances to ammonia. Okahara concluded that while the plant enzymes probably play the major role in breaking proteins down to peptones and albumose, the micro-organisms in the fluid may cooperate to reduce these substances into smaller molecules more readily utilized by the plant. Although micro-organisms in the fluid must contribute to the digestion of captured

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insects to some extent, the amount of digestion which is attributable to microbial action must vary in different pitchers depending on the number and type of micro-organisms present. Plummer and Jackson (1963) pointed out that the conditions under which proteolysis occurs are affected by:

a) the number of insects entering the pitchers,
b) the kinds of bacteria carried in,
c) the optimum environment for the respective enzymes,
d) the interchange of materials between the pitcher leaf and the sarcophagus,
e) the acid-alkaline reactions within the fluid,
f) the physiological activities of the plant, and
g) the climatic factors under which the particular leaf is growing;

as a result it is virtually impossible to generalize on the importance of bacteria in digestion.

e) Absorption

It has been demonstrated in all three of the pitcher plant genera studied (*Sarracenia*, *Darlingtonia*, *Nepenthes*) that nutrients and water are absorbed into the leaves from the pitcher fluid. Pitchers of *Sarracenia* and *Darlingtonia* absorb water less rapidly than nitrogenous compounds such as ammonium chloride, ammonium tartrate, acetamide, urea, asparagin, glycocoll, peptone and egg albumen; while phosphates and lithium ions are absorbed more slowly than water (Hepburn, St. John and Jones, 1920; 1927). Radioactively labelled zinc, iodine, cobalt, sulphur and calcium are also absorbed from the

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pitcher fluid in S. flava L., while phosphate, sulphate and amino acids derived from radioactively labelled insects fed to the plants accumulate in the leaves and rhizomes at different rates (Plummer and Kethley, 1964). Some individual amino acids fed to the plants were never recovered, suggesting that they are very rapidly utilized (Plummer and Kethley, 1964). Few experiments have been carried out on absorption in Nepenthes, but it has been shown that resorption of nutrients is specific and takes place in a definite order; thus Luttge (1964) showed that L-alanine was absorbed more rapidly than phosphate, which in turn was absorbed more rapidly than sulphate.

Clautriau, as early as 1900, showed that the digestive glands were the site of absorption in Nepenthes and this was confirmed by Luttge in 1965. Using microautoradiography, Luttge followed the absorption of radioactively labelled sulphate from the pitchers and found that within 24 hours all cells of the glands were heavily labelled and movement of sulphate into the plant was well advanced. Similar experiments on the absorption of radioactively labelled ferritin-derived iron and uranium within pitchers of Sarracenia purpurea L. demonstrated that the digestive glands specifically localized these metals within 20-45 minutes after feeding and that the rate of transport of these metals to the opposing surface of the leaf was independent of the concentration of the feeding solution (Panessa et al, 1976). The passage of ions across the gland head cells probably relies on active mechanisms and may be similar to the mechanism of uptake of nutrients by roots (Heslop-Harrison, 1976). In Sarracenia, the route of transport of both ferritin-derived iron and uranium is

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symplastic; that is, from cell to cell via the cytoplasm, although there are also indications that the vascular system may affect the amount of material transported (Panessa et al, 1976).

VI. The significance of carnivory

It is well established that carnivorous plants are usually found in very infertile soils which are often low in available nitrogen, thus Wherry (1929) found that although the soils of Sarracenia habitats had nitrogen concentrations of 2-3%, there was no detectable nitrate or ammonia present, indicating that the nitrogen present was relatively unavailable to the plants. Analysis of soil from the habitats of Dionaea musculipa also revealed that there was no nitrate and very little ammonia present (Roberts and Oosting, 1958). Other elements besides nitrogen may also be lacking or in short supply, particularly calcium, magnesium, phosphate, iron, manganese and potassium (Roberts and Oosting, 1958; Plummer, 1963).

Since carnivorous plants are able to thrive in poor soils it seems reasonable to assume that they are able to do so because they derive supplementary nutrients from their trapping activities. The first experiments to determine whether or not this trapping of insects conferred advantages to the plants were carried out by Francis Darwin in 1878. He showed that Drosera plants which were fed with insects were much more vigorous than those which were not and this was later confirmed by several authors (Kellerman and Raumer, 1878; Busgen, 1883; Behre, 1929). More recent experiments have shown that Drosera plants supplied with insects and stressed for inorganic nitrogen

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often grow more than plants raised on a complete inorganic medium without insects, which suggests that nitrogen-containing insect metabolites are more effective in enhancing growth than inorganic nitrogen (Chandler and Anderson, 1976a). The presence of nitrate may actually inhibit the growth of insect-fed plants, implying that there is competition between nitrate and insect metabolites in which nitrate is the poorer nitrogen source (Chandler and Anderson, 1976a).

Although the main benefit of carnivory to the plants is probably the supply of additional nitrogen, trapped insects must also be an important source of other minerals such as phosphorus and sulphur which are also in short supply in the soil. Insect feeding enhances the phosphate content of Drosera plants under all conditions (Chandler and Anderson, 1976a) and both radioactively labelled sulphur and phosphorus are absorbed into the plants when they are fed on labelled Drosophila (Chandler and Anderson, 1976b). In 1912, Weyland (cited by Lloyd, 1942) showed that there was little phosphorus or potassium in the roots of Drosera plants, while Schmid in the same year (cited by Lloyd, 1942) found that these elements were absent from the leaves before insect feeding, but were present afterwards. This indicated that both phosphorus and potassium were obtained from captured insects; however, Watson, Matthiessen and Springett (1982) have suggested that while insects are probably the major source of nitrogen and phosphorus in Drosera erythrorhiza Lindl., the principal source of potassium is the soil. This may apply to carnivorous plants in general as Christensen (1976) found that there was no detectable increase in the amount of potassium (nor of magnesium or calcium) in

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the tissues of Sarracenia flava after feeding with insects. Insects do not appear to be an important source of microelements as the application of insects to Drosera plants raised in the absence of molybdenum, copper, zinc, boron and manganese caused no significant increase in plant growth (Chandler and Anderson, 1976a).

There seems to be no doubt that the carnivorous habit is not obligate since most carnivorous plants grow in the absence of insects when inorganic nutrients are supplied (Pfeffer, 1877; Roberts and Oosting, 1958; Pringsheim and Pringsheim, 1962; Dore Swamy and Mohan Ram, 1969); however, growth is usually less vigorous than when the plants are supplied with insects. Pringsheim and Pringsheim (1962) could not induce Utricularia to flower and set seed when raised on a wholly inorganic medium and they concluded that some substance obtained only from organic sources was necessary for reproduction to take place. This is not true of all carnivorous plants since Drosera is capable of completing its life cycle on a completely inorganic medium (Small et al, 1977), as is Cephalotus follicularis (Dakin, 1917-1918).

The actual extent to which carnivory benefits insectivorous plants has been disputed for many years. Regel in 1879 (cited by Lloyd, 1942) thought that the carnivorous habit was a distinct disadvantage because he observed that the leaves of Drosera filiformis were often injured by feeding, and that fed leaves died sooner than unfed ones. However, excessive feeding often causes decay of the leaves and while fed leaves may die sooner than unfed leaves, they may contribute substantially more to the plant in their shorter life spans (Goebel - cited by Lloyd, 1942). Haberlandt (cited by Lloyd,

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1942), basing his conclusions on the small number of insects trapped by Nepenthes plants in Java, thought that carnivory was a semi-superfluous, luxury adaptation while Goebel (cited by Lloyd, 1942) thought that carnivory was useful but not obligatory. Lloyd, (1942) notes that carnivorous plants generally have very poor root systems and therefore have little means of obtaining adequate supplies of nutrients from infertile soils. Additionally, they may have depressed transpiration rates due to their situation in the habitat, making it necessary to have some other means of obtaining salts. In support of this he quotes the fact that leaves of Nepenthes when exposed to situations where transpiration can act freely, do not produce pitchers and have a higher ash content than those lower down on the plant and exposed to higher humidity. He therefore points out that while it may be true that experiments show that carnivorous plants can obtain all their requirements through their roots if plentifully supplied with nutrients, this does not necessarily mean that they are able to do so under natural conditions. Thus, although experimental evidence indicates that nutrients derived from captured insects are not necessary for growth provided sufficient mineral elements are available for uptake by the roots, this does not mean that carnivory is not necessary in the wild where conditions may be substantially different to those maintained in experiments. The importance of carnivory may also depend on the developmental state of the plants; thus it may be crucial for the establishment of young plants, as well as for mature plants which are flowering. Consequently, until experimentation is carried out under natural conditions taking all these factors into account, the degree to which carnivory benefits the plants cannot be determined.

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VII. Reproduction

Nepenthes plants are dioecious, bearing paniculate or racemose inflorescences which are terminal initially, but which later become lateral by the development of a branch in the axil of the uppermost leaf (Danser, 1928). The female inflorescences are usually shorter and more robust than the male (Danser, 1928) but the structure is otherwise very similar, with flowers spirally arranged on peduncles (Lim and Prakash, 1973). Each flower consists of four red or green tepals dotted with glands that secrete so much nectar that the base of the spoon-shaped tepals often becomes filled (Green, 1967); in the male flowers the stamens are united into a column and the anthers are sessile and crowded into one whorl (Danser, 1928), while the female flowers have a quadriloculate, ellipsoidal ovary (Danser, 1928) with a short style and a quadrified stigma (Lim and Prakash, 1973). Glandular nectaries are not confined to the tepals, but are also common on the inflorescence axis and the pedicels of the flowers (Lim and Prakash, 1973).

In *N.gracilis*, pollen grains are shed from the male flowers in permanent tetrads, with anthesis occurring in the evenings at 1600-1800h, accompanied by a heavy foetid odour (Lim and Prakash, 1973). Because of the floral structure and the dioecious habit of the plants, an insect would need to be large and winged in order to effect pollination (Green, 1967) and for this reason ants are unlikely to be the main pollinating agents, as suggested by Holttum (1954). The flowers are seldom visited by insects (Green, 1967) despite the large quantities of nectar secreted and it is probable that most of the

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pollination is by wind, as the pollen tetrads are small enough to be transported in this way (Green, 1967).

Each inflorescence of N. gracilis produces 50-200 fruits, depending on size (Lim and Prakash, 1973), with up to 10,000 seeds being produced on a single inflorescence (Green, 1967). The position of the fruits influences their size, thus the largest are at the base of the inflorescence and they have an average of 145 embryonated and 7 aborted seeds, while the smallest are at the tip and have only about 23 fertile seeds with as many as 71 being sterile (Lim and Prakash, 1973).

The seeds are long and thin, with the embryonated part in the centre occupying only about one eighth of the total length (Lim and Prakash, 1973), while the two wings at either end are hollow so that the seeds are light and buoyant and are easily carried by wind or water (Green, 1967). Most seeds germinate in the light within two to three weeks of sowing, although some may germinate up to six or seven months later (Green, 1967). The seeds appear to degenerate rapidly on storage as Garrard (1955) found that seeds kept for 14 days failed to germinate, while Lim and Prakash (1973) found that 80% of the seeds germinated if sown on the day of collection, but only 14% if sown 4 days later. Although these results suggest that most seeds must germinate immediately, Lim and Prakash (1973) do not give the length of time allowed for germination, while Garrard (1955) only left the seeds to germinate for a maximum of 50 days, so that these results may be incorrect in view of Green's observation that seeds may take 6-7 months to germinate.

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Germination is epigeal and the radicle is first to emerge followed 6 days later by the cotyledons which are green and presumably photosynthetic (Lim and Prakash, 1973). The first leaf is fully formed about a month later and is a small wing-like structure with a terminal minute pitcher (Lim and Prakash, 1973). The mouths of the first formed pitchers are bounded by a narrow corrugated rim formed by the growth and reflexion of the margin (Lim and Prakash, 1973) and the pitchers are fully functional with digestive glands in their cavities and nectar glands which are restricted to the rudimentary rim under the mouth (Green, 1967). In the early stages of development of the seedling the pitchers are formed as an integral part of the leaf blade but as the plant develops they become gradually more independent until the leaf is clearly demarcated into a laminar part and a pitchered part (Hooker, 1859).

Development of the seedling is slow; a tiny rosette of leaves is formed and the plant remains in this form for two or three years with successive leaves becoming larger and successive pitchers gradually attaining the mature form (Green, 1967). When the rosette of leaves is well grown the stem begins to elongate and climbs by twining of the pitcher tendrils around adjacent vegetation. The climbing habit has the effect of bringing the flowers out into the open, to the advantage of both pollination and seed dispersal, thus the inflorescences appear only where they can be fully exposed, so that they protrude from the tops and sides of trees and above the tops of bushes (Green, 1967). Flowering occurs at irregular intervals (but is always gregarious) and the stimulus may be dry weather following a wetter period (Holttum, 1954).

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Section B. Fauna associated with pitcher plants

I. Prey

The majority of animals trapped by pitchers of *Nepenthes* are insects belonging to the orders Collembola, Hymenoptera, Orthoptera, Hemiptera, Coleoptera, Lepidoptera and Diptera, although all the major orders of insects are represented, as well as arachnids, myriapods, isopods, occasionally molluscs and even small birds and mammals (Jensen, 1910; Guenther, 1913; Menzel, 1922; Dover, 1928; Erber, 1979). Winged seeds, bark and humus are often also found in pitcher residues, either being blown in by the wind, or carried in by ants which often form the greater part of the residue of trapped insects in the pitchers (Guenther, 1913; Dover, 1928; Erber, 1979). Most of the ants trapped belong to species which are attracted by nectar (Guenther, 1913; Erber, 1979), those species which are not seldom being found in the pitchers although they may often be observed foraging around the plants (Guenther, 1913). Nectar secretion does not however, appear to be the only lure which entices animals to enter the pitchers, as many of the victims in pitchers of *Sarracenia* were found to belong to species indifferent to sugary substances (Mellichamp, 1875). These species are perhaps attracted to odours of putrefaction emitted from pitchers containing excessive numbers of insects, or alternatively they may enter the pitchers out of curiosity or in search of prey, or purely accidentally due to physical proximity to the pitchers (Mellichamp, 1875; Jones, 1921; Swales, 1969). The taxonomic composition of the pitcher victims depends to some extent on the flora associated with the habitat (Swales, 1969) and it may reflect in part the fauna of the habitat occupied by the plants (Erber, 1979).

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The amount of prey captured varies considerably, depending to some extent on the plant habitat, the positioning of the pitchers and the pitcher age (Beaver, 1983). Pitchers in some habitats contain large numbers of insects while those in other habitats contain relatively few. Both Haberlandt (cited by Lloyd, 1942) and Clautriau (1900) observed that pitchers of Nepenthes in Java generally contained very little prey, although Clautriau did note that this was not universally true. Clautriau also noted that at low altitudes, where the vegetation was well developed, all the pitchers on Nepenthes plants contained insect remains, whereas at high altitudes, where there is little vegetation and few insects, pitchers containing captured insects were scarce. Within a particular plant habitat there may also be considerable variation in the amount and type of prey caught by individual pitchers, with ground pitchers generally containing large numbers of running and crawling insects, while pitchers suspended high in the air usually contain fewer animals, of which a higher proportion are flying insects (Guenther, 1913; Menzel, 1922).

The ability of pitchers to trap insects diminishes with age, thus in Sarracenia, most of the pitcher victims are trapped within the first thirty days after opening of the pitcher (Fish and Hall, 1978; Wolfe, 1981), and observations suggest (Beaver, 1983) that the input of prey to pitchers of Nepenthes follows a similar pattern, reaching a maximum within the first thirty days after opening. Consequently, a plant composed of leaves of different ages has only one or two leaves which are actually attracting and capturing insects and each leaf contains insects at different stages of decay (Fish and Hall, 1978). The decline in the trapping ability of the pitchers with age is probably

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related to a decrease in their attractiveness to insects, since old pitchers on plants with newly opened, highly attractive pitchers caught substantially more than those on plants with no new leaves (Wolfe, 1981).

II Pitcher Inhabitants

The first recorded account of animals living in Nepenthes is attributed to G.E. Rumphius in 1747 (Thienemann, 1932), although it was not until the early part of the twentieth century that any significant observations were made on the Nepenthes fauna. In 1900, Clautriau discovered larvae of two unidentified diptera inhabiting pitchers of Nepenthes in Java, and mosquito larvae were later found in Nepenthes pitchers in Malaysia and the Philippines by Leicester (1908) and Banks (1909), respectively (cited by Edwards, 1931). Subsequently, more detailed studies on the pitcher fauna were carried out by Jensen (1910), Meijere (1910), Guenther (1913) and later on by numerous researchers, all available information being summarized by Thienemann in 1932. In this summary, Thienemann divided Nepenthes animals into three categories; nepenthebiont species which occurred exclusively in Nepenthes pitchers; nepenthephil species which were often found in pitchers in large numbers, but which also occurred in other habitats; and nepenthexene species which were only rarely found in the pitchers, being more common in other habitats. He also distinguished between the aquatic fauna living in the pitcher fluid, and the terrestrial fauna living above the fluid level, pointing out that some animals may belong to both categories at different stages in their lifecycle. Numerous animals have been added to the list of Nepenthes inhabitants

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since Thienemann's summary, which has recently been updated by Beaver (1983). A more detailed summary of all information available on Nepenthes fauna to date is included below.

Aquatic Biota

Taxonomic composition

Protozoa

Most of the protozoa recorded from Nepenthes belong to the Sarcodina and they are largely shelled forms such as Difflugia and Arcella. The following amoebae have been recorded from Nepenthes:

Amoeba guttula Duj. (Oye, 1921)
A. nepenthesi v. Oye (Oye)
A. verrucosa Ehrbg. (Ghosh, 1928)
Arcella hemispherica Perty (Ghosh)
Ar. singaporensis n. sp. (Ghosh)
Ar. subconica n. sp. (Ghosh)
Ar. subhemispherica n. sp. (Ghosh)
Ar. triangularis n. sp. (Ghosh)
Ar. vulgaris Ehrbg. (Oye)
Centropyxis aculeata Stein (Oye)
Cochliopodium bilimbosum (Auerbach) Leidy (Oye)
Difflugia constricta (Ehrbg.) Leidy (Oye)
D. pyriformis Perty var. (Ghosh)
D. singaporensis n. sp. (Ghosh)

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D. subpyriformis (Ghosh)

D. suburceolata n. sp. (Ghosh)

Diplochlamys sp. (Ghosh)

Lesquereusia epistomium Penard (Oye)

Pyridicula klossi n. sp. (Ghosh)

The amoebae recorded by Oye originated from N. gymnamphora in Java, while those found by Ghosh were from pitchers of N. ampullaria in Singapore.

Thienemann (1932) found Chlamydomonadae and Mallomonas in pitchers of N. ampullaria in Sumatra, and Ghosh (1928), also noted the presence of unidentified flagellates in the same Nepenthes species in Singapore. Although Ghosh did not find any ciliates in the pitcher fluid, Dover (1928) found Paramecium. Menzel (1922) also found ciliates, in the form of Colpoda-like infusoria, in pitchers of N. gymnamphora in Java.

Thienemann (1932) considered all the protozoan species found in Nepenthes to be nepenthexene animals. Centropyxis aculeata, Difflugia pyriformis, Arcella vulgaris and Cochliopodium bilimbosum have all been recorded from treeholes (Lackey, 1940), while Ar. vulgaris and C. bilimbosum have also been recorded from ponds amongst algae and other plants (Ward and Whipple, 1959). Lesquereusia epistomium is also found in Sphagnum swamps (Ward and Whipple, 1959), so Thienemann's assumption is probably correct. The protozoa recorded from Nepenthes were all found in ground level pitchers and were probably introduced into the pitchers from the surrounding earth and pools of water (Thienemann, 1932).

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Algae

Dover (1928) found diatoms in pitchers of Nepenthes in Singapore, while Oye (1921) recorded eight algae from pitchers of N. gymnamphora in Java, of which six were also diatoms. These were: Epithemia sorex Kuetz: Achnanthes minutissima Kuetz; A. lanceolata Breb; Navicula elleptica Keutz; N. viridis (Nitzsch) Kuetz; and Cocconeis placentula Ehrbg. var. lineata Ehrbg. The only other algae recorded from Nepenthes are the blue green alga Merismopedium glaucum (Ehrbg.) and the desmid Euastrum (Oye, 1921). The low light intensity within the pitchers probably accounts for the relative scarcity of algae and it may also explain the predominance of diatoms in the species recorded, since diatoms are a group well known for their tolerance of low light intensities (Oye, 1921). The algae found by Oye were darkly pigmented, presumably to allow efficient utilization of the dim light penetrating the pitcher walls.

Rotifera

Rotifers have been recorded from Nepenthes pitchers by Dover (1928), Ghosh (1928), Thienemann (1932) and Beaver (1979a; b); however, the only rotifers which have been specifically identified were those found by Thienemann. These were: Lepadella patella Muller; Monostyla monostyla Daday; and Monostyla serrata n. sp., which were found in pitchers of N. ampullaria in Sumatra (Thienemann, 1932).

Nematoda

Menzel (1922) found five genera of nematodes in pitchers of N. gymnamphora in Java. Individuals belonging to the genera Plectus, Dorylaimus, Rhabditis and Diplogaster were found in ground level

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pitchers, the two former being nepenthephil species and the two latter, nepenthexene, while another nepenthephil nematode Anguillula nepenthicola Menzel was found to be restricted to pitchers hanging a few metres above the ground (Menzel, 1922; Thienemann, 1932). Dover (1928) and Beaver (1979a; b; 1983) have also noted the presence of nematodes in Nepenthes pitchers.

Oligochaeta

Oligochaetes have been found in pitchers of N. gymnamphora (Menzel, 1922) and N. ampullaria (Thienemann, 1932) in Java and also in Nepenthes pitchers in Penang (Beaver, 1979a), but no specific identifications are available.

Crustacea

Most of the crustacea recorded from Nepenthes are harpacticoid copepods. Menzel (1922) found a dead female of Epactophanes sp. in N. gymnamphora in Java, while Thienemann (1932) found Epactophanes Richardi Menzeli, Parastenocaris incerta and Viguirella caeca Menzel in N. ampullaria in Sumatra. Ghosh (1928) mentions finding two species of copepods and a cladoceran in N. ampullaria in Singapore and small crabs have occasionally been found in pitchers (Schuitemaker and Franssen, 1934; Beaver, 1983), although the latter are clearly accidental inhabitants (Beaver, 1983). Most of the crustacea found are probably nepenthexene species (Thienemann, 1932).

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Acarina

Anoetidae

Four nepenthebiont anoetid mites belonging to the genera Zwickia, Creutzeria and Anoetus have been found in the fluid of Nepenthes pitchers. Zwickia guentheri Oudemans was first described from pitchers of N. distillatoria in Sri Lanka by Oudemans (1915), and this species has since been found in N. gymnamphora in Java, N. mirabilis in Sumatra (Thienemann, 1932) and N. ampullaria, N. albo-marginata and N. gracilis in Penang, where it usually occurs together with Anoetus nepenthesiana (Hirst) (Beaver, 1979a; b; 1983). Anoetus nepenthesiana was first found in pitcher of N. ampullaria in Singapore (Hirst, 1928) and it has since been found in N. gymnamphora in Java and in N. mirabilis and N. tobaica in Sumatra (Thienemann, 1932). It may also have been found in pitchers of N. reinwardtiana in Sumatra (Erber, 1979), but the identification is extremely doubtful.

The genus Creutzeria was erected by Oudemans (1932) to accomodate mites collected from pitchers of N. tobaica in Java. This species, which he named Creutzeria tobaica Oudemans, has since been recorded from pitchers of N. madagascariensis in Madagascar (Paulian, 1961) and from pitchers of N. mirabilis in New Guinea (Beaver, 1983), while a related species, C. seychellensis Nesbitt, is found in pitchers of N. pervillei in the Seychelles (Nesbitt, 1979). Apart from the latter species, many of the records of these anoetid mites may be based on misidentifications (Beaver, 1983).

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Oribatei

A number of oribatid mites have been found in Nepenthes pitchers, in varying stages of decomposition. These include: Liebstadia

thienemanni Willmann; L. perforata Willmann; Protoribates clavatus Willmann; Rostrozetes foveolatus Sellnick; Oppia latifasciata Willmann; O neerlandica Oudms. var. sumatrensis Willmann; and Scheloribates praeincisus Berl. (Willmann, 1931). The above specimens originated from pitchers of Nepenthes in Java and Sumatra (Thienemann, 1932). Hirst (1928) and Erber (1979) have also noted the presence of partially digested oribatids in samples taken from Nepenthes pitchers in Singapore and Sumatra respectively. Willmann (1931) thought that the mites found by Thienemann were pitcher victims, however, as living oribatids have been found in pitchers of Sarracenia purpurea (Swales, 1972), it is possible that some of the oribatids which have been found in Nepenthes pitchers were originally pitcher inhabitants rather than pitcher victims.

Diptera

Diptera make up the largest component of the aquatic Nepenthes fauna, thus 130 species from twelve different families have been recorded from Nepenthes to date (Table 1). Of these 130 species, 96 are members of the Culicidae (Table 1), which is the dominant family both regionally, in terms of number of species, and locally, in terms of the number of individuals per pitcher (Beaver, 1983). Most of the Nepenthes diptera are probably nepenthebiont (68%), while only 8% are nepenthephil and 14% nepenthexene. The habits of 10% of the species recorded are unknown (Table 1).

Nepenthebiont species generally have a much more limited distribution than nepenthephil and nepenthexene species (Table 1). This is well illustrated by the distribution of Tripteroides species in the

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Table 1. Aquatic Diptera recorded from Nepenthes

Note: NB = Nepenthebiont, NP = Nepenthephil, NX = Nepenthexene species

- Malaya is taken to include West Malaysia and Singapore; Borneo to include Brunei, Kalimantan, Sabah and Sarawak; and New Guinea to include Papua New Guinea and West Irian.

- Where Total geographical distribution is unknown the column is left blank.

  * = Doubtful identification

** The genus Endonepenthia has not been synonymized with Megaselia as recommended by Disney (1981b) because Disney based his recommendation largely on the study of adult characteristics, stating that the morphology and habits of the immature stages of Megaselia are so diverse that it is not feasible to separate the two genera on the basis of the immature stages alone. However, the pupae at least, of Endonepenthia and Megaselia are so consistently different that it seems to me to be unreasonable to merge both genera into one without further study of all stages in their natural habitat.

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TABLE 1

Aquatic Diptera Recorded from Nepenthes pitchers

Dipteran Species	Ecological group	Total Geographical Distribution	Nepenthes Species	Locality	References
Culicidae	NB	Borneo	N. sp.	Borneo	16, 27, 41, 159.
Aedes (Alanstonea) brevitibia (Edwards)					
A. (Al.) treubi (de Meijere)	NB	Java, Thailand	N. gymnamphora Nees	Java	16, 25, 41, 49, 131 186, 187.
A. (Finlaya) gani Bonne-Wepster	NB	New Guinea	N. sp.	New Guinea	16, 104.
A. (Huades) medialis Brug	NB	New Guinea	N. sp.	New Guinea	16, 104, 187.
A. (Stegomyia) albopictus Skuse	NX	Australia, Somaliland, Hawaii, Japan Malagasy, New Guinea, Oriental region	N. ampullaria Jack	Malaya	10, 13, 16, 35, 41, 46, 186.
A. (S.) dybasi Bohart	NP				
A. (S.) maehleri Bohart	NB		N. mirabilis Druce	Palau Islands	16.
			N. mirabilis	Caroline Islands	16.
Anopheles sp.	NX	?	N. sp.	Malaya	14, 16, 55, 186.
Armigeres (Armigeres) conjungens Edwards	NX	Borneo, Malaya	N. sp.	Malaya	13, 16, 35, 41.
Ar. (Ar.) durhami Edwards	NX	Andaman Islands, India, Indo-china, Java, Sumatra, Malaya, Thailand	N. ampullaria	Malaya	10, 14, 61, 41.

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Table 1 - continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
Ar. (Ar.) giveni Edwards	NB	Malaya	N. ampullaria, N. rafflesiana Jack	Malaya	10, 14, 16, 41, 46, 51, 55, 186.
Ar. (Ar.) hybridus Edwards	NX	Borneo, Malaya	N. sp.	Malaya	13, 16, 35, 41.
Ar. (Ar.) kuchingensis Edwards	NX	Borneo, India, Indochina, Malaya Thailand	N. ampullaria	Malaya	10, 14, 16, 41.
Ar. (Ar.) malayi (Theobald)	NX	China, Indonesia, Malaya, Philippines, Thailand, Moluccas	N. sp.	Malaya	14, 16, 41, 55.
Ar. (Leicesteria) flavus (Leicester)	NX	Borneo, Burma, China, Bangladesh, Taiwan, India, Indochina, Java, Malaya, Sumatra Thailand, Philippines	N. sp.	Malaya	14, 16, 41, 55, 186.
Ar. (L) magnus (Theobald)	NP	Borneo, Burma, China, Sri Lanka, India, Taiwan, Indochina, Java, Malaya, Sumatra, Thailand, Philippines	N. mirabilis	Hong Kong	16, 32, 41.
Culex (Culiciomyia) shebbearei Barraud	NP?	Borneo, Sir Lanka, China, India,	N. rajah Hook. f.	Borneo	16, 41, 54, 186.
C. (Lophoceraomyia) acutipalus Colless	NB	Malaya	N. ampullaria	Malaya	13, 14, 16, 36, 41, 175.

Table 1 - continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes Species	Locality	References
C. (L.) brevipalpus (Theobald)	NB	Malaya	N. ampullaria, N. gracilis	Malaya	14, 16, 36, 41, 175.
C. (L.) coerulescens Edwards	NB	Borneo, Malaya	N. ampullaria, N. sp.	Malaya	14, 16, 36, 52, 186.
C. (L.) curtipalpis (Edwards)	NB	Borneo, Malaya, Viet Nam, Thailand, Sumatra	N. gracilis, N. mirabilis, N. ampullaria, N. albo-marginata Lobb	Thailand, Malaya, Viet Nam, Borneo, Sumatra	10, 13, 14, 16, 24, 25, 27, 36, 41, 52, 55, 175, 186.
C. (L.) eminentia (Leicester)	NB	Borneo, Malaya	N. ampullaria, N. gracilis, N. rafflesiana	Malaya	10, 14, 16, 35, 36, 41, 52, 55, 175, 186.
C. (L.) hewitti (Edwards)	NB	Borneo, Malaya, Sumatra	N. ampullaria	Malaya, Sumatra	10, 13, 14, 16, 36, 41, 49, 52, 55, 175, 186.
C (L.) jenseni (de Meijere)	NB	Borneo, Java, Malaya, Sumatra	N. gymnamphora, N. villosa Hook. f., N. - reinwardtiana Miq.	Malaya, Java, Borneo, Sumatra	14, 16, 25, 36, 41, 49, 55, 57, 131, 175, 186.
C (L.) lucaris Colless	NB	Malaya, Thailand	N. rafflesiana, N. gracilis, N. albo-marginata	Malaya, Thailand	13, 14, 16, 24, 36, 41, 175.
C. (L.) navalis Edwards	NB	Borneo, Malaya	N. ampullaria, N. rafflesiana, N. bicalcarata Hook. f.	Borneo, Malaya	10, 13, 14, 16, 27, 36, 41, 51, 52, 55, 175, 186.
C. (L.) sumatranus Brug	NB	China, Sumatra, Hong Kong, Viet Nam, Cambodia	N. mirabilis, N. sp.	Hong Kong, Viet Nam, Cambodia	16, 32, 41, 175.

Table 1 - continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
Mimomyia (Ravenalites) jeansottei (Doucet)	NX		N. madagscariensis Poir.	Madagascar	16, 73, 151.
Toxorhynchites (Toxorhynchites) acaudatus (Leicester)	NB?	Borneo, Malaya,	N. ampullaria, N. rafflesiana	Malaya	10, 14, 16, 41, 46, 49, 51, 55, 186.
T. (T.) ater (Daniels)	NB?	Malaya	N. rafflesiana	Malaya	14, 16, 41, 49, 86.
*T. (T.) aurifluus (Edwards)	NX?	Taiwan, Java, Sumatra	N. sp.	Sumatra	26, 41, 187.
T. (T.) coeruleus (Brug)	NB?	Sumatra	N. sp.	Sumatra	16, 41.
T. (T.) klossi (Edwards)	NB	India, Malaya,	N. ablo-marginata	Malaya	13, 14, 16, 41, 160.
T. (T.) metallicus Leicester	NX?	India, Indonesia, Malaya	N. sanguinea Lindl.	Malaya	14, 16, 41, 49, 113, 186.
T. (T.) nepenthicola Steffan and Evanhuis	NB?	New Guinea	N. sp.	New Guinea	180.
T. (T.) nepenthis (Dyar and Shannon)	NB	Philippines	N. sp.	Philippines	16.
T. (T.) nigripes (Edwards)	?	Borneo	? N. sp.	Borneo	16.
T. (T.) pendleburyi (Edwards)	NB?	Borneo, Malaya	N. sp.	Borneo, Malaya	16.
T. (T.) quasiferox (Leicester)	NX	Borneo, Java, Malaya, Sumatra	N. sp.	Malaya	16.
T. (T.) splendens (Wiedemann)	NX	Burma, Celebes, Sir Lanka, India Java, Malaya, Philippines, Fiji, New Guinea, Samoa	N. ampullaria, N. rafflesiana	Java, Malaya, New Guinea	14, 16, 41, 49, 113, 186.
T. (T.) sumatranus (Brug)	NB?	Sumatra	N. sp.	Sumatra	16, 42.

Table 1 - continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
Tripteroides (Polylepidomyia) caledonicus (Edwards)	NP?	South Pacific	N. mirabilis	New Caledonia	16, 19, 104, 111.
Tp. (P.) digoelensis Brug	NB	New Guinea	N. sp.	New Guinea	16, 104, 111.
Tp. (P.) microlepis (Edwards)	NB?	New Guinea	N. sp.	New Guinea	6, 7, 16.
Tp. (Rachionotomyia) aranoides (Theobald)	NX	Andaman Islands, Borneo, Burma, Taiwan, Sri Lanka, Hainan Island, India, Indo-china, Java, Malaya, Sumatra, Thailand	N. sp.	Malaya	16, 41, 127.
Tp. (R.) dofleini (Guenther)	NB?	Sri Lanka	N. distillatoria L.	Sri Lanka	16, 49, 74, 127.
Tp. (R.) nepenthis (Edwards)	NB	Borneo, Malaya	N. ampullaria, N. rafflesiana	Borneo, Malaya	10, 13, 14, 16, 41, 46, 49, 51, 55, 127, 186.
Tp. (R.) nepenthesimilis Mattingly	NB	Borneo, Malaya	N. ampullaria ?N. rafflesiana	Borneo, Malaya	16, 217.
Tp. (R.) tenax (de Meijere)	NB	Thailand, Malaya, Java	N. ampullaria, N. gracilis, N. rafflesiana, N. tobaica Dans, N. reinwardtiana, N. mirabilis, N. sanguinea, N. albo-marginata	Java, Thailand Malaya	10, 13, 14, 16, 25, 27, 35, 46, 49, 51, 55, 57, 113, 127, 186.
Tp. (R.) sp. 1 (Mattingly, 1981)	?	?	?N. rajah	Borneo	16, 217.
Tp. (R.) sp. 2 (Mattingly, 1981)	?	?	N. sp.	Borneo	16, 217.

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Table 1 - continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
Tp. (Rachisoura) adentata Assem	NB?	New Guinea	N. sp.	New Guinea	6, 16.
Tp. (Rs.) bisquamatus Lee	NP	New Guinea	N. mirabilis	New Guinea	6, 7, 16, 111.
Tp. (Rs.) brevirhynchus Brug	NB	New, Guinea, Australia	N. mirabilis	New Guinea, Australia	16, 104, 111.
Tp. (Rs.) cuttsi Assem	NB?	New Guinea	N. sp.	New Guinea	6, 16.
Tp. (Rs.) filipes (Walker)	NB	New Guinea, Australia	N. mirabilis	New Guinea, Australia	6, 16, 111.
Tp. (Rs.) flabelliger Bonne-Wepster	NB?	New Guinea	N. sp.	New Guinea	6, 16.
Tp. (Rs.) kingi Lee	NB?	New Guinea	N. mirabilis	New Guinea	6, 16, 111.
Tp. (Rs.) longipalpatus Lee	NX?	New Guinea	N. sp.	New Guinea	16, 111.
Tp. (Rs.) sp. nr. mathesoni Belkin	?	New Guinea	N. sp.	New Guinea	16.
Tp. (Rs.) obscurus Brug	NB	New Guinea	N. sp.	New Guinea	16, 104, 111.
Tp. (Rs.) pallidus Lee	NB?	New Guinea	N. sp.	New Guinea	16, 111.
Tp. (Rs.) papua Brug	NB	New Guinea	N. sp.	New Guinea	16, 111.
Tp. (Rs.) pilosus Lee	NB?	New Guinea	N. sp.	New Guinea	16, 111.
Tp. (Rs.) simplex Brug	NB	New Guinea	N. sp.	New Guinea	16, 104, 111.
Tp. (Rs.) subobscurus Lee	NB	New Guinea, Australia	N. mirabilis	New Guinea, Australia	16, 111.
Tp. (Tricholeptomyia) apoensis Baisas and Ubaldo-Pagayon	NB	Philippines	N. sp.	Philippines	8, 16, 127.
Tp. (Tr.) barraudi B. and U-P	NB	Philippines	N. sp.	Philippines	8, 16, 127.

Table 1 - continued

Dipteran species	Ecological Group	Total Geographical Distribution	Nepenthes species	Locality	References
Tp. (Tr.) belkini B and U-P	NB	Philippines	N. sp.	Philippines	8, 16, 127.
Tp. (Tr.) christophersi B and U-P	NB		N. sp.	Philippines	8, 16, 127.
Tp. (Tr.) delpilari B and U-P	NB	Philippines	N. sp.	Philippines	8, 16, 127.
Tp. (Tr.) microcala (Dyar)	NB	Philippines	N. sp.	Philippines	8, 16, 127.
Tp. (Tr.) nepenthicola (Banks)	NB	Philippines	N. alata Blanco	Philippines	8, 16, 49, 127, 186.
Tp. (Tr.) roxasi B and U-P	NB	Philippines	N. sp.	Philippines	8, 16, 127.
Tp. (Tr.) werneri B and U-P	NB	Philippines	N. sp.	Philippines	8, 16, 127.
Tp. (Tripteroides) bambusa (Yamada)	NP	China, Taiwan, Ryukyu Islands, Japan, Malaya	N. ampullaria, N. gracilis, N. albo-marginata	Malaya	13, 14, 16, 41.
Tp. (Tp.) bimaculipes (Theobald)	NP	New Guinea	N. sp.	New Guinea	7, 16, 104.
Tp. (Tp.) dyari Bohart and Farner	NP?	Philippines	N. sp.	Philippines	8, 16.
Tp. (Tp.) elegans Brug	NB?	New Guinea	N. sp.	New Guinea	16, 104.
Tp. (Tp.) intermediatus B and U-P	NB?	Philippines	N. sp.	Philippines	8, 16.
Tp. (Tp.) malvari B and U-P	NB?	Philippines	N. sp.	Philippines	8, 16.
Tp. (Tp.) mendacis (Daniels)	NB?	Malaya	N. sp.	Malaya	14, 16, 49.
Tp. (Tp.) reiseni Basio	NB	Philippines	N. sp.	Philippines	16.
Tp. (Tp.) simulatus B and U-P	NB	Philippines	N. sp.	Philippines	8, 16.
Tp. (Tp.) vicinus (Edwards)	NB	Borneo, China, Malaya, Sumatra	N. mirabilis, N. gracilis, N. sanguinea, N. lowii Hook. f.	Malaya, Sumatra, Borneo,	10, 14, 16, 25, 27, 41, 49, 54, 55, 113, 186.

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Table 1 - continued

Dipteran Species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
Uranotaenia (Pseudoficalbia) ascidiicola de Meijere	NB	Java	N. gymnamphora	Java	16, 25, 41, 49, 131, 153, 186.
U. (P.) belkini Grjebine	NB	Madagascar	N. madagascariensis Poiret	Madagascar	16, 73, 151.
U. (P.) bosseri Grjebine	NP?	Madagascar	N. madagascariensis	Madagascar	16, 73, 151.
U. (P.) brunhesi Grjebine	NB	Madagascar	N. madagascariensis	Madagascar	16, 73.
U. (P.) damasei Grjebine	NB?	Madagascar	N. madagascariensis	Madagascar	16, 73.
U. (P.) gigantea Brug	NB	Malaya, Sumatra	N. tobaica	Sumatra	16, 25, 41, 153, 186.
U.(P.) modesta Leicester	NX	Borneo, Malaya, Philippines, Thailand	N. sp.	Malaya, Thailand, Philippines	14, 153.
U. (P.) moultoni Edwards	NB	Borneo, Malaya, Sumatra	N. ampullaria, N. gracilis, N. rafflesiana	Borneo, Malaya, Sumatra	10, 13, 14, 16, 27, 41, 46, 49, 51, 55, 153, 186.
U. (P.) nepenthes (Theobald)	NB	Seychelles, ?Madagascar*	N. pervillei Blume ?N. madagascariensis*	Seychelles ?Madagascar*	16, 110, 128, 150*.
U. (P.) nivipleura Leicester	NP?	Sri Lanka, India, Java, Malaya, Laos, Cambodia, Ryukyu Islands, Hong Kong, Japan	N. distillatoria	Sri Lanka, Malaya	14, 16, 41, 49, 153, 186.
U. (P.) xanthomelaena Edwards	NB	Malaya	N. ampullaria, N. gracilis, N. rafflesiana	Malaya	10, 14, 16, 50, 55, 153, 186.

Table 1 continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
Chaoboridae					
Corethrella calathicola Edwards	NB	Borneo, Malaya	N. ampullaria	Malaya, Borneo	10, 13, 14, 16, 53, 186.
Ceratopogonidae					
Dasyhelea ampullariae Macfie	NB	Malaya	N. ampullaria, N. gracilis	Malaya	13, 14, 16, 41, 121, 204.
D. biseriata Wirth and Beaver	NB	Malaya	N. ampullaria	Malaya	14, 16, 204.
D. confinis Johannsen	NB	Sumatra	N. mirabilis	Sumatra	16, 41, 99, 129, 186, 187, 204.
D. nepenthicola Wirth and Beaver	NB	Malaya	N. albo-marginata, N. gracilis	Malaya	13, 14, 16, 204.
D. subgrata Tokunaga	NB	New Guinea	N. mirabilis	New Guinea	6, 16, 204.
?g. ?sp.	?	?	N. mirabilis	Hong Kong	16.
Cecidomyiidae					
Lestodiplosis syringopais (Hering)	NB	Malaya, Sumatra	N. gracilis, N. tobaica, N. albo-marginata	Malaya, Sumatra	13, 14, 16, 81, 186.
Chironomidae					
Metriocnemus sp.	?	?	N. sp.	Borneo	16.
?g. ? sp.	?	?	N. mirabilis	Hong Kong	16.

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Table 1 - continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
Phoridae					
**Endonepenthia cambodiae Borgmeier	NB?	Cambodia	N. sp.	Cambodia	16, 21.
E. campylonympha Schmitz	NB	Borneo, Sumatra	N. mirabilis	Borneo, Sumatra	16, 21, 129, 168, 169, 186.
E. gregalis (de Meijere)	NB	Java	N. gymnamphora	Java	16, 21, 64, 131, 186.
E. schuitemakeri Schmitz	NB	Borneo, Malaya, Sumatra	N. gracilis, N. mirabilis, N. albo-marginata	Borneo, Malaya, Sumatra	13, 14, 15, 16, 21, 168, 169, 186.
E. tobaica Schmitz	NB	Sumatra	N. tobaica	Sumatra	16, 21, 168, 186.
Megaselia bivesicata Schmitz	NX	Borneo, Malaya, Java	N. ampullaria	Borneo, Malaya, Java	13, 16, 168, 169, 186.
M. corkerae Disney	NB	Hong Kong	N. mirabilis	Hong Kong	16, 43.
M. decipiens (de Meijere)	NB	Java	N. gymnamphora	Java	16, 64, 131, 170, 186.
M. deningi Disney	?	Sri Lanka	N. distillatoria	Sri Lanka	16, 42.
M. nepenthina Schmitz	NB	Sumatra, Borneo, ?Malaya	N. mirabilis, N. gracilis, N. albo-marginata	Sumatra, Borneo, ?Malaya	13, 16, 170.
M. sp. (Thienemann, 1932)	?	?	N. tobaica	Sumatra	16, 186.
M. sp. (Lever, 1956)	?	?	N. gracilis	Malaya	14, 114.
Syrphidae					
Nepenthosyrphus capitatus (Sack)	NB	Sumatra, ?Malaya	N. tobaica, N. reinwardtiana	Sumatra, ?Malaya	13, 14, 16, 57, 87, 132, 165, 186, 187, 188.

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Table 1 - continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
N. malayanus Hippa	NB	Malaya	N. sp.	Malaya	14, 16, 87.
N. oudemansi de Meijere	NB	Borneo	N. ampullaria, N. rafflesiana	Borneo	16, 132, 187, 188.
N. venustus Thompson	NB?	Philippines	N. sp.	Philippines	16, 87, 188.
Xylota sp. (Beaver, 1979a)	NX	?	N. ampullaria	Malaya	13, 14, 16.
Chloropidae					
?g. ?sp. (Paulian, 1961)	?	?	N. madagascariensis	Madagascar	16, 151.
Lauxaniidae*					
?g. ?sp.	?	?	N. sp.	Java	16, 131.
Calliphoridae					
Nepenthomyia malayana Kurahashi and Beaver	NB	Malaya	N. ampullaria	Malaya	13, 14, 16, 105.

Table 1 - continued

Dipteran species	Ecological group	Total Geographical Distribution	Nepenthes species	Locality	References
Wilhelmina nepenthicola Villeneuve	NB	Borneo, Sumatra	N. ampullaria, N. rafflesiana	Borneo, Sumatra	16, 56, 105, 171, 172.
Sarcophagidae					
Pierretia urceola Shinonaga and Beaver	NB	Malaya	N. albo-marginata	Malaya	13, 14, 16, 174.
Sarcophaga sp. (Lever, 1956)	?	?	N. sanguinea	Malaya	14, 16, 114.
Muscidae					
Phaonia nepenthicola Stein	NB?	Java	N. gymnamphora	Java	16, 64, 131, 168, 186, 187.

TABLE 1 SUMMARY

TOTAL NUMBER OF DIPTERAN FAMILIES RECORDED		=	12
TOTAL NUMBER OF DIPTERAN SPECIES RECORDED		=	130
NEPENTHEBIONT SPECIES	67 + 22?	=	(68%)
NEPENTHEXENE SPECIES	15 + 3?	=	(14%)
NEPENTHEPHIL SPECIES	5 + 5?	=	(8%)
ECOLOGICAL GROUP UNKNOWN	13		(10%)

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Philippines, where only two species are common to both islands of Luzon and Mindanao, the rest being confined to Luzon, Palawan or Mindanao (Baisas and Ubaldo-Pagayon, 1953). This limited geographical range of nepenthebiont species may be explained by the fact that they probably develop in different areas through the progressive adaptation of a nepenthephil or nepenthexene species to the pitcher environment. Several such nepenthebiont species could arise from one wide ranging nepenthephil or nepenthexene species, the geographical range of each depending on the degree of geographical or ecological isolation of the Nepenthes plants which they inhabit.

Edwards (1926) noted that there appeared to be two distinct races of Tripteroides aranoides developing in Malaya, one breeding in bamboo and the other in Nepenthes, however, Mattingly (1981) has since provisionally separated these two forms into two different species; Tp. tenax breeding in Nepenthes and Tp. aranoides breeding in bamboo or only very rarely in Nepenthes. The two species appear to be distinct with the exception of some individuals from pitcher plants in Johore which show some intergrading of characters between the two species (Mattingly, 1981). This might suggest that the two species were hybridizing locally, but as this area is well south of the distribution of Tp. aranoides and since Tp. tenax occurs further north together with Tp. aranoides without any intergrading (Mattingly, 1981), it may instead suggest that Tp. tenax was originally a race of Tp. aranoides which has developed into a distinct nepenthebiont species. Barr and Chellapah (1963) note the presence of two distinct forms of Tp. aranoides (Tp. tenax sensu Mattingly, 1981) in Singapore, one more common in N. ampullaria and N. rafflesiana while the other usually

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occured in N. gracilis. Beaver (1979a) also found that the pupal period of Tp. aranoides (Tp. tenax sensu Mattingly, 1981) breeding in N. ampullaria pitchers was significantly different to those breeding in N. albo-marginata and N. gracilis, perhaps indicating continued genetic divergence of the species. A similar situation may exist in the case of Tp. vanleeuweni and Tp. bisquamata in New Guinea. Individuals of both species are very similar but the two species are nevertheless considered to be distinct (Assem, 1959). Tripteroides vanleeuweni breeds largely in bamboo, while Tp. bisquamatus is a nepenthephil species found in Nepenthes pitchers and Colocasia axils (Assem, 1959). Peters (1963) suggests that these species represent either two distinct but closely related species among which an appreciable degree of hybridization occurs, or a polymorphic species which is in the process of differentiating into two different species.

The development of large numbers of nepenthebiont species over a relatively small area is probably favoured by the fact that (as pointed out by Beaver, 1983), conditions within a patch of pitcher plants are generally very stable with a constant supply of new pitchers for colonization, thus reducing the necessity for diptera to travel between patches for oviposition and hence also reducing the risks of the dispersal phase. This may contribute to the evolution of species complexes in mosquitoes (Beaver, 1983).

The composition of the pitcher dipteran fauna may be affected by the structure of the pitchers of different species of Nepenthes, the amount of glandular tissue in the pitchers, and the degree to which the lid overhangs the mouth being the most important factors. In pitchers of species such as N. albo-marginata, N. gracilis and N. rafflesiana,

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the glandular tissue is confined to the lower half or two-thirds of the pitcher and the pitcher lid overhangs the mouth preventing large amounts of rainwater from entering, whereas in N. ampullaria the whole of the pitcher interior is glandular and the lid is thrown back away from the pitcher mouth so that rainwater can enter freely. These structural differences really only affect species which have aquatic larvae and terrestrial pupae which pupate on the pitcher wall above the fluid level. In N. ampullaria, the glandular tissue extends to the top of of the pitcher so that the only resting or pupation site is beneath the inturned rim, and flooding is also a danger to terrestrial fauna as the pitchers readily fill with rain (Beaver, 1979b). As a result, nepenthebiont Megaselia spp. and Lestodiplosis syringopais which all have terrestrial pupae, do not occur in pitchers of N. ampullaria (Table 1), while Nepenthomyia malayana is only able to breed in pitchers of N. ampullaria because the larvae pupate beneath the pitcher rim where air bubbles will be trapped should the pitcher become flooded (Beaver, 1979b). Species having aquatic larvae and pupae (Culicidae and Dasyhelea) are unlikely to be affected by differences in pitcher structure (Beaver, 1979b), with the exception of the nepenthexene fauna which often occurs only in pitchers of N. ampullaria (Table 1) because the fluid in these pitchers may be heavily diluted with rainwater, so that the pitcher habitat comes to closely resemble other container habitats. The nepenthebiont fauna is specifically adapted to live in the pitcher fluid, so that dilution is not an important factor, and since the composition of the fluid of different species of Nepenthes is probably very similar, faunistic differences between different species of Nepenthes growing in the same region are likely to be related to the

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habitats in which the plants grow and the preferences of the animals for particular habitats (Beaver, 1979b).

A number of the nepenthebiont diptera are restricted to particular species of Nepenthes, thus in Penang, Culex acutipalus is found only in N. ampullaria, and C. lucaris is restricted to N. albo-marginata (Beaver, 1979a). The fact that N. albo-marginata is generally found in open areas, whereas N. ampullaria usually occurs in more enclosed spaces may account for the separation of these two Culex species, since C. lucaris appears to be restricted to species of Nepenthes growing in open areas (Colless, 1965; Beaver, 1979a). In the Philippines, the mosquitoes Tp. christophersi and Tp. roxasi are restricted to ground pitchers of Nepenthes, while Tp. belkini and Tp. werneri are found only in arboreal species of Nepenthes (Baisas and Ubaldo-Pagayon, 1953). This separation of species is presumably also due to the preference of the adults for different habitats. It must be noted that where dipteran species are recorded from only one species of Nepenthes (Table 1), this does not necessarily mean that they are restricted to this species but may merely mean that this is the only species of Nepenthes which has been studied in a particular area.

Odonata

Libellulidae

A libellulid, Lyriothemus salva Ris has been recorded from Nepenthes in Sumatra. This animal is probably nepenthexene (Beaver, 1983).

Lepidoptera

Psychidae

Guenther (1913) found Nepenthophilus tigrinus Guenther living in

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pitchers of N. distillatoria in Sri Lanka and at first thought that it was a trichopteran larva, although he subsequently recognized that it was a psychid larva which constructs a case for itself of the chitin remains of insects captured by the pitchers. This animal has been considered to be nepenthebiont for many years, but Erber (1979) found a similar psychid in pitchers of N. reinwardtiana in Sumatra which had a case largely composed of leaf fragments (which would not be available to any great extent in the pitchers) and he also found similar cases around the plants, so that he concluded that the animal was not a true inhabitant. There is no evidence however, that this animal is the same as the one found by Guenther and therefore no justification for stating, as Erber does, that Nepenthophilus tigrinus is probably not a genuine associate of Nepenthes.

Batrachia

Bufonidae

Dover (1928) found very young batrachian larvae in ground pitchers of N. ampullaria in Singapore and although none lived to be definitely identified, they were possibly specimens of Bufo melanostictus Schneider. Dover thought that once the larvae grew past a certain stage they then transferred to nearby water, but it seems much more likely that the larvae were accidental inhabitants.

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Biology of the aquatic fauna

a) Colonization

Colonization of the pitchers may be active with the animals entering the pitchers directly, or passive, in which case the animals arrive in the pitchers through the mediation of some other transporting agency such as wind, water, or other animals. Important factors involved in the colonization process are the habitat in which the plants are growing, the structure of the pitcher, its age and the amount of food available (Beaver, 1983).

Pitchers are usually colonized as soon as they open wide enough to allow insects to enter and before there has been any accumulation of prey (Assem, 1959; Beaver, 1983). Diptera are normally the first to colonize the pitchers and they may be present within 24 hours of the pitcher opening (Assem, 1959). Gravid females of nepenthebiont diptera must be able to distinguish between pitchers and other container habitats and this may be due to a chemical cue located in the fluid, since Lambrecht (1971) found that females of Uranotaenia nepenthes would not oviposit in artificial pitchers containing water, but sometimes did so in those containing pitcher fluid. Assem (1959) also noted that eggs of the culicine Tripteroides bisquamatus took much longer to appear in freshly opened pitchers washed out and filled with distilled water, than in those containing fresh pitcher fluid. The females are probably also able to distinguish between new and old pitchers since the majority of species lay their eggs selectively in newly opened pitchers. There is great variation in the number of eggs laid per pitcher and the large numbers of eggs laid in some pitchers must originate from more than one female (Assem, 1959). There appears to be no distinct correlation

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between the size, or contents of the pitcher, and the number of eggs laid in it (Assem, 1959).

Early colonization is advantageous for carrion and filter feeders, although not essential, since it is likely that colonization by mosquitoes (but not carrion feeders) may continue over two or three months (Beaver, 1983). Detritus feeders (Ceratopogonidae) and predators living amongst the detritus (Chaoboridae) can be expected to colonize pitchers after some detritus has accumulated, thus larvae of these species usually appear 5-7 weeks after opening of the pitcher (Beaver, 1983). It is likely that in general, only one generation of each insect species develops within the life of a pitcher, although there may be exceptions amongst the fast developing species (e.g. Culex spp.). However, the decreasing availability of food and the changing conditions within the pitcher as it ages suggest that recolonization is not of frequent occurrence (Beaver, 1983).

The diptera actively colonizing the pitchers are also responsible for the dispersal of anoetid mites living in the pitchers. These mites possess specially adapted nymphs (deutonymphs) which attach themselves to the legs of the dipterans associated with the pitchers and are thereby passively transported from one pitcher to another (Vitzhum, 1931; Thienemann, 1932; Hunter and Hunter, 1964; Beaver, 1979a; 1983) The deutonymph is a non-feeding nymphal stage which follows on from the first nymphal instar and it is particularly well adapted for dispersal, both morphologically and behaviourally. The mouth and chelicerae in the deutonymph are absent and the gut is solid and non-functional. The body is dorsoventrally flattened and strongly sclerotized and the legs are usually short and stout with a modified chaetotaxy. There are also

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usually well developed suckers in the paraproctal region (OConnor, 1982). They are typically very active in comparison to the other stages in the life cycle and wander readily through and out of the preferred feeding area, attaching themselves to almost any moving object (OConnor 1982). In the Anoetidae, the deutonymphs use the posterior pair of legs for jumping onto the host (OConnor, 1982).

The development of the deutonymphs is dependent on external environmental conditions: Thus, when food is readily available, waste products are low in concentration, temperature and humidity are within tolerable limits and population densities are below a certain level, the protonymph may transform directly into a tritonymph at its next moult, however, if these conditions are not met the protonymph moults to the deutonymph (OConnor, 1982). The moult from deutonymph to tritonymph is similarly regulated, taking place under favourable environmental conditions (OConnor, 1982). This is illustrated by the fact that Swales (1972) found that while there were very few deutonymphs of Anoetus gibsoni in pitchers of Sarracenia in the summer, the numbers increased dramatically as temperatures fell and the population subsequently overwintered in the deutonymphal stage. Hunter and Hunter (1964) also found that deutonymphs of A. hughesi were most abundant in old pitchers of Sarracenia where only insect exoskeletons remained and where food scarcity was probably limiting development of the population.

The majority of nepenthephil and nepenthexene protozoa, algae, rotifers, nematodes, oligochaetes and crustacea found in pitchers, are probably passively introduced by wind or water, or on insects which fall into the pitchers. The wind may carry such diverse organisms as protozoa, rotifers, small oligochaetes, nematodes and micro-crustacea from

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one aquatic habitat to another (Maguire, 1971) and it is therefore likely to be an important vector in the transport of these organisms into the pitchers. Rain may be instrumental in washing disseminules out of the air and into pitchers, or it may create splashes of water from groundpools which then enter the pitchers carrying small organisms from the pool with them. Under wet conditions or where the Nepenthes plants are partly submerged, it is probably very easy for small organisms to either swim into the pitchers or to be carried in via water currents. Various insects have also been found to carry viable unicellular and filamentous algae, diatoms, ciliates, rotifers and nematodes (Menzel, 1922; Maguire, 1963; Stewart, Milliger and Solon, 1970; Wutthrich and Matthey, 1980), so that insects which fall victim to the pitchers may be carrying disseminules of freeliving organisms which subsequently establish themselves in the pitcher fluid. Hegner (1926) found that the normally freeliving ciliates, Paramecium and Colpoda, were able to survive and multiply in the pitcher fluid of Sarracenia when artificially introduced and it is probable that many small aquatic animals from other habitats which are passively introduced may also successfully colonize pitchers.

b) Nutrition

Food webs in the pitchers of pitcher plants are carrion-based, with the insect corpses in the pitchers providing food for all the pitcher inhabitants, either directly or indirectly. The pitcher communities are extremely diverse and may include carrion feeders, filter feeders, detritus feeders and predators (Beaver, 1979a), with competition for the same food resource being limited to some extent by the varied feeding habits of the inhabitants and their consumption of the

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drowned insects at different stages in their decay. Freshly drowned insects provide food for direct carrion feeders such as Endonepenthia schuitemakeri, Nepenthomyia malayana and Pierretia urceola (Beaver, 1979a), while culicine larvae in the genera Tripteroides, Uranotaenia and Culex are basically filter feeders, sieving off fine particles, including bacteria, protozoa and rotifers, from the pitcher fluid (Beaver, 1979b). The insect corpses which accumulate in the base of the pitcher, provide food for detritus feeders such as the anoetid mites Zwickia guentheri and Z. nepenthesiana, and larvae of Dasyhelea ampullariae and D. nepenthicola (Beaver, 1979a).

In Sarracenia pitchers, this consumption of the drowned insects at different stages in their decay leads to a spatial and temporal segregation of the pitcher inhabitants (Fish and Hall, 1978). Larvae of the sarcophagid, Blaesoxipha fletcheri (Aldrich), feed on newly captured insects floating on the surface of the fluid, free-swimming larvae of Wyeomyia smithii Coquillet feed on suspended particulate matter, and larvae of the chironomid Metriocnemus knabi Coq. feed on the accumlated insect remains at the bottom of the pitcher (Fish and Hall, 1978). The insects enter and leave the pitchers at slightly different times, as a result of differences in development times and oviposition habits, and although segregation is incomplete, with a few individuals of each species frequently being found in the same pitcher, the maximum number of each species appears to be correlated to the maximum abundance of their specific food type (Fish and Hall, 1978).

The only predators in Sarracenia pitchers are larvae of W. smithii which feed on small organisms such as bacteria and protozoa, but in

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Nepenthes pitchers, in addition to the filter feeding culicine larvae, there are often other predatory species which prey largely on dipteran larvae in the pitchers. Larvae of Toxorhynchites are predatory on other mosquito larvae (Bates, 1954; Beaver, 1979a), while larvae of Lestodiplosis syringapais and Corethrella calathicola in Nepenthes pitchers in Penang, feed chiefly on the smaller larvae of Endonepenthia schuitemakeri and Dasyhelea (Beaver, 1979a). Thienemann (1932) considered that true Nepenthes inhabitants were detritus feeders and assumed that predators found in the pitchers were nepenthexene or nepenthephil inhabitants; however, Beaver (1979a; b) notes several nepenthebiont animals which are definitely predatory. A number of culicine larvae, such as Culex brevipalpus (Sirivanakarn 1977), C. curtipalpus (Colless, 1965) and larvae of Tripteroides in the subgenus Rachisoura (Assem, 1959), appear to have mouthparts which are adapted to feeding directly on insect remains in the pitchers and it is easy to see how animals adapted to feeding on dead insects could instead turn to feeding on living animals. It is notable in this respect that many of the pitcher inhabitants, such as Tripteroides bambusa (Beaver, 1979a) and Uranotaenia spp. (Grjebine, 1979), are facultative predators. Larvae of Uranotaenia are not noted as predators (Bates, 1954), but several of the nepenthebiont species have mouthparts which show striking similarities to those of the exclusively predatory genus Toxorhynchites (Grjebine, 1979), perhaps suggesting a tendency for nepenthebiont diptera to change from browsing or carrion feeding to predation.

Community composition may be drastically altered by the feeding activities of predacious dipteran larvae, particularly by those filter feeding on small organisms in the fluid. Numerous authors have commented on the negative effect of mosquito larvae on communities of

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protozoa and micro-organisms (Kato, Toriumi and Sato, 1952; Kurihara, 1954; 1957; Maguire, Belk and Wells, 1968; Vandermeer et al, 1972; Addicott, 1974; Fish and Carpenter, 1982) and this may be the reason why these groups of organisms are usually restricted to old pitchers of Nepenthes from which the normal culicine inhabitants have already emerged (Beaver, 1979a).

The food supply in the pitchers is often irregular in both space and time, with some pitchers attracting a disproportionate amount of prey and with young pitchers usually trapping more than old pitchers (Beaver, 1979a). Many of the diptera have adapted to this irregularity in the food supply by acquiring the ability to suspend their development for long periods of time under starvation conditions, development proceeding normally when food is once more available. Larvae of Toxorhynchites klossi (Beaver, 1979a) and W. smithii (Wallis and Frempong-Boadu, 1967) can extend their developmental period for 3-4 months when food is scarce, while the life cycle of Tripteroides aranoides (T. tenax sensu Mattingly, 1981) can be extended to at least 7 months under similar conditons (Beaver, 1979a). The number of larvae of a particular species which can be supported by the limited food supply in individual pitchers is usually small, thus Assem (1959) noted that of the large number of Tp. bisquamatus larvae initially present in newly opened pitchers, only 21% finally reached the pupation phase. Cannibalism was largely responsible for regulating the number of larvae and this appeared to be related to the amount of food available, rather than to the overall density of the larvae (Assem, 1959). Cannibalism has also been noted in larvae of Tripteroides bambusa and Toxorhynchites klossi and in the latter case it is so extreme that the larvae are

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always solitary (Beaver, 1979a). Larvae of Pierretia urceola (Beaver, 1979a), and Blaesoxipha fletcheri (Forsyth and Robertson, 1975) are very aggressive and will attack any other larvae of the same species encountered, eventually resulting in the similar establishment of a solitary larva in each pitcher. This behaviour is unusual in sarcophagid larvae and since it occurs in larvae which both live in pitchers (the former in Nepenthes and the latter in Sarracenia), it is probably an adaptation to a limited food supply which would be insufficient to support the growth of several larvae to maturity (Beaver, 1979a). The solitary habit is confined to larger dipteran larvae, smaller larvae such as those of Corethrella calathicola, Lestodiplosis syringopais and Dasyhelea spp. being present in larger numbers in the pitchers (Beaver, 1979a).

The communities in pitchers of N. gracilis and N. albo-marginata in Penang appear to closely resemble each other, but are different to those normally found in pitchers of N. ampullaria, probably as a result of differences in the structure of the pitchers (Beaver, 1979b). As a result of these taxonomic differences in the communities, the components of the food webs are different in pitchers of N. ampullaria on the one hand and N. gracilis and N. albo-marginata on the other and ecologically equivalent species may differ considerably taxonomically (Beaver, 1979b). In some cases the differences only concern different species within the same genus (Tripteroides, Culex, Dasyhelea), but in other cases, different families are involved (Sarocophagidae, Calliphoridae) or sometimes even higher categories (Beaver, 1979b). The details of food webs in Nepenthes spp. in Penang are given by Beaver (1979b).

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c) Respiration

The aquatic inhabitants of Nepenthes pitchers can be divided into two groups in terms of their respiration; those which are air-breathing, and those which are dependent on dissolved oxygen for respiration. All Nepenthes-inhabiting aquatic insect larvae and pupae (apart from those of Dasyhelea spp.) are air-breathing (Thienemann, 1932) and many show a number of special adaptations to pitcher existence. Muscoid larvae living in pitchers are often characterized by elevation of the anal segment (Sanjean, 1957; Kurahashi and Beaver, 1979; Shinonaga and Beaver, 1979), which enables them to float at the surface respiring through the posterior spiracles, while still feeding in the base of the pitcher. This characteristic is unusual in sarcophagid larvae yet it is found in both Blaesoxipha fletcheri and Pierretia urceola which breed in pitchers of Sarracenia and Nepenthes respectively, so that it is perhaps a parallel adaptation of the larvae to similar habitats (Shinonaga and Beaver, 1979). In addition to the elevated anal segment, larvae may also possess hairs around the posterior spiracle (as for example in Nepenthomyia malayana) which clearly also aid in floatation (Kurahashi and Beaver, 1979).

In larvae of the Culicidae, the posterior spiracles are situated at the end of a respiratory siphon, which is usually of variable length although several of the Nepenthes-inhabiting mosquito larvae have come to resemble one another superficially through shortening of the siphon (Edwards, 1931). The larvae come to the surface to breathe periodically, but may remain submerged for considerable periods of time without direct access to air, depending to a large extent on cutaneous respiration. Hopkins (1936) notes that in well-aerated water, culicine larvae

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can remain alive for up to 35 days without access to the atmosphere. The degree of cutaneous respiration in mosquito larvae is determined by the oxygen concentration of the water, the species of mosquito and its developmental stage (Bates, 1954), but it has been noted that in general, larvae which are found in small container habitats spend much less time at the surface of the water than larvae which live in open habitats (Hopkins, 1936). Some larvae, such as those of Psorophora discolor which are found in rainpools, must rely almost entirely on cutaneous respiration since they have never been observed coming to the surface to breathe (Bates, 1954).

Cutaneous respiration must occur to some extent in all the dipteran larvae inhabiting the pitchers, but it is probably relatively unimportant except in Dasyhelea spp. and in larvae of the Chironomidae which do not possess functional spiracles (Imms, 1957). These animals are therefore totally dependent on dissolved oxygen for respiration, as are the protozoa, rotifers, nematodes, oligochaetes, crustacea and mites found in the pitchers. All these animals are small with a relatively large surface area over which gaseous exchange can take place and most lack specialized respiratory systems. In Sarracenia pitcher fluid, dissolved oxygen concentrations are consistently in excess of 77% saturation despite a high community respiration rate (Cameron, Donald and Paterson, 1977) and, if this is also true of Nepenthes pitcher fluid, the inhabitants can have no problem obtaining sufficient oxygen for respiration.

d) Reproduction and Life cycles

The reproduction and life cycles of most Nepenthes inhabitants are very poorly known. Female diptera usually oviposit in newly opened

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pitchers, as already noted, but little is known about the pattern of oviposition of different species. Mogi and Mokry (1980) noted that females of W. smithii laid small numbers of eggs in several pitchers of Sarracenia, a pattern of oviposition which they termed 'skip oviposition'. Skip oviposition is probably common in most small conainer breeders as it lessens the number of unoccupied habitats as well as reducing intraspecific competition (Mogi and Mokry, 1980) and it is likely that most female culicines breeding in Nepenthes oviposit in a similar manner. Eggs are laid either in or on the pitcher fluid, or alternatively on the pitcher wall above the fluid level. Tripteroides spp. (Beaver, 1979a) and Uranotaenia ascidiicola (Meijere, 1910) oviposit on the fluid surface, while Culex spp. (Beaver, 1979a) and Aedes treubi (Meijere, 1910) oviposit on the pitcher wall. The eggs of A. treubi are laid in small groups with the long axis against the pitcher wall (Meijere, 1910). Adult females of Armigeres have been observed to have a very curious oviposition habit. Egg masses have several times been found on the hind legs of the female mosquitoes, each egg containing a protruding larva (Strickland; Barraud - cited by Bates, 1954). The females deposit the eggs by methodically dipping their hind legs into water whereupon all the larvae swim away (Bates, 1954). Barraud (cited by Bates, 1954), observed with regard to Ar. flavus, that this method of oviposition would enable the larvae to be introduced through small holes into the bamboo internodes which are their normal habitat. Presumably this method of oviposition also enables Nepenthes-breeding species to oviposit with ease in the pitchers, with colonization occurring very rapidly if larvae are deposited rather than eggs.

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Growth rate and development times of the larvae are largely dependent on the amount of food available in individual pitchers. Larvae of Culex spp. living in Nepenthes pitchers in Penang develop fairly rapidly, with pupae of C. acutipalus sometimes being present in pitchers which have only been open three weeks (Beaver, 1979a). Under normal conditions, with an adequate food supply, the life cycle from egg to adult in Tripteroides spp. breeding in Nepenthes, is approximately 5-6 weeks, although in T. aranoides (Tp. tenax sensu Mattingly, 1981) the life cycle may be extended to an observed maximum of seven months when food is scarce (Beaver, 1979a). Larvae of Toxorhynchites klossi are also capable of extending their larval developmental period up to 3 or 4 months when food is in short supply and this is probably characteristic of nepenthebiont species (Beaver, 1979a).

The larvae generally pupate over a wide size range, depending on the amount of food available. Thus, larvae of W. smithii with access to large quantities of food remained as larvae past the minimum size for pupation, eventually achieving a larger pupal size (Istock, Wasserman and Zimmer, 1975). Larvae of Endonepenthia schuitemakeri also pupate over a wide size range, some larvae under laboratory conditions pupating at sizes too small to produce a viable adult (Beaver, 1979c).

Culicine pupae are all aquatic and the pupal period is generally short, with the pupal period in a given species being purely a function of temperature (Bates 1954). In Tx. klossi and U. moultoni the pupal period ranges from 5-7 days, while in Tp. aranoides (Tp. tenax sensu Mattingly, 1981) it is 6-8 days and in Tp. bambusa and Tp. nepenthis, 4-6 days (Beaver, 1979a). The pupal period of the Culex species breeding in Nepenthes in Penang is 3-4 days (Beaver, 1979a). Pupae of Dasyhelea

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spp. are also aquatic, remaining at the bottom of the pitcher when young, but later floating up to the surface (Beaver, 1979a). They are capable of slight wriggling motions which appear to be primarily defensive rather than locomotory (Beaver, 1979a). D. ampullariae has a pupal period of 4-8 days, while in D. nepenthicola it is 5-8 days (Beaver, 1979a).

Apart from pupae of Wilhelmina nepenthicola which float on the fluid surface (Schmitz and Villeneuve, 1932a and b), the pupal stages of other Nepenthes diptera are terrestrial and are usually found under the rim of the pitcher, or on the pitcher walls above the glandular area. The puparia of Endonepenthia are usually closely placed in one or more rows around the inner wall of the pitcher above the glandular tissue (Meijere, 1910; Schuitemaker and Franssen, 1934; Schmitz, 1955; Beaver, 1979a) and are U-shaped, with the long hind end bent up away from the fluid (Beaver, 1979a). The majority of adults of E. schuitemakeri emerge 13-15 days after the larva has attached itself, although a small proportion may emerge after 23-36 days (Beaver, 1979a). Lestodiplosis syringopais also pupates on the pitcher wall inside a small, silk, cocoon-like covering constructed by the larva (Beaver, 1979a), whereas the pitcher rim is the favoured site for pupation of Nepenthomyia malayana (Beaver, 1979a), as well as of most Megaselia species, although some species may pupate on the pitcher lid and outer surfaces of the pitcher or even further afield (Meijere, 1910; Beaver, 1979a). Larvae of Pierretia urceola crawl out of the pitchers when mature and pupate in the soil (Beaver, 1979a).

Less is known of the adult stages than of the immature insects. Beaver (1979a) states that none of the mosquitoes or midges bred from

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Nepenthes pitchers in Penang could be induced to bite man and, as field caught adults contained no traces of blood in the gut, the majority of species probably feed on plant secretions, decaying fruits or carrion. Adults of W. smithii in the northern United States are generally autogenous (non-haematophagous), while those in the south are capable of autogenous development, although they may also feed on blood (Bradshaw 1980a). Bradshaw suggests that in the north, there are fewer density induced constraints and the larvae are relatively well fed, whereas in the south, densities are higher and larvae are not so well nourished, so that haematophagy in the adults may substantially increase reproductive success. Larvae of Nepenthes culicines presumably obtain relatively large amounts of high quality protein during their development so that the necessity for haematophagy for successful reproduction in the adult stage is removed.

Very little is known about the reproduction and development of other nepenthebiont animals such as the anoetid mites Zwickia, Anoetus and Creutzeria. In anoetids in general, a hexapod larva hatches out from the egg and subsequently passes through two nymphal stages in the normal course of events, although some individuals may pass through an extra instar (the deutonymph) between the first nymphal instar and the penultimate stage of the life cycle (Hughes, 1959). OConnor (1982) notes that anoetid mites have evolved haplodiploid sex determination which enables them to rapidly colonize new habitats, since a single female deutonymph can found a new colony.

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e) Adaptations of pitcher inhabitants

Antienzyme?

Early investigators of digestion in Nepenthes and Sarracenia argued that the presence of living animals in the fluid was evidence for the absence of digestive enzymes, but Clautriau (1900) and Vines (1901) disagreed and were of the opinion that it indicated instead that the larvae were specially adapted to the digestive environment of the fluid. The parallel nature of the habitat of Nepenthes pitcher inhabitants and that of intestinal parasites stimulated Jensen (1910) to investigate the nature of the resistance to digestion in Nepenthes fauna. There appeared to be no detectable differences in thickness between the cuticle of mosquito larvae living in puddles and those living in Nepenthes pitchers, so Jensen investigated the possibility that the Nepenthes larvae contained an antienzyme which protected them against digestion. He tested the effect of press juices obtained from Nepenthes-dwelling mosquito and fly larvae on the digestive action of pepsin and pancreatin and found that the extract from fly larvae substantially decreased the activity of both pepsin and pancreatin, while the mosquito press juices adversely affected pepsin activity only. Fluid extracts obtained from larvae living in puddles were found to have no effect on pepsin activity. Similar experiments were carried out on mosquito larvae from Nepenthes pitchers in Singapore (Dover, 1928) and on Sarcophaga larvae from pitchers of Sarracenia (Hepburn and Jones, 1919), which indicated that the Sarcophaga larvae contained an antipepsin and an antitrypsin, while the Nepenthes-dwelling larvae possessed only an antipepsin.

Parasitic intestinal worms of man and domestic animals have been shown to possess antipepsin and antitrypsinases (Fischer, cited by

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Hepburn and Jones, 1919; Mendel and Blood, 1910; Green, 1957), so that the presence of antienzyme activity in pitcher inhabitants is not surprising when it is considered that larvae of other species of Sarcophaga (for example S. haemorrhoidalis) are parasites of the human digestive system, causing intestinal myiasis (Hepburn and Jones, 1919). Larvae of a species of Megaselia which is closely related to the Nepenthes inhabitant M. deningi (M. trivialis (Brues.)), have also been found as parasites in man (Disney and Kurahashi, 1978; Disney, 1981a), so that it is quite probable that many of the diptera inhabiting pitchers are capable of producing antienzymes, although it must be noted that this has been by no means proved, since the results of the experiments above are somewhat suspect. Dover himself notes (1928) that neutral salts in the tissues of the larvae would retard peptic digestion and thus, the decrease in activity of the pepsin may not necessarily have been due to the presence of antipepsins.

Thienemann (1932) was not convinced that antienzymes existed in Nepenthes fauna, nor did he consider that there was any necessity for them, pointing out that it was extremely unlikely that nepenthephil and nepenthexene animals suddenly developed antienzymes when living in the pitchers rather than in other more normal habitats. As Thienemann (1932) and Swales (1969) have both noted, the essential difference between the pitcher prey and the pitcher inhabitants is that one is terrestrial and drowns in the pitcher fluid, while the other is aquatic and in a natural medium. Animals which do not drown in the fluid and which are not affected by its acidity can survive in it for long periods, thus Beaver (1979a) was able to rear Aedes albopictus (a species not normally found in Nepenthes) from egg to adult, in

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freshly opened pitchers of N. albo-marginata in which no dilution of the fluid had occurred, within the normal time span and with no suggestion of increased mortality. He also found that corixid bugs were able to survive for more than two weeks in pitcher fluid in the laboratory. Contrary to this, Jensen (1910) found that mosquito larvae from freshwater habitats, as well as tadpoles and water beetles, died when immersed in pitcher fluid, but this may have been due to an inability to tolerate the low pH rather than as a result of the digestive activity of the fluid.

Pitcher victims and pitcher inhabitants are both protected externally by a cuticle which is very resistant to enzyme attack, but the terrestrial pitcher victims die and are thus subject to digestion by enzymes entering the mouth and anus and working from the inside, outwards (Swales, 1969). The living inhabitants may also aid in the digestion of captured animals by helping to break up the bodies so that the enzymes can reach the softer, more readily digestible tissues (Guenther, 1913). While the pitcher fauna is protected from enzymes externally by the cuticle, it would be impossible for them to prevent their entry into the digestive tract during feeding; however, enzymes entering through the mouth would come into contact with the living epithelium of the gut, resistant to its own digestive enzymes and possibly also to introduced foreign ones, particularly if the pH in the gut was such that the pitcher enzymes were inhibited (Swales, 1969). It therefore seems that, although some of the nepenthebiont diptera may produce antienzymes, the majority of aquatic arthropods are probably resistant to the digestive enzymes anyway, by virtue of their chitin cuticle, and that they are more likely to die from lack of suitable food if they accidentally enter the pitchers

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than as a result of digestion by the fluid.

The resistance to digestion of other pitcher inhabitants such as nematodes, oligochaetes, rotifers and crustacea is more difficult to explain since most do not possess such resistant cuticles as insects and, as the majority are probably nepenthexene, they are unlikely to possess specific antienzymes. Most of the records of these inhabitants are either from pitchers of N. ampullaria where the fluid may be heavily diluted with rainwater, or from very old pitchers of other Nepenthes species in which the fluid has probably lost its digestive activity. These animals may therefore be only occurring in pitchers where the enzyme activity is minimal and unlikely to affect them.

Adaptations to the temporary nature of the pitcher environment

All inhabitants of temporary aquatic environments possess adaptations for living in an unstable environment, including an enhanced ability to survive temperature extremes and desiccation, and the presence of clearly defined resting stages in the life cycle which are capable of remaining dormant for long periods (Belk and Cole, 1975). Although the pitcher habitat is permanent in the sense that pitchers are always readily available for colonization by pitcher fauna, individual pitchers are clearly temporary aquatic habitats since they have limited lives as water holding containers. Thienemann (1932) thought that the pitchers probably only functioned for a few days but Beaver (1983) notes that the maximum life of a pitcher is probably about one year.

The volume of fluid contained in the pitchers is usually small and as a result the temperature within the fluid is likely to fluctuate over a wide range. The fluid temperature of Sarracenia pitchers in open sunlight ordinarily fluctuates from a low of 10-15°C to a high of 30-35°C

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in a single summer day (Istock et al, 1975), with the mean daily amplitude being 14.5^{o}C (Bradshaw, 1980b). Apart from isolated measurements of pitcher temperature (Thienemann, 1932), there is no information on the range of temperatures found in Nepenthes pitcher fluid, but it is likely that, as in Sarracenia, the temperature fluctuates greatly with very high temperatures being common in pitchers exposed to full sun. The pitcher inhabitants must be able to withstand these large fluctuations in temperature and indeed, W. smithii appears to be specifically adapted to these conditions, since Bradshaw (1980b) found that when individuals were reared under fluctuating temperature conditions, they showed a 58% greater capacity for increase over those reared under constant temperature regimes, despite the fact that development was faster in the latter treatment. In other insects, fluctuating temperatures are known to have an accelerating effect on development (Bates, 1954), but as pitcher plant culicines probably depend on the larval stage for collection and storage of most of the food reserves eventually directed towards reproduction,a decrease in larval development time would be detrimental to the reproductive success of the species. The slowing of development of W. smithii under fluctuating temperature conditions may thus represent a specific adaptation of the larvae to normal conditions in the pitchers.

In addition to being subject to wide fluctuations in fluid temperature, Nepenthes and Sarracenia pitchers must also be very susceptible to desiccation. Kingsolver (1981) showed under simulated conditions, that desiccation frequency was inversely related to leaf size in Sarracenia, the size distribution of pitchers in the field being such that the majority of pitchers were likely to desiccate one to three

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times a season, while smaller pitchers might average eight times a season. As pitchers of Nepenthes are generally smaller than those of Sarracenia (5-30cm in length - Lloyd, 1942 - compared to 15-90cm in length for Sarracenia - Slack, 1979), they are probably even more likely to dry out.

The ability of mosquito larvae to tolerate desiccation appears to be correlated to the size of the habitat they normally live in and the likelihood of it drying out, thus Bick and Penn (1947) found that larvae of W. smithii were much more tolerant of desiccation than those of Anopheles walkeri (which are normally found in swamps or lakes) or those of Aedes vexans which are temporary pool inhabitants. Larvae of W. smithii and A. vexans were found to secrete a mucous covering over their bodies when free water was removed, which must be an adaptation enabling them to survive periods of drought, since larvae of An. walkeri, which presumably are rarely if ever subjected to desiccation, did not (Bick and Penn, 1947). Although the larvae of pitcher plant diptera must have some measure of tolerance to drought, this tolerance may be very limited, as the maximum observed survival time of W. smithii was only 192 hours under conditions of continuous drought (Bick and Penn, 1947), so that if pitchers dry out, most of the larvae they contain are likely to die unless rain refills them fairly rapidly. Brug (1931) observed that once first instar larvae had developed within eggs of Aedes treubi, A. argenteus and A. albopictus, they were able to endure a month-long desiccation and it is therefore likely that the eggs are the main guarantee of survival of culicine species breeding in pitchers.

Nematode inhabitants of temporary pools such as Dorylaimus spp. and Actinolaimus spp. appear to be able to withstand almost total removal of water from their tissues (Lee, 1961) and seem to be cryptobiotic in the

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sense of Hinton (1951; 1960). Individuals belonging to the genera Plectus, Dorylaimus and Cephalobus found in mosses kept dry for two years, were found to be alive when wetted (Menzel, cited by Lee, 1961), and live nematodes were also obtained from a sample of moss kept dry for four and a half years (Hyman, 1951), demonstrating that many nematodes are extremely resistant to desiccation. The genera Plectus and Dorylaimus, both noted for their desiccation tolerance, have been recorded from Nepenthes pitchers (Menzel, 1922) and are probably particularly suited to temporary environments as a result of their ability to survive long periods of drought in both the adult and juvenile stages. Crustacea, rotifers and protozoa found in pitchers probably survive desiccation in the egg stage or in cysts which are very resistant to drying and which are capable of long periods of dormancy. Nematodes, crustaceans, rotifers and protozoa are all characteristic of temporary aquatic environments (Rzoska, 1961; Maguire, 1971; Bayly, 1982) and this is probably mostly as a result of the desiccation tolerance of certain stages in their lifecycle.

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Terrestrial Fauna

Taxonomic Composition and Biology

a) Diptera

Mycetophilidae

Xenoplatyura beaveri Matile occurs in pitchers of N. ampullaria in Penang (Beaver, 1979a; b) and is the only mycetophilid to be found living in pitcher plants (Matile, 1979). The larvae are solitary, presumably as a result of larval interactions, and each one spins an irregular web above the surface of the pitcher fluid, on which it deposits droplets of a highly acid sticky secretion (Beaver, 1979a). Small insects trapped by the pitchers, or those emerging from the pitcher after development in the fluid, become entangled in the web, are killed by the acid and then eaten by the larva (Beaver, 1979a). Larvae of X. beaveri are never found in the same pitchers as those of Nepenthomyia malayana, presumably because these larvae often climb out of the pitcher fluid and move around the pitcher walls and in so doing may damage the web or may even attack the mycetophilid larva (Beaver, 1979a). The latter usually remains in the same pitcher during development but, if the pitcher is flooded or dies,it can move to another nearby (Beaver 1979a). Before pupation (which takes place under the rim of the pitcher) the larva thickens the web around itself and then pupates suspended in it for a period of 4-5 days (Beaver, 1979a). The adult remains quiescent in the web for a further 1-2 days (Beaver, 1979a).

Tachinidae

Succingulum fransseni Schmitz and Villeneuve was found in N. mirabilis in Borneo (Schmitz and Villeneuve, 1932b; Thienemann, 1934). According to Beaver (1983) this dipteran is a member of the terrestrial pitcher fauna.

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Cecidomyiidae

The cedidomyiid Lestodiplosis syringopais (Hering) has been recorded from pitchers of N. tobaica in Sumatra (Hering, 1930; Thienemann, 1932) and from N. albo-marginata and N. gracilis in Penang (Beaver, 1979a; b). According to Hering (1930) larvae of this cecidomyiid were parasitic on the leaf mining lepidopteran Phyllocnistis nepenthae Hering, but Beaver (1979a) notes that the larvae are clearly aquatic and have no association with leaf miners. This dipteran is therefore not part of the terrestrial fauna as reported by Thienemann (1932), except in the pupal stage.

Many of the diptera breeding in Nepenthes pitchers, which have aquatic larvae, also have terrestrial pupae (Phoridae, Calliphoridae, Sarcophagidae) so that at different stages of their life cycle they belong to both the aquatic and the terrestrial fauna. However, they are normally considered to be part of the aquatic fauna, since most of their feeding and development takes place in the aquatic stage (Beaver, 1979a).

b) Lepidoptera

Phyllocnistidae

Leaf mining larvae of Phyllocnistis nepenthae Hering have been found in pitchers of N. tobaica in Sumatra (Hering, 1930; Thienemann, 1932) and possibly in N. albo-marginata in Penang, although this is not certain since only leaf miner galleries were found and it was not possible to identify the maker (Beaver, 1979a). This species is probably nepenthebiont (Beaver, 1983).

Noctuidae

Dover (1928) found larvae of a small noctuid, Eublemma radda Swinhoe, living and pupating on the smooth inner conducting surface of pitchers of

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N. rafflesiana in Singapore and this species has also been found in N. albomarginata in Penang (Beaver, 1979a; b). The type-locality of the species is Borneo (Tams, 1928; Dover, 1928) and further specimens of this moth have also been found in Sumatra and Thailand (Beaver, 1979a). There is evidence for regular association of the species with Nepenthes, although it is not certain that it is exclusive (Dover, 1928). In this connection, it is interesting to note that this moth belongs to the same subfamily (Erastriinae as the North American species of the genus Exyra, which are exclusively associated with Sarracenia (Tams, 1928).

c) Hymenoptera

Formicidae

Beaver (1983) notes that there are three formicids which are associated with Nepenthes in Borneo: Camponotus schmitzi Starcke is associated with N. bicalcarata Hook. f., N. gracilis and N. mirabilis; Camponotus sp. with N. bicalacarata; and Dolichoderus bituberculatus Mayr with N. mirabilis and N. gracilis. All three species are nepenthexene.

Ichneumonidae

Meer-Mohr (1932) found an unspecified ichneumonid (possibly ?Allocata sp. n. - Beaver, 1983) parasitizing egg cocoons of the spider Thomisus nepenthephilus in Sumatra. The female ichneumonids laid their eggs among the eggs of the spider, which provided nourishment for the larvae as they developed (Meer-Mohr, 1932).

Chalcidoidea

Meer-Mohr (1932) also found a small chalcid in the egg cocoons of T. nepenthephilus, which was either parasitic on the eggs of the spider, or hyper-parasitic on the eggs of the ichneumonid mentioned above. Thienemann

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(1932) notes that an elachertine chalcid was found in the burrows of Phyllocnistis nepenthae in Sumatra.

Encyrtidae

Several specimens of an unidentified encyrtid (?gen. nov. nr. Tachinaephagus) were found parasitizing puparia of Endonepenthia schuitemakeri from pitchers of N. albo-marginata and N. gracilis in Penang (Beaver, 1979a). Thienemann (1932) also extracted an unidentified encyrtid from a puparium of E. tobaica in Sumatra.

Proctotrupidae

An unidentified proctotrupide is mentioned by Meijere (1910) as being parasitic on E. gregalis from N. gymnamphora in Java, although the family identification of this hymenopteran is doubtful (Beaver, 1983).

Diapriidae

Beaver (1979a) bred a single specimen of Trichopria from a puparium of Megaselia sp. A from N. ampullaria but, as the host was a nepenthexene species, it is unlikely that the parasite has any particular association with Nepenthes.

d) Acarina

Anystidae

Dead mites identified as Snartia nepenthus Oudemans were found in pitchers of N. tobaica in Sumatra (Oudemans, 1936) but, as no other information is available on this mite, it is uncertain whether it is a true associate of Nepenthes pitchers or not.

e) Araneae

Thomisidae

Several spiders which appear to be exclusively found in Nepenthes

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pitchers have been observed living and reproducing in the upper regions of the pitchers. Misumenops nepenthicola (Pocock) has been found in Singapore, apparently restricted to pitchers of N. gracilis, and in Borneo in a species which may have been N. gracilis (Fage, 1928). In Sumatra, this spider was found in pitchers of N. reinwardtiana Miq. and N. tobaica (Meer-Mohr, 1932), and in Penang in N. albo-marginata, N. gracilis and N. rafflesiana (Beaver, 1979a), so that it is not in fact restricted to any particular species of Nepenthes as first thought by Fage (1928). The spider is usually found in the interior of the pitcher, a little below the peristome, where it weaves a light web which allows it to move around easily on the steep, slippery walls (Fage, 1928). When disturbed, the spiders let themselves fall into the base of the pitcher, descending into the fluid and wandering around amongst the insect debris before returning to their webs (Fage, 1928). Normally a pitcher contains only one spider (Meer-Mohr, 1932; Beaver, 1979a), although after emergence of the eggs, many small spiders may be found which eventually disperse to other pitchers (Beaver, 1979a). Another species of Misumenops, M. thienemanni, which is very similar to M. nepenthephilus, has been found living in pitchers of N. tobaica in Sumatra (Reimoser, 1931; Thienemann, 1932).

Thomisus nepenthephilus Fage has also been found in pitchers of N. tobaica in Sumatra, where it weaves a vertical web, behind which it attaches its cocoons to the inner wall of the pitcher by means of short threads (Meer-Mohr, 1932). Reimoser (1931) maintained that T. nepenthephilus and T. callidus (Thor.) were identical, in which case the name T. callidus should take precedence (Thienemann, 1932). If this is the case then the spider is nepenthephil and not nepenthebiont as formerly thought, since T. callidus is found outside the pitcher environment (Thienemann, 1932).

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Theridiidae

Decary (1928) found spiders later identified as Theridion decaryi Fage (Fage, 1930) in pitchers of N. madagascariensis. They normally constructed a vertical web inside the pitchers and typically sheltered under the pitcher peristome when disturbed (Fage, 1930). This spider is not a nepenthebiont animal as it is found outside the range of Nepenthes in Madagascar and lives normally on small bushes (Decary, 1928; Fage, 1930). Another species, Theridion sp. n., has been found in Nepenthes pitchers in Borneo, but the status of this animal is unknown (Beaver, 1983).

General Remarks on the terrestrial fauna

The terrestrial fauna is almost exclusively found in non-ampullaria type pitchers where there is a substantial area above the pitcher fluid which is free of glands and hence safe to walk on. In the ampullaria type of pitchers, animals walking about over the surface of the pitcher walls would come into contact with the glands, stimulating digestive secretions (Fage, 1928) and, in addition, immobile animals or those with very limited powers of movement would be in danger of drowning if the pitcher flooded. Xenoplatyura beaveri is the exception to the rule that terrestrial fauna lives in non-ampullaria type pitchers, being found exclusively in pitchers of N. ampullaria (Beaver, 1979a); however, individuals are suspended in the middle of a web so that they never come into contact with the glandular sides and, if the pitcher floods, they are capable of moving to a new one (Beaver, 1979b). Terrestrial animals in normal type pitchers are usually confined to the smooth non-glandular area above the pitcher fluid, but may extend lower down if the pitcher dries out as a result of evaporation or damage, thus leaf mines of Phyllocnistis nepenthes may take over the whole pitcher under these circumstances (Hering, 1930).

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GENERAL INFORMATION ON NEPENTHES IN HONG KONG

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Distribution of Nepenthes mirabilis in the South China Region

Nepenthes mirabilis has been recorded from a number of places in the South China region, including various localities in Kwangtung (mostly unspecified), Hainan Island, Macau and Hong Kong (Table 2).

TABLE 2

Recorded locations of Nepenthes mirabilis in the South China area

China - Kwangtung province	British Museum (Natural History) Herbarium
	Hong Kong Herbarium
	Forbes and Hemsley (1889-1902)
(Szetsushan, Sanning)	Dunn and Tutcher (1912)
Hainan Island	BM (NH) Herbarium
	Hong Kong Herbarium
Macau	BM (NH) Herbarium
	Dunn and Tutcher (1912)
Hong Kong	
Shun Ling Sze ge Shan (Lion Rock mountain)	Hong Kong Herbarium
Tai Lam Chung	Hong Kong Herbarium
	Herklots (1951)
Lantau Island	
Location east of Keung Shan	Hong Kong Herbarium
Locality near Tai O	Hong Kong Herbarium
two unspecified valleys	Herklots (1951)

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The known distribution of plants of N. mirabilis in Hong Kong is shown in Figure 2A. The occurrence of plants on Lion Rock mountain and east of Keung Shan on Lantau (Table 2) has not been confirmed personally, but the latter location is close to sites 9 and 10 where Nepenthes is known to occur (Fig. 2A), so it is probable that the plants are to be found in small patches all over this area.

Nepenthes seems to be restricted to the western half of Hong Kong (Fig. 2A) and this is probably related to the geology of the region since the plants occur mostly in granitic areas (Fig. 2A; B). The apparent association of the plants with granite is strengthened by the fact that they grow in profusion on the mainly granitic island of Chep Lap Kok (Fig. 2A), but do not appear to occur on the two islands known as The Brothers (Griffiths, 1982), which are slightly to the north of Chep Lap Kok and which are composed of Tai O formation sandstone, shale and siltstone (Fig. 2B). Weathering of granite produces a material which is easily eroded (Grant, 1960), so it is possible that the plants occur in granitic areas because it is usually these areas which are most heavily eroded (Fig. 2B; C). The level of plant nutrients is generally low in hillside soils in Hong Kong (Grant, 1960) and where loss of topsoil has occurred the soil must be extremely infertile. Carnivorous plants characteristically grow in infertile soils, so this may explain why the plants are always found in heavily eroded areas (Fig. 2A; C) in the western regions, where urban development is less intense.

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Figure 2. Factors affecting the distribution of N. mirabilis in Hong Hong.

A. The distribution of N. mirabilis in Hong Kong.

B. Simplified geological map of Hong Kong.
(Redrawn from Hong Kong minerals by C.J. Peng. Published 1978, Government Printer, Hong Kong).

C. Erosion in Hong Kong.
(Redrawn from Grant, 1960)

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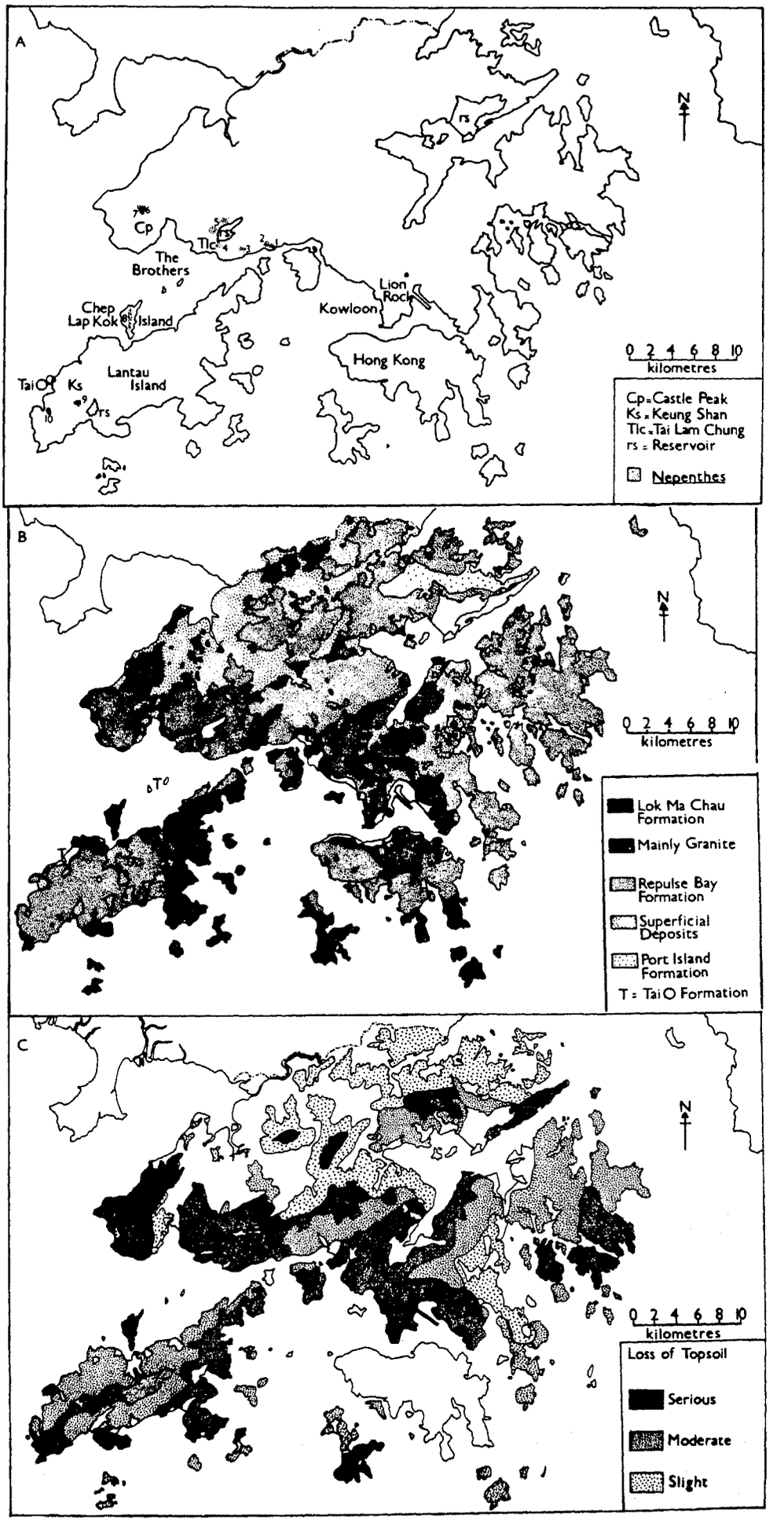

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Habitat

Nepenthes mirabilis in Hong Kong occurs at elevations of 100-400m, along the banks of streams and in river valleys, or in seepage areas on hillsides which are usually south-facing. The plants are normally found in areas which are waterlogged all year round, although a few stunted plants were found in regions which were apparently dry for some time in the winter (the dry season in Hong Kong).

A number of plant species always occurred together with N. mirabilis (although not exclusively), thus the sedge Lepidosperma chinense Nees is a constant associate of Nepenthes in Hong Kong, to such an extent that it can often be used as an indicator of the presence of Nepenthes. The pitcher plants grow amongst the sedge which usually acts as the major support for climbing plants, since it is rare that taller vegetation is available to act as a support. Drosera burmanni Vahl is often also present in the same habitats, together with the bamboo orchid Arundina chinensis Bl.. A number of other plants which are common on shrub covered hillsides in Hong Kong are often found in the dryer areas around the water logged patches of Nepenthes and Lepidosperma. Thus, the following are all common associates: Baeckia frutescens L.; Rhodomyrtus tormentosa (Ait.) Hook.; Melastoma sanguineum Sims; M. candidum D. Don; Dicranopteris linearis (Butm. f.) Underw.; and Lycopodium cernuum L.. Green (1967) also notes that the two latter species are associated with Nepenthes in Singapore. Small trees of Pinus massoniana Lamb and Schefflera octaphylla (Lour.) Harms are sometimes also present.

The regions where N. mirabilis grows are often in areas which are subject to hillside fires. On one occasion (at site 8b), mature plants were found growing in an area which had obviously been burnt in the

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recent past, so that N. mirabilis must be able to survive fire to some extent. Since the plants develop from an underground rhizome, it is probable that while the aerial parts of the plant may be destroyed by fire, the rhizome (usually in very wet ground) remains undamaged, producing new growth once the fire is over. Fire may actually be beneficial to subsequent growth in that it may cause a rapid release of nutrients formerly tied up in plant tissues and decaying matter, in the form of ash, to the soil.

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Site descriptions

Site 1

The *Nepenthes* plants at site 1 (Fig. 3A) are situated along a stream bank. Very few plants are present and most of these are relatively stunted and in poor condition with few functional pitchers. The reason for the poor growth of these plants is unclear, but it was noted that all the plants seemed to suffer from severe insect damage and almost all of the pitchers, even those which had recently opened, were dry as a result of herbivores eating away the base of the pitchers. The animal causing this damage was never found.

Site 2

Site 2 (Fig. 3A) is situated on a south-facing hillside overlooking the coast and it is one of the most prolific in terms of the number of *Nepenthes* plants present. These grow along the banks of two small streams running down the hillside and in the waterlogged areas in between. The plants here reached the greatest height of any plants seen in Hong Kong, climbing in trees of *Pinus massoniana* and *Schefflera octaphylla* to heights of 3m or more.

Site 3

The plants at site 3 (Fig. 3B) occur along the sides of a steep, rocky stream which has a small tributary entering to one side. Several plants are also found along this tributary which is heavily enriched with organic waste from a farm higher up on the hillside.

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Figure 3. Geographical Locations of Nepenthes plants in Hong Kong

A. Sham Tseng; sites 1 and 2.

B. Tai Lam Chung; sites 3. 4 and 5.

C. Castle Peak; sites 6 and 7.

D. Chep Lap Kok island; site 8.

E. Lantau island; sites 9 and 10.

Key

SM = San Miguel Brewery

GB = Garden Bakery

R = Restricted road

CPH = Castle Peak Hospital

KYT = Kwun Yam Temple

---- = Footpath

--- = Boundary of military firing range

* = location of Nepenthes plants

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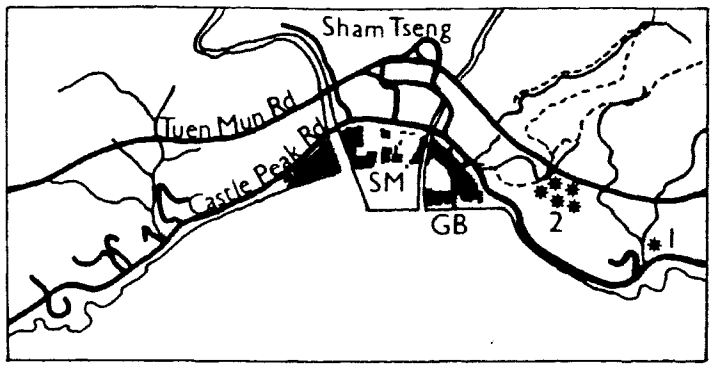
A



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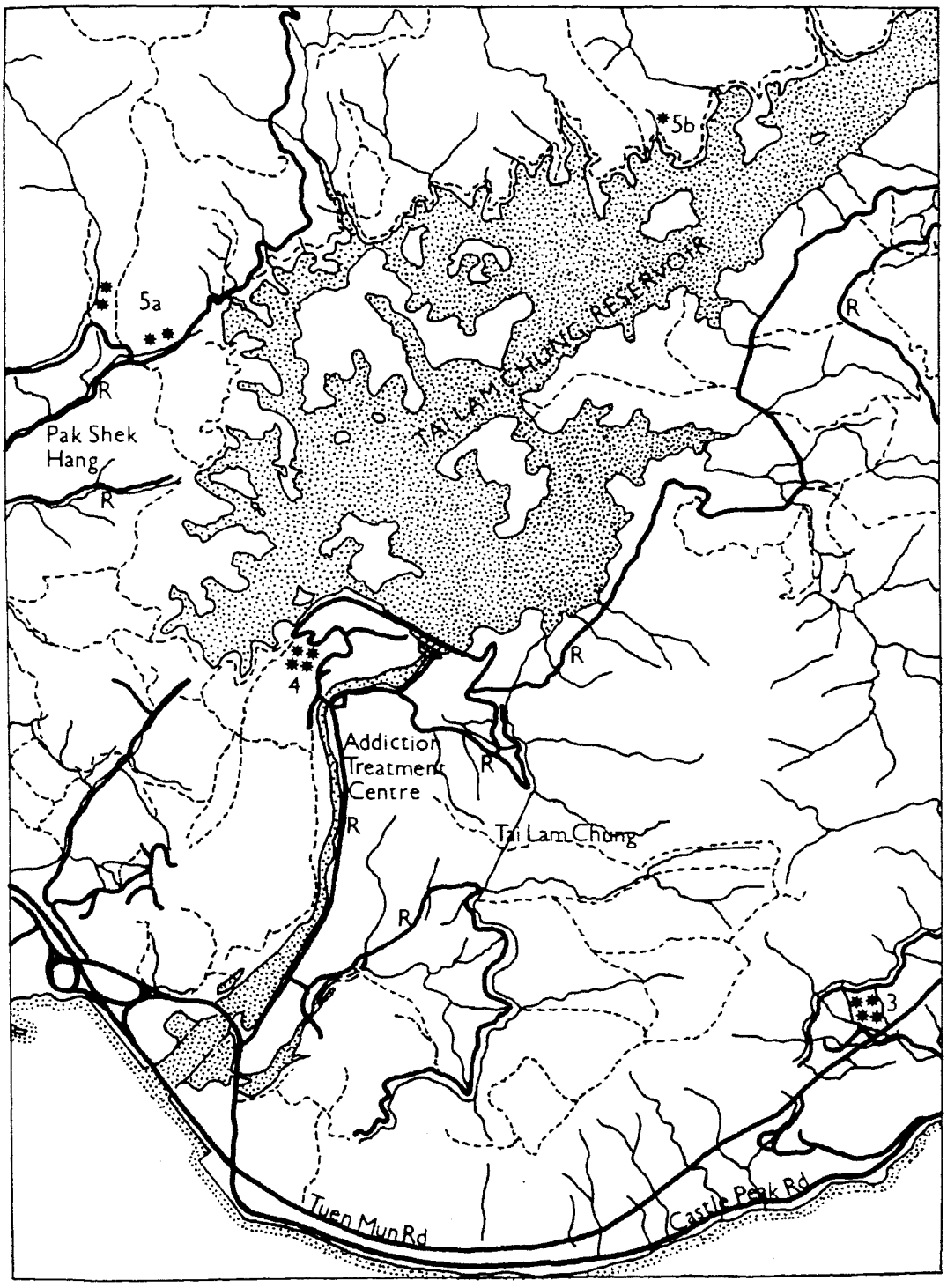

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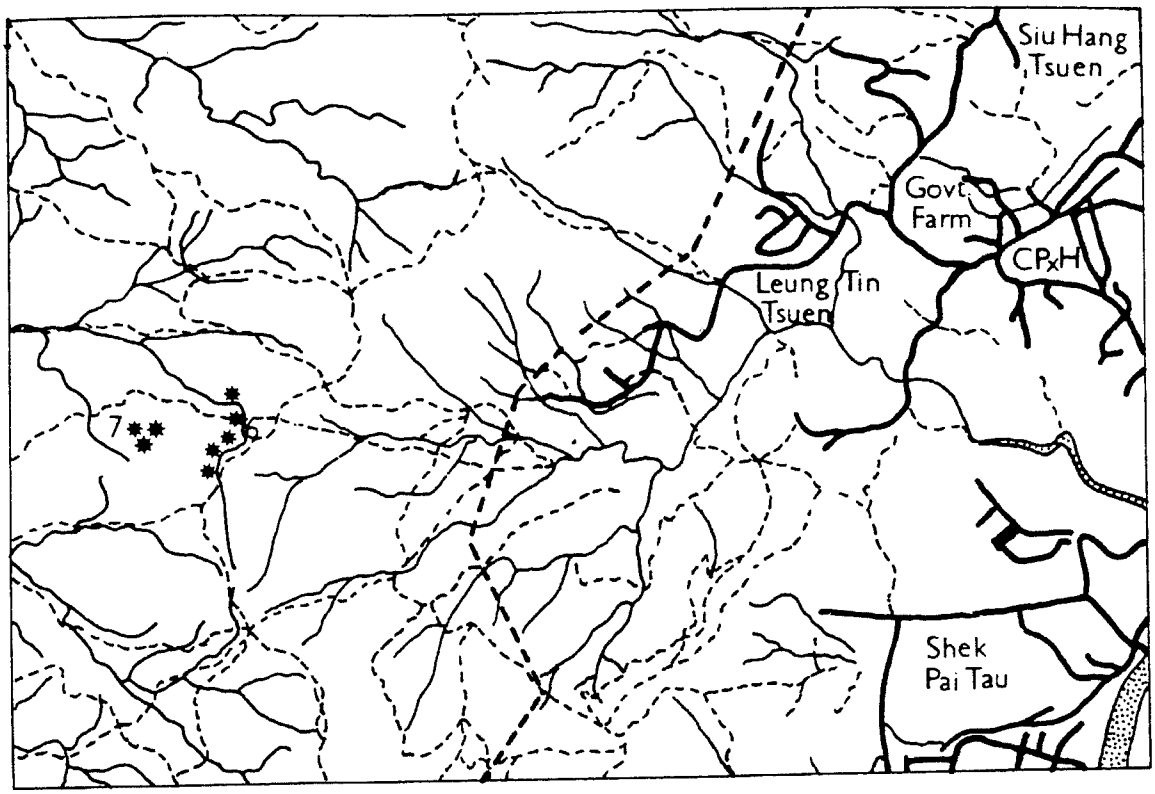
Fig. 3

C



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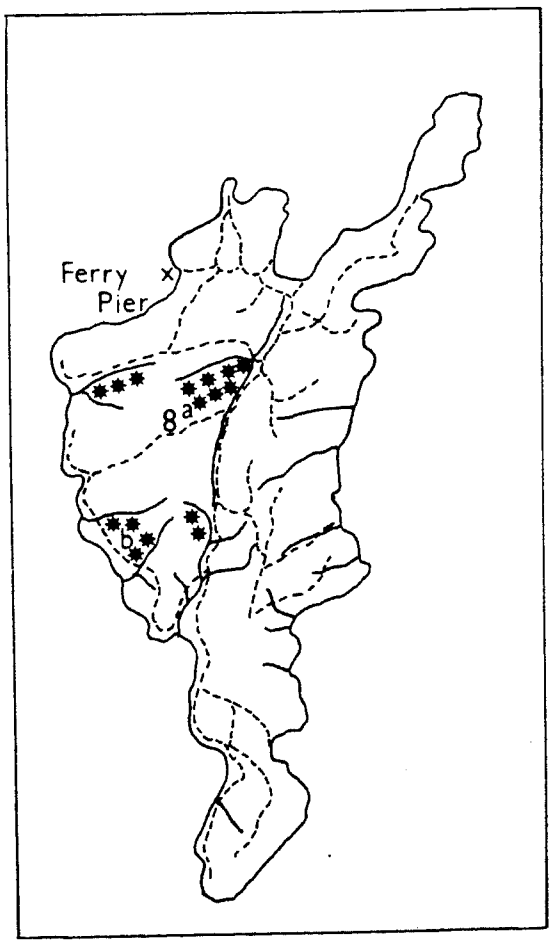

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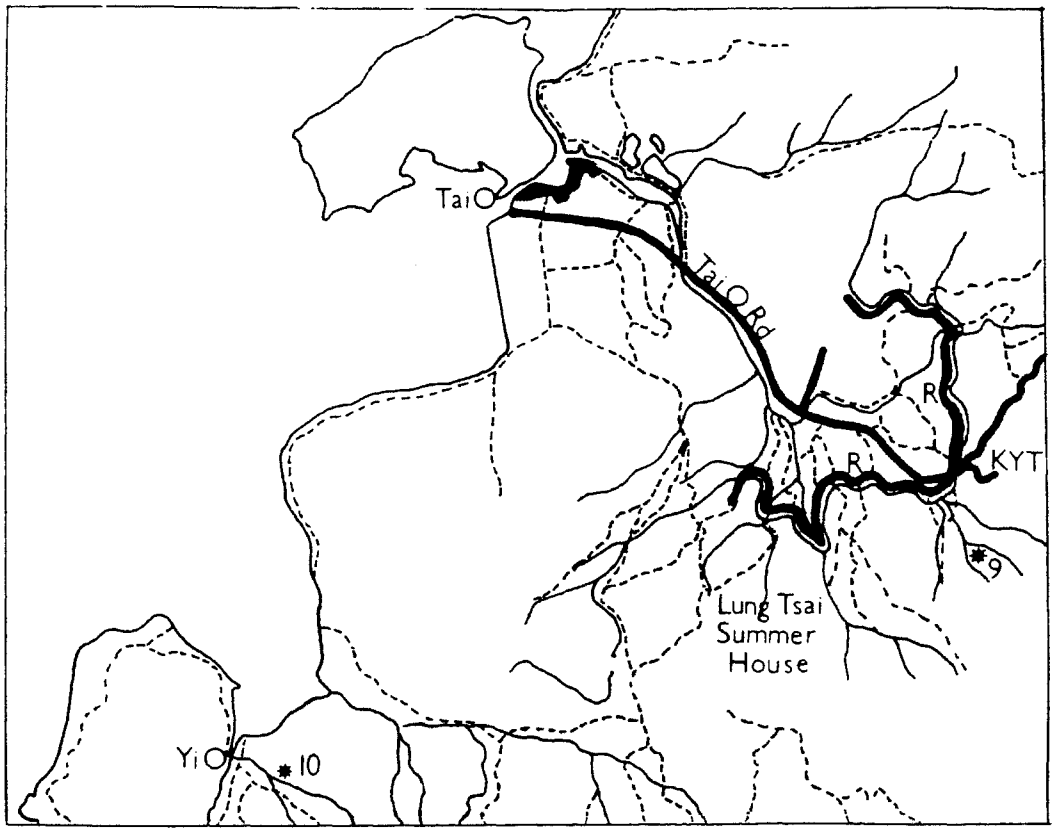
Fig 3 E



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Site 4

Site 4 (Fig. 3B) is located within the Tai Lam Chung drug addiction treatment Centre, in a seepage area near a stream, on a south/southeast-facing hillside. Periodically the plants are completely cut back by Government authorities in an attempt to control the mosquitoes breeding in the pitchers, so that they rarely grow very tall but are mostly in the form of rosette-like clumps, although a few plants which escape cutting may reach heights of 1m or more.

Site 5

At site 5a (Fig. 3B) plants grow along a stream and on a small seepage area on the hillside. Few plants are present. At site 5B (Fig. 3B) a few large plants occur along the steep banks of a stream which is dry in winter (when the site was examined). Most of the pitchers on the plants had dried out.

Sites 6 and 7

Sites 6 and 7 (Fig. 3C) are very close together within a military firing range, so that access is limited. The plants at site 6 grow along the banks of a small stream and in the wet areas surrounding it, while those at site 7 grow in a seepage area on a southwest-facing hillside. These plants are well away from any form of human habitation and are seldom disturbed.

Site 8

The largest aggregation of Nepenthes plants in Hong Kong was found at site 8a (Fig. 3D), which is a flat, sandy river valley with an area

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of about 200m^2, colonized by over 500 plants of N. mirabilis. All plants at other sites on Chep Lap Kok were found along stream banks, although those at site 8b (Fig. 3D) were in a very arid, eroded area which was dry at the time of examination. This area had been burnt in the recent past, but mature plants of Nepenthes were still present.

Sites 9 and 10

Only 4 or 5 plants were found initially at site 9 (Fig. 3E) and this number was reduced to 2 by the end of the study. To begin with, small seedlings were present but these were eventually eliminated. Competition from other plants is probably responsible for the gradual extinction of Nepenthes in this area, as the vegetation grew substantially over the three year period of study, from short scrub into the beginnings of woodland which completley overshaded and choked the Nepenthes plants.

A few small plants were also found at site 10 by a rocky stream near Yi O (Fig. 3E), but they were very inaccessible and few of them had any functional pitchers.

Site 11

Site 11 was located in Macau on the island of Coloane, inside the experimental agricultural farm run by the Forestry and Agriculture Service of Macau. A small patch of Nepenthes plants occurred in a wet area below a dam. Most of the plants appeared to be derived from a single rhizome.

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SECTION II

Plant growth and reproduction

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Introduction

In Hong Kong, temperatures range from a minimum of around 6°C in the winter months of December, January and February, to a maxiumum of 35°C in June, July and August, when most of the annual rainfall is also recorded. This is in direct contrast to most other purely tropical regions where Nepenthes grows, where the climate varies little seasonally. Despite the fact that N. mirabilis is a widespread species, which tolerates a wide range of climatic conditions, it is likely that it is primarily adapted to tropical conditions. As a result, the extremes of temperature and rainfall in Hong Kong are likely to affect growth of the plants, as well as the production and lifespan of pitchers, which will obviously also affect the pitcher fauna. It has been established that Nepenthes plants require high humidity and a limited amount of light for good growth (Green, 1967), but plant growth in relation to other climatic factors has never previously been studied. This investigation was therefore undertaken to determine such factors as growth rate of the plants, frequency of pitcher production and lifespan of the pitchers, in relation to temperature and rainfall.

Numerous studies on the morphological and anatomical development of pitchers of Nepenthes have been carried out, but the timescale of development and the changes in fluid volume and pH which take place throughout the life of a pitcher have never been studied, although many isolated measurements of pH have been made (Zeeuw, 1934; Morrissey, 1955; Nakayama and Amagase, 1968; Tokes et al, 1974). Heslop-Harrison (1975) studied fluid volume and pH changes in developing pitchers of N. chelsonii but did not continue the study to include changes taking place in mature open pitchers. As the activity of protease enzymes secreted by the

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pitchers is dependent on the fluid pH (Tokes et al, 1974), a study of the sequential changes in fluid pH in open pitchers, might shed some light on whether the plant enzymes or the pitcher microflora are more important in the digestion of trapped prey. Changes in fluid volume and pH were therefore studied in both developing and open pitchers of N. mirabilis up until the death of the pitchers.

In tropical regions, such as Malaysia, flowering of Nepenthes is non-seasonal, occurring at irregular intervals (Holttum, 1954), however, in the South China region, N. mirabilis appears to have a specific flowering period in August (Dunn and Tutcher, 1912), which is presumably due to the seasonal nature of the climate. The factors affecting flowering in Nepenthes are largely unknown (although Holttum (1954) speculated that dry periods following heavy rainfall might stimulate flowering), therefore investigations on the flowering of Nepenthes in Hong Kong in relation to climatic factors were also carried out. Seed germination was also investigated to determine whether it followed the same pattern as that of Nepenthes in other regions.

Materials and Methods

1. Seasonal Growth

A total of 25 Nepenthes plants were selected for studies on seasonal growth and flowering, of which 15 were from site 4 and 10 from site 2. The only criteria used in selecting plants were that they should be matur and capable of flowering, as well as readily accessible. The plants from site 4 were first marked in February, 1982, while those at site 2 were not selected and marked until April, 1982, since it was decided after the start of the marking program that plants from at least two sites

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should be studied to decrease the possibility that all marked plants might be destroyed by vandalism or natural disasters. The number of plants studied was relatively small, but as marking plants and recording growth was very time consuming, 25 was the maximum number that could be handled in the time available.

Each plant was numbered, the initial height was measured and open pitchers containing fluid were numbered in sequence from the oldest at the base to the youngest at the top of the plant. The relative ages of each of the pitchers were determined using the positioning of their respective leaves on the plant stem as a guide; that is, a leaf arising on the plant stem above another, was younger than the leaf below it and hence its pitcher was also assumed to be younger than the one carried on the lower leaf. The plants were examined at approximately monthly intervals for 13 months and the increase in height of each plant was noted, any new pitchers were labelled and numbered in sequence, and their sizes were noted. Each month, the number of pitchers capable of trapping (those pitchers secreting nectar, or with an intact lid and peristome), as well as the number of pitchers containing fluid was determined for each plant. In July, 1982 it was discovered that all the marked plants at site 4 had been destroyed and in August, 1982, 2 plants at site 2 were vandalized, so that the data for the months August, 1982 to March, 1983 are based solely on the remaining 8 plants (as there was not enough time to mark replacement plants and begin again).

2. Development, and fluid volume and pH changes in pitchers of *N. mirabilis*

Pitcher development was studied by marking and numbering 40 immature

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pitchers (ranging in size from 0.6-4.0cm in length) and subsequently noting changes in size, daily for one week, and then at weekly intervals until each pitcher was fully developed and open. The growth rate in cm per day was calculated from the total increase in length of the pitcher, divided by the length of time taken to reach maximum size, and a mean growth rate for developing pitchers was calculated from these figures.

Changes in the volume and pH of fluid secreted by immature pitchers were investigated by examining 60 unopened pitchers ranging in length from 3.0-13.7cm. Pitchers shorter than 3cm contained no fluid while those over 13cm in length were usually open. The fluid from each pitcher was drawn into a syringe through a needle inserted into the pitcher cavity and the volume of the fluid and the length of the pitcher from which it originated were noted. The pH of each sample was measured immediately using a Beckman Expand-Mate pH meter, except where the fluid volume was too small to permit measurement (less than 0.1mL).

The sequence of changes in fluid volume and pH which take place between pitcher opening and death were studied in 32 pitchers. One day in July, 1982, the maximum number of pitchers which could be found (32) which had just opened (as shown by the pitcher lid being closely applied but not attached to the pitcher peristome) were marked with tape and numbered. The pitchers were divided into two groups, 1-15 and 16-32. In the first group, all the pitcher fluid was removed from the pitchers, the pH and volume of each sample was measured and the fluid was then immediately returned to the correct pitcher. Measurements were carried out at intervals of 1, 2, 3, 4, 5, 7, 8, 10, 14, 21, 35, 45, 60 and 80 days after opening. Removal of fluid from the pitchers proved to be the only way to measure changes in the fluid volume because, although the

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fluid level was usually visible, continued growth and changes in shape and orientation of the pitchers after opening meant that changes in the fluid level in the pitcher did not accurately reflect changes in the fluid volume. It was not known whether repeated removal of the fluid from the pitchers would alter the normal succession of pH changes in the pitcher fluid (as a result of mechanical stimulation of the pitchers, or exposure to the atmosphere outside the pitchers), so the second group of pitchers were used solely to determine pH changes in the fluid. Measurements were carried out directly on the fluid *in situ*, by placing the probe of a Beckman Expand-Mate pH meter directly into the pitcher, taking care to minimize disturbance to the pitcher. Measurements of pH were made at the same time intervals as for the first group of pitchers. The experiment was ended after 80 days as most of the pitchers were dead 100 days after opening.

The range of pH and fluid volumes found in *Nepenthes* pitchers in Hong Kong were determined over a period of two years, by isolated measurements of the pH and fluid volume of over 400 pitchers which varied in age from newly opened to senescent. Fluid was collected in small vials, the volume was measured and the pH determined in the laboratory within a few hours of collection.

3. Flowering and germination

The production of inflorescences in the 25 plants marked for studies on seasonal growth at sites 2 and 4, was followed at monthly intervals, and rough estimates were also made of the number of plants bearing inflorescences at each of these sites at the same time.

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An inflorescence bearing fruits which had just begun to shed their seeds, was collected and kept in the laboratory and the seeds which fell naturally from it were gathered and stored. The percentage of seeds which germinated when sown at intervals of 24, 48, 72 and 96 hours; 1, 2 and 3 weeks; and 1, 2, 3 and 4 months after collection of the inflorescence was determined using the following method. Two lots of 100 seeds were selected, excluding those which were damaged or abortive, at each of the times noted above and as the seeds are very small and light and difficult to manipulate singly, each lot of seeds was placed in a folded piece of filter paper to enable them to be handled as a group. Each filter paper was placed in 0.5% mercuric chloride for 30 seconds to surface sterilize the seeds and it was then successively transferred through four petri-dishes of sterile, distilled water, remaining in each for five minutes, to remove all traces of mercuric chloride. After this,each filter paper was placed in a sterile petri-dish containing sterile soil water taken from the site where the seeds were collected, and it was unfolded to allow the seeds to float freely in the water. The petri-dishes were sealed with tape and one was left under natural daylight conditions on a window sill, while the other was kept in constant darkness, both at a room temperature of 25°C. The percentage of germination in each dish was determined after a minimum of 4 weeks, or when a substantial number of seeds had germinated in the dish. A dissecting microscope was used when counting the seeds, to ensure that seeds containing germinating embryos which had not yet broken through the seed coat, were not missed.

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Results

1. Seasonal growth

The average annual increment in height of the plants studied was

3.1m, with maximum growth occurring in the months of May, August and September (Fig. 4A). At first glance, the growth rate of the plants appears to be directly related to rainfall (Fig. 4A; B); however, the correlation coefficients calculated for growth and rainfall and growth and temperature show that growth is more significantly related to temperature than to rainfall (Table 3). Growth was positively correlated to temperature and in particular to temperature maxima (Table 3), so that the increase in height of the plants was greatest when temperatures were high (Fig. 4A; C). There was also a significant positive correlation between increase in height of the plants and temperature minima (Table 3), so that although growth decreased when temperatures were low (Fig. 4A; C), it never actually ceased, indicating that minimum temperatures in Hong Kong are within the tolerance limits of N. mirabilis. Although the partial correlation coefficient between growth and temperature when rainfall was held constant was significant ($r_{GT.R} = 0.7573$, $P < 0.005$), the partial correlation coefficient between temperature and rainfall when growth was constant, was not significant ($r_{TR.G} = 0.2430$), indicating that there is no relationship between rainfall and temperature. As the partial correlation coefficient between growth and rainfall when temperature was constant was also not significant ($r_{GR.T} = 0.1881$), the effects of temperature and rainfall on growth of N. mirabilis are obviously independent of one another.

An average of 21 pitchers were produced per plant annually, with new pitchers developing continuously throughout the year. The greatest number of new pitchers per plant were produced in May and July, with very few maturing in the winter months (Fig. 4D). It was noticed that pitchers produced during the winter were often deformed by having deep, thumb-like indentations in one or both sides of the pitcher, which often

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Figure 4 Seasonal changes in various parameters of plant growth, in relation to rainfall and temperature

A. Increase in height of the plants

B. Rainfall

C. Temperature maxima and minima

D. Number of new pitchers produced per plant

E. Size of new pitchers produced

F. Number of pitchers containing fluid per plant

G. Number of trapping pitchers per plant

Climatic data is taken from monthly weather summaries issued by The Royal Observatory, Hong Kong. Figures used were calculated for each sampling period and not for the calendar month. The points on graphs 4A, D, E, F and G represent mean values $\pm$ I SE.

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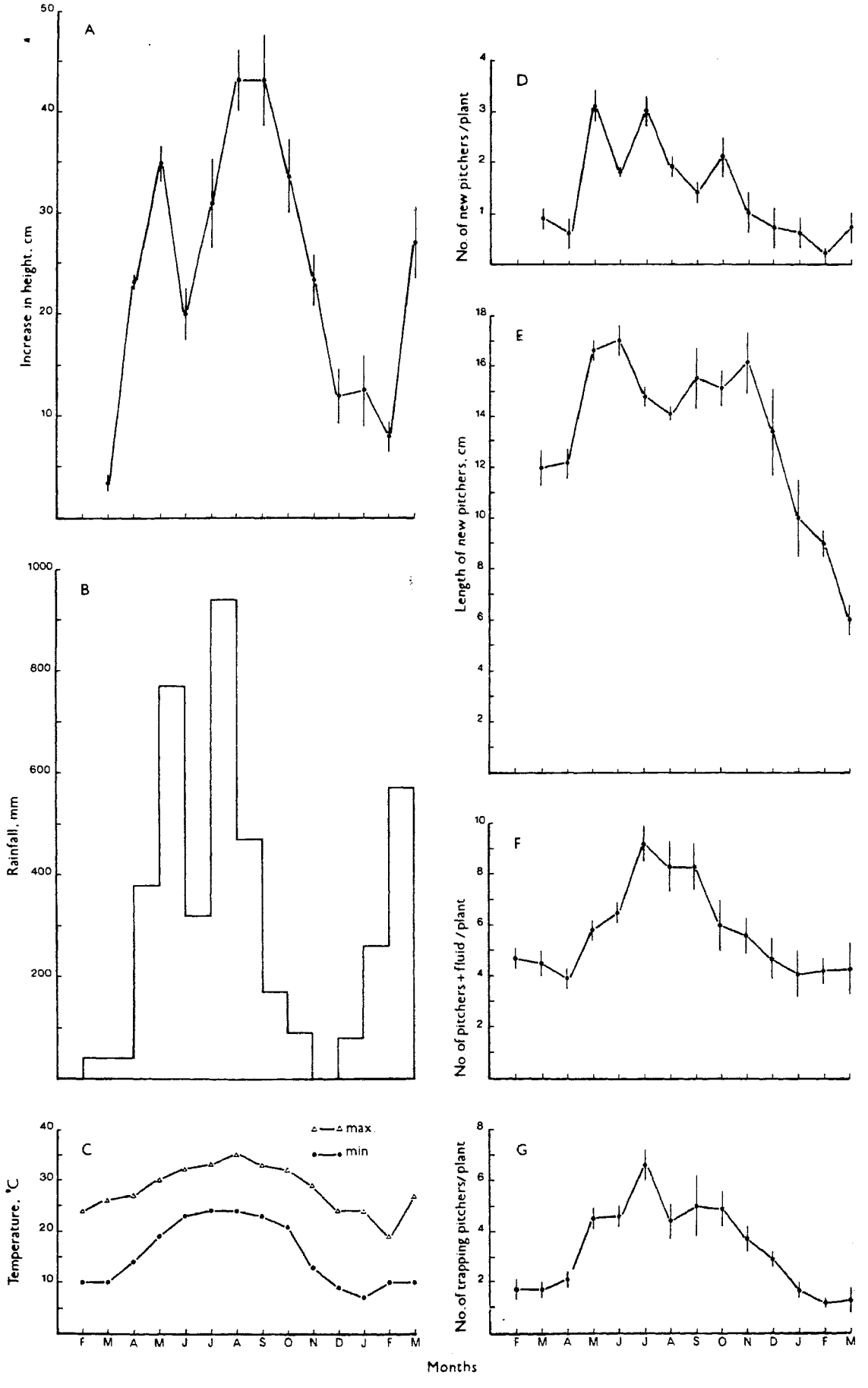

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Table 3. Correlation coefficients and levels of significance for the relationships between plant growth, pitcher production and the number of trapping and digesting pitchers, related to climatic factors

G	= mean increase in height of the plants
N	= mean number of new pitchers produced per plant
S	= mean size of new pitchers produced per plant
F	= mean number of fluid-containing pitchers per plant
Tr	= mean number of trapping pitchers per plant
T max	= Absolute maximum temperature
T min	= Absolute minimum temperature
R	= Rainfall
r	= correlation coefficient
P<	= Significance level
*	= highly significant

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TABLE 3

r \ P<	G	N	S	F	Tr	T max	T min	R
G		0.05	NS	0.005	0.01	0.001*	0.002	0.05
N	0.6292		0.02	0.01	0.001*	0.005	0.002	NS
S	0.4266	0.6642		0.05	0.001*	0.02	0.01	NS
F	0.7246	0.7175	0.5951		0.001*	0.001*	0.001*	0.05
Tr	0.6895	0.8594*	0.8067*	0.8924*		0.001*	0.001*	NS
T max	0.8429*	0.7319	0.6478	0.8273*	0.8410*		0.001*	0.05
T min	0.7775	0.7828	0.7036	0.8822*	0.8964*	0.8844*		0.05
R	0.5876	0.3827	0.1481	0.5683	0.3618	0.6011	0.6281	

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substantially reduced the volumetric capacity of the pitchers and prevented large insects from falling into the pitcher fluid in the base. This phenomenon was observed over three consecutive years, but the reasons for the deformity (although they are presumably temperature related), are unknown.

The number of new pitchers produced was significantly positively correlated with increase in height of the plants and was also highly correlated with temperature, although not with rainfall (Table 3). The correlation between the number of pitchers produced and temperature minima was more significant than for temperature maxima (Table 3) indicating that low temperatures may inhibit the production of new pitchers. As the number of pitchers produced per plant decreased in September when growth of the plants was at its peak and when temperatures reached a maximum level (Fig. 4A; C; D), it is likely that very high temperatures also limit pitcher production.

The largest pitchers were produced in May, June and November and the smallest in January, February and March (Fig. 4E). Pitcher size was positively correlated to the number of pitchers produced, but whereas pitcher production was related to plant growth, pitcher size was not. This may be explained by the fact that the significance level of the correlation between pitcher production and plant growth was relatively low (Table 3). Pitcher size was also positively correlated with temperature and, as for pitcher production, the correlation was greatest between pitcher size and minimum temperatures (Table 3). Extremes of temperature may therefore cause a reduction in pitcher size, as well as reducing the number of pitchers produced.

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The number of fluid-containing pitchers per plant (i.e. those which are digesting) was greatest in July, with a reduction of approximately 50% in number in the winter months (Fig. 4F). There was a highly significant positive correlation between the number of fluid-containing pitchers and temperature (Table 3), so that high temperatures do not appear to have a negative effect on the number of fluid containing pitchers (due to evaporation), as would be expected. As there were significant positive correlations between the number of fluid-containing pitchers and plant growth, pitcher production and pitcher size, all of which are positively correlated to temperature (Table 3), it is likely that the positive effects of higher temperatures in increasing the number and size of pitchers produced and hence the number of fluid-containing pitchers, outweighs the negative effect of high temperatures in increasing the evaporation of fluid from pitchers. The number of fluid-containing pitchers was also significantly correlated to rainfall (Table 3), since when it rains a certain amount of rainwater must enter the pitchers increasing the volume of pitcher fluid, or rehydrating pitchers which have dried out.

The number of trapping pitchers per plant followed a similar pattern to that of the number of fluid-containing pitchers per plant, with the maximum number occurring in July (Fig. 4G). The number of trapping pitchers was highly correlated to the number of pitchers produced (Table 3), since usually only the youngest pitchers were capable of trapping prey. As a result of this highly significant correlation, there were also significant correlations between the number of trapping pitchers per plant and pitcher size, and temperature, both of which are significantly correlated to pitcher production (Table 3).

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2. Development, and fluid volume and pH changes in pitchers of N. mirabilis

New, open pitchers were produced on a plant approximately once every 17 days (calculated by dividing the number of days in a year by the mean number of pitchers produced per plant annually - i.e. - 365 ÷ 21). Pitchers normally developed in sequence according to the age of the leaves. However, some remained as pitcher initials for a much longer period of time than normal and eventually developed into mature pitchers out of sequence, although this was rare, as most initials which failed to develop in sequence never developed into mature pitchers. Once development of the pitcher initials began, they grew at a mean rate of 0.6 cm per day, so that an average pitcher measuring 14cm in length on opening, would have taken approximately 23 days to develop from a pitcher initial.

During the early stages of development of a pitcher initial, the sides of the pitcher are closely adpressed to each other so that there is no internal cavity, but as the pitchers grow, the sides gradually separate forming a cavity in which fluid begins to accumulate. As individual pitchers vary in size, young pitchers of the same length are not necessarily at the same stage of development. Nevertheless, there was a clear linear relationship between the volume of fluid present in unopened pitchers, and pitcher size (Fig. 5A), demonstrating that as pitchers grow, increasing quantitites of fluid are secreted. Developing pitchers smaller than 3.0cm in length never contained any fluid, but there were small quantities of fluid (less than 1mL) in pitchers of between 3-5cm in length and up to 4mL of fluid in some of the larger pitchers which must have been close to opening (Fig. 5A). There was also a

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Figure 5. Fluid volume and pH changes in developing pitchers of N. mirabilis

A. Fluid volume in relation to pitcher size, with a best fitting line fitted by the method of least mean squares.

B. Fluid pH in relation to pitcher size, with a best fitting line fitted by the method of least mean squares.

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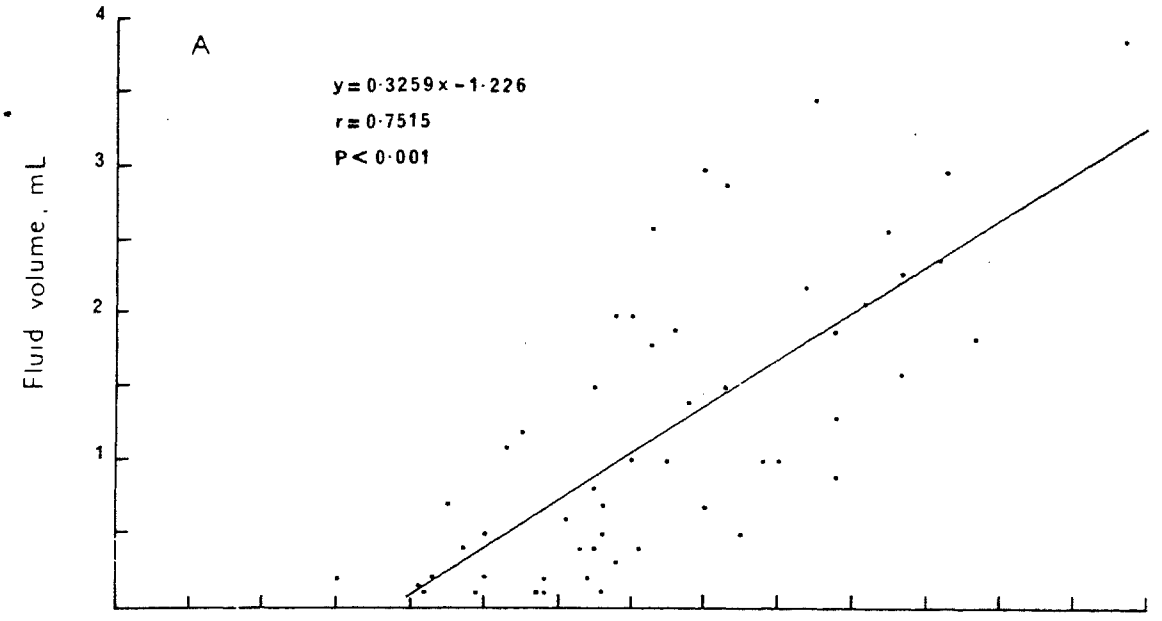

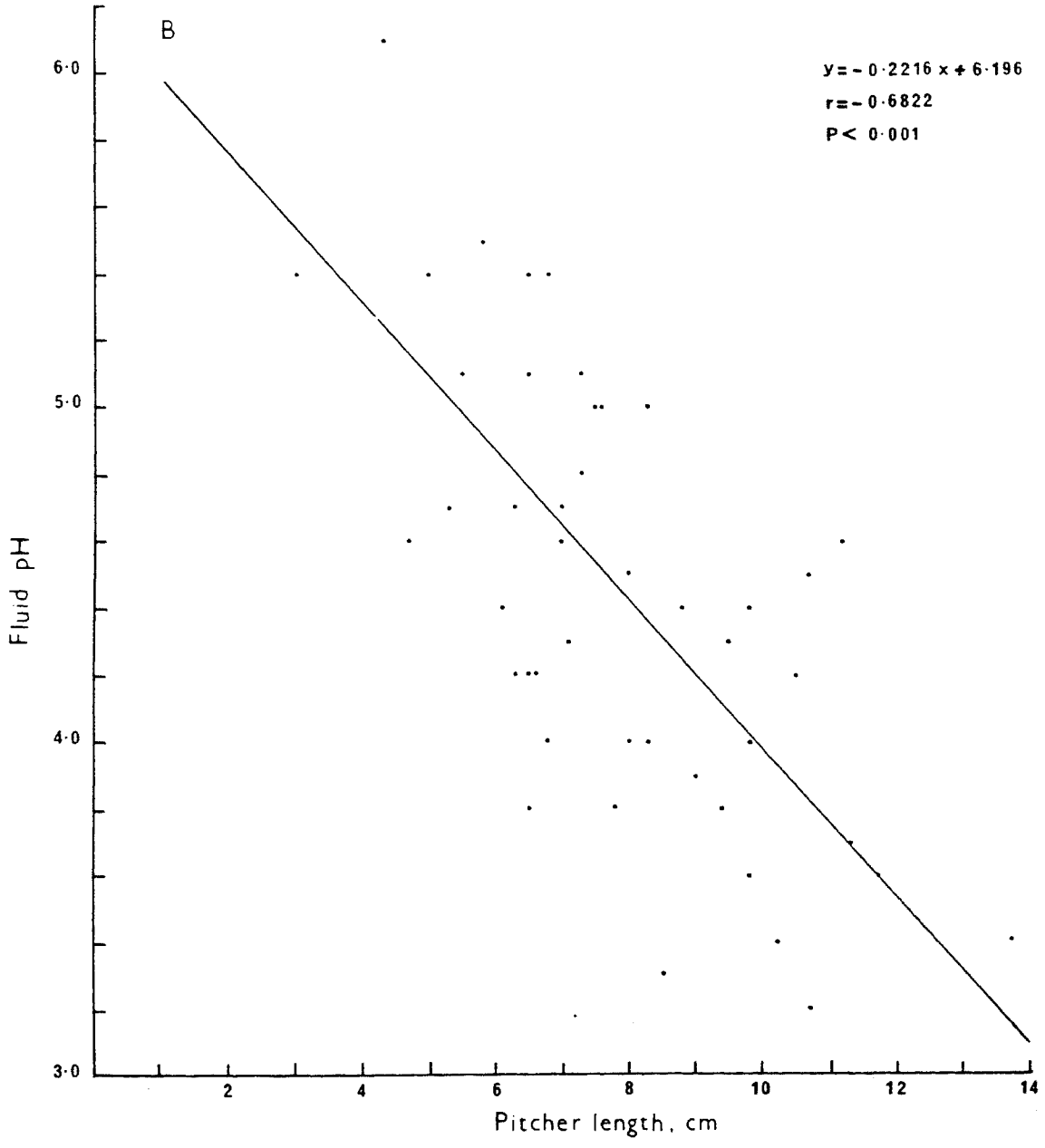

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linear relationship between pitcher size and the pH of the fluid secreted in unopened pitchers (Fig. 5B). The fluid first formed is weakly acidic (pH 5-6), but the pH decreases steadily as the pitchers grow, dropping to 3.0 - 3.5 in the larger unopened pitchers (Fig. 5B). As already noted, pitchers of the same size may be of different developmental stages and, as the correlation coefficient between pitcher size and fluid pH is lower than that for pitcher size and fluid volume (Fig. 5), it may be that the pH of the fluid secreted is more dependent on the developmental stage of the pitcher, than is the fluid volume, which is probably more related to pitcher size.

The fluid initially secreted by the pitchers is colourless, but on opening of the pitchers, it acquires a bright yellow colouration which persists for 4-5 days, before fading to a pale tea-colour. If the yellow fluid is removed from the pitchers and kept in vials, the yellow colouration disappears overnight, so that it must be due to some substance secreted continuously by the pitchers for the first few days after opening. Pitchers may continue to increase in length for the first 10 days after opening, although most cease growing after 4 days. The maximum increase in growth recorded subsequent to pitcher opening was 4.0cm but the mean increase in length was only 1.2cm.

The range of fluid pH recorded in open pitchers of N. mirabilis in Hong Kong was 1.6-8.0, the former recorded in newly opened pitchers and the latter in senescent pitchers. Fluid volume varied from a few drops up to 75mL, which must have been mostly rainwater. In the newly opened pitchers studied, the initial fluid volume was approximately 3.0mL but this increased steadily in the first week to about 6.0mL, while the pH decreased from an initial level of 3-4 to 2-3 in the same period of time (Fig. 6A; B). As the only rainfall in this week occurred on the

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Figure 6. Fluid volume and pH changes in open pitchers of *N. mirabilis*, in relation to rainfall and temperature

A. Fluid pH (means are given ± I SE)

B. Fluid volume (means are given ± I SE)

C. Rainfall

D. Maximum temperature

Climatic data are taken from The Royal Hong Kong Observatory monthly weather summaries.

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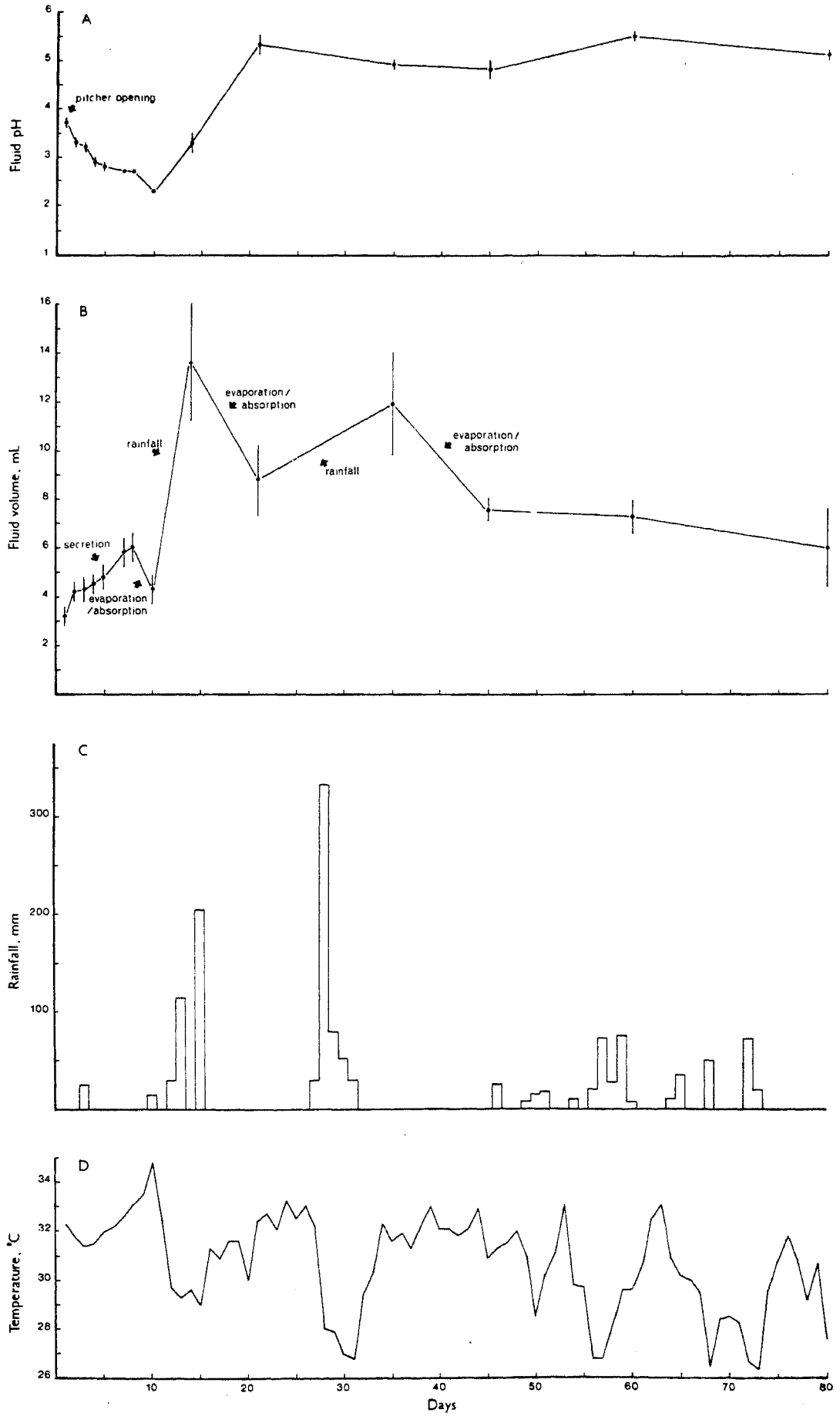

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second day after opening (Fig. 6C), the increase in fluid volume could only have been due to continued secretion of fluid by the pitchers, while the decrease in pH must have been due to the secretion of acid. The fluid volume decreased slightly between 7 and 10 days after opening, which may have been a result of evaporation, as temperatures were very high during this period (Fig. 6B; D), or it may have been due to absorption of fluid by the pitchers. There was a period of heavy rainfall between 10 and 14 days after opening, and this probably accounted for the rapid increase in fluid volume, since the latter was accompanied by an increase in pH rather than by a decrease, as would be expected if the additional fluid had been secreted by the pitchers (Fig. 6A; B; C). Fluid secretion and the maintenance of a low fluid pH appeared to be restricted to the first two weeks after opening since, after this period, fluctuations in fluid volume seemed to be largely related to changes in temperature or to the amount of rainfall, while the fluid pH, either due to the accumulation of alkaline products of digestion, or to the entrance of rainwater, increased to approximately 5.0 within 3 weeks after opening and showed only minor fluctuations for the remainder of the period of study (Fig. 6). It must be noted however, that in the first group of pitchers (1-15) where all the fluid was removed from the pitchers and subsequently replaced, the fluid pH was consistently lower in the first 2 months after opening than for the second group of pitchers (16-32) where fluid pH was measured <u>in situ</u> (Fig. 7). This may indicate that each time fluid was removed, the pitchers were stimulated to secrete acid so that the fluid pH was always lower than that measured for the second group. In this case the pitchers must be capable of secreting acid for at least the first two months after opening, although this may have been masked by the heavy rainfall through the period of study.

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Figure 7. pH changes in pitchers of groups 1 (1-15) and 2 (16-32)

Figure 8. A. Pitcher lifespan (frequency)

B. Pitcher lifespan related to time of production (means are given ± I SE)

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Fig.7

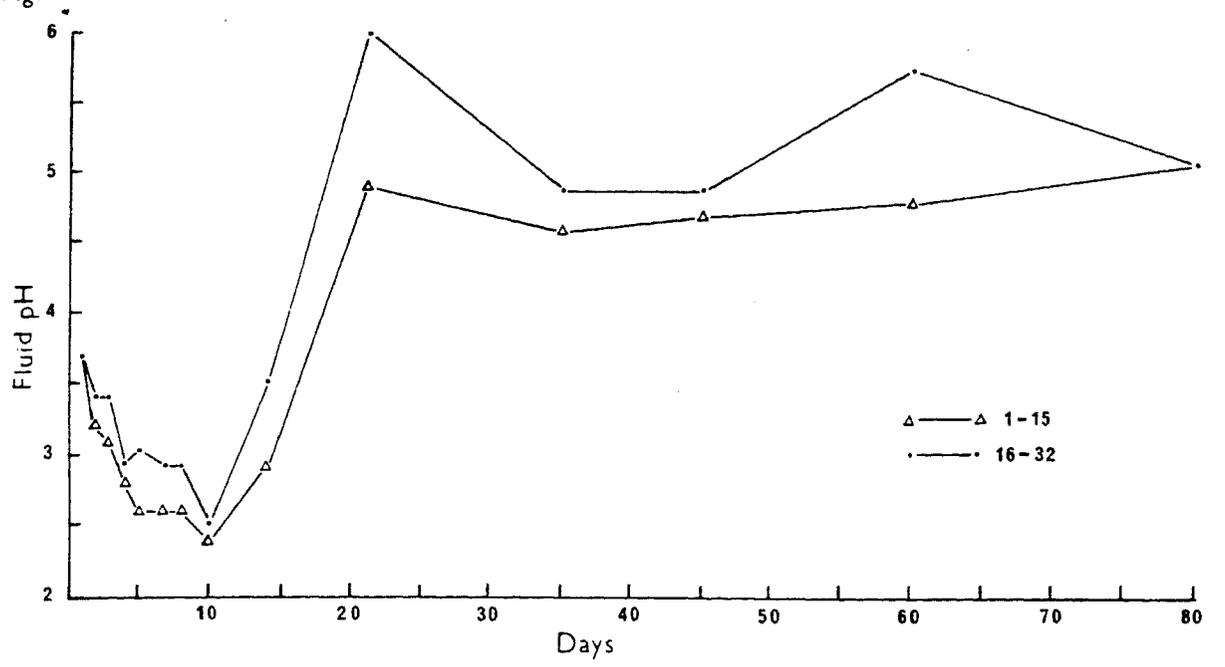
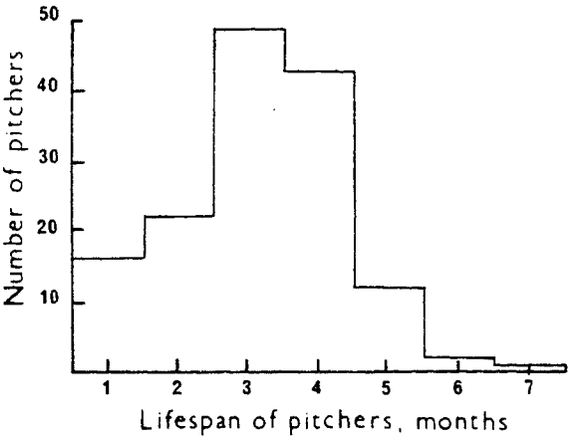
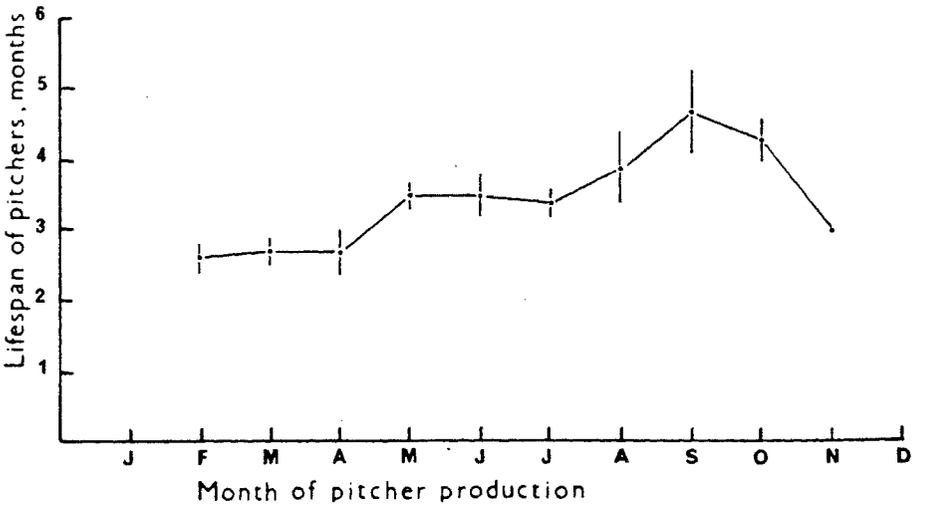


Fig.8 A



B



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Most of the 32 pitchers studied were dead within 100 days of opening, which is the average length of life of a pitcher in Hong Kong. A few pitchers survive for less than a month, usually killed by insect damage, but most live for 3 or 4 months, although occasionally a few pitchers may survive for up to 7 months (Fig. 8A). Pitchers produced in the months of February, March and April had a much shorter length of life than those produced later on in the year (Fig. 8B). Pitchers produced in these months were smaller than those produced during the summer (Fig. 4E) and therefore must have been more susceptible to desiccation and drying out, particularly since this is a dry time of year (Fig. 4B). However, size and susceptibility to desiccation cannot be the only factors involved, as the larger pitchers produced in the wet months of May, June and July (Fig. 4B; E) had only a slightly increased lifespan (Fig. 8B). The longest lived pitchers were those produced in September (Fig. 8B), which were of intermediate size (Fig. 4E), but which were produced when growth of the plants was most vigorous (Fig. 4A). Unfortunately there is no information on the length of life of pitchers produced in December and January because the experiment was terminated before these pitchers had died. The lifespan of a pitcher must depend to some extent on its size and on such factors as temperature and humidity, which may affect evaporation, and it must also depend on rainfall, which may either increase the fluid volume or rehydrate pitchers which have dried out. However, the most important factor may be the vigour of the pitchers produced, so that those produced in periods when temperatures are extreme or when there is little plant growth probably have a shorter life than those produced when temperatures are favourable and the plants are growing vigorously.

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3. Flowering and germination

Nepenthes flowers all year round in Hong Kong (even when the marked plants had no inflorescences, there were always a few unmarked plants flowering), but the major flowering period was in June, July and August (Fig. 9A) when, in addition to the marked plants, virtually all the other plants at the two sites studied were flowering. Each marked plant produced an average of two inflorescences a year, often in quick succession within one or two months of each other.

Flowering in N. mirabilis apppears to be related to temperature and daylength but not to rainfall (Fig. 9) which is confirmed by the fact that there are significant correlations between flowering and minimum temperature and flowering and daylength, but no significant correlation between flowering and rainfall (Table 4). Since flowering was significantly correlated with minimum temperature only and not with maximum temperature (Table 4), it is probable that the production of inflorescences in Nepenthes in Hong Kong is often limited by low temperatures, so that in the coldest months, flowering in the majority of plants is inhibited. As some plants do flower all year round, minimum temperatures obviously never reach the lower limits of thermal tolerance of N. mirabilis, but they must at times be close to a critical value below which flowering will not occur. Although temperature and daylength both influence flowering, daylength appears to be the most important factor since it was more significantly correlated with flowering than temperature (Table 4). Both factors affect flowering independently and do not interact, since although there was a significant partial correlation between daylength and temperature when flowering was constant ($^{r}DT.$ F=o.668, P<0.02), the partial correlation coefficients for flowering and daylength when temperature was

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Figure 9. Flowering in N. mirabilis, related to climatic factors

A. Percentage of marked plants flowering

B. Rainfall

C. Temperature maxima and minima

D. Daylength

Climatic data is taken from The Royal Hong Kong Observatory monthly weather summaries.

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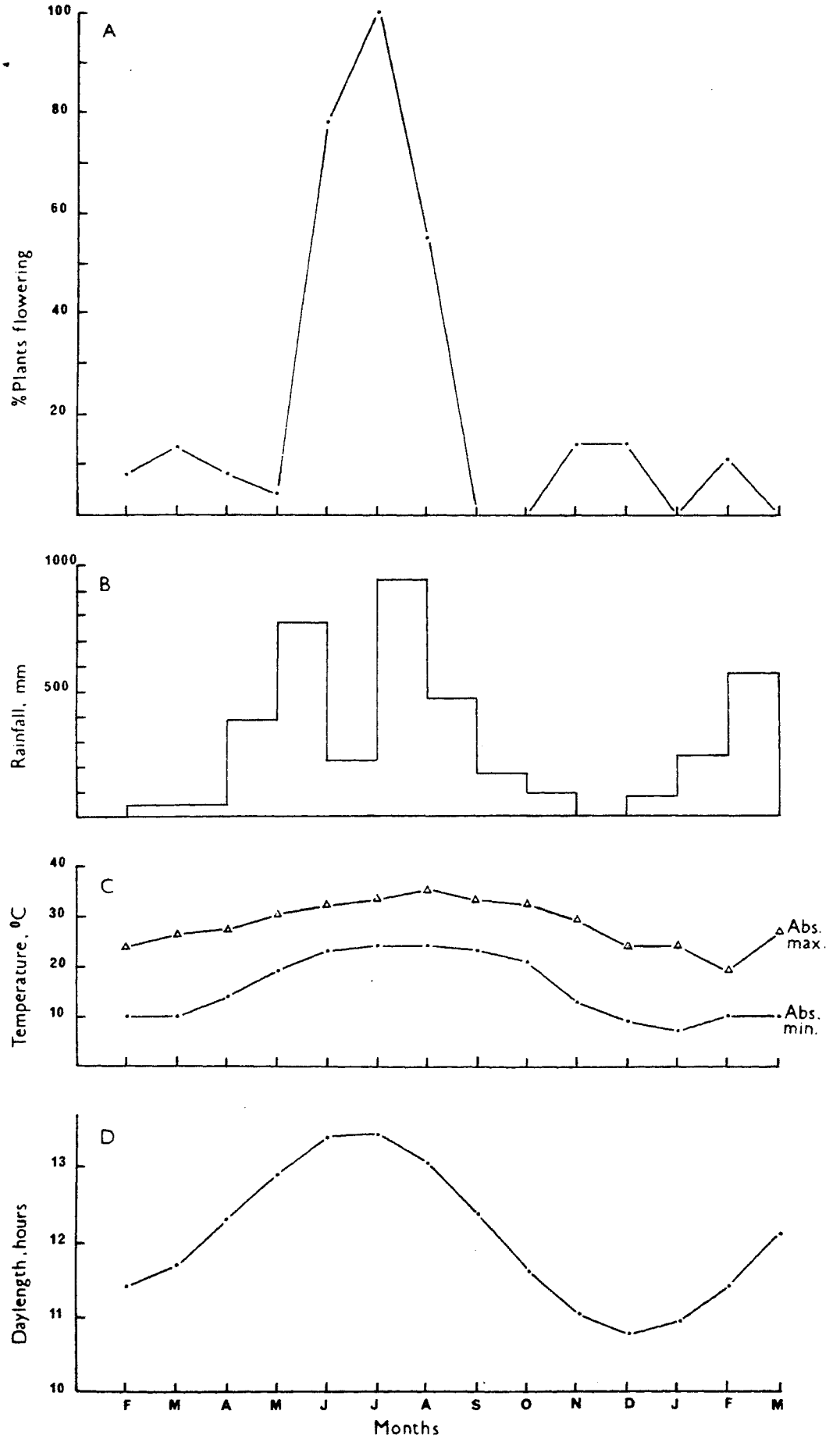

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Table 4

Correlation coefficients and significance levels for the relationships between flowering and climatic factors

r \ P<	F	T max	T min	R	DL
F		NS	0.05	NS	0.01
T max	0.4785		0.001*	0.05	0.005
T min	0.5875	0.8844*		0.05	0.005
R	0.4733	0.6011	0.6281		0.005
DL	0.6944	0.7273	0.7969	0.7551	

F = % plants flowering, T max = Absolute maximum temperature, T min = Absolute minimum temperature, R = rainfall, DL = mean daylength, * = highly significant, r = correlation coefficient, P< = significance level

Table 5

Percentage of seed germination related to period of storage

No seed germination in the dark treatment. * = Fungal contamination.

Length of time seeds stored	% germination	Period of time elapsed before % germination
24 hours	0	59 days
48 hours	8	58 days
72 hours	19	57 days
96 hours	17*	56 days
1 week	24	52 days
2 weeks	2*	45 days
3 weeks	42	38 days
1 month	54	31 days
2 months	84	54 days
3 months	0*	/
4 months	58	4 months

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constant, and flowering and temperature with constant daylength, were not significant ($r_{FD.\ T} = 0.470$, $r_{FT.\ D} = 0.078$).

Development of both male and female inflorescences takes about one month. The flowers have a strong mousy odour which may attract the large diptera which were often seen visiting the flowers together with hymenoptera presumably attracted by the large quantities of nectar secreted by the inflorescences. Few other insects were seen visiting the flowers, so it is probable that diptera and hymenoptera are the main pollinating agents, although some wind pollination may also occur since isolated, unisexual stands of female plants, produced by vegetative propagation of a single rhizome, still produced seed.

The fruit capsules which develop on female inflorescences after fertilization, persist for a long time and shed seeds over a period of several months. The seeds remain viable for at least 4 months, since a substantial percentage of seeds germinated when sown 4 months after collection (Table 5). The longer the period of storage the greater the percentage of seeds which germinated, up to 2 months after seed collection (Table 5). In seeds stored for longer than 2 months, the percentage of germination decreased while the time required for germination was greatly increased (Table 5). Unfortunately the germination experiment was terminated after 4 months so the maximum period of viability of the seeds was not determined. Seeds which were sown 24 hours after collection failed to germinate, while only a small percentage of those sown 48 and 72 hours after collection germinated, producing small, brown seedlings which subsequently died. Seeds stored for longer periods of time produced healthy, green seedlings, all of which survived. Light is required for germination since none of the seeds kept in the dark germinated.

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In general, there were very few Nepenthes seedlings at any of the sites studied in Hong Kong, so it seems likely that vegetative propagation is responsible for the spread of the species in established habitats, and that seed production and the development of seedlings are only important in the initial dispersal of the species.

Discussion

Growth of N. mirabilis in Hong Kong is positively related to temperature, so that maximum growth of the plants occurs when temperatures are highest in the summer months, while very little growth takes place in the winter when temperatures may be well below 10°C. Growth is also related to a lesser extent to rainfall, although as the plants already grow in wet, marshy areas where water is rarely in short supply, it is difficult to see why rainfall should positively influence growth. It is possible that heavy rainfall may promote plant growth by increasing the level of nutrients in the soil water of the plant habitats, due to increased water run off and leaching of nutrients from higher areas. As the maximum numbers of digesting pitchers per plant were found in July, August and September when rainfall was also high, it may be that an increased supply of nutrients from two sources - the soil water, and trapped prey - interacts with high temperatures to promote maximum growth of the plants. In general, the greater the increase in plant height, the greater the number of new, trapping pitchers produced per plant, although extreme of temperature tended to inhibit pitcher production and to decrease the size of pitchers produced.

The fluid in developing pitchers of N. mirabilis is secreted continuously once the pitcher cavity has formed, 3-4mL of fluid being present on opening of the pitchers. The actual amount of fluid present is dependent on pitcher size. The pH of the fluid initially secreted is

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between 5 and 6, but this decreases to 3-4 as the pitchers mature and become ready to open. Developing pitchers of N. chelsonii appear to differ considerably from those of N. mirabilis since the pH of the fluid initially secreted in the former species is 7.5, decreasing to 2.5 on opening, while the fluid volume may reach as much as 20mL in mature pitchers about to open (Heslop-Harrison, 1975). Tokes et al (1974) found that the fluid pH of open and closed pitchers of N. macferlanei was much lower than that of the secretions of other species, which suggests that the fluid pH may differ in different species of Nepenthes. This seems to be borne out by the above findings, although unfortunately, it is difficult to compare the fluid volume and pH changes in developing pitchers of N. mirabilis and N. chelsonii critically, because the latter results are presented graphically (Heslop-Harrison, 1975) and it is not stated how the results were obtained.

Differences in the aquatic fauna of Nepenthes species having pitchers with similar structures and growing in the same areas, have been attributed by Beaver (1979b) to differences in the habitat of the plant species involved, since he considered that the constitution of the pitcher fluid of different species was likely to be similar. However, if the fluid pH differs in different species of Nepenthes, as suggested above, it is possible that differences in the pitcher communities of similar Nepenthes species growing in the same area may be attributable to differences in fluid composition, as well as to habitat differences.

In N. mirabilis, fluid secretion continues for at least ten days after opening and the fluid pH decreases, reaching an average level of 2.0-3.0, indicating continued acid secretion. This may be a result of stimulation of the pitchers by prey capture since it has been demonstrated

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conclusively that the addition of protein to pitcher fluid in situ leads to an increase in acidity (Zeeuw, 1934). Unfortunately, it is not certain for how long the pitchers continue to secrete fluid, because the introduction of large amounts of rainwater to the pitchers as a result of heavy rainfall soon after opening, and throughout the period of study, greatly increased the fluid volume and pH, masking any further secretion by the pitchers. Thus, three weeks after opening, the pH of the pitcher fluid had increased to 5.0 (which is the average pH of rainwater in Hong Kong - Gott, 1976) and it remained at this level, with only minor fluctuations, for the remainder of the life of the pitchers. Although the pH was consistently lower for the first two months after opening in pitchers 'stimulated' by the frequent removal and replacement of fluid (which suggests continued acid secretion), the ability of the pitchers to buffer the fluid pH obviously decreases with age since the fluid pH never decreased to the low levels observed soon after opening.

The optimum pH for the protease enzymes secreted by Nepenthes pitchers is 2.2 (Steckelburg et al, 1967), so that enzyme activity must be greatest in the first ten days after opening when the fluid pH is at its lowest level. Since there is only 10% of the maximum protease activity when the fluid pH is 4.0 (Tokes et al, 1974), by the time the pitchers have been open for two or three weeks, the amount of digestion of prey attributable to the pitcher enzymes must be negligible and most of the subsequent digestion which takes place must be due to the activities of symbiotic microflora in the fluid.

The average length of life of pitchers in Hong Kong (three months) is much shorter than that of pitchers in Malaysia, which have a maximum lifespan of about one year (Beaver, 1983). It is possible that specific differences

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may affect the lifespan of the pitchers but this is unlikely since Beaver (1979a; b) studied three species of Nepenthes in Malaysia and although it is not stated (Beaver, 1983) whether the average length of life of the pitchers was determined for one or all three species, it must be assumed that the lifespan of one year quoted, applies to all three. As it is therefore unlikely that specific differences account for the shorter lifespan of pitchers of N. mirabilis, the decrease in the average length of life of the pitchers is presumably due to the seasonal nature of the climate in Hong Kong.

Most plants of N. mirabilis flowered in June, July and August, although a few plants at each site were flowering all year round. Despite the fact that flowering in Nepenthes in Hong Kong was only studied for one year, it must be usual for the plants to flower at this time since Dunn and Tutcher (1912) noted that plants of N. mirabilis in the South China region flowered in August. Nepenthes species in Malaysia flower at irregular intervals, but always gregariously, apparently in response to dry weather following a wetter period (Holttum, 1954); however, flowering of Nepenthes in Hong Kong was found to be positively correlated with minimum temperature and daylength, so that flowering was inhibited by short day lengths and low temperatures and it was apparently unrelated to rainfall. In other regions where N. mirabilis occurs, such as Malaysia, the average daylength varies only twenty minutes annually, ranging from 11 hours and 57 minutes to 12 hours and 17 minutes (Ooi and Chia, 1974), and absolute minimum temperatures encountered there and in Borneo, Sumatra, Java and the Philippines, where N. mirabilis also occurs, are rarely belo $20^{o}C$ (Meteorological Office, 1966). Flowering is therefore probably inhibited when daylength and minimum temperatures in Hong Kong are well

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below the normal daylength and minimum temperatures encountered in most places where N. mirabilis grows, so that most of the plants only flower when daylength and minimum temperatures are above twelve hours and 20°C, respectively. Since the only period in Hong Kong when both these factors are favourable is June-August, most of the plants flower in this period, although as daylength and temperature are not interdependent, a few plants may flower at other times when either daylength or temperature are marginally favourable. In the truly tropical regions where N. mirabilis grows, daylength and temperature are presumably never limiting so that other factors must be involved in the control of flowering. This is also apparent from the study on flowering of N. mirabilis in Hong Kong, since a few plants were still flowering when temperature and daylength appeared to be severely limiting. The nature of other controlling factors is unknown, but the alternation of periods of rainfall and drought may be important, as suggested by Holttum (1954), and the nutrient status of the plants may also be involved.

The flowers must be insect pollinated to some extent since many diptera and hymenoptera were observed visiting the inflorescences. However, interpatch insect pollination is probably infrequent, since it is unlikely that insects would fly long distances in search of a new source of food when an ample supply was already available. As isolated, unisexual stands of female plants still produced seed, it is therefore likely that some wind pollination also takes place, as suggested by Green (1967).

In comparison to N. mirabilis, seeds of N. gracilis appear to have a very limited viability. Thus seeds of N. gracilis are apparently viable for a maximum period of two weeks (Garrard, 1955), whereas seeds of N. mirabilis are viable for at least four months. The results obtained

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by Garrard may be slightly misleading in that he only allowed 50 days for seed germination to take place and, as some seeds may take 6-7 months to germinate (Green, 1967), some viable seeds may have been overlooked. However, this cannot account for the observed differences between seed viability in N. mirabilis and N. gracilis because most seeds of N. mirabilis had germinated within 50 days (apart from those stored for four months, which required a much longer period of time for germination). Other differences between seed germination in N. gracilis and N. mirabilis are also apparent, in that maximum germination is obtained in seeds of N. gracilis when they are sown immediately after collection (Lim and Prakash, 1973), whereas few seeds of N. mirabilis germinate when sown soon after collection and the percentage germinating increases with storage time, while in N. gracilis it declines very rapidly (Lim and Prakash, 1973).

Nepenthes gracilis is limited to purely tropical areas (Borneo, Sumatra, Malaya) where climatic conditions are fairly constant all year round and as a result there is no advantage to be gained by having seeds which are capable of germinating over long periods of time. However, as N. mirabilis grows in subtropical, as well as tropical areas, it is important that the seeds are viable for long periods so that some at least of the seedlings may emerge when conditions are favourable. It therefore seems likely that the differing range of climatic conditions encountered by the two species is responsible for the fact that seeds of N. gracilis usually germinate as soon as they are developed and shed from the fruit capsules, whereas those of N. mirabilis appear to be adapted to longer periods of dormancy before germination.

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Section III. Fauna associated with Nepenthes mirabilis in Hong Kong

Chapter 1. Preliminary investigations on the taxonomic composition and biology of the Nepenthes fauna

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Introduction

Nepenthes mirabilis is a very widespread species which extends from South China and Hong Kong throughout Southeast Asia to New Guinea, Australia and New Caledonia. The fauna associated with *N. mirabilis* has been studied in a number of these areas (Brug, 1931; 1934; Johannsen, 1931; Schmitz and Villeneuve, 1932; a; b; Thienemann, 1932; Assem, 1959), revealing that the composition of the fauna is usually different in different regions. Thus, only 6 species out of the 27 recorded from *N. mirabilis* in different parts of its range occur in more than one country (Beaver, 1983). The fauna of *N. mirabilis* in Hong Kong has never been studied in any detail, but it is likely that its composition differs substantially from that of other areas, due to the relative isolation of the species in the South China area, and to the seasonal nature of the climate which would eliminate the purely tropical *Nepenthes* fauna of other regions.

Herklots (1951) mentioned finding mosquito larvae of a type not previously recorded in Hong Kong, in pitchers on Lantau island, while Chau (1982) notes that there are 2 species of mosquito (*Armigeres magnus* (Theobald) and *Culex sumatranus* Brug) which breed in *Nepenthes* pitchers in Hong Kong. As this was the only information available on the Hong Kong *Nepenthes* fauna, the composition of the fauna, as well as seasonal changes in population levels, were investigated by sampling a number of pitchers at monthly intervals for a period of 16 months. Any animals found living in the pitchers were identified and counted and the biology of the most common species was studied. Animals living on aerial parts of the plants were also observed and collected for identification.

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Materials and Methods

A number of pitchers, which varied from 8-30 although the usual number was 10 (Fig. 13), were sampled at monthly intervals beginning in December, 1979 and ending in March, 1981. Initially, Nepenthes plants were only known to occur at 4 sites (1, 4, 6, and 7) and as site 1 consisted of only a few poorly developed plants, most of the pitchers were sampled from sites 4, 6 and 7. Six additional sites were subsequently discovered and additional pitchers were sampled from these sites when they were first discovered, accounting for the increase in the number of pitchers sampled in some months. The number of pitchers sampled per month was very small, but at the start of the sampling program it was not known how long pitchers took to develop, nor how many were produced annually by each plant. Consequently, only a small number were sampled each month and these were taken from different sites to avoid damaging the plants and depleting the animal populations.

The approximate age of each pitcher sampled was determined and each was placed into one of three categories: young (newly opened), mature (open for several weeks), or old (senescent), on the basis of the external appearance of the pitcher. Young pitchers were usually bright green, contained clear, yellow fluid and secreted copious quantities of nectar; mature pitchers were usually red and contained dark, turbid fluid, while old pitchers were easily recognized by the drying, senescent pitcher tissue. The length, diameter of the pitcher mouth and temperature of the fluid of each pitcher sampled were measured and the fluid was poured into a plastic vial labelled with the pitcher number. The contents remaining in the base of the pitcher were washed into another labelled vial using distilled water and the original fluid in the pitcher was replaced with

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distilled water. The pitcher was then labelled to prevent resampling. Any other animals found living on the aerial parts of the plant were also collected for identification.

In the laboratory, the pH of each fluid sample was measured immediately using a Beckman Century S-S I pH meter. Living animals were picked out of the fluid and debris using a Leitz dissecting microscope and were preserved in 70% alcohol for identification and counting at a later date. Samples of the fluid and debris were also examined for the presence of protozoa, rotifers and algae using a Leitz compound microscope. Samples were sorted as rapidly as possible, to minimize changes in the number of animals in the sample due to predation since, although the samples could have been preserved immediately after collection to eliminate this factor, it was preferable to sort the samples live, as many of the smaller animals, particularly the mites, could not be seen in the debris unless they were active and moving around. Once all the animals had been removed, the volume of the pitcher fluid was measured. Preserved animals were later identified and counted and the length of culicine larvae was determined to facilitate determination of the instar number. The number of each species per mL of original fluid was calculated for each pitcher to eliminate numerical differences resulting from differences in pitcher size.

Live animals were collected from a number of pitchers not included in the sampling program and these were kept in small petri-dishes in the laboratory for observation. The gut contents of a number of animals were examined to determine what they were feeding on and the feeding habits of the live animals were noted. The minimum time taken for eggs of C. sumatranus and A. magnus to develop into adults, and the length of time spent in each larval instar, was determined by collecting eggs from

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pitchers in the field and placing them in separate petri-dishes of fresh, filtered pitcher fluid. The dishes were observed daily and instar changes were noted, as well as the average pupal period. Debris, in the form of large hymenoptera trapped by pitchers, was placed in each dish to provide a food supply for the developing larvae. A number of larvae were also collected and kept in pitcher fluid without food to determine the tolerance of the larvae to starvation. Development in the anoetid mites, Zwickia sp. and Anoetid A, was also studied in a similar manner. Ten females of Zwickia were placed in one dish of fresh, filtered pitcher fluid and ten females and ten males in another dish (both containing large hymenoptera to act as food for the mites) while twenty adults (sex ratio unknown) of Anoetid A were placed in another petri-dish of pitcher fluid. The proportion of males to females in the latter species was not fixed because it is extremely difficult to sex adults of this species without first killing them, whereas males and females of Zwickia are morphologically different and easily identifiable. The Anoetid A mites were fed on a 1% killed yeast suspension daily and all the dishes were observed daily for the appearance of eggs, larvae and nymphal stages. Ten Zwickia females were also placed in pitcher fluid in a petri-dish without food to see how starvation affected development.

It was discovered from the monthly sampling of pitchers that there were definite seasonal fluctuations in the population levels of four of the animals living in the pitchers. These appeared to be related to environmental temperature changes, so temperature tolerance experiments were carried out on three of these species (C. sumatranus, A. magnus and Zwickia). Unfortunately it was not possible to obtain enough larvae of the fourth species (Megaselia corkerae Disney) at one time in order to carry out the experiments.

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Temperature tolerance in C. sumatranus and A. magnus

The effect of seven different temperatures (8, 12, 25, 31, 37, 40 and 44°C) on the survival of first and fourth instar larvae of both species was investigated using incubators set at the required temperatures. Larvae were collected from pitchers in the field and for each temperature investigated, one dish containing ten first instar larvae and one containing ten fourth instar larvae, in 10mL of fresh, filtered pitcher fluid, was set up for each species. First instar larvae were fed on 0.1mL of a killed yeast suspension daily, until they became large enough to be fed on the chironomid larvae (bloodworms normally fed to aquarium fish) which were fed to the fourth instar larvae. The amount of food per dish was standardized, so that one chironomid larva was added per two culicine larvae initially, and at periodic intervals afterwards when all the available food had been consumed. The larvae were observed over a period of six weeks and the percentage of larvae surviving, as well as the percentage of emergence of adults in each treatment, was determined.

Unfortunately it was impossible to find enough larvae of M. corkerae for all temperature experiments to be carried out, however, ten fourth instar larvae were obtained and these were placed in a petri-dish containing 10mL of pitcher fluid in the 8°C incubator to determine their degree of tolerance to low temperatures.

Temperature tolerance of Zwickia sp.

Ten females and ten males of Zwickia were placed in each of ten petri-dishes containing 10mL of fresh, filtered pitcher fluid. The effect of five different temperatures on the population levels in the dishes, was investigated using incubators set at 8, 12, 25, 31 and 35°C. Two dishes were used for each temperature treatment, one to be counted after

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one week and one to be counted after two weeks, since it was virtually impossible to count the number of mites present accurately without first preserving them. The mites were fed on 0.1mL of a killed yeast suspension daily, rather than on carrion, because it would otherwise have been virtually impossible to standardize the amount of food available in each dish. The number of mites present in one dish from each of the temperature treatments was determined after one week, while the number of mites in the remaining dishes was determined after two weeks.

Results

Protozoa

Ciliates, flagellates and shelled rhizopods were all found living in the pitcher fluid. The diversity of species and the number of organisms present was often so great that no attempt was made to identify individual species or to sample them quantitatively. Ciliates were found in 16% of the pitchers sampled, usually in either very young or very old pitchers (Fig. 10A), while flagellates occupied 28% of all pitchers sampled, with no apparent discrimination between pitchers of different age groups (Fig. 10B). Shelled rhizopods, resembling *Euglypha*, were found in 6% of the pitchers sampled, usually in mature or old pitchers (Fig. 10C) which contained considerable quantities of sand and quartz particles. The most diverse group found in the pitchers was the ciliates, which were free-swimming in the fluid, while only a few species of flagellates were found, normally attached to particles of debris in the pitcher base.

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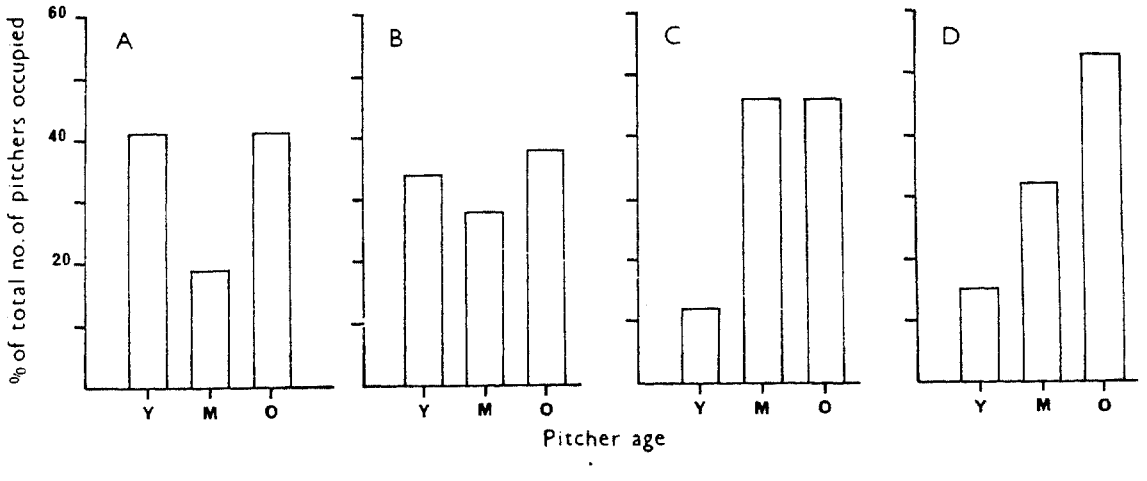
Algae

Unidentified benthic diatoms were found in 3% of the pitchers sampled. They were found only in very young pitchers which contained clear fluid and which had very little debris in the base to obscure the light penetrating the pitcher walls. Unicellular green algae were also found in 3% of the pitchers and a filamentous green alga was found on one occasion.

Rotifera

Bdelloid rotifers were found living amongst the debris in the base of the pitchers in 9% of the pitchers sampled. The rotifers occurred in great numbers, usually in old pitchers (Fig. 10D) lacking the normal culicine fauna.

Figure 10. Distribution of microfauna according to pitcher age
A. Ciliates. B. Flagellates. C. Rhizopods. D. Rotifers
(Y = Young, M = Mature, O = Old pitchers.)



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Nematoda

Large numbers of juveniles and adults of Rhabditis sp. were found feeding on micro-organisms and protozoa amongst the pitcher debris, in 3 (1%) of the pitchers sampled. All 3 pitchers were senescent.

Oligochaeta

An oligochaete, tentatively identified as Pristina foreli Piguet, was found reproducing in 3 senescent pitchers.

Crustacea

On one occasion, several specimens of the cladoceran, Monospilus dispar Sars, were found together with numerous copepods, identified as Phyllognathopus vigueri Maupas. The pitcher in which they were found was in the centre of a stream and it was flooded with water, which may indicate that both crustaceans were stream inhabitants which were washed into the pitcher accidentally, although P. vigueri was subsequently found in several pitchers so that it appears to be a distinct nepenthexene species.

Insecta

Collembola

Five different collembola were found living on the surface of the pitcher fluid. These were:

Paronellidae sp. A	(1 pitcher)
Paronellidae sp. B	(2 pitchers)
Entomobryidae - Lepidocyrtus sp.	(1 pitcher)
Entomobryidae - ?genus ?species	(3 pitchers)
Sminthuridae - Sminthurus sp.	(1 pitcher)

These collembola are obviously all accidental inhabitants since very few pitchers were occupied by each species; however, as there were usually

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numerous individuals, including newly hatched nymphs, present in each of the pitchers, this suggests that they are able to live and reproduce successfully in the pitchers once they have been trapped inside.

Thysanoptera

Thysanopteran nymphs (?*Scirtothrips dorsalis* Hood) were found on two occasions crawling around amongst the debris in the base of the pitcher. The nymphs were kept alive for several days in the laboratory and were clearly aquatic. Dead adults of the same species were also found amongst the debris of other pitchers, so it is likely that this is a nepenthexene species.

Diptera

Culicidae

Two species of mosquitoes were found breeding in the pitchers. Larvae and pupae of *Armigeres magnus* were found in 60% of the pitchers, while the immature stages of *Culex sumatranus* occupied 44% of the pitchers sampled. Of those pitchers containing immature culicines, 42% contained both mosquitoes, 40% contained *A. magnus* alone and 18% *C. sumatranus* alone.

The eggs of *C. sumatranus* are 0.7mm long and are roughly conical in shape. They are laid in newly opened pitchers, in groups of 5 or 6, with the blunt end attached to the inner surface of the pitcher walls in the smooth, non-glandular zone. Eggs collected from the sides of pitchers in the field hatched within 24 hours of being placed in pitcher fluid, although some eggs hatched over a week later. The mortality rate for first instar larvae hatching out was extremeley high and relatively few

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successfully escaped from the egg cases. Development of first instar larvae into third instars took place very rapidly with third instars being present less than a week after hatching of the eggs (Fig. 11A). The greatest length of time was spent in the fourth instar which lasted for a minimum of 7 days (Fig. 11A). Most larvae pupated when they reached a length of 5.5-6.0mm, but a few did not pupate until they reached lengths of up to 8mm. The pupal period for C. sumatranus was 3-4 days and the minimum time taken for eggs to develop into adults was 17 days.

Eggs of A. magnus are roughly crescent-shaped and are much larger than those of C. sumatranus (1.2mm in length). They are also laid in newly opened pitchers, in groups of about 6, on the fluid surface. Eggs collected from pitchers in the field took much longer to hatch than those of C. sumatranus, so that first instar larvae were not present until 3 days after collection. Hatching also took place over a much longer period of time with some eggs hatching up to two weeks later. As for C. sumatranus, the greatest length of time was spent in the fourth larval instar (a minimum of 11 days), while only 6 days were required for the first instar larvae hatching out to develop into fourth instar larvae (Fig. 11B). Pupation of fourth instar larvae took place over a size range of 10-13.5mm and the pupal period was 5-6 days. The life cycle length of A. magnus is longer than that of C. sumatranus and a minimum of 23 days was required for the development of eggs into adults.

Larvae of A. magnus are primarily carrion feeders, while larvae of C. sumatranus are basically filter feeders, although they also feed on carrion. Both species are also facultative predators. Thus, A. magnus preys on the smaller larvae of C. sumatranus and both species prey on other dipteran larvae in the pitchers. The negative effect of the

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Figure 11. Minimum Duration and size range of mosquito larval instars

A. *Culex sumatranus*

B. *Armigeres magnus*

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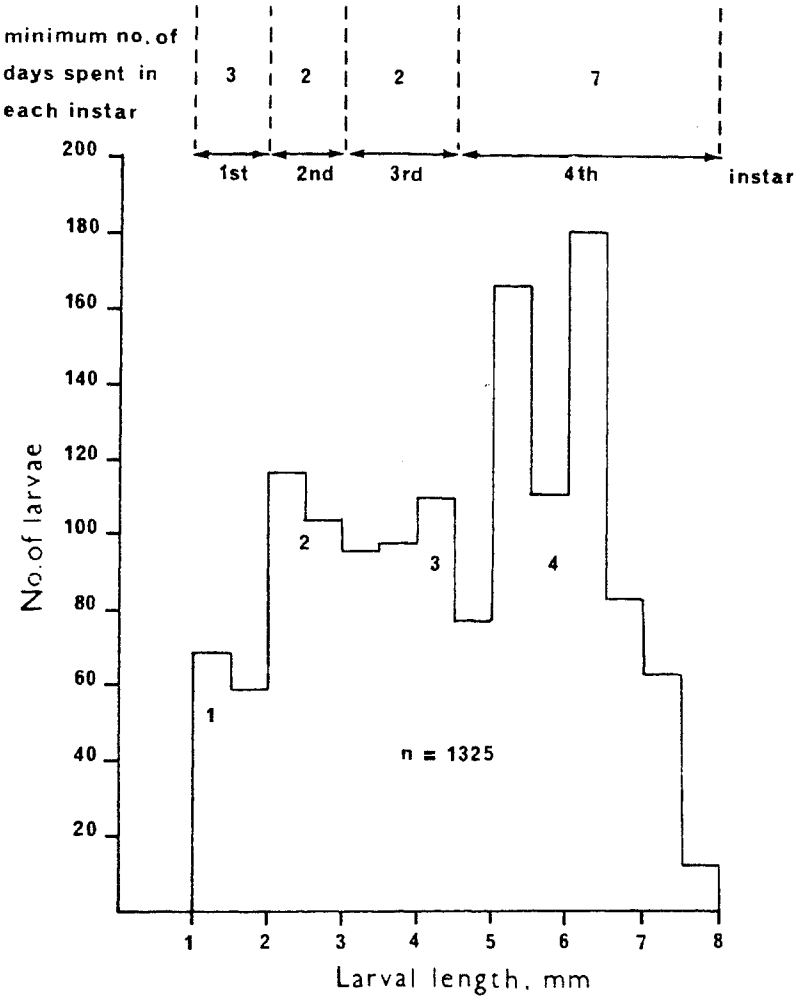
A



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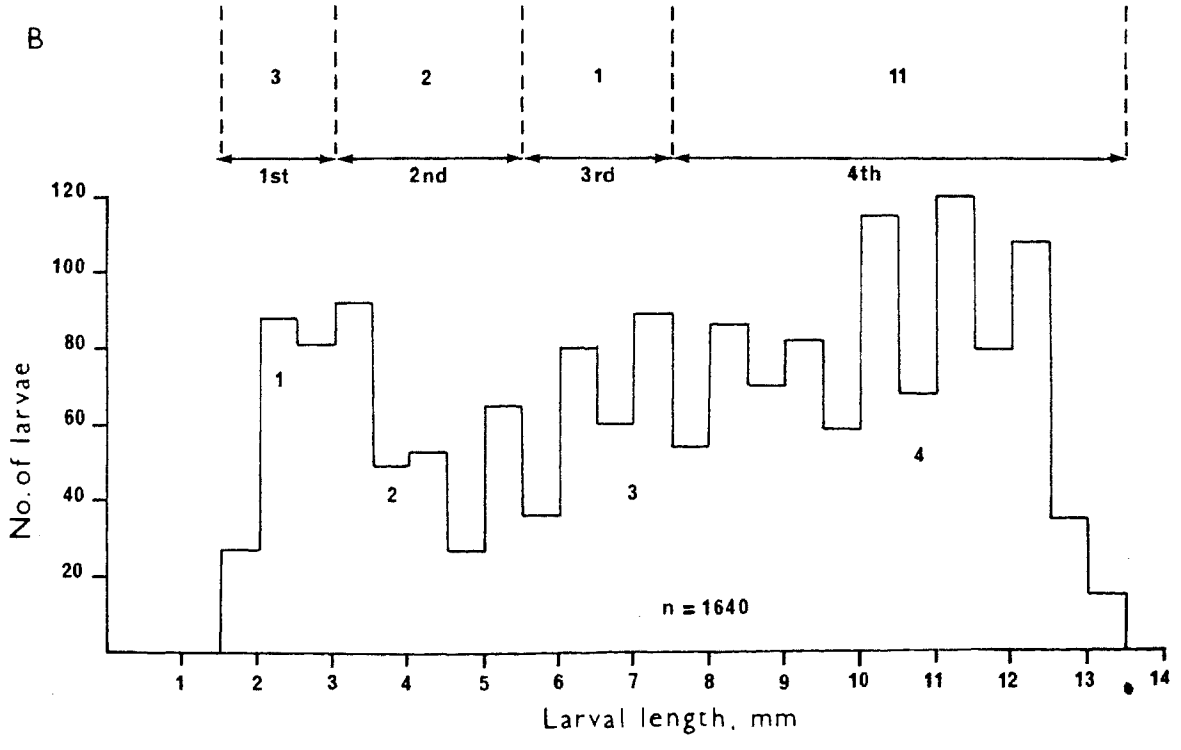

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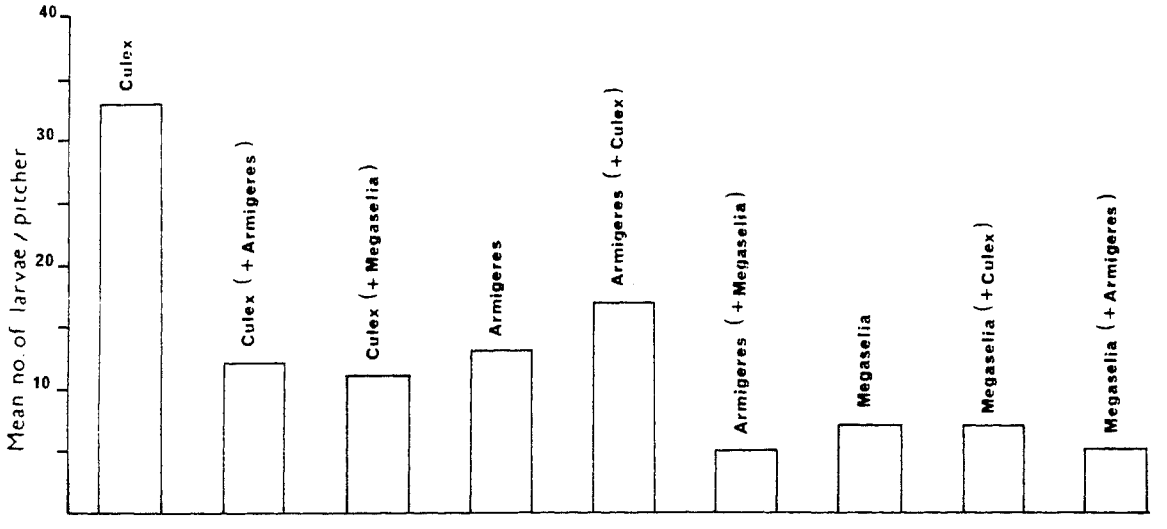
predacious A. magnus larvae on C. sumatranus is immediately apparent, in that the number of larvae of C. sumatranus found in pitchers which contained A. magnus larvae, was greatly reduced in comparison to pitchers where the Culex larvae occurred on their own (Fig. 12). There was a slight increase in the number of A. magnus larvae found in pitchers containing C. sumatranus over those where A. magnus occurred on its own (Fig. 12), possibly as a result of the increase in the amount of food available.

Figure 12. The effect of species interactions on dipteran larval numbers in the pitchers



There was great variation in the number of mosquito larvae found in individual pitchers. Young pitchers usually contained large numbers of first instar larvae of both species, while older pitchers contained comparatively few larvae of the later instars. This suggests that larval wastage is high and that few of the larvae initially hatching out surviv

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to pupate and emerge. In general, pitchers usually supported larger populations of C. sumatranus larvae (the maximum number recorded from a single pitcher was 275, in comparison to 70 for A. magnus) and this is probably due to the difference in size of the two species. Larvae of A. magnus are much larger than those of C. sumatranus (Fig. 11), so presumably fewer larvae can be supported by the limited food resources in the pitchers. It was noted that larvae of A. magnus were occasionally cannibalistic and this may be a method of regulating larval numbers in the pitchers to acceptable levels. Larvae of both species kept under starvation conditions survived for over three months showing that both species are capable of extending larval development indefinitely when food is scarce.

A. magnus and C. sumatranus breed throughout the year, but their numbers are greatly reduced in the winter months of February and March (Fig. 13A). During very cold weather, virtually no live larvae or pupae were found in the pitchers, while large numbers of dead adults were found in the pitcher debris. It is likely that only the eggs survive these cold periods and that it is from these that the populations eventually build up again as the weather becomes warmer. Throughout the remainder of the year the population levels of both species fluctuated widely (Fig. 13A). However, this is probably a reflection of the sampling method used rather than of real fluctuations in the populations as a whole, since the age of the pitchers was not taken into account when sampling and, as already noted, the number of larvae present in pitchers of different ages may vary considerably. The inadequate method of sampling is reflected in the large standard errors obtained for the mean values plotted (Table A; Appendix 1). There was no correlation between the mean number of A. magnus larvae and the mean number of C. sumatranus larvae, indicating that the

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Figure 13. Seasonal population fluctuations of the Nepenthes diptera, related to temperature

A. Mean monthly larval numbers of *A. magnus*, *C. sumatranus* and *M. corkerae*. (Standard errors of the means are given in Table A; Appendix 1).

B. Monthly temperature maxima, means and minima. (Information derived from Royal Hong Kong Observatory monthly weather summaries.)

n = number of pitchers sampled.

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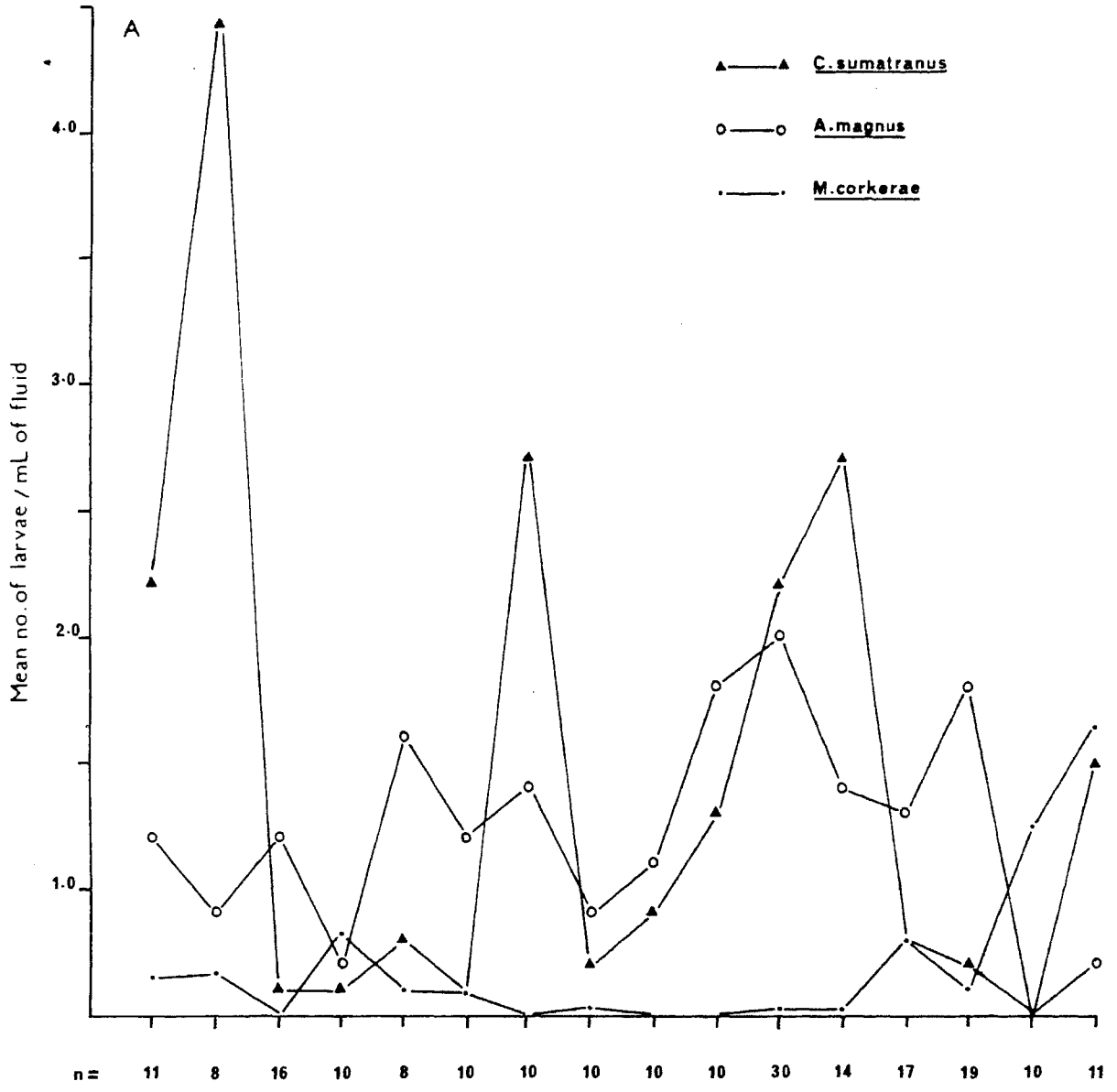

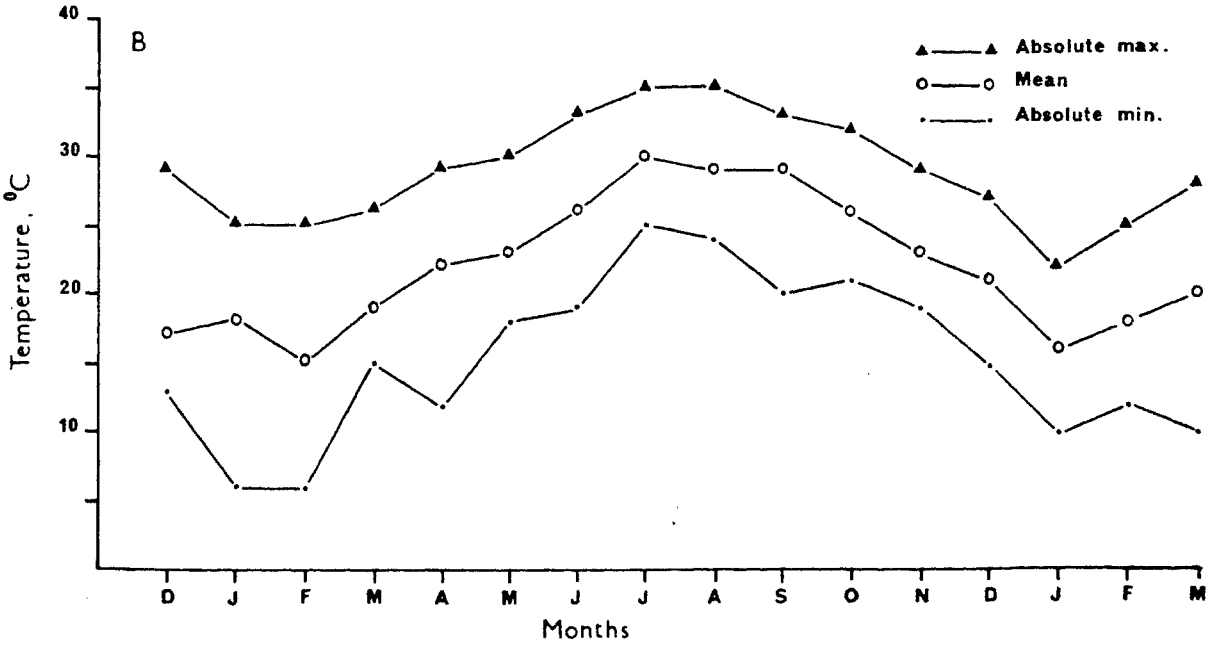

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predacious larvae of A. magnus do not have a significant negative effect on the population levels of C. sumatranus and equally, that C. sumatranus larvae are not an important source of food for A. magnus.

Temperature tolerance experiments showed that the optimum temperature for development of both C. sumatranus and A. magnus is about 25°C, since the greatest number of larvae survived to pupate and emerge at this temperature, although in the case of Culex, development at 25°C was marginally slower than at 31°C (Table 6). Temperatures of 37°C and above, sustained for more than one week, were fatal to larvae of both species (Table 6). This limited tolerance of high temperatures is reflected in the fact that the mean number of larvae of both species decreased in July and August when temperatures were highest (Fig. 13). The maximum temperature recorded in the pitcher fluid during this period was 41.5°C, which if sustained for any length of time would be lethal to all C. sumatranus larvae and to most A. magnus larvae (Table 6). Larvae of A. magnus are more tolerant of high temperatures than C. sumatranus (Table 6) and this is reflected in the higher population levels of A. magnus compared to those of C. sumatranus in July and August (Fig. 13A). A. magnus larvae are also more tolerant of cold temperatures than those of C. sumatranus (Table 6), although development of both species is limited at temperatures below 12°C. At temperatures of 12°C, all the larvae ceased feeding and they remained in this state indefinitely, with the number of larvae surviving gradually decreasing. It is interesting to note that tolerance of low temperatures was increased in the older fourth instar larvae, but that tolerance of high temperatures was decreased (Table 6).

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Table 6

Percentage survival of dipteran larvae at different temperatures

A. Culex sumatranus

(E = Emerged)

Temp. °C	instar	Time (days) 1	2	3	4	5	7	14	21	28	35	42
8	1	100	100	90	60	30	0					
	4	100	100	100	100	100	100	70	20	0		
12	1	100	100	100	100	100	60	60	60	10	0	
	4	100	100	100	100	100	100	80	60	60	60	60
25	1	100	100	100	100	100	100	100	90	90E		
	4	100	100	100	100	100	100	100	100E			
31	1	100	100	100	100	100	100	70	60	40E		
	4	100	100	100	100	100	90	90E				
37	1	100	100	100	100	0						
	4	70	0									
40	1	0										
	4	0										

B. Armigeres magnus

8	1	100	100	100	90	50	30	0				
	4	100	100	100	100	100	90	80	60	40	10	0
12	1	100	100	100	100	100	70	60	40	30	30	0
	4	100	100	100	100	100	100	100	90	80	80	80
25	1	100	100	100	100	100	100	90	90	80	80E	
	4	100	100	100	100	100	100	90	90E			
31	1	100	100	100	100	100	100	90	80	70	60	60E
	4	100	100	100	100	100	100	90	60	60E		
37	1	100	100	100	100	100	10	0				
	4	100	100	90	90	80	0					
40	1	100	80	80	30	0						
	4	90	80	10	0							
44	1	0										
	4	0										

C. Megaselia

8	4	100	100	100	100	100	100	100	80	50	40	40

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Phoridae

Larvae and pupae of Megaselia corkerae were found in 18% of the pitchers sampled, usually in pitchers uninhabited by A. magnus or C. sumatranus since both these species prey on Megaselia larvae. However, C. sumatranus does not appear to be a significant predator of this species since the population levels of Megaselia were apparently unaffected by the presence of C. sumatranus larvae, although it is notable that in pitchers where Megaselia larvae occurred together with Culex larvae, the population levels of the latter were always lower than normal (Fig. 12). Megaselia larvae were only found together with those of A.magnus when the population levels of the latter were very low and the number of Megaselia larvae present in such pitchers was reduced (Fig. 12).

Very little is known about the development of M. corkerae as the adults were never observed ovipositing and the eggs were never identified with certainty. Larvae were also relatively rare, usually being restricted to old pitchers from which the culicine fauna had already emerged and, as they occurred in small numbers, it was difficult to obtain enough larvae to allow development studies to be carried out.

The larvae normally live amongst the pitcher debris, feeding on small particles of detritus and associated fungal material, but they occasionally swim to the surface where they hang vertically, respiring through the posterior spiracles. When ready to pupate, they climb the sides of the pitcher and pupate on the smooth inner walls beneath the rim of the pitcher.

The population levels of M. corkerae were extremely low throughout the year in comparison to those of A. magnus and C. sumatranus, apart from the months of February and March when there was a dramatic increase

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in the number of larvae occupying the pitchers (Fig. 13A). This increase coincided with the virtual elimination of larvae of A. magnus and C. sumatranus from the pitchers due to cold weather (Fig. 13).

Fourth instar larvae of Megaselia are more tolerant of low temperatures than those of A. magnus and C. sumatranus (Table 6) particularly as larvae kept at a temperature of 8°C continued to feed while the culicine larvae became quiescent and ceased feeding at these temperatures. The population levels of Megaselia therefore increased substantially in the winter months due to the almost total absence of predation, and in spite of the low temperatures, which must also limit the development of Megaselia larvae to some extent. There was no correlation between the mean number of C. sumatranus larvae and the mean number of Megaselia larvae, but there was a significant negative correlation between the mean number of A. magnus larvae and the mean number of Megaselia larvae (Table A; Appendix I). This confirms that while Culex larvae are not important predators of Megaselia, Armigeres larvae may have a significant negative effect on the population levels of Megaselia. The limitation of Megaselia larvae to old pitchers for much of the year is not due to feeding preferences of the larvae or to oviposition habits of the adults, but is purely a result of predation by culicine larvae since, during the winter months, larvae of Megaselia were found in pitchers of all ages. Several larval instars were often found together in the same pitchers, which suggests that the females oviposit indiscriminately in pitchers and do not select pitchers of any particular age group.

Psychodidae

Two species of psychodid were found breeding in the pitchers. The first (?Pericoma type) was found in 3 pitchers while the second (?Psychoda type) was found in only 2. Attempts to rear the larvae for identification

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failed. Both types of larvae were present in very large numbers, but as many of them were dead and semi-digested it is likely that the pitchers were not a normal habitat.

Other Diptera

On one occasion, 2 mycetophilid larvae were found living in the pitcher fluid amongst large quantitites of a filamentous green alga. In addition, 3 ceratopogonid larvae (?*Culicoides* type) were found once, and chironomid larvae (?*Metriocnemus* sp.) 3 times. Attempts to rear the larvae for identification were unsuccessful.

Lepidoptera

Psychidae

One specimen of a psychid larva was found, which had a case made up of insect debris from the base of the pitcher. Unfortunately it was semi-digested making identification impossible.

Noctuidae

A noctuid larva was found on several occasions at site 4, eating the leaves and pitchers of the plants. Larvae inside the pitchers attached themselves to the pitcher walls with a vertical sheet of silk to prevent themselves falling into the fluid, and ate away the pitcher tissue above the fluid level causing a windowing effect. Attempts were made to rear the larvae for identification but, although the larvae pupated, none of the pupae emerged.

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Eucleidae

A eucleid larva which carried poisonous spines on the dorsal surface was found feeding on leaves of pitcher plants at site 2. Larvae were only ever found at this site and during attempts to rear them it was discovered that the larvae would only eat leaves from this site, rejecting leaves collected from other sites. None of the larvae were reared successfully and so the species remains unidentified.

Other Lepidoptera

Unidentified lepidopteran larvae were discovered in the seed capsules of plants at site 8. The caterpillars were heavily parasitized by mites (*Pediculoides sp.*) making identification impossible.

Acarina

Prostigmata

Bdellidae

Adults and nymphs of *Bdellodes sp.* were found living on the fluid surface in 21% of the pitchers sampled. These mites were also observed running about on the aerial parts of the plant, so that, while it is fairly certain that the mites are associated with the plants, they are probably only accidental pitcher inhabitants.

Anystidae

Mites belonging to the genus *Anystis* were found living on the fluid surface in 4% of the pitchers sampled, occasionally occurring together with *Bdellodes sp.*

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Hydrachnellae

On two separate occasions, nymphs belonging to the family Anisitsiellidae were found living in the base of pitchers. No adults were present so it was not possible to identify the mites, although it is probable that they belong to an as yet undescribed species.

Sarcoptiformes

Acaridae

In 3% of the pitchers sampled, acarid mites belonging to the *Tyrophagus putrescentiae* Schrank complex were found swimming around in the pitcher fluid. Only one or two specimens occurred in each pitcher and this, together with the small number of pitchers occupied, indicates that this mite is a nepenthexene form.

Anoetidae

Three anoetid mites were found living in the pitchers, of which two were aquatic and one terrestrial. The most common species was *Zwickia sp.* (possibly conspecific with *Z. guentheri* Oudemans), which was found swimming in the fluid of 80% of the pitchers sampled. Unidentified mites (Anoetid A) were found in 15% of the pitchers, crawling about amongst the debris in the base, while a third species, *Creutzeria sp.*, was found living on the fluid surface and on the pitcher walls of 4% of the pitchers sampled. As the latter two species were not discovered until long after the start of the sampling program, it is possible that specimens may have been overlooked in the earlier months of sampling and that the mites were actually more common than the results suggest. *Zwickia sp.* is a carrion feeder and was normally found in greatest numbers in newly opened pitchers,

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while both Creutzeria and Anoetid A are detritus feeders usually found in older pitchers where there was a substantial accumulation of detritus.

The life cycle of Zwickia and Anoetid A takes approximately two weeks to complete. Eggs of Zwickia are laid singly on the walls of the pitcher above the fluid level, while those of Anoetid A are laid singly or in groups of up to 25 amongst the debris in the base of the pitcher. Males are not necessary for eggs to be laid since the mites are haplodiploid - that is the males are haploid and the females diploid. Eggs laid parthenogenetically develop into males while fertilized eggs develop into females. The normal ratio of females to males in Zwickia is 3 : 1, while in Anoetid A it is 1 : 1. Hatching of the eggs takes place within one or two days in both species and the emerging larvae change into primary nymphs within one day. Most individuals seemed to pass directly from the primary nymphal stage into the tertiary nymphal stage without passing through the intermediate deutonymphal stage. Newly developed adults were present within two weeks of eggs being laid and they lived for over two weeks, although the exact length of life is not known. There is some indication that the life cycle length is dependent on the amount of food available, since although eggs laid by females placed in a dish with very little food developed into larvae within two days, these larvae still had not moulted into primary nymphs two weeks later, whereas in the dishes where food was plentiful, development of the eggs was complete and adults were already present. Unfortunately nothing is known of the development of Creutzeria sp. because the mites proved very difficult to rear in the laboratory and could not be kept alive for long.

Data on the seasonal changes in population levels of only one species (Zwickia sp.) were obtained, since there were not enough samples of Anoetid

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A and Creutzeria to draw conclusions about changes in population levels throughout the year. Unfortunately the data obtained for monthly Zwickia population levels is relatively meaningless because it is so variable, probably as a result of the fact that pitcher age was ignored in sampling. This is illustrated by the high standard errors of the mean monthly population values (Fig. 14A). Nevertheless, one clear pattern did emerge and that was that the number of mites present in the pitchers was greatly reduced in the coldest months of the year (Fig. 14A; C), indicating that the mites are intolerant of low temperatures. This was confirmed by the results of the temperature tolerance experiment which showed that at temperatures of 12°C and below, most of the mites are killed and no reproduction takes place (Fig. 15). Temperatures above 35°C are also fatal to the mites (Fig. 15), which must account for the lowered population levels in the pitchers in July and August (Fig. 14A; C). The optimum temperature for development of Zwickia sp. appears to be about 31°C (Fig. 15). The level of deutonymphs in the population was relatively low throughout the year but there was a substantial increase in the number of deutonymphs present in January, 1981, despite the fact that the total population level decreased (Fig. 14A; B). It is therefore possible that adverse conditions such as low temperatures increase the number of nymphs passing through the deutonymphal stage.

Oribatei

Galumnidae

In 2% of the pitchers examined, individuals of Galumna sp. were found floating on the surface of the pitcher fluid. One specimen was kept alive in the laboratory for over 3 months, presumably feeding on micro-organisms in the fluid.

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Figure 14. Seasonal population fluctuations in Zwickia, in relation to temperature

A. Monthly population levels (all stages). Means are given ± I SE.

B. Monthly population levels of deutonymphs. Means are given ± I SE.

C. Temperature maxima, means and minima. (Information derived from Royal Hong Kong Observatory monthly weather summaries).

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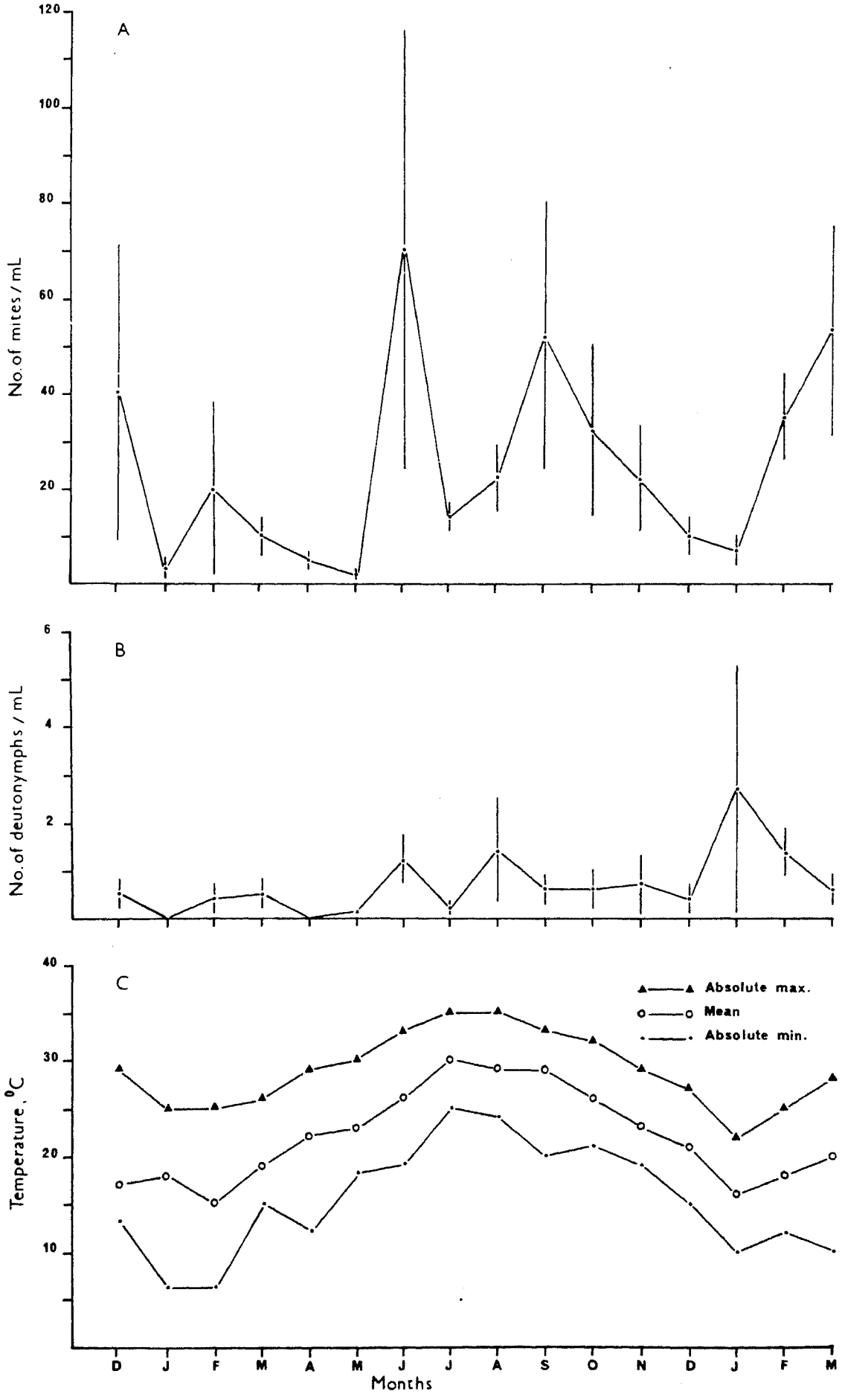

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Figure 15. The effect of temperature on population levels of *Zwickia sp*.

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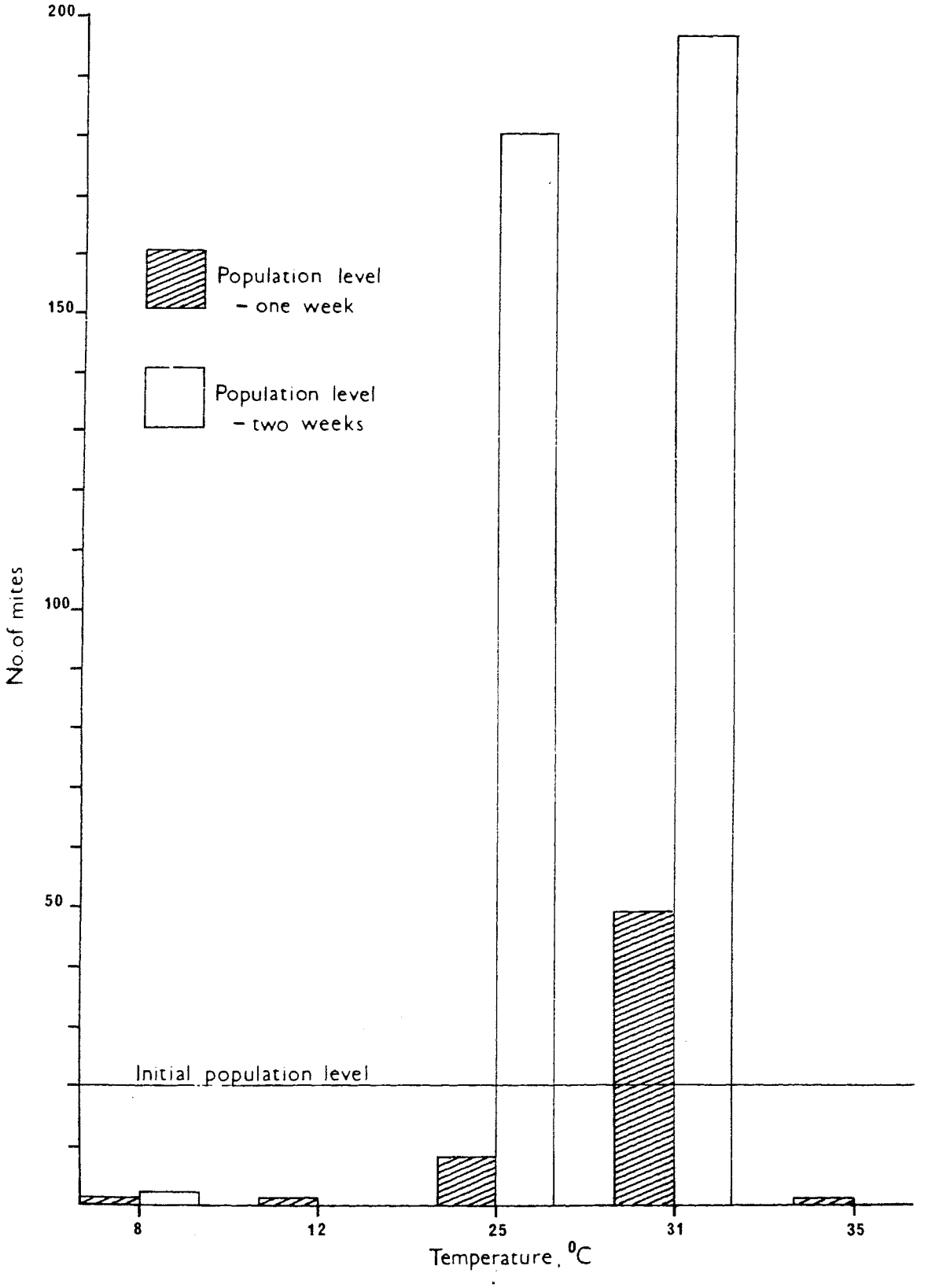

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Scheloribatidae

Siculobata sp. occurred in 4% of the pitchers. All specimens found were dead and partially digested so that it is not certain whether this mite actually lives in the pitcher as an accidental inhabitant or is merely part of the pitcher prey.

Oribatulidae

Several dead specimens of Zygoribatula sp. were found in 4% of the pitchers sampled, many of them very well preserved. This mite may be an accidental inhabitant or a pitcher victim.

Arachnidae

Theridiidae

Two spiders belonging to the family Theridiidae were found living inside pitchers. The most common was Coleosoma sp. which builds an irregular zig zag web below the pitcher mouth, sometimes filling the whole pitcher interior. One spider occupies each pitcher and the eggs are laid in cocoons just beneath the pitcher rim. The spider was also found walking around on the aerial parts of the plant. Argyrodes sp. was found on two occasions sitting inside pitchers, but is probably not a true pitcher inhabitant.

Discussion

Thirty four animals (apart from protozoa, rotifers and algae) were found on aerial parts of the plants or living in the pitchers. Most of these animals are nepenthexene forms which either fall into the pitchers accidentally (Collembola, Anystis, oribatids), or are aquatic forms which

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are normally found in other habitats. The latter are usually only found in old pitchers where the digestive activity of the fluid is much reduced, thus the nematode, Rhabditis, and the oligochaete, Pristina foreli, were found only in old pitchers. The genus Pristina appears to be characteristic of phytotelmata, since another species P. rosea Piguet has been found occupying phytotelmata in plants such as Crinum, Hymenocallis and Pandanus (Thienemann, 1934). Psychodids have never been found breeding in Nepenthes pitchers before, although mycetophilids, ceratopogonids and chironomids form part of the Nepenthes fauna in other areas (Table 1). Only one mycetophilid has been found previously in Nepenthes pitchers. This species is Xenoplatyura beaveri, which is a nepenthebiont species which suspends itself on a web above the pitcher fluid (Beaver, 1979a) in contrast to the species found in Hong Kong which is nepenthexene and aquatic. The ceratopogonid found in Hong Kong was also nepenthexene, whereas those found elsewhere (Dasyhelea spp.) are all nepenthebiont. The nepenthexene chironomid breeding in Nepenthes in Hong Kong probably belongs to the genus Metriocnemus which has been found in Nepenthes pitchers in Borneo (Table 1) and which is characteristic of container habitats.

In comparison to the number of nepenthexene animals recorded from the plants, the number of nepenthephil and nepenthebiont animals found was relatively small. Only two definite nepenthephil species were found in the pitchers; the culicine A. magnus and the prostigmatid mite Bdellodes. Armigeres magnus has a wide geographical range (Table 1), but is only associated with Nepenthes in Hong Kong. It has been recorded recently from bamboo stumps and tree holes in Hong Kong (Chau, 1982), but was previously known only from pitcher plants. The large number of

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pitchers occupied and the obvious preference of the adults for breeding in this habitat indicate that, although the species must be considered nepenthephil overall, it may be in the process of evolving into a nepenthebiont species in the Hong Kong region. Bdellodes mites were found in a relatively large number of pitchers and were often seen running about on aerial parts of the plants, so they are probably associated with Nepenthes, although it is not known whether or not the association is exclusive. The spider Coleosoma may be a nepenthephil or a nepenthexene species, but as it does not appear to be solely associated with the pitchers it is unlikely to be nepenthebiont. Members of only two families of arachnids (Thomisidae and Theridiidae) have been found living in Nepenthes pitchers to date (Beaver, 1983) and it seems that these are the only families which are able to adapt to the pitcher environment, since both spiders found in Nepenthes pitchers in Hong Kong belong to the family Theridiidae.

Seven of the animals found in this preliminary study appear to be exclusively associated with the plants. Culex sumatranus breeds in Nepenthes pitchers throughout its range (Table 1), while Megaselia corkerae may be a nepenthebiont species since it is a new species described from specimens found in pitchers in Hong Kong and is not known to occur in other habitats. Anoetid mites associated with Nepenthes in other areas are all nepenthebiont (Beaver, 1983) and so it is probable that the three anoetids found in the pitchers in Hong Kong (which belong to the same genera as those associated with Nepenthes elsewhere) are also nepenthebiont.

It is likely that the two lepidoptera found feeding on Nepenthes are similarly nepenthebiont species since they seem to be specifically adapted to feeding on the plants. In the case of the noctuid larvae, this

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involved adaptations of the larvae to enable them to feed inside the pitchers without falling into the fluid, while the eucleid larvae seemed to be so limited in their choice of food plant that they would only eat Nepenthes leaves from one site. This suggests that the chemical composition of the leaves differs at different sites and, had sufficient time been available, it would have been interesting to investigate this further. The psychid larva found in the pitchers had a case composed of insect remains from the debris in the pitcher and it appeared to be superficially very similar to Nepenthophilus tigrinus, described by Guenther (1913). Unfortunately as only one semi-digested specimen was found it is impossible to speculate on whether it is the same psychid or a related species.

Disregarding the nepenthexene species which do not form part of the true pitcher fauna, four predators were found in the pitchers, of which two were terrestrial (Bdellodes and Coleosoma), feeding on insects falling into the pitchers and on emerging Nepenthes diptera, and two aquatic (larvae of A. magnus and C. sumatranus). Larvae of A. magnus and C. sumatranus feed on other dipteran larvae in the pitchers and on small organisms such as protozoa and rotifers. The controlling influence of mosquito larvae on protozoan communities in phytotelmata is well documentec (Kato et al, 1952; Kurihara, 1957; Maguire et al, 1968; Vandermeer et al, 1972; Addicott, 1974) and it is illustrated in this case by the fact that ciliates usually only occurred in newly opened pitchers not yet containing larvae, or in old pitchers from which the culicine fauna had already emerged. Flagellates did not appear to be restricted to pitchers of any particular age group, but it is possible that their attachment to particles of debris in the base of the pitchers protects them to a certai degree from the filter feeding activities of the mosquito larvae.

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Although the culicine larvae may be predatory, the bulk of their food appears to consist of carrion, which is also the main food source of Zwickia mites. Since most prey is apparently caught soon after the pitchers open (Beaver, 1983) young pitchers contain the largest amounts of carrion and as a result these three animals were most abundant in young pitchers. In older pitchers where there has been some time for digestion of the prey initially trapped, the pitcher debris consists mostly of detritus, so that the three detritus feeders in the pitchers (Megaselia, Anoetid A and Creutzeria) were usually found in older pitchers. In the case of M. corkerae, this restriction to old pitchers seemed to be largely due to the predatory activities of the mosquito larvae rather than to feeding preferences of the Megaselia larvae, or to oviposition habits of the adults.

Females of C. sumatranus and A. magnus oviposit selectively in newly opened pitchers. The eggs of A. magnus are deposited on the surface of the fluid, while those of C. sumatranus are laid on the pitcher walls, well above the fluid level. Presumably the high humidity in the pitchers and the condensation of water on the walls provides enough moisture to allow the eggs to hatch and the larvae to wriggle down the walls into the fluid in the base of the pitcher. Unfortunately Armigeres adults were never observed ovipositing so it is not certain whether they have the same curious method of oviposition as other container-breeding species of Armigeres, although they do not deposit first instar larvae as reported by Bates (1954).

Large numbers of eggs are laid by both species in individual pitchers and from these, large numbers of first instar larvae hatch out. Relatively few of these larvae survive to pupate and emerge because, as

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pointed out by Assem (1959), the number of eggs laid cannot be correlated to the amount of food which will eventually become available to the larvae, particularly as there is so much variation in the amount of prey caught by individual pitchers. Thus, Assem (1959) found that on average, only 21% of the larvae of Tripteroides bisquamatus initially present in pitchers of N. mirabilis in New Guinea, survived to pupate and emerge. However, although larval wastage is high, those larvae which die of starvation provide food for those remaining, so that they all contribute to the survival of the species.

The minimum length of time required for development of eggs to adults is 17 days for C. sumatranus and 23 days for A. magnus under laboratory conditions, with the greatest proportion of time being spent in the fourth larval instar. The duration of each instar may vary considerably and although this was not determined for C. sumatranus and A. magnus, Assem (1959) quotes figures for Tp. bisquamatus which demonstrate that the fourth larval instar is the most variable. The duration of each larval instar is related to the amount of food available so that when food is scarce the larvae are able to delay development. This ability to extend the larval lifespan appears to be characteristic of nepenthebiont diptera and many species are able to survive for several months without food, particularly in the last larval instar (Assem 1959; Beaver, 1979a; 1983). Culex sumatranus and A. magnus were also able to survive for at least three months under starvation conditions and this is another indication that A. magnus is adapting to the pitcher habitat in Hong Kong. The ability to extend the developmental period when food is scarce appears to be a feature of nepenthebiont animals in general, as Zwickia mites also appeared to be able to survive for some time in a

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state of arrested development when starved.

Few conclusions can be drawn regarding seasonal changes in the population levels of A. magnus, C. sumatranus, M. corkerae and Zwickia sp. from the monthly population data obtained for each of these animals since, in retrospect, the method of sampling was wholly inadequate. Pitchers were taken in varying proportions from different sites, so that geographical variation may have affected the results and the number of pitchers sampled each month was unnecessarily small, as well as being inconsistent. Perhaps the most important factor which was overlooked initially was that pitchers of different ages may have substantially different faunas and, since the age of the pitchers was not kept constant from one sampling period to the next, the comparison of population data obtained in different months is not particularly valid. These inconsistencies in sampling are reflected by the high values obtained for the standard error of the mean number of animals present each month. Despite the inadequacy of the sampling method however, a few trends did emerge from the data obtained. The numbers of both Culex and Armigeres larvae in the pitchers declined in the winter months of February and March, due to the intolerance of both species to low temperatures, while there was a great increase in the number of the more tolerant Megaselia larvae. This sudden increase in the population levels of Megaselia was a direct result of the almost total absence of predatory mosquito larvae in the pitchers and it appears to be an annual event since it was observed two years running. The mosquito larvae were also found to be intolerant of high temperatures and therefore their numbers decreased in the hottest months of July and August. It must be noted that the tolerance of larvae to different temperatures was determined under constant temperature conditions, whereas the

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temperatures in the pitcher fluid must have a wide daily range, so that larvae are never exposed to very high or low temperatures for any length of time. However, if atmospheric temperatures are extreme for long periods, the fluid temperatures must also become more extreme, eventually reaching levels which severely inhibit or damage the larvae.

The variability of the population data obtained for Zwickia mites makes it difficult to draw conclusions on seasonal population changes, but there appeared to be a drop in the number of mites present in the coldest months, coincident with an increase in the number of deutonymphs present. The moult from protonymph to deutonymph or tritonymph is controlled by environmental factors so that when conditions are unfavourable, protonymphs transform into deutonymphs rather than directly into tritonymphs (OConnor, 1982). This increase in the number of deutonymphs of Zwickia must therefore be a response of the mites to low temperatures which are unfavourable for the species. Swales (1972) also found that the number of deutonymphs of Anoetus gibsoni increased in pitchers of Sarracenia purpurea as temperatures fell, and that the population overwintered in the deutonymphal stage, so it is likely that Zwickia similarly survives periods of extreme cold in Hong Kong in the deutonymphal stage.

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Chapter 2. Faunal succession in the pitcher communities

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Introduction

Environmental conditions within Nepenthes pitchers are dynamic and constantly changing throughout the life of a pitcher, from the moment it opens, to the moment when it ceases functioning as a water-holding container. It is therefore to be expected that the pitcher communities will also be dynamic and that the composition of the communities will change as environmental conditions in the pitchers alter.

The fluid in newly opened pitchers is extremely acid and it contains digestive enzymes which are active in the acid environment of the fluid. However, as the pitchers age, the fluid pH becomes gradually more alkaline due to the build up of alkaline digestion products and to the entrance of rainwater, and as a result the digestive enzymes secreted by the pitchers become largely ineffective, since they require a low pH for optimum activity. Nepenthexene animals which are unable to tolerate very acid conditions, or which are susceptible to the digestive enzymes in the fluid, are therefore likely to be restricted to older pitchers containing alkaline or highly diluted fluid and hence inactive protease enzymes.

Young pitchers secrete large quantitites of nectar and are thus highly attractive to insects and other animals, but as they become older, nectar secretion decreases and the pitcher tissue begins to wither and desiccate so that they are no longer particularly attractive to potential prey. This results in prey capture being limited to a relatively short period of time after opening. In Sarracenia, the trapping ability of the pitchers peaks approximately two weeks after opening and then declines rapidly so that most of the prey caught by individual pitchers is trapped within the first thirty days after opening (Fish and Hall, 1978; Wolfe, 1981). The pattern of prey capture in Nepenthes also appears to be

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similar, with the maximum prey input taking place three weeks after pitcher opening when the number of individuals living in the pitchers is also at a maximum (Beaver, 1983). Most of the prey is therefore caught in a relatively short period after opening and it subsequently decomposes slowly into detritus as the pitchers age. Pitchers of different ages therefore contain different amounts of prey at different stages of decomposition.

Since there are effectively no primary producers in the pitchers of pitcher plants, the insects and arachnids living in the pitchers are all dependent on the input of captured prey for food. In Sarracenia purpurea, the insect inhabitants of the pitchers consume captured insects at different stages of decomposition, with the maximum number of each insect coinciding with the abundance of their specific food type (Fish and Hall, 1978). Differences in oviposition patterns and development times facilitate temporal segregation between the three species involved, although this segregation is never complete and individuals of all three species may sometimes be found together (Fish and Hall, 1978). A similar situation may exist in Nepenthes pitchers since the pitcher fauna includes carrion feeders, filter feeders and detritus feeders, which must feed on captured insects at different stages of their decay.

The variation in the amount and type of food available in pitchers of different ages, differences in the oviposition habits of adult diptera and species interactions within the pitchers are all likely to affect the composition of the pitcher communities, resulting in different animals being abundant in pitchers of different ages. The results of the preliminary sampling program indicated that this was indeed the case, so in order to investigate the faunal succession in pitchers more fully, all

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the fluid-containing pitchers on 25 plants were sampled. Pitchers of the same relative ages from different plants were grouped into age classes and comparisons were made between the faunas of pitchers of different age classes.

Materials and Methods

Over a period of 19 months beginning in November, 1980 and ending in June, 1982, a total of 25 plants were sampled. The plants were chosen from several different sites (2-8) on the basis of the number of fluid-containing pitchers they possessed, those with the maximum number available being sampled. Plants were taken from a number of sites to avoid depleting populations of animals in one area, and also because in many cases each site had only a small number of plants suitable for sampling at any one time. Plants suitable for sampling were taken to be those bearing a minimum of 5 fluid-containing pitchers (the maximum number found on one plant was 10). It was not possible to sample all the plants at the same time because the amount of time involved in sampling all the pitchers on a plant and subsequently sorting samples in the laboratory was enormous. As a result, there may have been seasonal differences in the number of animals present in the pitchers of different plants, as well as variation in the composition of the fauna due to differences in the geographical location of the plants. However, as the purpose of sampling was to detect changes in the fauna of pitchers of different ages on the same plant, any variation between the fauna of individual plants, due to seasonal or geographical effects, would not alter the relative proportions of animals in different pitchers on the same plants, but would merely increase the variability of data obtained when pitchers of the same relative ages from different plants were grouped together.

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Leaves of Nepenthes are produced spirally from the apex of the plant, so that leaves at the top of the plant are the youngest and a leaf which is attached to the stem above another leaf is younger than the one below it. It is therefore easy to determine the ages of the leaves relative to each other and hence also that of the pitchers, since pitcher development normally follows the same pattern as that of the leaves. Occasionally pitcher initials fail to develop, or do not develop until much later, so that the pitcher does not follow the same age sequence as the leaves, but this is rare and is usually very noticeable since the pitchers have characteristic appearances at different ages.

The pitchers on each plant sampled were numbered according to relative age, with pitcher number 1 being the youngest open pitcher on a plant. None of the plants sampled appeared to have pitchers which had developed out of sequence so it was assumed that pitcher age corresponded to leaf age. The length of each pitcher was measured and the contents were removed by pouring the fluid into a plastic vial labelled with the plant number and pitcher number. The remainder of the contents were washed into another similarly labelled vial with repeated rinsings of distilled water. Once the pitchers were empty, distilled water was added to replace the fluid removed and the plant was left intact with the minimum of disturbance. In the laboratory each sample was sorted in the same way as for the preliminary sampling program, except that insect debris was also preserved and the wet weight determined at a later date. Wet weight was determined rather than dry weight because variable amounts of debris were lost during sampling and sorting procedures. As a result it was impossible to obtain valid comparisons of the amount of debris present in

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different pitchers using dry weights, which must necessarily be measured extremely accurately.

Dipteran larvae contained in each pitcher were identified, counted and measured, the acarine fauna was identified and the number of individuals of each species was determined. The number of adults, primary, deuto- and tertiary nymphs of the anoetid mites Zwickia and Creutzeria were determined for each pitcher (any larvae present were included in the primary nymph category), and the same was done for Anoetid A except that in this case only adults, nymphs and deutonymphs were counted since it was difficult to separate primary and tertiary nymphs of this species except on the basis of size, which was unsatisfactory. Nematodes, turbellarians and copepods occurred infrequently but in very large numbers so that only their presence was noted.

For each pitcher, the percentage of the total dipteran population accounted for by each dipteran species and the percentage of the total anoetid population accounted for by each of the three anoetid species was determined. The number of individuals of each species per mL of pitcher fluid was also worked out for each pitcher in order to eliminate numerical differences in the fauna due to pitcher size variation. Pitchers bearing the same number were grouped together into age classes, thus all the youngest pitchers from each plant, bearing the number one, were grouped into age class one, all the second youngest pitchers formed the second age class and so on. In practise not all pitchers in the same age class were of exactly comparable ages, but they were of the same relative ages. Mean values for population percentage and number per mL for each species were determined for each of the pitcher age classes, as well as mean values for pH, fluid volume and amount of debris.

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It would obviously have been preferable to mark large numbers of pitchers about to open and to subsequently sample subgroups of these pitchers at different intervals so that the exact age of the pitchers would be known; however, it was not possible to carry out the succession study in this way because at any one time relatively few pitchers are of exactly the same age and it was therefore impossible to obtain enough pitchers at the same stage of development to carry out the study.

Results

For a plant to be suitable for sampling it had to possess a minimum of 5 fluid-containing pitchers, therefore the pitcher age classes 1-5 each contained 25 pitchers. Age class 6 contained 23 pitchers; class 7, 19 pitchers; class 8, 15 pitchers and class 9, 9 pitchers. Only 2 of the 25 plants sampled possessed 10 fluid-containing pitchers and so this age class was ignored.

Fluid volume and pH changes

The size of a pitcher affects the volume of fluid secreted, and so to obtain values for fluid volume independent of pitcher size, the amount of fluid in each pitcher was divided by the length of the pitcher to give an index value representing the number of mL of fluid per cm of pitcher length. Mean values for fluid volume per cm of length were determined for each of the pitcher age classes.

The volume of fluid contained in pitchers of age class 2 was substantially higher than that found in pitchers of age class 1 (Fig. 16A), while the mean fluid pH was slightly lower (Fig. 16B), indicating that both fluid and acid are secreted by the pitchers after opening. This secretion

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Figure 16. Changes in fluid volume, pH and wet weight of debris with pitcher age

A. Fluid volume (means are given ± I SE)

B. Fluid pH (the line joins the mean values for each age class)

C. Debris (means are given ± I SE)

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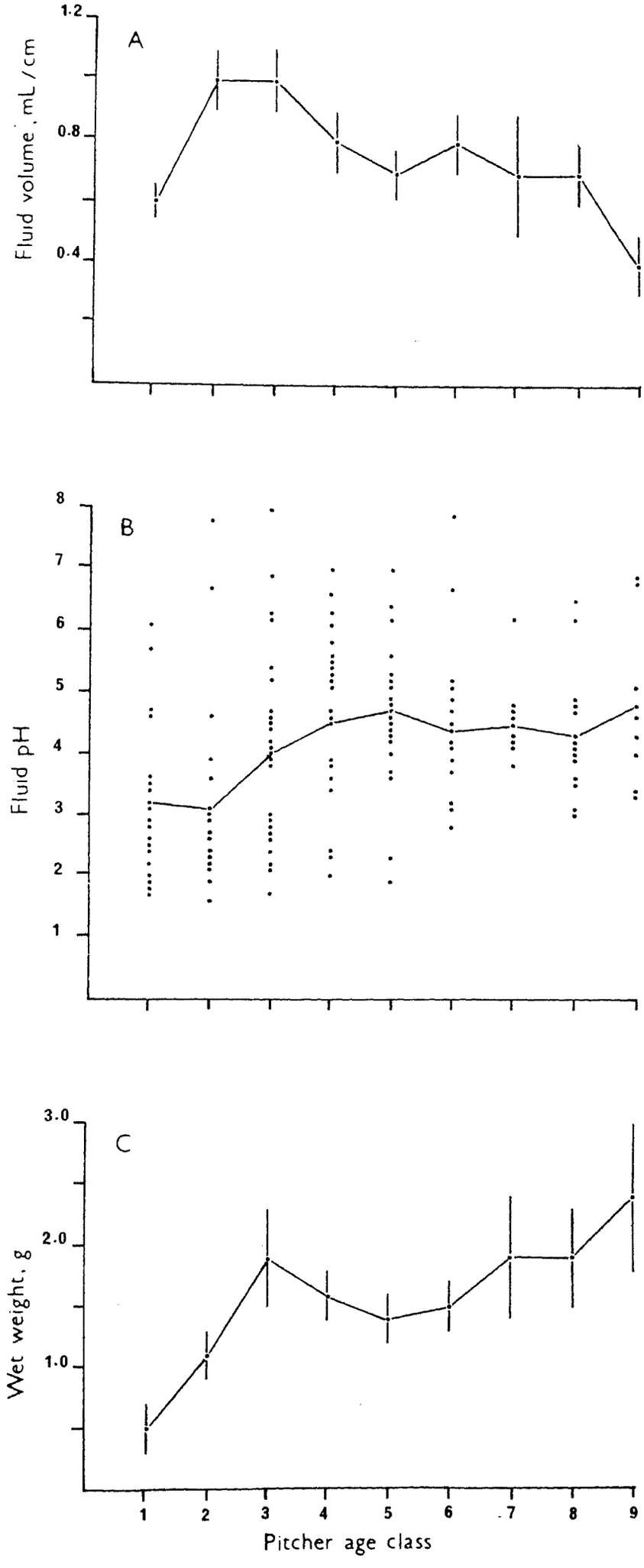

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of fluid may be a response to the stimulation of prey capture since the amount of debris present in pitchers in age class 2 was greater than that in age class 1, showing that prey capture had occurred. The fluid pH in pitchers of age classes 1 and 2 was generally very acidic although a few pitchers had abnormally high pH values (Fig. 16B), which may have resulted from excessive prey capture and putrefaction. The pH becomes gradually more alkaline in pitchers in older age classes (Fig. 16B), demonstrating that the ability of the pitchers to buffer the fluid pH decreases as they age. Fluid volume decreased in older pitchers (Figure 16A), as a result of absorption of fluid by the pitchers and probably also as a result of evaporation.

Pitcher debris

The amount of debris contained in the pitchers increased gradually in pitchers of age classes 1-3, reaching a maximum in age class 3 (Fig. 16C). This indicates that prey capture was taking place in pitchers of all three age classes. The greatest increase in the amount of debris present occurred between age classes 2 and 3 (Fig. 16C), which must correspond to the period of maximum prey capture in the pitchers. The mean weight of pitcher debris declined in age classes 4-6 (Fig. 16C) demonstrating that very little prey was being caught by these pitchers and that the prey caught soon after opening was decomposing, or being consumed by the pitcher inhabitants. It is difficult to explain the increase in mean debris weight in pitcher age classes 7-9 as it is very unlikely that the pitchers in these age classes were capable of catching large amounts of prey; however, the high standard errors for the mean values (Fig. 16C) indicate that there was great variability in the amount of debris present

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in individual pitchers and it is likely that the high mean values resulted from a few pitchers containing abnormally large amounts of debris, probably as a result of excessive prey capture soon after opening.

Diptera

The three diptera commonly found breeding in *Nepenthes* pitchers in Hong Kong (*C. sumatranus*, *A. magnus* and *M. corkerae*) were found in pitchers of all ages; however, the relative proportions of the three species altered with pitcher age. The youngest pitchers contained the highest proportion of *A. magnus* larvae and pupae, thus *A. magnus* accounted for 60-75% of the dipteran population in pitchers of age classes 1-4 (Fig. 17A) and a high percentage of pitchers in age classes 2-5 contained individuals of this species (Fig. 17C). The predominance of *A. magnus* in younger pitchers is due to the fact that the adult females oviposit preferentially in newly opened pitchers. Large numbers of first instar larvae were found in pitchers of age class 1 and to a lesser extent in those of age class 2 (Fig. 18A), and the number of individuals and percentage of pitchers occupied increased between age classes 1 and 2 (Fig. 17B; C), demonstrating that oviposition takes place in pitchers of both age classes.

The larvae must develop very rapidly, since fourth instar larvae were present even in pitchers of the youngest age class (Fig. 18A), while pupae were first observed in pitchers of age class 2 (Fig. 19). Pupation reached a maximum level in pitchers of age classes 3-5 (Fig. 19) and this resulted in a decrease in the number of individuals and percentage of pitchers occupied in the older age classes (Fig. 17 B; C). A few individuals were usually present in older pitchers however (Fig. 17B), due to continuing oviposition and possibly also as a result of delayed

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Figure 17. Changes in the relative proportions of the Nepenthes diptera, in relation to pitcher age

Armigeres magnus - A. Percentage of the total dipteran population.

B. Mean number of individuals per mL.

C. Percentage of pitchers occupied.

Culex sumatranus - D. Percentage of the total dipteran population.

E. Mean number of individuals per mL.

F. Percentage of pitchers occupied.

Megaselia corkerae - G. Percentage of the total dipteran population.

H. Mean number of individuals per mL.

I. Percentage of pitchers occupied.

(Points represent mean values ± I SE)

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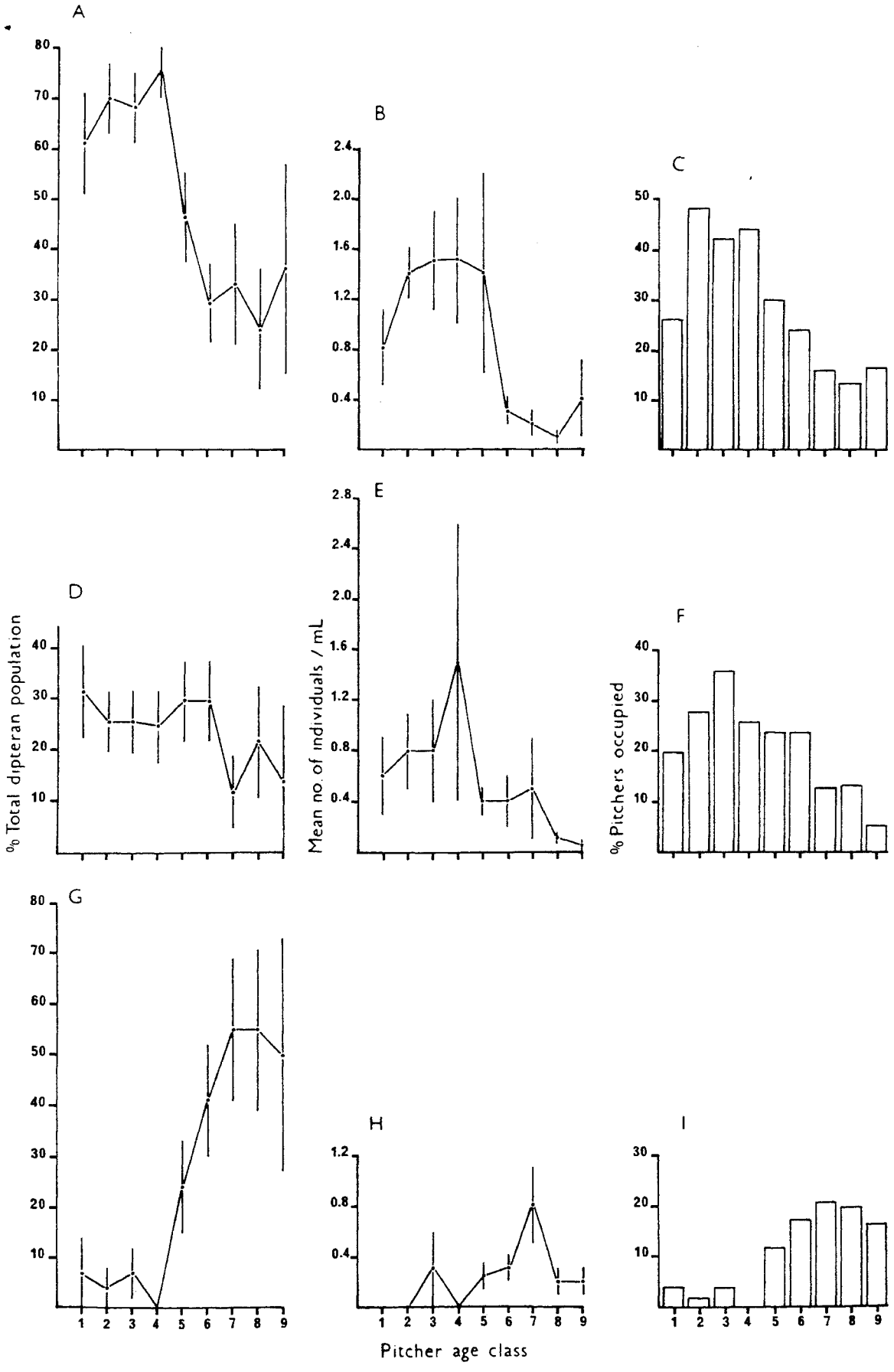

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Figure 18. Size ranges of dipteran larvae found in pitchers of different ages

A. *A. magnus*.

B. *C. sumatranus*.

C. *M. corkerae*.

(P1 = age class 1, P2 = age class 2, etc.)

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Fig 18 A

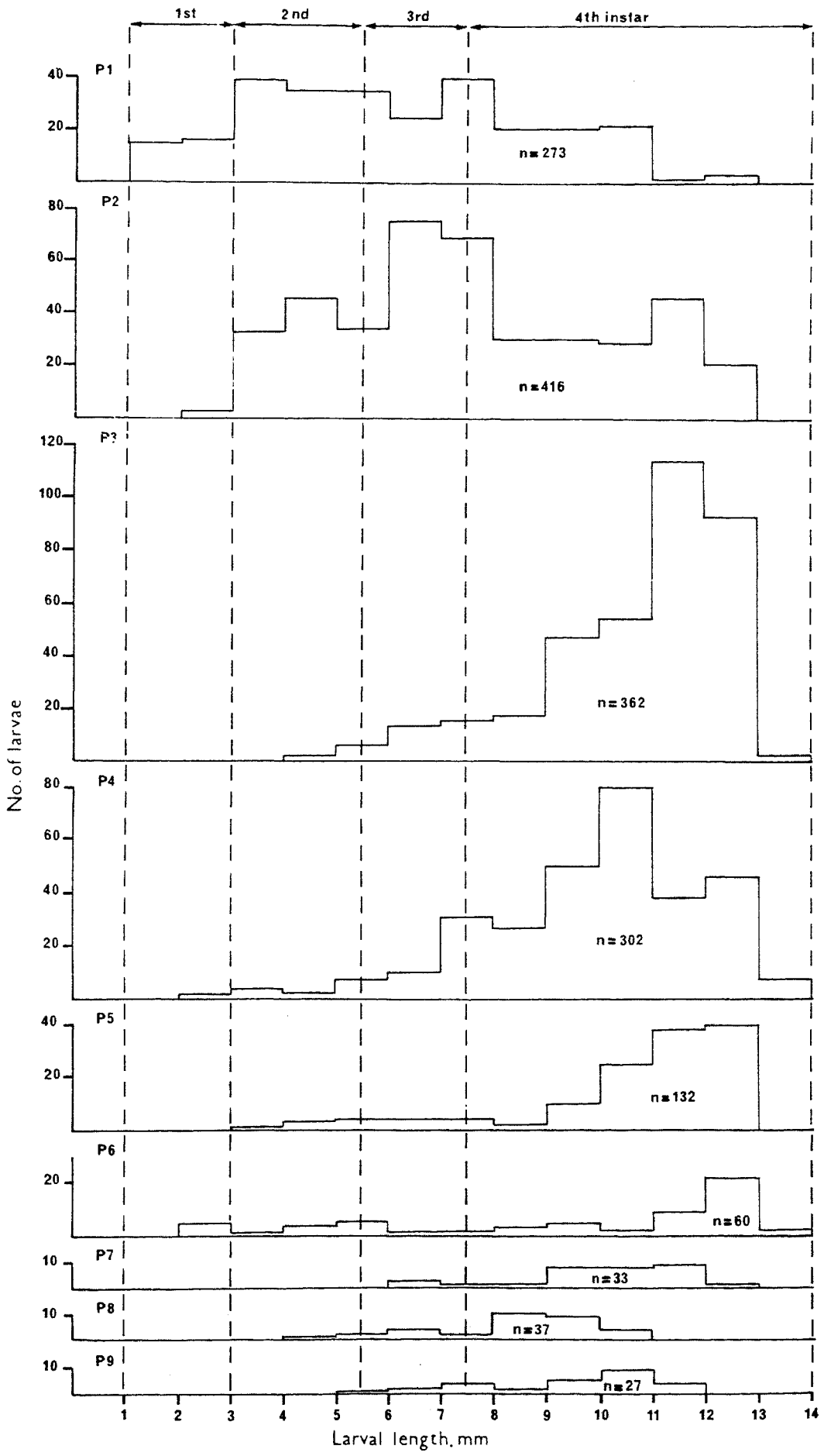

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Fig. 18 B

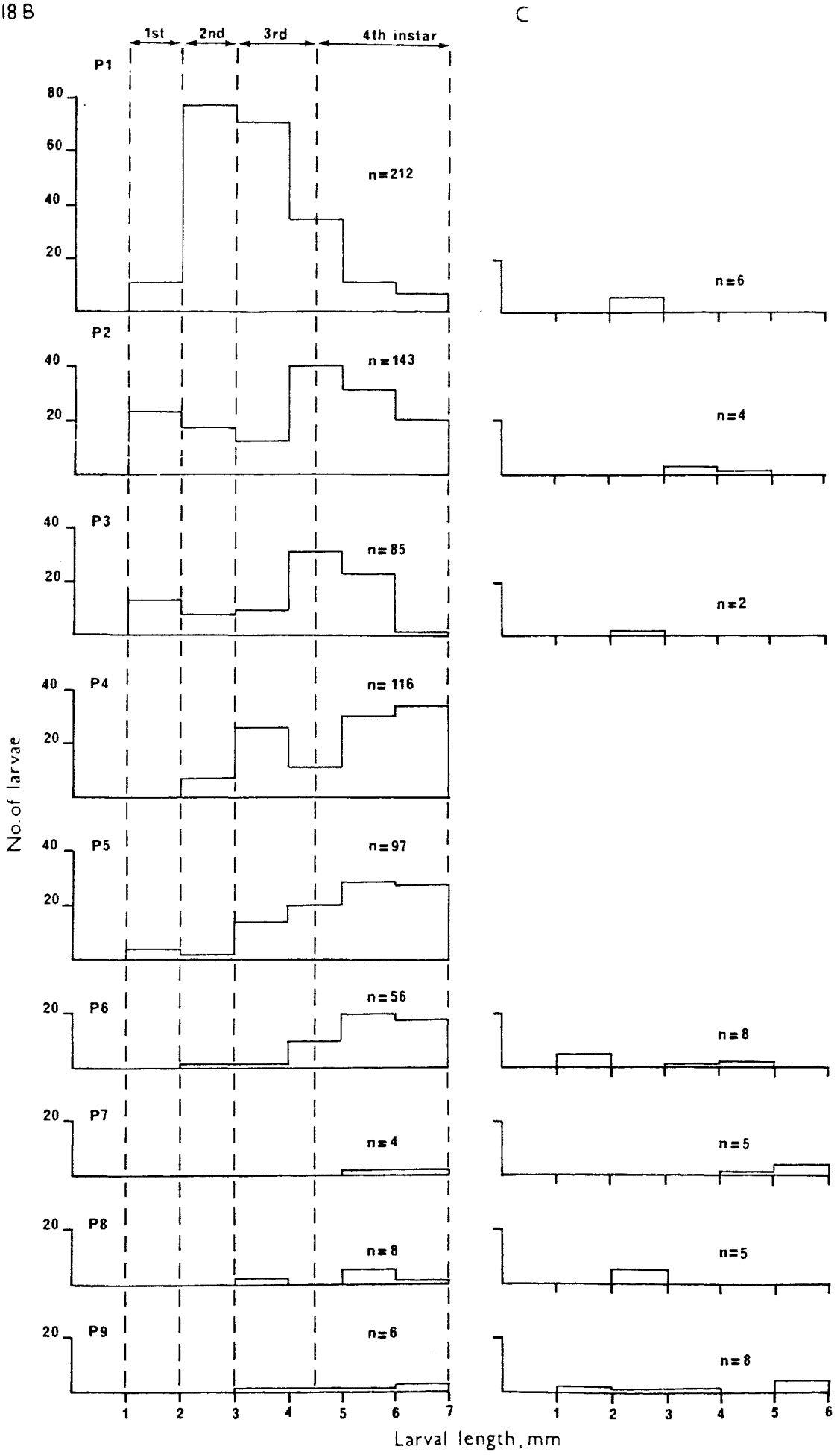

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Figure 19. The effect of pitcher age on the number of dipteran pupae in pitchers

(Standard errors of the mean values are given in Table B, Appendix A).

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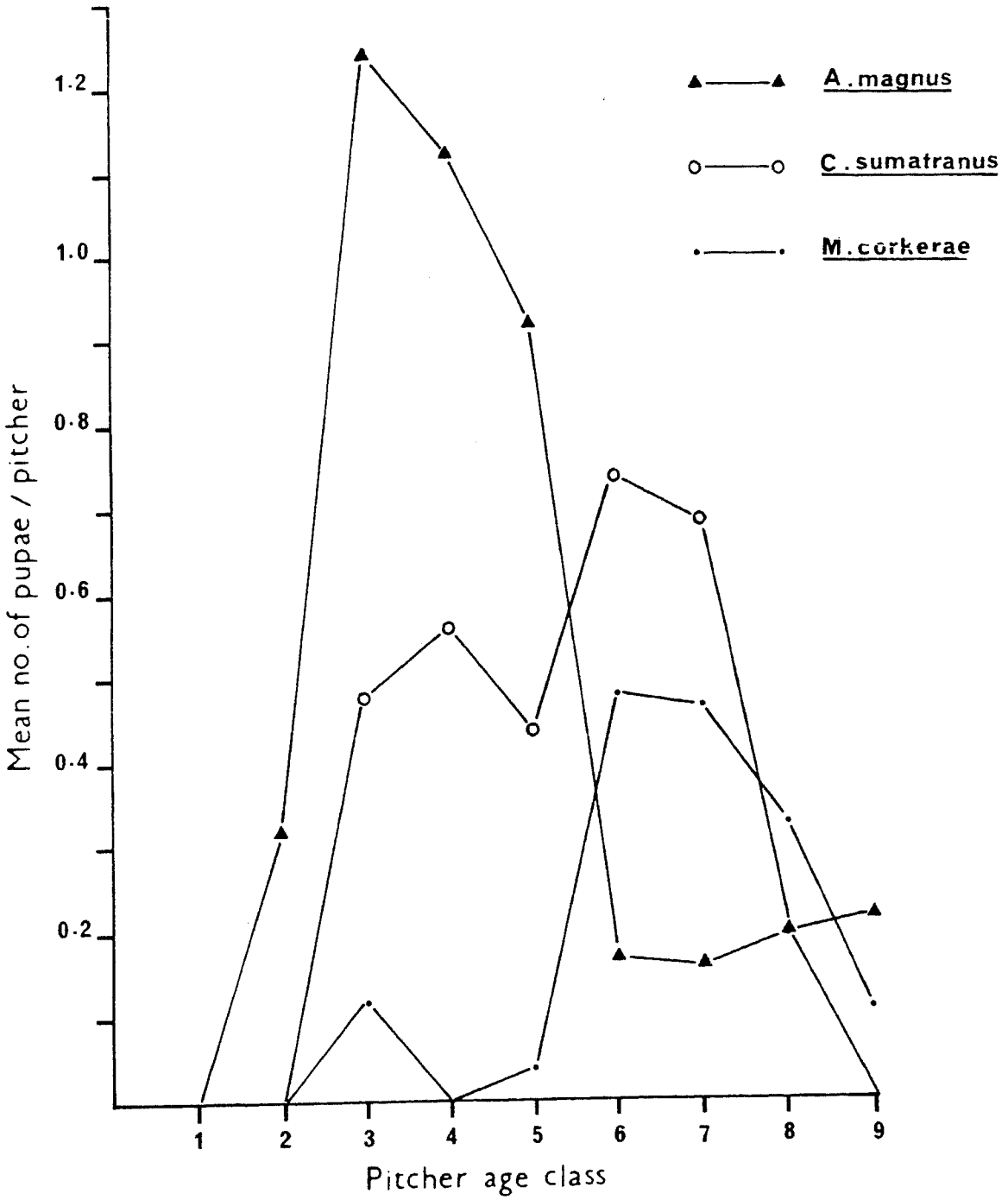

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development of larvae due to starvation. Very little oviposition takes place in older pitchers, but a few first instar larvae were found in pitchers of age classes 4 and 6 (Fig. 18A), so that some eggs must have been laid in these pitchers.

Larvae and pupae of C. sumatranus accounted for a remarkably constant percentage of the total dipteran population in pitcher age classes 1-6, varying only between 25 and 31% (Fig. 17D). The highest percentage of the population accounted for by C. sumatranus occurred in the youngest pitchers of age class 1 (Fig. 17D), because, as for A. magnus, the youngest pitchers are usually selected for oviposition. Culex females appear to be slightly less discriminating about the age of the pitchers which they select, since first instar larvae were present in pitchers of age classes 1-3 (Fig. 18B), and the percentage of pitchers occupied increased to its maximum level in age class 3 (Fig. 17F), indicating that oviposition occurs in pitchers of all three of the youngest age classes. The percentage of the dipteran population attributable to C. sumatranus decreased between age classes 1 and 4 (Fig. 17D), despite continuing oviposition in these pitchers and this may have been as a result of predation by A. magnus larvae since the number of individuals and the percentage of pitchers occupied by A. magnus were at their maximum level in pitchers of these age classes (Fig. 17B; C). In spite of this decline in the percentage of the population accounted for by C. sumatranus, the number of individuals present increased; however, very high values were obtained for the standard error of the mean values (Fig. 17E), indicating that there was great variation in the number of larvae found in individual pitchers. It is possible that the mean values obtained were abnormally high due to the presence of large numbers of larvae in a few pitchers lacking larvae of A. magnus.

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Although larvae of C. sumatranus developed rapidly, with fourth instar larvae being present in pitchers of age class 1 (Fig. 18B), pupae were first found in the much older pitchers of age class 3, whereas pupae of A. magnus were first found in pitchers of age class 2 (Fig. 19). This suggests that larvae of C. sumatranus suffer when in direct competition with A. magnus for limited food resources, so that larval development is delayed due to starvation. There were two peaks of pupation for C. sumatranus, one in pitchers of age class 4 and one in pitchers of age classes 6 and 7 (Fig. 19). Presumably the first peak is formed by the pupation of faster developing larvae hatching out from eggs laid in pitchers of age classes 1-3, while the second is due to the pupation of slower developing larvae, which are only able to complete their development once most of the A. magnus larvae have pupated and emerged reducing competition. A certain amount of oviposition must take place in older pitchers since first instar larvae were found in pitchers of age class 5 (Fig. 18B), so these larvae may also contribute to the second peak of pupation.

Changes in the mean percentage of the total dipteran population accounted for by M. corkerae and in the percentage of pitchers occupied, appear to be virtually mirror images of changes occurring in the population percentage and percentage of pitchers occupied by A. magnus (Fig. 17G; I; A; C), illustrating the strongly negative effect which A. magnus has on M. corkerae due to predation. Thus, the percentage of the dipteran population accounted for by M. corkerae was exceptionally low (0-7%) in pitchers of age classes 1-4, but it increased to 55% in pitchers of age classes 7 and 8 (Fig. 17G), with the maximum number of individuals also occurring in age class 7 (Fig. 17H) when most A. magnus larvae had

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completed their development. Larvae of different sizes (and hence instars) appeared to be fairly randomly distributed in pitchers of different ages (Fig. 18C) suggesting that oviposition is random and is not dependent on pitcher age. It must be noted that many of the Megaselia larvae found were kept for experimental work and were not measured, so that Fig. 18C does not represent all the larvae found. Nevertheless, from the larvae measured, there does not appear to be any distinct pattern in changes in larval size with pitcher age. Since the population levels of M. corkerae only built up in older pitchers, very few pupae were observed in young pitchers and most pupation occurred in the older pitchers of age classes 6 and 7 (Fig. 19).

In addition to the three commonly found Nepenthes diptera, chironomid larvae (?Metriocnemus sp.) were also found in two pitchers, one in age class 7, and one in age class 8. This species is nepenthexene so it may be restricted to older pitchers by an inability to tolerate the low pH and digestive nature of the fluid in young pitchers, or alternatively, it may be restricted to older pitchers for the same reasons as M. corkerae - that is - because of the negative effects of predation by A. magnus larvae.

Anoetidae

The relative proportions of the three anoetid mites found in Nepenthes pitchers in Hong Kong (Zwickia sp., Creutzeria sp. and Anoetid A) changed markedly according to the age of the pitchers being sampled. Zwickia mites occurred in far greater numbers in the pitchers than either Creutzeria or Anoetid A (Fig. 20B; E; H), so that they accounted for a hig percentage of the anoetid population in pitchers of all ages (Fig. 20A),

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Figure 20. Changes in the relative proportions of anoetid mites, in relation to pitcher age

Zwickia	A.	Percentage of the total anoetid population.
	B.	Mean number of individuals per mL.
	C.	Percentage of pitchers occupied.
Creutzeria	D.	Percentage of total anoetid population.
	E.	Mean number of individuals per mL.
	F.	Percentage of pitchers occupied.
Anoetid A	G.	Percentage of the total anoetid population.
	H.	Mean number of individuals per mL.
	I.	Percentage of pitchers occupied.

(Points represent mean values ± I SE).

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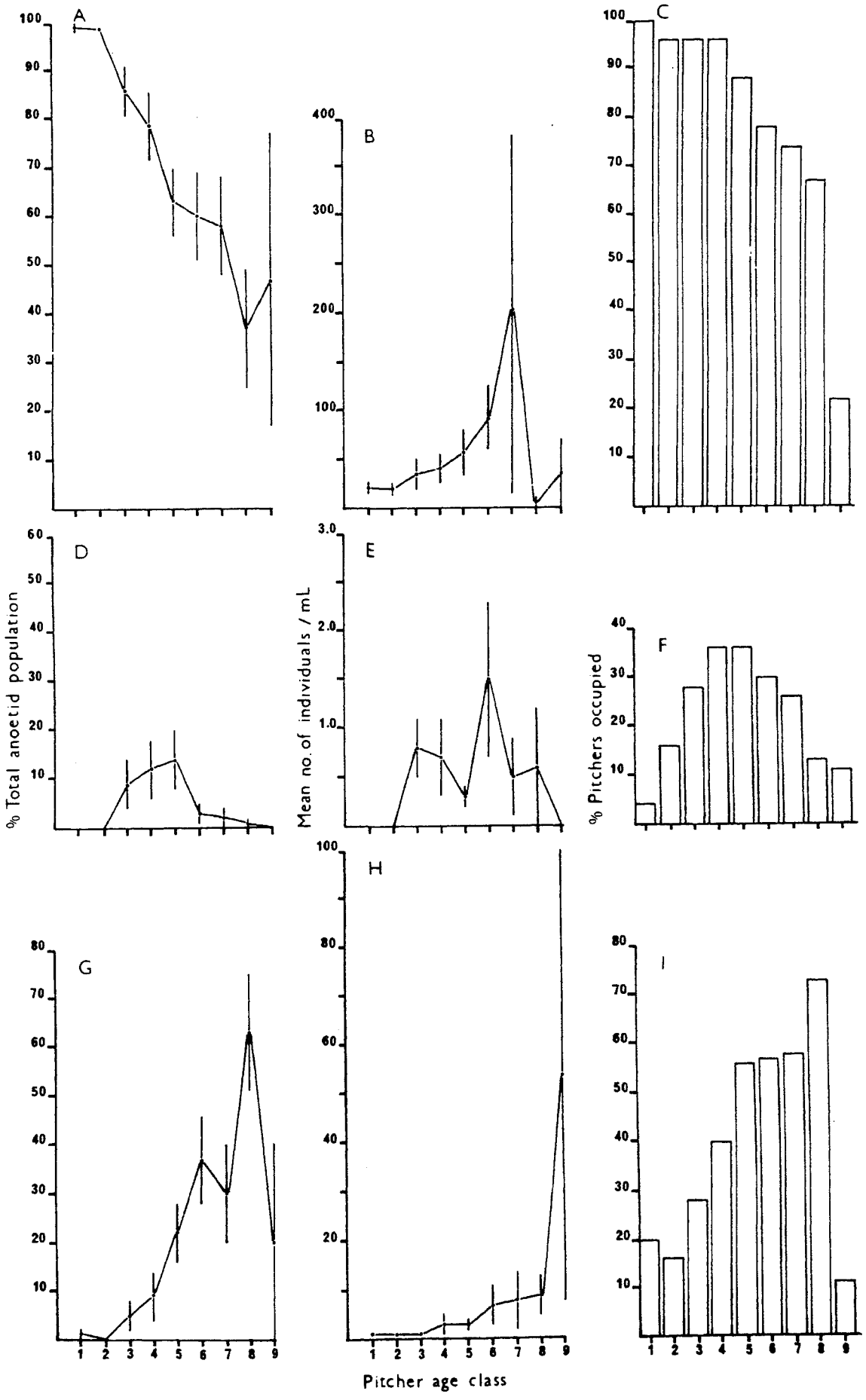

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but in spite of this, definite patterns of distribution depending on pitcher age were apparent for all three species. The youngest pitchers in age classes 1 and 2 contained the highest proportion of Zwickia (Fig. 20A) and virtually all pitchers sampled in these age classes contained mites of this species (Fig. 20C). The percentage of the total anoetid population accounted for by Zwickia and the percentage of pitchers occupied decreased in older pitchers (Fig. 20A; C), suggesting that conditions are most favourable for this species in young pitchers, although the number of mites instead of declining in older pitchers as would be expected, increased, reaching a maximum in pitchers of age class 7 (Fig. 20B). Fewer pitchers were occupied in this age class and the standard error for the mean number of individuals was extremely high (Fig. 20B; C), so it is likely that the mean value was influenced by a few abnormally high population levels. This might result from a few pitchers catching excessive amounts of prey initially, so that large mite populations could be sustained for longer than normal. In this respect it is worth noting that the amount of debris present in pitchers of age class 7 was greater than that recorded for any of the younger pitcher age classes (Fig. 16C).

Creutzeria sp. usually occurred in very small numbers in the pitchers and therefore accounted for a low percentage of the anoetid population in pitchers of all ages (Fig. 20D). Nevertheless, the percentage of the anoetid population attributable to Creutzeria followed a definite pattern, reaching a maximum level in pitchers of age classes 4 and 5 (Fig. 20D). The percentage of pitchers occupied was also at a maximum in these age classes (Fig. 20F). Only one or two mites were present in a few pitchers of the youngest and oldest age classes, resulting in mean values of virtually zero for the number of mites present in pitchers of age classes 1,

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2 and 9, while the maximum number of mites were found in pitchers of age class 6 (Fig. 20E).

While Zwickia was most common in young pitchers and Creutzeria in mature pitchers which had been open for some weeks, Anoetid A was most abundant in pitchers of the older age classes. Thus, the percentage of the anoetid population attributable to Anoetid A, the mean number of mites present and the percentage of pitchers occupied all increased with pitcher age (Fig. 20G; H; I). Pitchers in age class 8 contained the greatest number of mites (the higher mean value for the number of mites present in pitchers of age class 9 has been ignored because it is obviously not representative of the majority of pitchers in this age class) and were the most frequently occupied pitcher age group (Fig. 20H; I).

Colonizing deutonymphs formed the greater part of the populations of Creutzeria and Anoetid A in pitchers of age class 1 (Figs. 21; 22), although the actual percentage of pitchers occupied in this age class was low (Fig. 20F; I), suggesting either that most of the colonizing deutonymphs die, or that relatively few young pitchers are colonized by the deutonymphs. In contrast to Creutzeria and Anoetid A, the percentage of deutonymphs in Zwickia populations in pitchers of age class 1 was low (Fig. 23C), however, the percentage of adults was high (Fig. 23A), indicating that colonizing deutonymphs develop very rapidly into adults under the favourable conditions in these pitchers. Virtually all pitchers in the youngest age classes were occupied (Fig. 20C), demonstrating that colonization is very successful.

In all three species there appeared to be three generations of mites developing from the incoming first generation of deutonymphs in pitchers of age class 1 (Figs. 21; 22; 23). Generally, the percentage of deutonymphs in the populations of Creutzeria and Anoetid A followed fluctuations in the percentages of the other life cycle stages (Figs. 21; 22),

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Figure 21. Fluctuations in the relative proportions of the life cycle stages of Creutzeria sp. in relation to pitcher age

A. Adults

B. Primary nymphs (larvae are also included in this category)

C. Deutonymphs

D. Tritonymphs

Points represent mean values ± I SE.

(The numbers on the graph represent generation numbers; that is - 1 represents the colonizing generation, 2 the second generation etc.)

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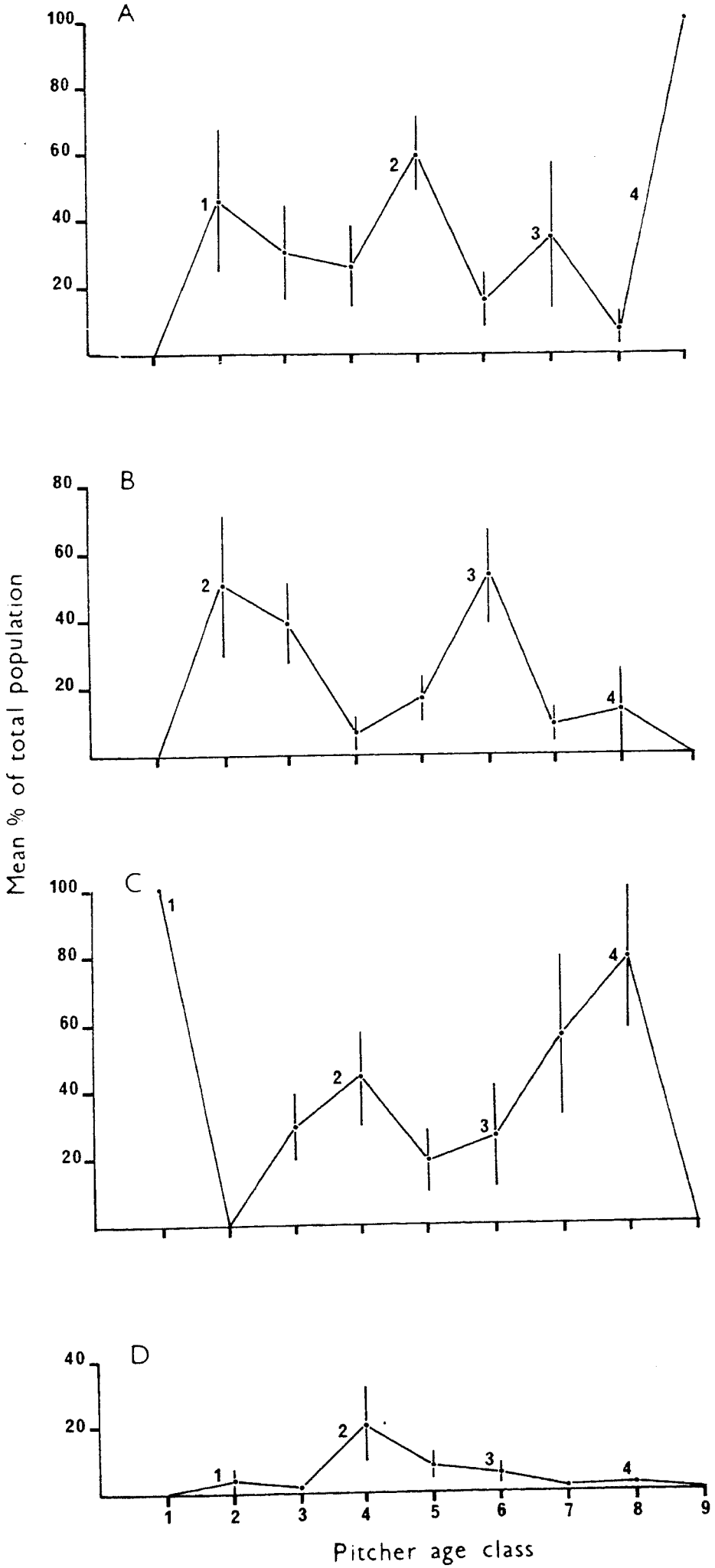

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Figure 22. Fluctuations in the relative proportions of the life cycle stages of Anoetid A, in relation to pitcher age

A. Adults

B. Deutonymphs

C. Larvae and nymphs other than deutonymphs

Points represent mean values ± I SE.

(The numbers on the graph are generation numbers.)

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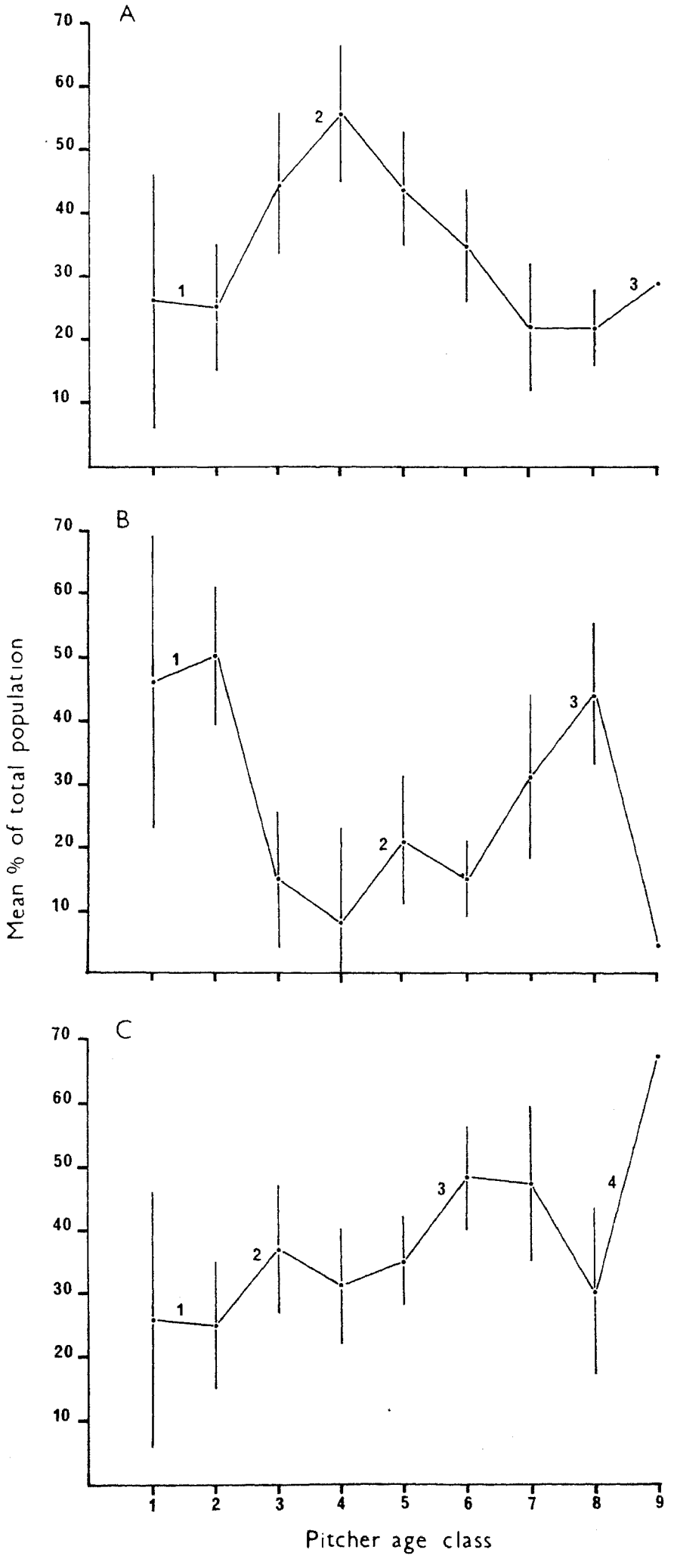

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Figure 23. Fluctuations in the relative proportions of the lifecycle stages of Zwickia sp., in relation to pitcher age

A. Adults

B. Primary nymphs (including larvae)

C. Deutonymphs

D. Tritonymphs

Points represent mean values ± I SE.

(The numbers on the graphs are generation numbers.)

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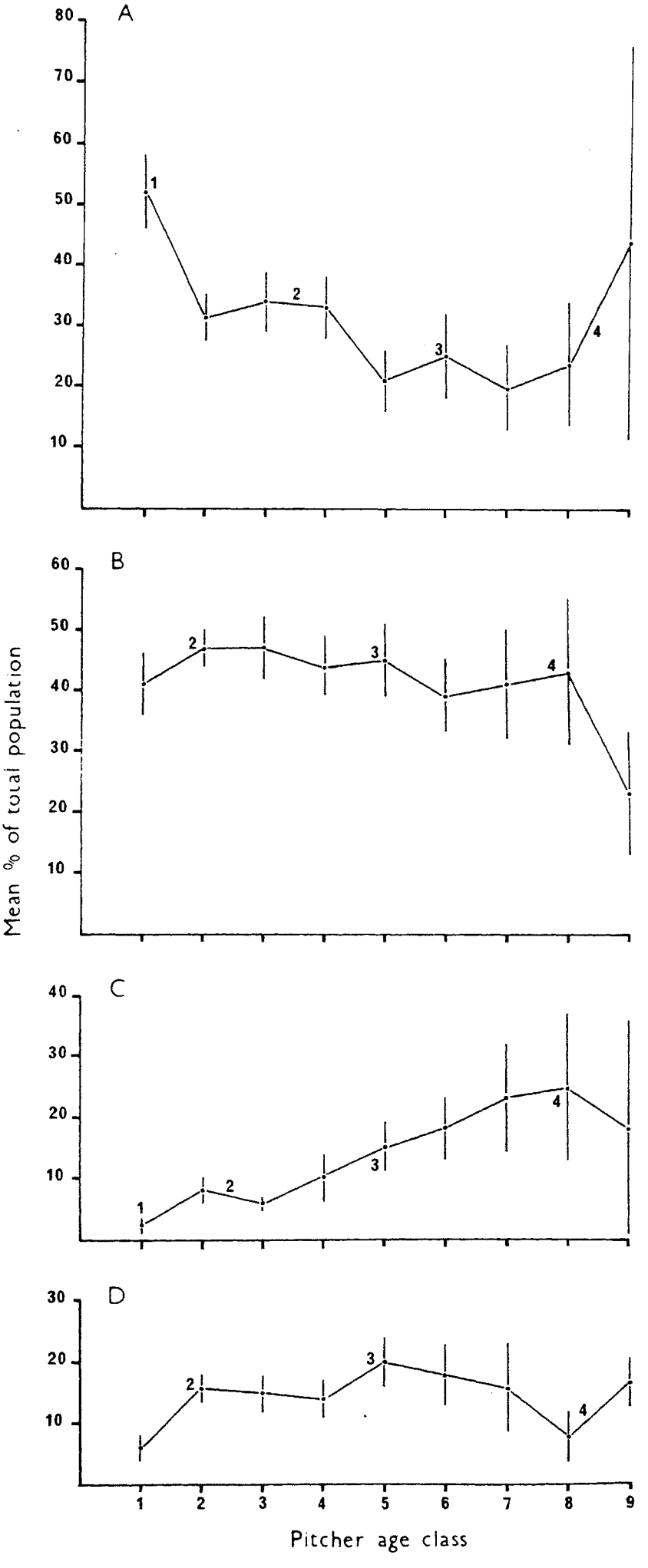

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indicating that many of the individuals automatically pass through the deutonymphal stage. This gave rise to two peaks of deutonymph production, in pitchers of age class 4 and 8 for Creutzeria (Fig. 21C) and 5 and 8 for Anoetid A (Fig. 22B). The second peak was always higher than the first (Fig. 21C; 22B), possibly because conditions in the pitchers were deteriorating so that more individuals developed into deutonymphs. The percentage of deutonymphs of Zwickia did not appear to follow fluctuations in the other life cycle stages in the pitchers, but instead increased steadily with pitcher age (Fig. 23). This indicates that few individuals pass through the deutonymphal stage when conditions are favourable, but that as conditions become more adverse, the percentage of the population developing into deutonymphs increases. Deutonymph production peaked in age class 8 (Fig. 23C), coincident with peaks in the production of Creutzeria and Anoetid A deutonymphs.

Miscellaneous fauna

A number of nepenthexene animals occurred infrequently in the pitchers, but often in great numbers. These animals included rotifers, ciliates, nematodes (Rhabditis sp.), copepods (Phyllognathopus vigueri) and turbellarians (?Catenula). The percentage of pitchers occupied by these animals always increased with pitcher age (Fig. 24). Rotifers and ciliates were occasionally found in young pitchers of age classes 1-3, but they occurred more frequently in old pitchers of age classes 7-9 (Fig. 24A; B), probably because the feeding activities of mosquito larvae usually eliminate them from younger pitchers. Copepods and turbellaria were restricted to old pitchers of age classes 7-9 (Fig. 24D; E) and this is probably due to the inability of the animals to tolerate the low pH

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Figure 24. Distribution of nepenthexene fauna in pitchers of different ages

A. Rotifers

B. Ciliates

C. *Rhabditis sp.*

D. *Phyllognathopus vigueri*

E. Turbellaria - ?*Catenula sp.*

Figure 25. Species diversity in relation to pitcher age

Points represent mean values ± I SE.

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Fig.24

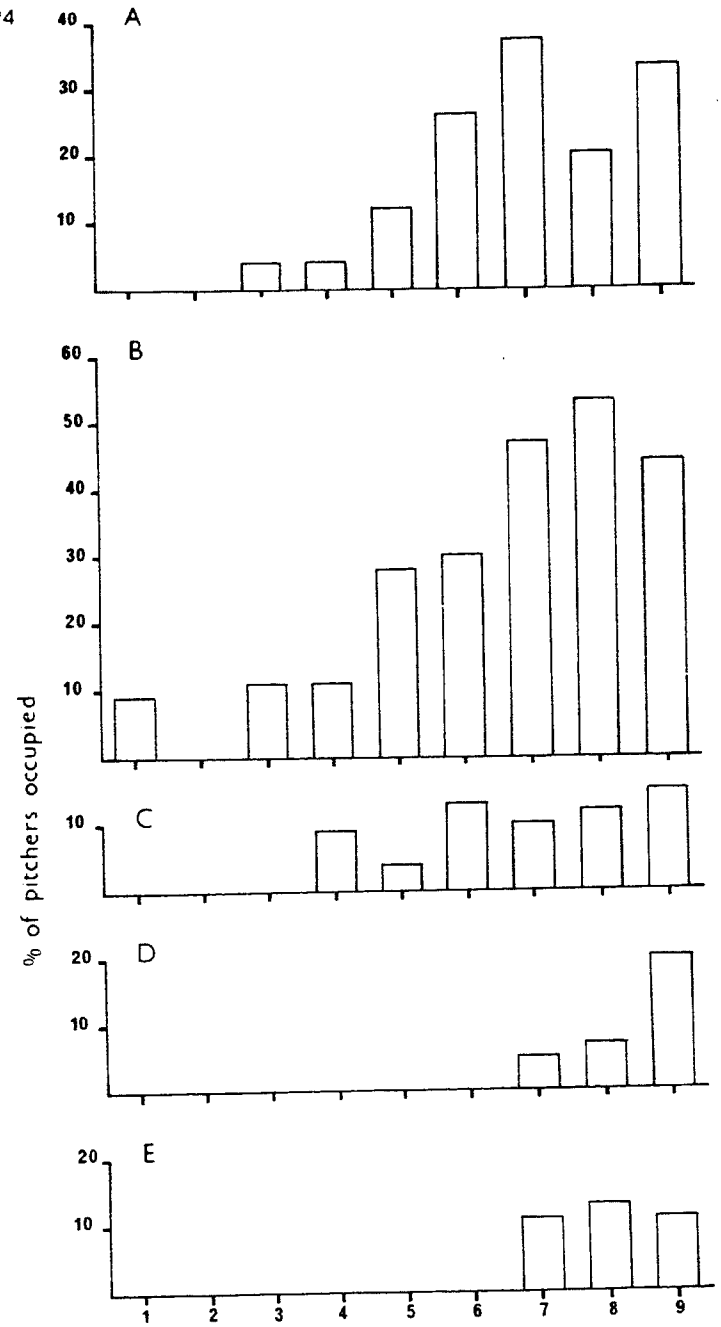
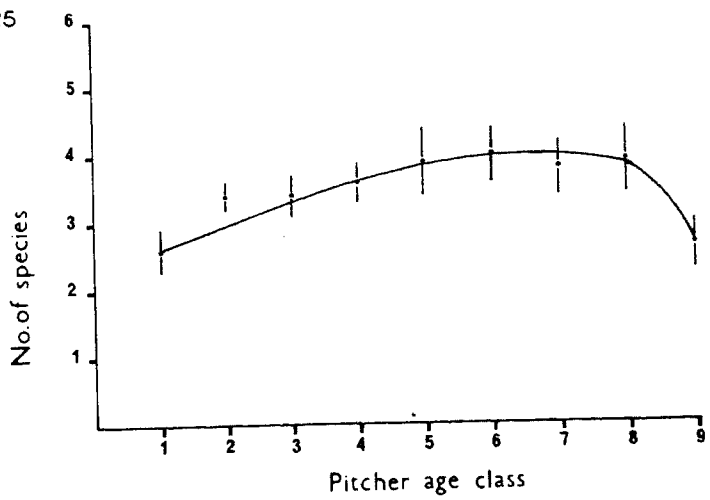


Fig.25



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and digestive nature of the fluid in young pitchers. Nematodes may be restricted to the older pitchers of age classes 4-9 (Fig. 24C), both as a result of predation by mosquito larvae and possibly also because of a limited ability to tolerate undiluted pitcher fluid. A large number of nepenthexene mite species were also found in older pitchers but since there were usually only one or two specimens of each species, occurring in a very small number of pitchers, they were ignored in this study.

As a result of the increase in the number of nepenthexene animals found in older pitchers, species diversity increased with pitcher age, with maximum diversity occurring in pitchers of age classes 5-8 (Fig. 25). Species diversity was relatively low in young pitchers because there are few nepenthebiont animals in Hong Kong which are able to tolerate conditions in the fluid of newly opened pitchers. It was also low in pitchers of age class 9, presumably because there is little food left in the pitchers so that diverse pitcher communities can no longer be supported.

Discussion

Pitchers of age class 2 contained more fluid, at a slightly lower pH than those of age class 1, indicating that fluid secretion takes place for some time after opening of the pitchers. (Had the increased quantity of fluid been attributable to rainwater, the pH would presumably have increased rather than decreased). Pitchers are produced approximately once every 17 days, so the pitchers in age class 2 may range in age from 17-34 days old. Thus, fluid secretion and buffering of the fluid pH must continue for at least one month after opening and is not confined to the first 10 days after opening as the earlier results of the experiment on pH changes in open pitchers suggested (see section II). The

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discrepancy between the two values for the length of time over which secretion takes place, may be explained by the fact that heavy rainfall soon after opening masked the secretion of fluid by pitchers in the first experiment. The pH of pitchers in age classes 3 and above became increasingly more alkaline, confirming that as the pitchers age, their ability to buffer the fluid pH decreases.

Trapping of prey took place largely in pitchers of age classes 1-3, with maximum prey capture occurring in pitchers of age class 2 - that is - approximately two weeks to one month after pitcher opening. The amount of debris in pitcher age classes 4-6 decreased demonstrating that little prey is caught by pitchers more than 50 days old and, that the prey caught initially is gradually decomposed or eaten by pitcher inhabitants. Beaver (1983) observed that the input of prey into pitchers of Nepenthes in Penang appeared to peak approximately 20 days after opening, which agrees well with the results obtained in this study.

Since young pitchers have the greatest trapping ability, they therefore contain the greatest amounts of carrion. As larvae of A. magnus are predominantly carrion feeders, while those of C. sumatranus, although basically filter feeders, also feed on carrion, the adults of both species oviposited preferentially in newly opened pitchers. This allows the larvae to develop rapidly, utilizing the large amounts of carrion entering the pitchers soon after opening. Beaver (1983) notes that although early colonization may be advantageous for carrion and filter feeders, it is likely that colonization by mosquitoes (although not by direct carrion feeders) may continue for two or three months. This is confirmed by the fact that both A. magnus and C. sumatranus occasionally

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oviposited in older pitchers. Adult females of A. magnus appeared to be more discriminating in their choice of pitchers for oviposition than those of C. sumatranus, usually choosing only newly opened pitchers and, since larvae of A. magnus are predominantly direct carrion feeders, this seems to confirm Beaver's observation that oviposition of direct carrion feeders is more likely to be confined to young pitchers.

Gravid females are obviously able to distinguish between pitchers of different ages and this is probably due to a chemical cue located in the pitcher fluid. Thus, Lambrecht (1971) found that females of Uranotaenia nepenthes would not oviposit in artificial pitchers containing water, although they sometimes did so in those containing pitcher fluid. Assem (1959) also noted that eggs of Tripteroides bisquamatus took much longer to appear in freshly opened pitchers washed out and filled with distilled water, than in those containing fresh pitcher fluid. It has already been noted that the pitcher fluid in newly opened pitchers is bright yellow, due to some substance secreted by the pitchers for a short period after opening, and this phenomenon was also noted by Assem (1959). It is therefore possible that the substance responsible for the colouration acts as a chemical cue to Nepenthes diptera. The colouration gradually fades with time, suggesting that the concentration of the substances is decreasing, and this may be the reason why oviposition decreases in older pitchers. Presumably small amounts of the cue may remain in some older pitchers, accounting for late oviposition in these pitchers.

In laboratory studies, it was found that the minimum life cycle length of C. sumatranus was 17 days, while that of A. magnus was 23 days. However, under field conditions, larvae of A. magnus developed more

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rapidly than those of C. sumatranus with pupae being present in pitchers of age class 2, within one month of pitcher opening, while pupae of C. sumatranus were first found in pitchers of age class 3 which were at least fifty days old. The life cycle length of C. sumatranus is therefore more than doubled when the larvae are developing under natural conditions. In the laboratory studies, food was never limiting, whereas in the pitchers, food is probably comparatively scarce and the larvae of both species are also in direct competition with each other for the same food resources. Larvae of A. magnus are much larger and more aggressive than those of C. sumatranus so presumably they are more competitive and therefore monopolize the food resources. As a result A. magnus larvae complete their development more rapidly than those of C. sumatranus.

The number of mosquito larvae in older pitchers was greatly reduced in comparison to young pitchers, as a result of larval mortality due to starvation (and predation in the case of C. sumatranus), and also as a result of pupation and emergence. Nevertheless, a small number of larvae were usually found in old pitchers, due to continuing oviposition at a reduced rate and to delayed larval development if food is scarce. However, as there was a great reduction in the number of predatory mosquito larvae in old pitchers, Megaselia larvae were normally found in pitchers in the older age classes. The distribution of M. corkerae in pitchers of different age classes was virtually a mirror image of that of A. magnus, demonstrating that larvae of A. magnus have a severe negative effect on the population levels of M. corkerae due to predation. Larvae of M. corkerae are detritus feeders and so it would be advantageous for them to be in older pitchers where there has been time for detritus to

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accumulate; however, their predominance in these pitchers appeared to be purely a result of predation and not of specific oviposition habits of the adults, since the females apparently oviposited indiscriminately in pitchers of any age. Detritus feeding chironomid larvae (?Metriocnemus) also appeared to be restricted to pitchers in the older age classes but whether this was due to specific oviposition habits of the females, or to predation was not clear.

The nepenthebiont anoetid mites found in the pitchers showed very pronounced patterns of distribution depending on pitcher age. Zwickia sp., which is a carrion feeder, was found primarily in young pitchers where the mites could take advantage of the large amounts of carrion trapped by the pitchers, while the detritus feeding Creutzeria and Anoetid A were largely restricted to older pitchers where there was some accumulation of detritus. Creutzeria and Anoetid A showed spatial as well as partial temporal segregation, thus Creutzeria was normally found on the fluid surface of mature pitchers, while Anoetid A was found in the base of old pitchers. Creutzeria may be more abundant in mature pitchers because the amount of detritus on the fluid surface is likely to peak soon after the maximum trapping period of the pitchers, whereas the amount of detritus in the base of the pitchers presumably peaks much later when all the debris has settled to the bottom. Interspecific competition for the same food resource must be negligible due to the spatial and temporal segregation of the two species.

It is generally assumed that anoetid mites living in the pitchers are totally dependent on diptera associated with the pitchers for dispersal. However, the results of subsequent experiments (see Chapter 3)

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showed that deutonymphs of both Zwickia and Anoetid A are capable of active colonization of pitchers and that it is also probable that they are able to distinguish between pitchers of different ages. Nevertheless, some phoretic transport of these deutonymphs probably also takes place either via dipteran adults, or via potential prey wandering about on the plants. Creutzeria appears to be totally reliant on passive dispersal and therefore has no control over the age of the pitchers colonized by the deutonymphs, but is instead dependent on the oviposition habits of the dipteran vectors used.

Since A. magnus and C. sumatranus are the most common dipteran inhabitants of the pitchers, phoretic deutonymphs of all three species would usually be carried to young pitchers, with only a few entering older pitchers attached to Megaselia adults or to late colonizing mosquitoes. Zwickia and Anoetid A deutonymphs, phoretic on potential prey animals, would also tend to be transported to young pitchers since these are the most attractive to insects. While these conditions are ideal for Zwickia in that all deutonymphs, whether actively or passively, are colonizing pitchers of the most suitable age group, the same is not true for Creutzeria and Anoetid A since there is little food available for mites of these species in young pitchers. In actual fact, few of the youngest pitchers were occupied by either of these species, which in the case of Anoetid A suggests that very few deutonymphs are transported phoretically and that most instead actively colonize pitchers of a more suitable age. If this is so, then the peaks of deutonymphs noted for Anoetid A in pitchers of age classes 5 and 8 may be composed of colonizing deutonymphs rather than of deutonymphs developing from mites already present in the pitchers. It would make sense for colonizing deutonymphs to enter

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pitchers before the food supply peaks, so that populations would already be established and able to rapidly exploit increasing food resources. It is therefore possible that the first peak in pitchers of age class 5 is largely due to incoming deutonymphs, while the second, larger peak in pitchers of age class 8 is a response of the mite population already present to deteriorating conditions in the pitchers.

The highest proportions of deutonymphs of all three species were found in pitchers of age class 8 and this probably is due to the fact that environmental conditions within the pitchers deteriorate as they age and near the end of their lifespan, so that the number of anoetid primary nymphs passing through the deutonymphal stage increases. Food availability is probably the most important factor regulating deutonymph development, thus Hunter and Hunter (1964) found that the greatest number of deutonymphs of Anoetus hughesi were found in old pitchers of Sarracenia where only insect exoskeletons remained, so that the food supply must have been almost nonexistent. The proportion of Zwickia deutonymphs increased very steadily with pitcher age, reaching a maximum in pitchers of age class 8 and it is likely that the decreasing availability of carrion was the major factor causing this increase. The high proportion of deutonymphs in pitchers of age class 8 presumably facilitates dispersal of the anoetids to new pitchers before death of the pitcher already occupied, either by active movement or by phoretic transport via late emerging mosquitoes or Megaselia adults.

As Creutzeria is thought to be totally dependent on dipteran vectors for dispersal, it is difficult to explain why so few of the youngest pitchers were occupied by this species. Possibly only those deutonymphs

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which are transported to pitchers of the correct age give rise to colonies of mites, while the majority which are carried to young pitchers die or fail to develop. This seems unlikely as the deutonymph is a resistant non-feeding stage and it is therefore difficult to see why it should die instead of remaining quiescent until conditions became favourable. However, it was impossible to rear the mites in the laboratory so it appears that they require very specific conditions for development. This may be one reason why the abundance of the mites overall was so much more limited than the other two species of anoetids. The only other possible explanations for the low percentage of young pitchers occupied are that some predator of the species, found solely in young pitchers, eliminates the mites from these pitchers (however, the mites did not appear to have any predators and in any case there are no animals which are found solely in young pitchers), or that the deutonymphs are able to actively colonize pitchers of the correct age. The latter explanation is also unlikely as all evidence points to the fact that the deutonymphs are passively dispersed (see Chapter 3).

Nepenthexene animals such as protozoa, rotifers, nematodes, turbellaria and crustacea were rarely found in young pitchers, but occurred most commonly in pitchers of the oldest age classes. Beaver (1979b) also noted that protozoans, rotifers, nematodes and crustaceans were usually only found in old pitchers which had already been abandoned by insects and arachnids. In the case of protozoa, rotifers and possibly also nematodes, this is probably because populations in younger pitchers are eliminated by the feeding activities of mosquito larvae, whereas it is likely that the turbellarians and copepods are restricted

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to old pitchers because they are unable to tolerate the environmental conditions in young pitchers.

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Chapter 3

The effect of pitcher size on the composition of the pitcher fauna

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Introduction

Nepenthes pitchers vary greatly in size depending both on the species of *Nepenthes* and on the developmental state of the plant on which the pitchers are borne. In Hong Kong, open pitchers of *N. mirabilis* range in length from 1.5 to 22.0cm. The seedlings which are in the form of a small rosette, bear minute pitchers which are fully functional with digestive glands in their cavities. As the rosettes grow, successive leaves and pitchers become gradually larger until the plant is mature and the stem begins to elongate and climb. Pitchers on these mature plants gradually attain the mature form (opening outwards away from the plant and with reduced or absent wings) and reach maximum size. Different environmental conditions may also affect pitcher size to some extent, thus Kurata (1976) noted that the maximum size of *N. mirabilis* pitchers growing on Mount Kinabalu in East Malaysia was 16cm; however, the developmental state of the plants is the most important factor regulating pitcher size.

The pitcher fauna of *N. mirabilis* in Hong Kong is dominated by the mosquitoes *Armigeres magnus* and *Culex sumatranus*, both of which have predatory larvae which may alter the composition of the communities of individual pitchers. Larvae of *A. magnus* in particular are very aggressive and, when they are present, they often have a significant negative effect on the population levels of other dipteran species in the pitchers. The mouths of the pitchers in the smallest size ranges are of very narrow diameter, so it is possible that adults of both species (and particularly those of *A. magnus* which are comparatively large) may be unable to enter these pitchers to oviposit, resulting in the exclusion of predatory mosquito larvae from the smallest pitchers. The mouths of

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pitchers in the smallest size ranges are also very close to ground level so it would be easy for animals living in the environment around the pitchers to enter the pitchers and form part of the nepenthexene fauna. As a result, the communities of the smallest pitchers may be substantially different to those of larger pitchers.

Since there is to my knowledge no published literature dealing with the effect of pitcher size on the composition of pitcher communities, this aspect of community ecology was studied by sampling a series of pitchers ranging in length from 2 to 20cm. Comparisons were then made between the occurrence and abundance of different animals in pitchers of varying size.

Materials and Methods

Ten pitchers from each of the following size classes: 2-3, 3-4, 4-5 ..... 10-11, 12-13, 14-15, 17-18 and 20-21cm in length were sampled from site 4 in June. This site was chosen because the plants had been cut back six months prior to sampling and they had regenerated into large rosettes so that there were numerous pitchers of the smaller size classes available for sampling, as well as larger pitchers from plants which had escaped previous damage. All pitchers sampled were of approximately the same age (mature) in order to minimize differences in the composition of the pitcher fauna due to pitcher age. Mature pitchers (that is, those corresponding approximately to pitcher age class 4 of the faunal succession study) were chosen because they were most likely to contain all the elements of the normal pitcher fauna together. Individual pitchers were selected for sampling using external appearance as a guide to pitcher age. As far as possible all pitchers were taken from ground

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level in order to minimize any differences in the pitcher fauna which might result from the pitchers being at varying heights from the ground. This was virtually impossible in the case of pitchers in the largest size classes of 17 and 20 since these were invariably found on climbing plants and not on the rosettes, but pitchers sampled from these size classes were never more than 50cm off the ground. Sampling of all 130 pitchers was carried out within a period of 2 weeks to avoid any seasonal variation in the abundance of different animals. Sampling methods were the same as those used previously, except that pitchers in the smaller size classes were removed from the plants and taken to the laboratory for study since it was impossible to remove all the contents while they were attached to the plant. In the laboratory, all samples were sorted live and the animals were counted and identified as far as possible.

Data from this series of pitchers were used, together with data from all those pitchers sampled in previous investigations, to construct histograms for each species showing the percentage of pitchers in each size class occupied. However, the mean number of individuals of each species per mL of pitcher fluid was calculated for each size class only using the data obtained by sampling pitchers of different sizes at the same time. Pitchers sampled in previous investigations could not be used for this purpose since they were sampled from different sites at different times of the year and were of disparate ages.

Results

Diptera

Larvae of *A. magnus* were generally restricted to pitchers larger than 6cm in length, although on one occasion larvae were found in a

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pitcher of size class 4 (Fig. 26A). The average length of an A. magnus adult is 7mm (excluding antennae) while the mean wingspan is 8mm, thus as pitchers in size classes 2 and 3 have mouth diameters of less than 6mm (Table 7) it would clearly be difficult, if not impossible, for an adult female to enter pitchers in these size classes in order to oviposit. Pitchers of 4-5cm in length have mouth diameters ranging from 5-10mm (Table 7) so it would just be possible for an adult female to enter larger pitchers in this size class, accounting for the presence of larvae in one pitcher in this class. The minimum mouth diameter of pitchers in size classes 6 and above is 7mm (Table 7) so that there is no restriction on the entrance of A. magnus females to pitchers of 6cm or more in length. The percentage of pitchers in each size class occupied by A. magnus increased with pitcher size (Fig. 26A), probably as a result of increased ease of access and also due to the fact that large pitchers are more readily visible than small ones which are often hidden amongst foliage and detritus. Relatively few individuals of A. magnus were found in pitchers of size classes 6-10 (Fig. 26B) because of the small volume of fluid present (Fig. 27A) and hence limited available space, and also because very limited amounts of debris were present in these pitchers (Fig. 27B) to provide food for the developing larvae. The mean number of individuals per mL of fluid was greatest in pitchers of size class 14 (Fig. 26B), presumably because these pitchers contained large quantities of food in the form of insect debris (Fig. 27B) and could therefore support large populations of larvae. Although the largest pitchers would be expected to contain the most insect debris by virtue of the fact that they have the largest attraction zone for potential prey, as well as the largest internal volume, it was found that pitchers in the size range 12-14cm

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Figure 26. Distribution and abundance of diptera according to pitcher size

A. magnus	A. Percentage of pitchers occupied.
	B. Mean number of individuals per mL.
C. sumatranus	C. Percentage of pitchers occupied.
	D. Mean number of individuals per mL.
M. corkerae	E. Percentage of pitchers occupied.
	F. Mean number of individuals per mL.
?*Metriocnemus*	G. Percentage of pitchers occupied.
	H. Mean number of individuals per mL.

(Points represent mean values ± I SE)

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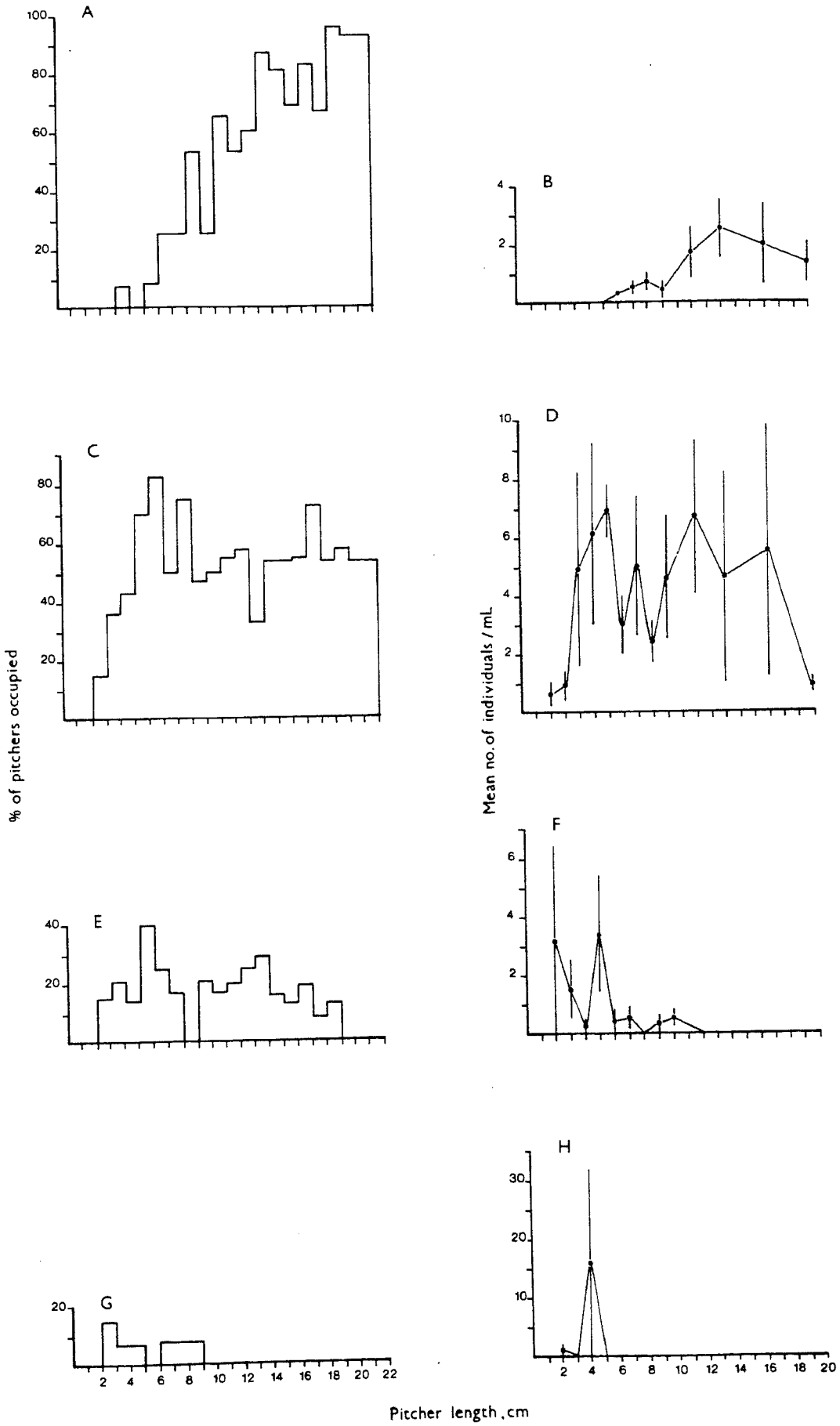

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Table 7

Pitcher length and mouth diameter in different size classes

Pitcher size	Pitcher length (cm)	Pitcher mouth diameter (mm)	Total no. of pitchers sampled
2	2-3	2-3	13
3	3-4	5-6	14
4	4-5	5-10	14
5	5-6	5-11	10
6	6-7	7-12	12
7	7-8	8-15	12
8	8-9	12-20	12
9	9-10	12-20	19
10	10-11	15-25	24
11	11-12	15-25	20
12	12-13	15-30	40
13	13-14	15-32	42
14	14-15	20-32	76
15	15-16	20-35	54
16	16-17	20-37	42
17	17-18	25-37	40
18	18-19	25-40	24
19	19-20	25-40	24
20	20-22	27-50	13

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Figure 27. Changes in fluid volume and amount of debris in pitchers of varying size

A. Fluid volume

B. Wet weight of debris

(Points represent mean values ± I SE)

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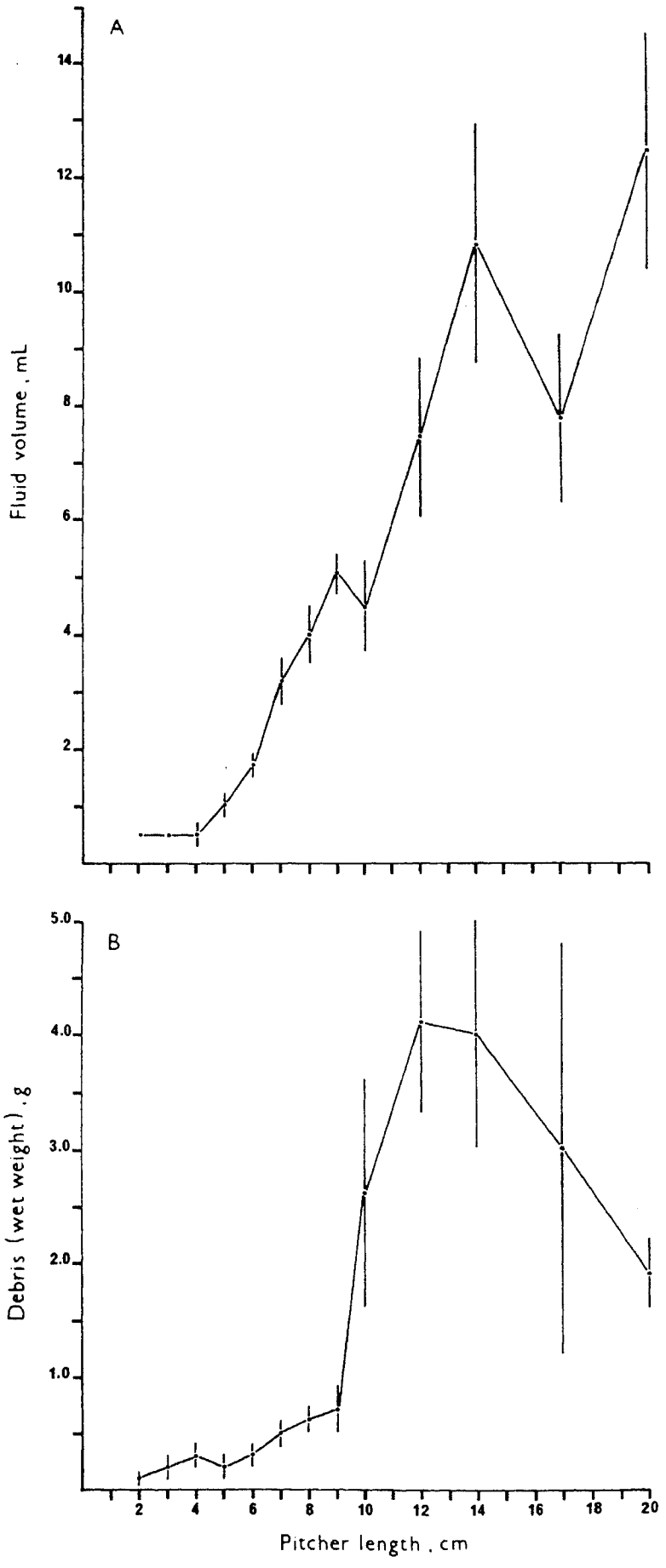

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contained the greatest amounts of insect debris (Fig. 27B). This may be explained by the fact that these pitchers were at ground level and they attracted vast numbers of ants which often half-filled the pitcher interior, while the larger pitchers in size classes 17 and 20 were above ground level and thus were more dependent on flying insects than on ants for prey. Although some of the flying insects caught by these pitchers were relatively large, the actual number caught was small, so that the weight of debris did not approach that of ground level pitchers.

Adults of C. sumatranus are much smaller than those of A. magnus, with an average body length of 4mm and an average wingspan of 5mm. Pitchers in size class 2 had a mouth diameter marginally smaller than the average size of a C. sumatranus female, but pitchers in all other size classes had mouth diameters of sufficient size to allow the entry of the females (Table 7). As a result, pitchers of all size classes contained larvae of C. sumatranus (Fig. 26C). Although the mouth diameter of pitchers in size class 2 was smaller than the wingspan and body length of adults of C. sumatranus, a few of these pitchers were occupied by Culex larvae (Fig. 26C) demonstrating that the adults are capable of crawling through very small spaces to oviposit. The number of larvae present in pitchers of different size classes fluctuated widely and was very variable even within pitchers of the same size class (Fig. 26D). Nevertheless, the greatest number of larvae were found in pitchers of size class 6 (Fig. 26D), and the percentage of pitchers occupied was also at its maximum level in this size class (Fig. 26C), despite the fact that the fluid volume and amount of insect debris available as food in these pitchers was considerably less than in larger pitchers (Fig. 27A; B). The decrease in the number of individuals, and in the number of pitchers occupied in the

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larger size classes, was presumably due to the fact that most of these pitchers were occupied by A. magnus larvae, which reduce the number of Culex larvae present both through predation and through competition for the same food resource. A. magnus larvae were more or less excluded from pitchers less than 7cm in length, and thus, in these pitchers the populations of C. sumatranus could build up in the absence of predation and competition for limited food resources.

Larvae of Megaselia corkerae occurred in pitchers of all size classes except the largest (Fig. 26E). The predatory larvae of A. magnus greatly deplete the populations of Megaselia in pitchers, and thus the absence of Megaselia from pitchers in the largest size classes was probably due to the fact that almost all these pitchers contained A. magnus larvae (Fig. 26A). Although larvae of C. sumatranus also prey on Megaselia, they have a much less significant effect on the population levels of this species than A. magnus, thus the greatest numbers of M. corkerae larvae were found in pitchers of size classes 2 and 5 (Fig. 26F) despite the presence of relatively large numbers of C. sumatranus larvae in the latter (Fig. 26D). In larger pitchers Megaselia larvae occurred only in individual pitchers which did not contain larvae of A. magnus.

Chironomid larvae (?Metriocnemus) were also found in the pitchers sampled but they occurred only in pitchers smaller than 9cm in length (Fig. 26G), with the maximum number of larvae occurring in pitchers of size class 4 (Fig. 26H). Chironomid larvae were never found in pitchers containing mosquito larvae so presumably they are confined to small pitchers by the predatory activities of both C. sumatranus and A. magnus, which occupy almost all of the larger pitchers. Because most pitchers, even those in the smaller size ranges, contain larvae of one or other of

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the two culicines, a very small percentage of pitchers were occupied by chironomid larvae, although sometimes large numbers of larvae were found in those pitchers which were inhabited by this species (Fig. 26H).

Acarina

Sarcoptiformes

Anoetidae

Virtually all pitchers in every size class contained mites of *Zwickia sp.* with very little variation in the percentage of pitchers occupied in different size classes (Fig. 28A), although the number of mites in pitchers of different size classes varied considerably (Fig. 28B); thus large numbers of mites were found in pitchers of size classes 2-6 and 10-12, while relatively few individuals were found in pitchers of other sizes (Fig. 28B). The most interesting fact to emerge from this study was that *Zwickia* mites were often found in small pitchers which contained no evidence that any of the normal dipteran fauna had been present at any time. Other animals which are not part of the pitcher fauna, which fall into the pitchers and drown, are unlikely to act as vectors for anoetid deutonymphs because they would have to enter one pitcher and emerge unscathed to visit another, which must happen very rarely if at all; therefore the mites present in pitchers lacking any dipteran fauna must have entered the pitchers by themselves. Subsequent examination of a number of open, undisturbed pitchers revealed *Zwickia* deutonymphs climbing up the internal walls and crawling about on the pitcher lids and exteriors. A number of pitchers about to open were also examined and many of them were found to have *Zwickia* deutonymphs attached to the pitcher peristome. It therefore seems certain that the deutonymphs are able to actively

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Figure 28. Distribution and abundance of anoetid mites, in relation to pitcher size

Zwickia	A.	Percentage of pitchers occupied.
	B.	Mean number of individuals per mL.
Anoetid A	C.	Percentage of pitchers occupied.
	D.	Mean number of individuals per mL.
Creutzeria	E.	Percentage of pitchers occupied.
	F.	Mean number of individuals per mL.

(Points represent mean values $\pm$ I SE)

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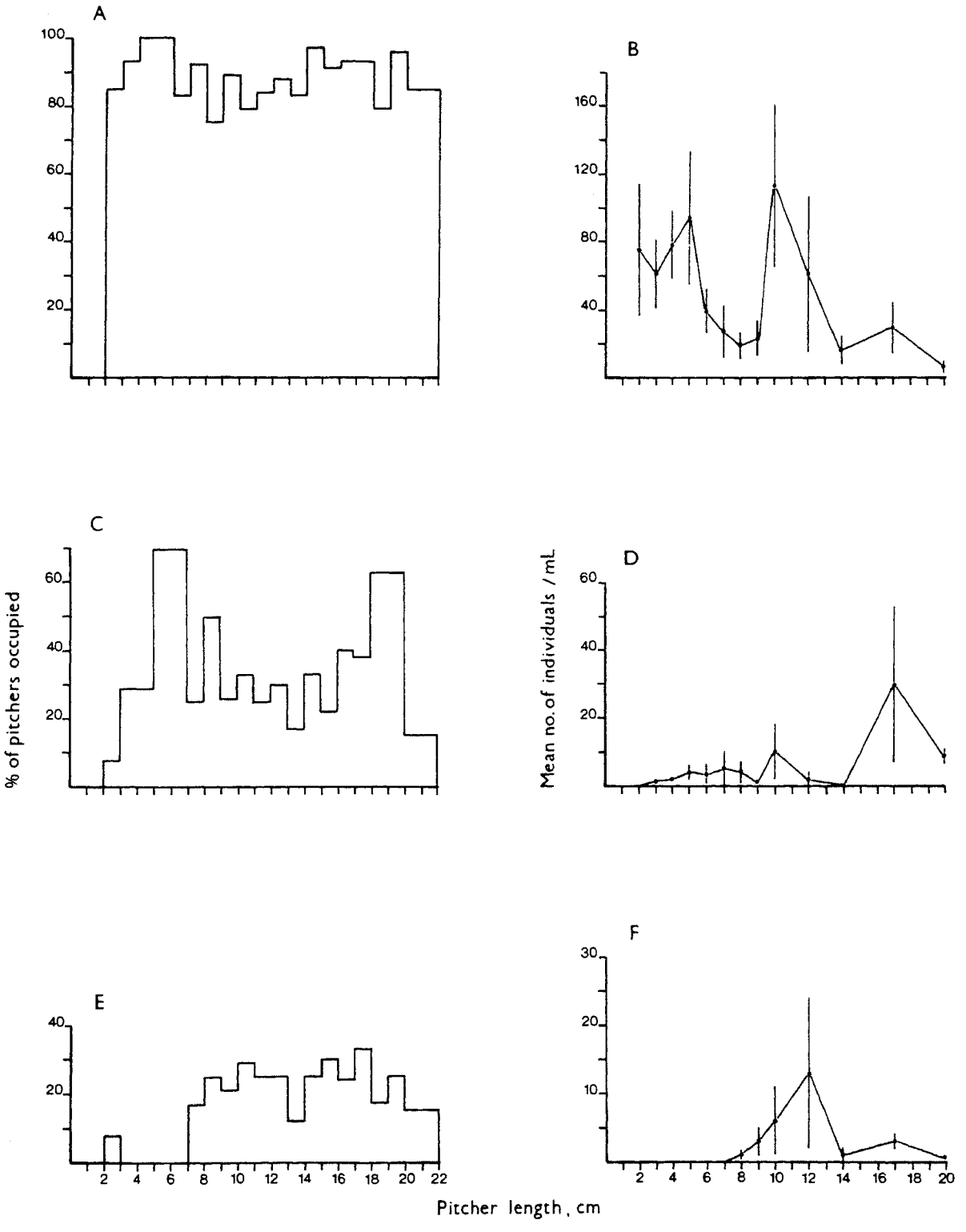

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colonize pitchers without relying on other animals as vectors. Undoubtedly Nepenthes diptera must sometimes act as vectors (although examination of adult diptera never revealed any attached deutonymphs) and walking or crawling animals may also pick up deutonymphs on the external surfaces of the pitchers, but the mites are not totally reliant on phoretic transport for dispersal as has been thought previously. The large number of mites found in pitcher size classes 2-6 (Fig. 28B) may thus be explained by the fact that these pitchers are all small and close together in rosettes at ground level, so that it would be relatively easy for large numbers of deutonymphs to crawl from one pitcher to another, resulting in large mite populations in these pitchers. The greater the size of the pitchers, the more difficult it must be for deutonymphs to transfer from one pitcher to another, so that fewer deutonymphs are likely to colonize large pitchers and they may rely mostly on vector transport in this case. The large number of mites found in pitcher size classes 10 and 12 (Fig. 28B) may be a result of the fact that these pitchers contained large quantities of insect debris (Fig. 27B) which would support a large population of mites, and as the debris was largely composed of ants it is also possible that large numbers of deutonymphs entered the pitchers initially, carried on ants which had picked them up while wandering about on the plants before falling into the pitchers.

Mites of Anoetid A were also found in small pitchers which did not contain any diptera, therefore it seems likely that deutonymphs of this species are similarly able to actively colonize pitchers. There were two main peaks in the percentage of pitchers occupied by this species, one in size class 6 and one in size class 19 (Fig. 28C); however, the actual number of individuals in size class 6 was very small and the maximum number

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of mites were instead found in the large pitchers of size class 17 (Fig. 28D). This may be a result of the fact that there is more space available in the larger pitchers as well as more food, which would support larger mite populations. However, Anoetid A deutonymphs are much smaller than those of Zwickia, so active movement from pitcher to pitcher must be much more difficult for this species and it is therefore possible that they are more reliant on vector transport for dispersal. If this is the case, then the large percentage of pitchers occupied and the large number of mites in pitchers in the bigger size ranges can also be explained by the fact that a high percentage of these pitchers were occupied by Nepenthes diptera which would act as the major vectors.

Creutzeria sp. deutonymphs were never observed climbing up and out of pitchers and the mites were never found in pitchers without dipteran larvae and were mostly restricted to pitchers larger than 7cm in length (Fig. 28E). This suggests that they rely totally on Nepenthes diptera for dispersal and in particular on adults of A. magnus, since larvae of this species were also usually absent from pitchers less than 7cm in length (Fig. 26A). The percentage of pitchers occupied by Creutzeria was generally much lower than for either Zwickia or Anoetid A (Fig. 28E) probably because total reliance on other animals for dispersal is much less effective than a combination of both active and passive dispersal. The largest populations of these mites were found in pitcher size classes 10 and 12 (Fig. 28F) which may be related to the large amount of debris available in these pitchers, (Fig. 27B).

Oribatei

Twelve genera of oribatid mites from eleven different families were found living in pitchers of all sizes, although most genera were confined

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Figure 29. Distribution and abundance of oribatid and mesostigmatid mites, in relation to pitcher size

A. Percentage of pitchers occupied.

B. Mean number of individuals per mL.

i. *Galumna sp.* (Galumnidae)

ii. *Carabodes sp.* (Carabodidae)

iii. *Neoliodes sp.* (Liodidae)

iv. *Hoplophthiracarus sp.* (Phthiracaridae)

v. *Peloribates sp.* (Haplozetidae)

vi. *Rostrozetes sp.* (Haplozetidae)

vii. *Zetorchestes sp.* (Zetorchestidae)

viii. *Zygoribatula sp.* (Oribatulidae)

ix. *Paralamellobates sp.* (Oribatellidae)

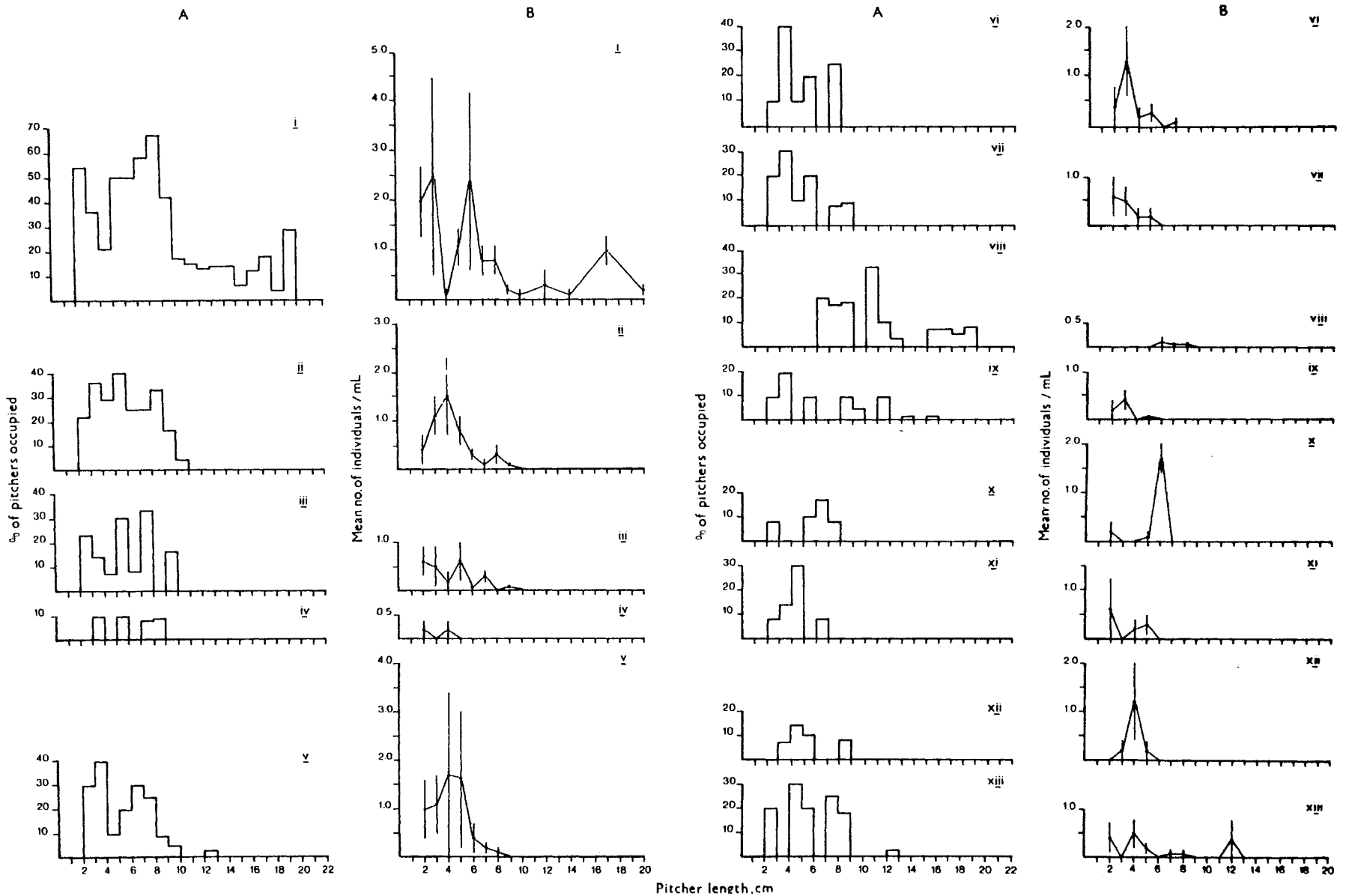
x. *Oppia sp.* (Oppiidae)

xi. *Hermannia sp.* (Hermanniidae)

xii. *Tetracondyla sp.* (Otocepheidae)

xiii. *Deraiophorus sp.* (Mesostigmata, Uropodidae)

Points represent mean values ± I SE


A
B
A
B
% of pitchers occupied
Mean no.of individuals / mL
% of pitchers occupied
Mean no.of individuals / mL
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
xiii
Pitcher length.cm

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to pitchers less than 10cm in length. The mites which occurred most frequently were individuals of Galumna sp. which were found in pitchers of all sizes, often occupying a large percentage of the pitchers sampled (Fig. 29A; i). Most of the other oribatid mites were found only in pitchers under 10cm in length, with the maximum percentage of pitchers occupied and maximum number of individuals occurring in pitchers in the smallest size classes (Fig. 29A; B). Mites belonging to the genera Zygoribatula, Paralamellobates and Galumna were the only oribatid mites found in pitchers larger than 12cm in length (Fig. 29A; i; viii; ix), although, as for the other oribatid mites, the maximum number of individuals were found in pitchers in the smallest size classes (Fig. 29B; i; viii; ix). In general, the percentage of pitchers in each size class occupied by each mite species was relatively low and the number of individuals found in each pitcher was small (Fig. 29A; B), particularly when compared to the mean number of anoetid mites found in pitchers (Fig. 28B; D; F). This suggests that the Nepenthes pitchers are not a normal habitat for most of the oribatids, which belong to families whose members often inhabit soil and litter. It is therefore likely that most of the oribatids found in the pitchers normally live in the water-logged soil and rotting vegetation surrounding the plants (although examination of soil and litter samples did not yield any specimens of the mites found in the pitchers). Most of these oribatids probably become pitcher inhabitants accidentally, but several individuals of the same species were often found living in the same pitcher (which is unlikely based on chance alone) and nymphal stages were often present, so it is possible that the mites not only survive in the pitcher fluid but may actually reproduce as well.

Oribatid mites do not possess a deutonymphal stage and are therefore dependent on active movement for dispersal. Presumably the degree of

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normal activity of each species determines the maximum size of the pitchers in which they occur, with the most active species being found in large pitchers and relatively inactive species being confined to the smallest rosette pitchers. There was no correlation between mean mite species size and the size of pitchers occupied, so the ability to colonize large pitchers is unrelated to size.

Mites of Galumna sp. were extraordinarily successful in colonizing large pitchers, being present even in pitchers of size classes 17 and 20 (Fig. 29A; i), which were often well above ground level. As it is difficult to imagine that the mites are able to crawl such relatively vast distances to subsequently fall accidentally into pitchers, it is possible that these mites may cling onto other animals for dispersal, eventually entering the pitchers attached to animals which fall into the fluid and drown. This may also be true of Zygoribatula and Paralamellobates which were also found in pitchers in the largest size classes (Fig. 29A; viii; ix).

In addition to the oribatid mites, a mesostigmatid mite, Deraiophorus sp. (Uropodidae), was found living in pitchers up to 12cm in length. The percentage of pitchers occupied by this species was highest in size classes 4-8, while the maximum number of individuals were found in size class 4 with a further small peak in size class 12 (Fig. 29; xiii). Since these mites were most often found in the smallest pitchers, it seems likely that, as for the oribatids, they actively crawl into the pitchers, although since uropodid mites possess a deutonymphal stage dispersed by insects, they may also be carried into pitchers on the bodies of pitcher victims. The isolated peak in the number of individuals of this species in size class 12 (Fig. 29B; xiii) may thus have resulted

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from several deutonymphs being carried into these pitchers on the bodies of the ants of which the greater part of the pitcher debris was composed.

Miscellaneous fauna

Ciliates, bdelloid rotifers and nematodes (Rhabditis sp.) were found in pitchers of all size classes, except that Rhabditis sp. was never found in pitchers larger than 17cm in length (Fig. 30C). However, the percentage of pitchers occupied by all three types of animals was highest in pitchers less than 10cm in length (Fig. 30). Since these animals are all nepenthexene forms which are probably normally found in the wet environment around the pitcher plants, the higher percentage of small pitchers occupied must be due to the fact that these pitchers are readily colonized by living animals swimming through water films, or carried in in splash droplets. Colonization of larger pitchers is probably accomplished via small cysts or resistant stages carried by wind or insects and it is likely to be less frequent. As a result of the increase in the number of nepenthexene species colonizing small pitchers, species diversity was much higher in these pitchers. Thus the total number of species found in pitchers of size classes 2-8 greatly exceeded the number found in pitchers in the larger size classes (Fig. 31).

Discussion

Small rosette pitchers of Nepenthes were found to harbour a considerably more diverse fauna than large pitchers and this appeared to be primarily due to the proximity of small pitchers to the soil and humus surrounding the plants, rather than to the absence of the predatory mosquito larvae. Nevertheless, as expected, A. magnus was more or less

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Figure 30. Distribution of miscellaneous fauna in pitchers of different sizes

A. Ciliates

B. Rotifers

C. Nematodes (*Rhabditis sp.*)

Figure 31. Species diversity in pitchers of different sizes

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Fig. 30

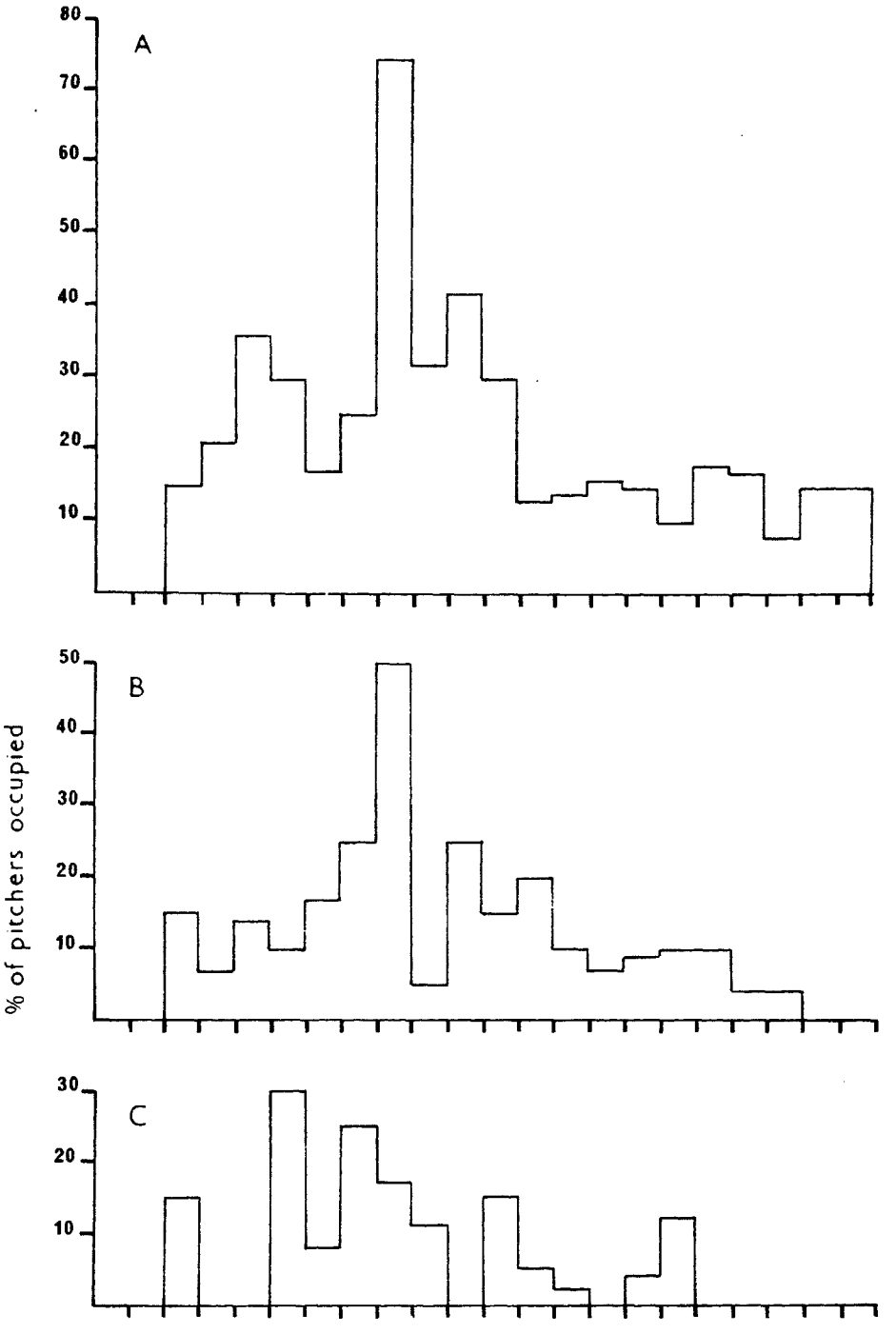
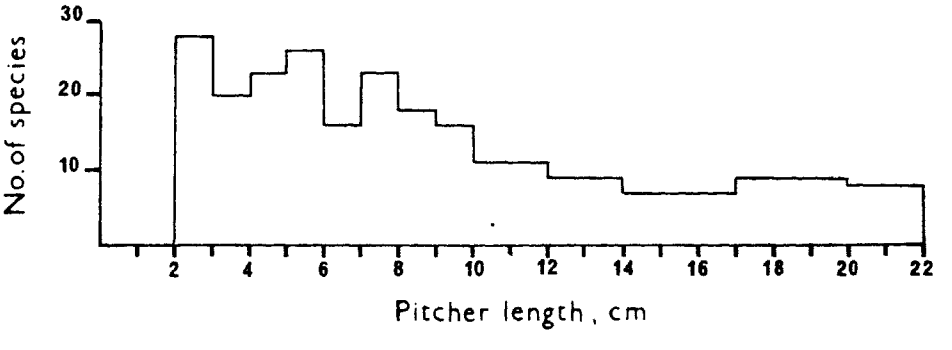


Fig. 31



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excluded from pitchers smaller than 6cm in length due to the large size of the adults and, as a result, these pitchers contained a more diverse dipteran fauna. The smaller adults of C. sumatranus were able to freely enter pitchers of any size to oviposit so that larvae were found in pitchers of all sizes, although the number of pitchers occupied and the number of individuals present reached its peak in pitchers of size class 6, despite the small space and amount of food available. This was presumably solely due to the absence of the predatory and extremely competitive larvae of A. magnus. Pitchers less than 6cm in length also contained the largest populations of M. corkerae and the chironomid ?Metriocnemus. Although larvae of C. sumatranus prey on those of M. corkerae, they are not such serious predators of this species as are larvae of A. magnus, so that despite the large number of Culex larvae in pitchers smaller than 6cm, large populations of Megaselia larvae were still able to coexist in the same pitchers. The chironomid larvae are preyed upon by both A. magnus and C. sumatranus, and so they were never found together with either of these species. However, fewer of the small pitchers were occupied by culicine larvae so that populations of the chironomid built up in pitchers usually less than 5cm in length which lacked the normal culicine fauna. These results demonstrate that the restriction of chironomid larvae to old pitchers in the succession study was a result of predation rather than of specific oviposition habits of the adult females.

It has been generally assumed that anoetid mites living in the pitchers of pitcher plants colonize new pitchers using adult diptera associated with the pitchers as vectors (Vitzhum, 1931; Thienemann, 1932; Hunter and Hunter, 1964; Swales, 1972; Beaver, 1979a). That phoretic transport of deutonymphs does occur, has been demonstrated by the fact

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that Beaver (1979a) found deutonymphs of Zwickia attached to the legs of an adult Endonepenthia schuitemakeri sitting in pitchers of N. albomarginata. However, in some species at least, it appears that it is not the only means of dispersal of the mites. Vitzhum (1931) argued that the structure of the legs of Zwickia deutonymphs was such that it was unlikely that they were capable of active colonization, but deutonymphs of Zwickia in Hong Kong were observed crawling up and out of open pitchers, as well as on the external surfaces of pitchers about to open and, since they were found in pitchers lacking any dipteran fauna, it seems fairly certain that this species is capable of active colonization of pitchers. Young pitchers are the most favourable habitat for Zwickia mites and as deutonymphs tended to be clustered around the mouths of pitchers about to open, it is likely that the deutonymphs are able to distinguish between pitchers of different ages, so that they colonize the most favourable pitchers. Undoubtedly some phoretic transport must also take place, either via Nepenthes diptera or on potential victims of the pitchers, and the efficiency of this combination of active and passive transport is reflected in the extraordinarily high percentage of pitchers occupied by this species.

Anoetid A also appears to be capable of actively colonizing pitchers although, as deutonymphs of this species are much smaller than those of Zwickia, active colonization must be much more difficult and hazardous. This may result in phoretic transport being more important, although the results of the succession study indicated that few deutonymphs are transported passively and that most actively colonize older pitchers. Creutzeria appeared to be totally reliant on phoretic transport for its dispersal and did not usually occur in pitchers smaller than 7cm in length.

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This suggests that this species normally selects adults of A. magnus for dispersal, since A. magnus was also usually absent from pitchers less than 7cm in length. Anoetid deutonymphs are able to recognize potential hosts and behave accordingly (OConnor, 1982) and so it is possible that the deutonymphs do normally attach themselves to A. magnus adults. However, later studies (see Chapter 4) showed that Creutzeria was most abundant at site 9, where A. magnus was rarely found, so that it is unlikely that the mites are specifically associated with A. magnus.

Thienemann (1932) found dead specimens of seven different oribatids in pitchers of Nepenthes in Java and Sumatra. Three of these species (Oppia latifasciata, O. neerlandica var. sumatrensis and Scheloribates praeincisus) were very poorly preserved and the legs and setae had already been digested, but extremely well-preserved specimens of Liebstadia thienemanni, L. perforata, Protoribates clavatus and Rostrozetes foveolatus were also found (Willmann, 1931; Thienemann, 1932). Willmann (1931) considered all these oribatids to be pitcher victims rather than inhabitants and surmised that they were all heliotropic species which habitually climbed up plants and hence fell into pitchers accidentally. He did, however, observe that it was strange that two such closely related species of Liebstadia should be found in pitchers of Nepenthes from different geographical areas. Although all the specimens found by Thienemann were dead, it is likely that the oribatids had been actually living in the pitchers prior to their death and subsequent digestion, since twelve different oribatids, including Oppia and Rostrozetes, (species of which were originally found by Thienemann) were found living in pitchers in this study. Swales (1972) also found several genera of oribatids living in pitchers of Sarracenia purpurea in Canada, so there

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is no doubt that oribatids not normally considered to be aquatic are capable of living in the pitcher fluid. Most of the oribatids found living in the pitchers are probably heliotropic species as suggested by Willmann (1931). A species of Neoliodes was found living in the pitchers and since Neoliodes vermicularis is known to be a positively heliotropic species (Jacot - cited by Willmann, 1931) it seems likely that these mites climb about on the aerial parts of the plants and occasionally fall into the pitchers. This may explain why specimens of the mites found living in the pitchers were not found in soil and litter samples taken from around the plants, since most of the mites are probably normally on the vegetation, rather than in the surrounding soil.

Most of the mites found in the pitchers belong to families usually inhabiting soil and litter, which are generally considered to be non-aquatic; however, many truly aquatic oribatids are opportunist members of chiefly terrestrial families (Ward and Whipple, 1959), and so the fact that most of the mites belong to terrestrial families does not mean that they are incapable of living in aquatic habitats. The only oribatids found which are considered to be truly aquatic (Ward and Whipple, 1959) were specimens of Hermannia, which probably originated from the water-logged soil surrounding the plants.

While it is almost certain that most of the oribatids found are accidental pitcher inhabitants, they are able to survive and may even reproduce in the pitchers. They are protected from the digestive action of the fluid by an extremely tough, resistant cuticle, which remains intact long after the soft body parts have been digested following death and, since they were usually only found in pitchers smaller than 10cm in length, where the fluid volume was relatively small, it is likely that

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they have no problem obtaining oxygen from the fluid, which presumably is well aerated. Although the mites probably occurred in small pitchers primarily due to the fact that these are more easily entered accidentally, these pitchers also contained the greatest quantities of vegetation and organic debris on which oribatids normally feed (Willmann, 1931), because they are closer to soil level where it is easier for bits of plant matter to be washed into the pitchers. Additionally, oribatids are never found in putrid environments (Willmann, 1931) and, since small pitchers rarely catch enough prey to cause putrefaction, the mites may thrive in these pitchers, whereas in larger pitchers where putrefaction quite often occurs, the mites would be killed. While most of the oribatids are nepenthexene forms, Galumna was found in such numbers and in such a large number of pitchers that it must be considered to be a nepenthephil animal. Since this species was found in pitchers of all sizes, many of them considerable distances off the ground, it is possible that these mites are not solely reliant on active movement for colonization of pitchers but may also be transported phoretically.

Besides the majority of oribatid mites, the nepenthexene fauna found in the pitchers also included ciliates, rotifers and nematodes (Rhabditis). These animals were also more common in small pitchers than in large ones, probably because the proximity of these pitchers to the soil and humus allows active colonization of the pitchers through water films and splash droplets, whereas larger pitchers are more likely to be colonized passively via the wind or insect vectors. The higher percentage of small pitchers occupied by ciliates, rotifers and nematodes may also be a result of the fact that small pitchers were less frequently occupied by predatory mosquito larvae which tend to eliminate these animals from the pitcher communities.

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Chapter 4

Taxonomic composition, abundance, feeding habits and geographical distribution of Nepenthes pitcher fauna, in the Hong Kong region

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Table 8 lists the species recorded from pitchers of Nepenthes mirabilis in Hong Kong, together with their abundance (percentage of pitchers occupied), feeding habits and geographical distribution (presence or absence) at each of the eleven sites studied. The abundance values for each species at these eleven sites are given in Appendix II, Table A.

Including the many unidentified protozoan species, over 60 different species of animals were found inhabiting the pitchers of N. mirabilis in Hong Kong and Macau. Most of these animals were nepenthexene forms (50+) and were found in a very small percentage of pitchers (Table 8), whereas only 8 species were regularly associated with the pitcher environment. The most common Nepenthes associate was the nepenthebiont anoetid mite, Zwickia sp., which occurred in approximately 88% of all the pitchers sampled (Table 8). Other nepenthebiont species included the anoetid mites, Creutzeria sp. and Anoetid A, which occurred in a much smaller percentage of the pitchers, and the mosquito Culex sumatranus which was found in 50% of all pitchers sampled (Table 8). Armigeres magnus, the other mosquito species found breeding in the pitchers, must be considered to be nepenthephil overall since it is not associated with Nepenthes elsewhere in its wide geographical range, but in Hong Kong, its association with Nepenthes appears to be virtually exclusive so that it may be evolving into a different nepenthebiont species in this region. The percentage of pitchers occupied by this species (56%) was actually higher than for the nepenthebiont C. sumatranus, which seems to support this theory. Megaselia corkerae may also be a nepenthebiont species but, as it is a new species described from the pitcher habitat, there is no information on its general breeding habits, and it is possible that it is also

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Table 8. Species recorded from pitchers of Nepenthes mirabilis in Hong Kong, their distribution, abundance and feeding habits

NB = nepenthebiont

NP = nepenthephil

NX = nepenthexene

C = carrion feeder

D = detritus feeder

F = filter feeder

P = Predator

PP = primary producer

* = Terrestrial species

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TABLE 8

Species	% of pitchers occupied	Ecological group	Feeding habits	Site no. 1	2	3	4	5	6	7	8	9	10	11
Protozoa														
Rhizopoda	3.3	NX	D	+	+	+	+		+	+	+			+
Flagellata	20.4	NX	F	+	+	+	+	+	+	+	+			+
Ciliata	18.7	NX	F	+	+	+	+	+		+	+	+		+
Algae														
Bacillariophyta	2.2	NX	PP			+	+		+	+				
Platyhelminthes														
?*Catenula*	1.0	NX	?		+		+							
Oligochaeta														
Pristina foreli Piguet	0.7	NX	D						+					
Rotifera														
Bdelloidea	11.2	NX	F		+	+	+		+	+	+	+	+	+
Nematoda														
Rhabditis sp.	4.0	NX	D		+	+	+		+		+	+		+
Crustacea														
Phyllognathopus vigueri Maupas	1.9	NX	D		+		+		+					+
Monospilus dispar Sars	0.2	NX	F						+					
Insecta														
Collembola														
Paronellidae														
*?genus sp. A	0.4	NX	D?						+		+			
*?genus sp. B	1.3	NX	D?	+						+	+	+		
Entomobryidae														
**Lepidocyrtus sp.*	0.2	NX	D?							+				
*?genus ?sp.	0.6	NX	D?					+		+				

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TABLE 8 - continued

Species	% of pitchers occupied	Ecological group	Feeding habits	Site No. 1	2	3	4	5	6	7	8	9	10	11
Sminthuridae														
*Sminthurus sp.	0.2	NX	D?						+					
Thysanoptera														
Scirtothrips dorsalis Hood	3.7	NX	D		+	+	+		+	+	+			
Phlaeothripidae														
?genus ?sp.	0.2	NX	D											+
Diptera														
Culicidae														
Culex sumatranus Brug	50.3	NB	P/C/F	+	+	+	+	+	+	+	+	+		+
Armigeres magnus (Theobald)	56.2	NB?	P/C	+	+	+	+	+	+	+	+	+		+
Ceratopogonidae														
?genus ?sp.	0.2	NX	?						+					
Chironomidae														
?Metriocnemus	2.2	NX	D		+		+		+	+				
Phoridae														
Megaselia corkerae Disney	15.7	NB?	D	+	+	+	+	+	+	+	+			+
Psychodidae														
?genus ?sp. A	0.6	NX	?			+			+					
?genus ?sp. B	0.4	NX	?			+								
Mycetophilidae														
?genus ?sp.	0.2	NX	?						+					
Lepidoptera														
Psychidae														
?genus ?sp.	0.2	?	?						+					

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TABLE 8 - continued

Species	% of pitchers occupied	Ecological group	Feeding habits	Site no. 1	2	3	4	5	6	7	8	9	10	11
Acari														
Mesostigmata														
Parasitidae														
*Pergamasus sp.	1.2	NX	P		+		+							
Uropodidae														
Deraiophorus sp.	2.6	NX	?				+							
Oplitis sp.	0.9	NX	?			+	+				+			
Trombidiformes														
Bdellidae														
*Bdellodes sp.	10.3	NP	P	+	+	+	+	+	+	+	+	+		
Anystidae														
*Anystis sp.	3.5	NX	P	+	+	+	+	+	+	+	+			
Cheyletidae														
*Hemicheyletia sp.	0.6	NX	P		+				+	+				
Cunaxidae														
*Cunaxoides sp.	0.6	NX	P		+	+								
Hydrachnellae														
Anisitsiellidae														
?genus ?sp.	0.3	NX	?						+	+				
Sarcoptiformes														
Acaridae														
Tyrophagus putrescentiae Schrank complex	2.7	NX	D		+	+	+		+	+				
Glycphagidae														
Blomia sp.	0.6	NX	D				+			+				
Anoetidae														
Zwickia sp.	86.7	NB	C	+	+	+	+	+	+	+	+			+
Creutzeria sp.	18.4	NB	D	+	+	+	+	+	+	+	+	+		+
Anoetid A	32.2	NB	D	+	+	+	+	+	+	+	+	+		+

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TABLE 8 - continued

Species	% of pitchers occupied	Ecological group	Feeding habits	Site no. 1	2	3	4	5	6	7	8	9	10	11
Oribatei														
Malaconothridae														
Malaconothrus sp.	0.2	NX	D				+							
Trimalaconothrus sp.	0.6	NX	D		+									
Hermanniidae														
Hermannia sp.	1.1	NX	D				+							
Liodidae														
Neoliodes sp.	2.8	NX	D				+		+					
Zetorchestidae														
Zetorchestes sp.	1.8	NX	D				+							
Oppiidae														
Oppia sp.	0,9	NX	D				+		+					
Carabodidae														
Carabodes sp.	5.1	NX	D				+							
Otocepheidae														
Tetracondyla sp.	0.6	NX	D				+							
Oribatellidae														
Paralamellobates sp.	2.2	NX	D		+		+		+					
Scheloribatidae														
Scheloribates sp.	1.7	NX	D		+	+	+		+					
Liebstadia sp.	0.2	NX	D				+							
Oribatulidae														
Zygoribatula sp.	4.8	NX	D		+	+	+		+	+	+			
Phauloppia sp.	2.2	NX	D	+		+				+				
Mochlozetidae														
Podoribates sp.	5.1	NX	D				+	+						
Haplozetidae														
Rostrozetes sp.	2.0	NX	D				+							

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TABLE 8 - continued

Species	% of pitchers occupied	Ecological group	Feeding habits	Site no. 1	2	3	4	5	6	7	8	9	10	11
Peloribates sp.	3.7	NX	D				+							
Galumnidae														
Galumna sp.	14.3	NP	?	+	+	+	+		+		+			+
Arachnida														
Theridiidae														
**Coleosoma sp.*	1.3	NP?	P	+	+	+								
**Argyrodes sp.*	0.4	NX	P		+	+								

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found in other container habitats, in which case it is only nepenthephil. This species was found in a relatively small percentage of pitchers (Table 8), which suggests that it may indeed be nepenthephil although, since it is heavily preyed upon by larvae of A. magnus, the small percentage of pitchers occupied may simply be a result of predation. Two other species were also regularly associated with the pitcher environment; these were the nepenthephil mites Bdellodes and Galumna. It is possible that the spider Coleosoma is also nepenthephil but it was found in such a small percentage of pitchers (Table 8) that this is unlikely and it is probably actually a nepenthexene species, as is Argyrodes.

The majority of the nepenthexene animals found living in the pitchers occurred in a very small percentage of the pitchers sampled, the most common forms (excluding protozoa which were not separated into individual species) being bdelloid rotifers, Rhabditis and the mites Anystis, Carabodes, Zygoribatula and Podoribates (Table 8). The nepenthexene animals were for the most part opportunist forms, which having accidentally entered the pitchers, were able to survive and reproduce, most of them utilizing the detritus accumulated in the pitchers as food. Although most of the nepenthexene animals found were detritus feeders, a number of terrestrial mites such as Anystis, Pergamasus, Hemicheyletia and Cunaxoides were predators (Table 8) living on the fluid surface. The terrestrial pitcher community in Hong Kong is unusual in this respect as mites have never previously been recorded as forming part of the terrestrial Nepenthes fauna. Individual nepenthexene species generally occurred in very few pitchers and they contribute little to the food webs operating in pitchers so they have therefore been excluded from the food web depicted in Figure 32, except where they form part of the food of the regular

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Nepenthes associates. The lepidoptera have also been excluded since they are feeding on plant tissue and are not involved in the food webs operating in the pitchers.

The food web in pitchers of N. mirabilis, as in other Nepenthes pitchers, is based on the input of living animals which are trapped by the pitchers (Fig. 32). These trapped animals provide food directly for terrestrial predators such as the spider Coleosoma, and the mite Bdellodes which may feed on the smaller trapped insects (Fig. 32). Those insects which are not consumed by the terrestrial predators, fall into the fluid and drown and are fed on by carrion feeders before any appreciable decomposition takes place. The major carrion feeders in pitchers of N. mirabilis are larvae of A. magnus and C. sumatranus and the anoetid mite Zwickia (Fig. 32). Larvae of A. magnus and C. sumatranus which are also facultative predators, were the only aquatic predators in the pitchers. Both species feed on other dipteran larvae, oligochaetes and nematodes, and they may also filter feed on bacteria and protozoa (Fig. 32). Armigeres is more aggressive and predatory than Culex and consequently is the top aquatic predator in the system (Fig. 32). The drowned insects are gradually digested by bacterial and plant enzyme action so that organic debris builds up in the base of the pitcher, providing food for detritus feeders such as larvae of M. corkerae and ?Metriocnemus and the oligochaete, Pristina foreli (Fig. 32). Creutzeria and Anoetid A are also detritus feeders, but Anoetid A is confined to the base of the pitchers while Creutzeria feeds on accumulated detritus on the fluid surface. The anoetid mites appear to have no predators, but bdellid mites are normally predacious on other mites as well as on small insects (Baker and Wharton, 1952) so it is quite possible that Bdellodes may feed on Creutzeria and

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FIGURE 32. Food web in pitchers of *N. mirabilis* in Hong Kong

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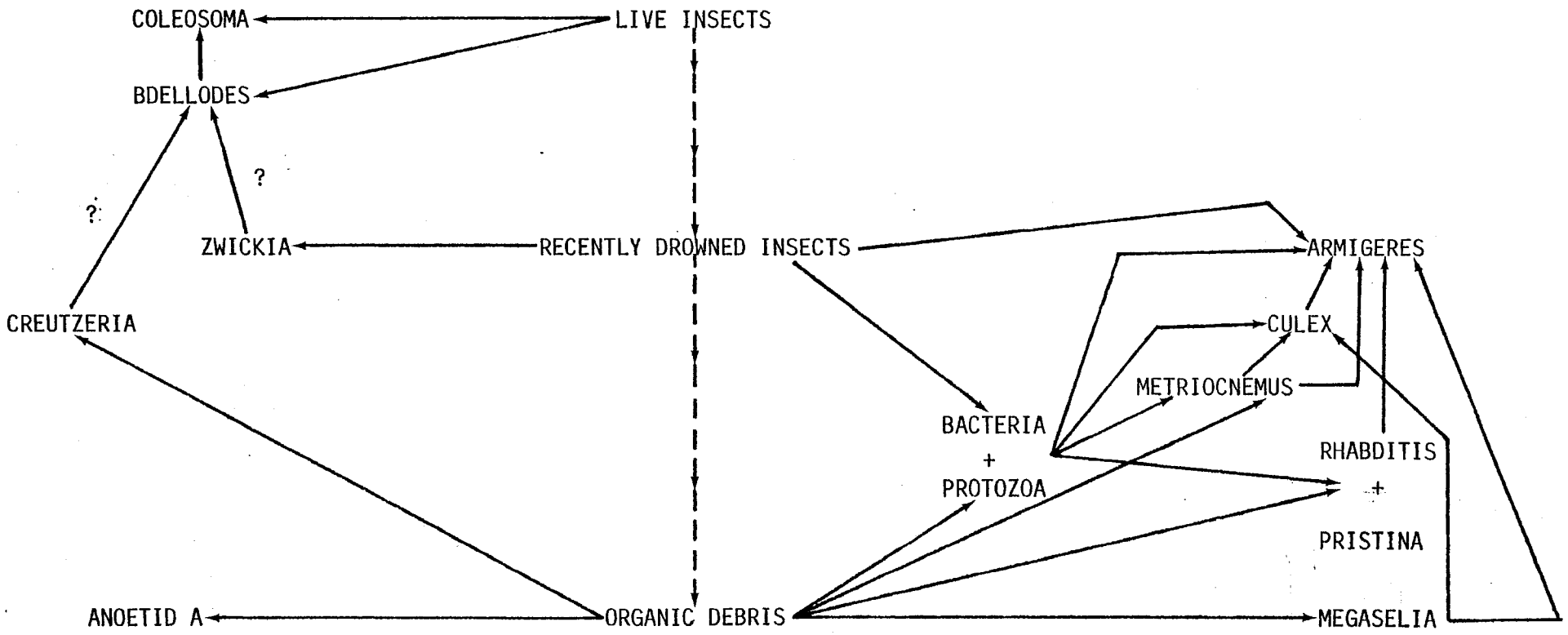
COLEOSOMA
LIVE INSECTS
BDELLODES
?
?
ZWICKIA
RECENTLY DROWNED INSECTS
ARMIGERES
CREUTZERIA
CULEX
METRIOCNEMUS
BACTERIA
+
PROTOZOA
RHABDITIS
+
PRISTINA
ANOETID A
ORGANIC DEBRIS
MEGASELIA

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Zwickia (Fig. 32). Anoetid A, by virtue of the fact that it occurs only in the base of the pitchers, would never be fed upon by the terrestrial Bdellodes, except possibly in the deutonymphal stage, although this is unlikely since the deutonymphs are heavily armoured. The terrestrial predators living on or above the fluid surface may also feed on diptera emerging from the pitchers after completing development.

The functional components of the food webs in N. mirabilis pitchers in Hong Kong are the same as those in pitchers of N. ampullaria and N. albo-marginata in Malaysia, apart from the apparent absence of terrestrial parasitoids in pitchers of N. mirabilis (Table 9). However, differences are immediately obvious when the number of species which make up each functional component of the food webs is considered. Thus, in N. ampullaria and N. albo-marginata, large numbers of carrion and filter feeders are present whereas in N. mirabilis there are only one or two (Table 9). This difference is a direct result of the relative paucity of regular Nepenthes associates in Hong Kong (8), when compared to the number of nepenthebiont and nepenthephil animals (23, - Beaver, 1979a) found in pitchers of the Malaysian Nepenthes. In addition, there are no true obligate aquatic predators in pitchers of N. mirabilis and the only aquatic predators present are the facultative predators, A. magnus and C. sumatranus. The species found in N. mirabilis often do not fall neatly into ecological categories because they tend to be opportunistic feeders and will feed on whatever is available in the pitchers, so that A. magnus and C. sumatranus could be placed in any one of three categories - that is - carrion feeder, filter feeder or aquatic predator. Beaver (1983) notes that towards the edge of the range of Nepenthes the food webs in the pitchers appear to be simplified, so that some functional components may be absent and the number of species making up a component is reduced, and this is borne out by the above observations on the pitcher communities in Hong Kong.

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TABLE 9

Comparison between the functional components of the food webs in N. ampullaria and N.albo-marginata in Pulau Pinang, West Malaysia, and N. mirabilis in Hong Kong

(Information on the functional components of the food webs of N. ampullaria and N. albo-marginata in Malaysia is taken from Beaver, 1983).

NB = nepenthebiont

NP = nepenthephil

NX= nepenthexene

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TABLE 9

Functional component	N. ampullaria	N. albo-marginata	N. mirabilis
Direct carrion feeder	Nepenthomyia malayana NB (Calliphoridae)	Pierretia urceola NB (Sarcophagidae)	Armigeres magnus NB (Culicidae)
		Endonepenthia schuitemakeri NB (Phoridae)	
	Megaselia bivesicata NX (Phoridae)	M. nepenthina NB? (Phoridae)	
	Xylota sp. NX (Syrphidae)	Nepenthosyrphus capitata NB (Syrphidae)	
			Zwickia sp. NB (Anoetidae)

Functional component	N. ampullaria	N. albo-marginata	N. mirabilis
Filter feeder	Tripteroides tenax NB (Culicidae)	Tp. tenax NB	
	Tp. bambusa NP	Tp. bambusa NP	
	Tp. nepenthis NB		
	Culex acutipalus NB (Culicidae)	C. curtipalpis NB	C. sumatranus NB
	C. hewitti NB	C. lucaris NB	
	C. navalis NB		
	Uranotaenia moultoni NB (Culicidae)		

TABLE 9 - continued

Functional component	N. ampullaria	N. albo-marginata	N. mirabilis
Detritus feeder	Dasyhelea ampullariae NB (Ceratopogonidae)		Megaselia corkerae NB? (Phoridae)
	D. nepenthicola NB	D. nepenthicola NB	?Metriocnemus NX (Chironomidae)
	Anoetidae 2 spp.	Anoetidae 2 spp.	Creutzeria sp. NB (Anoetidae)
			Anoetid A NB
Aquatic predator	Corethrella calathicola NB (Chaoboridae)	Toxorhynchites klossi NB (Culicidae)	A. magnus NP C. sumatranus NB (Culicidae)

Functional component	N. ampullaria	N. albo-marginata	N. mirabilis
Terrestrial predator	Xenoplatyura beaveri NB (Mycetophilidae)	Misumenops nepenthicola NB (Arachnida, Thomisidae)	Coleosoma sp. NP? (Arachnida, Theridiidae)
			Bdellodes sp. NP (Acari, Bdellidae)
Terrestrial parasitoid	Trichopria sp. NX (Hymenoptera, Diapriidae)	G. nr. Tachineaphagus NB (Hymenoptera, Encyrtidae)	

Ecological equivalents in pitchers of different species often differ considerably taxonomically, even within the same geographical area (Table 9). In Malaysia, the differences between ecological equivalents in pitchers of N. ampullaria and N. albo-marginata were thought by Beaver (1979b) to be largely a result of differences in the structure of the pitchers, since in N. albo-marginata the glandular area is confined to the lower half of the pitchers, whereas in pitchers of N. ampullaria the whole interior is glandular, which greatly restricts the occurrence of pitcher inhabitants that are either wholly terrestrial or that have terrestrial stages in their life cycle. Pitchers of N. mirabilis have a similar structure to those of N. albo-marginata, so that ecological equivalents would be expected to be similar (although obviously not the same in view of the difference in geographical location). This is true in so far as aquatic predators in N. albo-marginata and N. mirabilis differ only at the generic level, whereas the components in the two latter species and N. ampullaria differ at the family level (Table 9). Terrestrial predators in N. albo-marginata and N. mirabilis are also similar in that Coleosoma and Misumenops are both arachnids whereas the terrestrial predator in N. ampullaria belongs to the Insecta (Table 9). There is no ecological equivalent to Bdellodes in either N. ampullaria or N. albo-marginata (Table 9). The chironomid ?Metriocnemus is not a true ecological equivalent to Dasyhelea nepenthicola because it is a nepenthexene species whereas D. nepenthicola is nepenthebiont (Table 9). Beaver (1983) also notes that Megaselia bivesicata and M. nepenthina, and Xylota and Nepenthosyrphus capitatus, are not ecological equivalents for the same reason (Table 9).

Food webs in pitchers of N. mirabilis throughout the Hong Kong region are all essentially the same, no matter in which geographical area the

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plants occur, because all the nepenthebiont and nepenthephil animals associated with the pitchers occurred at virtually all sites (Table 8), including site II which was on the island of Coloane in Macau (Fig. 33). Although the composition of the fauna was similar at all the sites studied (except sites 9 and 10) it was found that the proportions of the species present altered between sites. The dominant dipteran species was usually A. magnus, although at sites 1, 4 and 9 C. sumatranus was the dominant species (Fig. 34A). A. magnus was very rare at site 9 (Table A. Appendix 2) and C. sumatranus was usually the only dipteran present (Table 8). Megaselia corkerae and Zwickia were never found at site 9 (Table 8), so that the Nepenthes fauna at this site was much less diverse. None of the normal Nepenthes fauna was found at site 10, although this may be a function of the small number of pitchers sampled at this site (only 3 pitchers were found). The impoverished fauna of the pitchers of plants growing at sites 9 and 10 is difficult to explain because, although both sites are on Lantau which is an island some distance away from the mainland (Fig. 33), the fauna of pitchers at site 8 on Chep Lap Kok, which is also an island (Fig. 33), was very similar to that of the sites located on the mainland (Table 8). Chep Lap Kok is also very close to Lantau island (Fig. 33) so there is virtually no barrier to the spread of the fauna from Chep Lap Kok to Lantau, particularly since the distance between the two latter is negligible in comparison to the distance between the mainland and Chep Lap Kok (Fig. 33). Sites 9 and 10 are both poor sites in terms of the number and vigour of plants growing there, and so it is possible that their impoverished pitcher fauna is a result of the fact that most species have abandoned these sites in search of more favourable habitats. The paucity of pitchers available for colonization

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Figure 33. Geographical location of Nepenthes sites in the South China region

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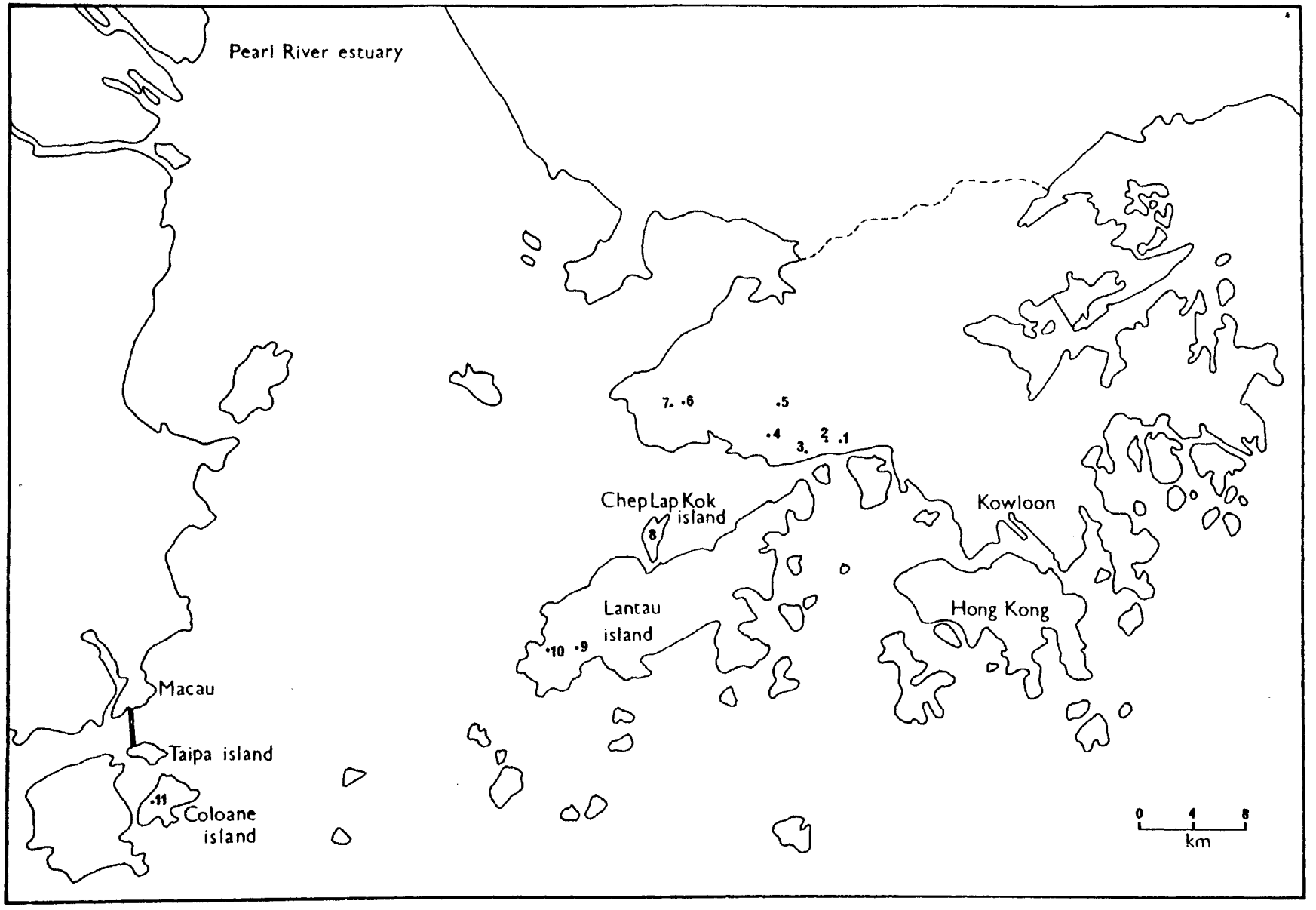
Pearl River estuary
7.
6
5
4
3.
2
1
Chep Lap Kok island
8
Kowloon
Lantau island
Hong Kong
10
9
Macau
Taipa island
11
Coloane island
0
4
8
km

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Figure 34. Geographical distribution and abundance of the Nepenthes diptera and anoetid mites in the South China region

A. Diptera

B. Anoetid mites

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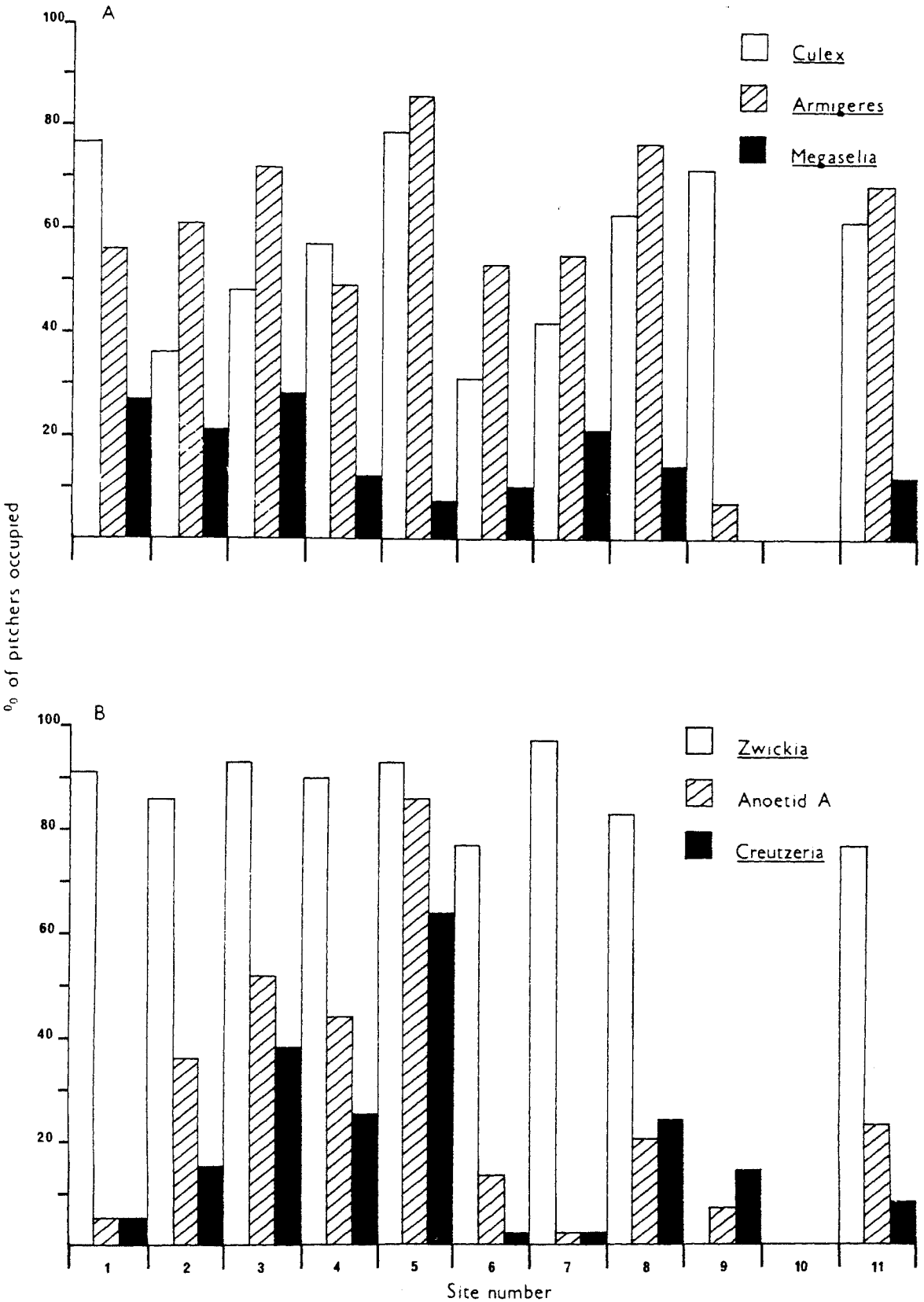

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and the isolation of the sites may also have led to the sites being overlooked or rejected by colonizing fauna from other areas. Other sites where Nepenthes grows are known to exist on Lantau but unfortunately the exact location of these was never discovered, so that it was not possible to compare the fauna from these sites with that of sites 9 and 10. However, Herklots (1951) mentions finding larvae of only one species of mosquito in pitchers on Lantau island, so that A. magnus may be rare throughout the island and not merely at sites 9 and 10. A few larvae of A. magnus were found at site 9 on one occasion, so that their absence from most of the pitchers cannot be explained by the total absence of the species from the island. It is possible that on Lantau, other container habitats are utilized in preference to the pitchers, although if this is so, it is not known why this should occur only in this region.

The dominant anoetid in the pitchers was usually Zwickia, although at site 9, Zwickia was absent and Creutzeria was the dominant species (Fig. 34B). The percentage of pitchers occupied by Zwickia at each site varied little apart from at sites 9 and 10 where this species did not occur (Fig. 34B). This demonstrates that once a particular site has been colonized by Zwickia deutonymphs, the mites are able to rapidly colonize most of the pitchers available within the site. The absence of Zwickia from sites 9 and 10 presumably indicates that these sites have never been colonized. Although the percentage of pitchers occupied by Zwickia altered little with geographical location, the relative abundance of Creutzeria and Anoetid A varied greatly between sites (Fig. 34B). Both anoetids were rare at site 1, but the proportion of pitchers occupied increased to a maximum at site 5 before again decreasing to a low level at sites 6 and 7 (Fig. 34B). A decrease in the relative abundance of the 3 diptera was

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also noted between sites 5 and 6 (Fig. 34A), which may be due to the fact that the distance between sites 5 and 6 is substantially greater than between any of sites 1-5 (Fig. 33), which would tend to reduce regular interpatch colonization. The reasons for the great variation between the percentage of pitchers occupied by Creutzeria and Anoetid A at different sites are obscure, since conditions within the pitchers must be uniform at all sites and, once a site has been colonized initially, there should be no barrier to the further colonization of pitchers within the habitat. The only other factor which could affect the relative abundance of the two anoetids would be the presence or absence of predators; however, the abundance of the two species is not significantly negatively correlated to that of Bdellodes and to my knowledge no other predator exists within the pitchers.

The similarity between the faunas of the II different sites studied was determined using the modified Sorensen coefficient (Southwood, 1978) $C = \frac{2W}{aN+bN}$; where aN is the sum of the percentage of pitchers occupied by (i.e. the relative abundance of) all species found at site a; bN is the same at site b and W is the sum of the lesser values for the species common to both habitats. The nepenthexene species were not taken into account when working out the coefficient because they are not true Nepenthes associates and their inclusion would have led to underestimation of the similarity between sites. Consequently, the only species used for calculation of the coefficient were the 8 species regularly associated with N. mirabilis in Hong Kong and Macau (A. magnus, C. sumatranus, M. corkerae, Zwickia, Creutzeria, Anoetid A, Bdellodes and Galumna). Site 10 was ignored in these calculations because none of these species occurred there. It is apparent that there is a high similarity between

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the faunas of most of the sites studied, although site 9, as would be expected due to its impoverished fauna, had a very low similarity with all other sites (Table 10). Site 5 also had a relatively low similarity to most other sites (Table 10), but the reason for this is not known. The relative similarity between sites did not appear to be related to the distance between sites; thus, the Macau pitcher fauna (site 11) was very similar to that of Hong Kong despite the comparatively great distance between the two regions (Table 10). The most similar site to Macau was site 8 (Table 10), which was also located on an island where colonizing fauna would have to cross water (Fig. 33) so it is likely that the geographical location of the plants and the type of habitat in which they occur is more important in determining the similarity between faunas than the actual distance between sites.

It is difficult to compare the species richness of different sites, taking into account all species found in the pitchers, because the number of pitchers sampled greatly affects the number of animal species found. This is because there is considerable variation in the composition of the faunas of individual pitchers even after the age of the pitchers has been taken into account (Beaver, 1983). There was great variation in the number of pitchers sampled at different sites (Table 11), so the differences in species diversity between sites are likely to be partially a result of differences in the number of pitchers sampled. However, when the cumulative frequency of the number of species found in relation to the number of pitchers sampled was worked out, it became apparent that 70% of all species found at a site are found in the first twenty pitchers sampled. The only exception to this was site 4 because this site was the only site where small pitchers were studied and, as the fauna in

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TABLE 10

Similarities between the faunas of different sites related to the distance between sites

Site	1	2	3	4	5	6	7	8	9	11
1	C / D	0.3	2.5	4.4	4.4	12.4	12.6	12.8	20.2	70
2	0.78		2.2	3.9	4.1	12.0	12.2	12.0	20.0	70
3	0.79	0.85		1.7	2.6	8.3	8.5	10.6	17.6	68
4	0.77	0.87	0.85		1.4	6.3	6.5	9.0	16.0	65
5	0.69	0.70	0.82	0.75		6.5	6.7	11.2	20.0	70
6	0.57	0.80	0.72	0.73	0.61		0.2	8.8	14.4	68
7	0.88	0.79	0.76	0.72	0.60	0.85		8.8	14.4	68
8	0.82	0.84	0.85	0.82	0.78	0.79	0.77		6.4	60
9	0.48	0.35	0.36	0.43	0.40	0.35	0.34	0.49		55
11	0.81	0.86	0.80	0.84	0.72	0.80	0.75	0.91	0.46	

D = distance between sites in km.

C = similarity coefficient

TABLE 11

Species diversity at different sites

Site No.	Number of pitchers sampled	Total number of species found
1	23	12
2	108	26
3	29	22
4	178	34
5	14	11
6	62	30
7	62	20
8	35	16
9	14	8
10	3	1
11	25	11

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small pitchers is much more diverse, a great number of species were found in these pitchers, which were sampled last. If the species found, and the pitchers sampled in this part of the study, are excluded, then 70% of all species found were also present in the first twenty pitchers sampled from this site. Thus, some comparisons can be made between the diversity of faunas at sites where more than twenty pitchers were sampled (i.e. excluding sites 5, 9 and 10).

A number of sites had a relatively impoverished fauna, notably sites 1, 8 and 11 (Table 11). There were relatively few plants at site 1 and these were not very vigorous in their growth, so that the diversity of species living in the pitchers may have been reduced, while sites 8 and 11 were both on islands where a number of species which are normally able to colonize the pitchers may be absent. In comparison to site 6, site 7 had a much less diverse pitcher fauna (Table 11), despite the fact that the two sites are very close together (Table 10) and that the same number of pitchers were sampled from each site (Table 11). This may be related to differences in habitat since, at site 6 the plants grew alongside and in a stream, whereas at site 7 the plants were growing on a seepage area on the hillside. Presumably the diversity of species at site 6 was much greater within the whole habitat and not just within the pitcher environment, because of the greater range of niches available, thereby resulting in an increase in the diversity of the pitcher fauna. Site 4 had the most diverse fauna of all, but as already noted, this must be a reflection of the fact that the greatest number of pitchers were sampled from this site (Table 11), including a large number of small pitchers which have been shown to have a more diverse fauna anyway.

Individual nepenthexene species tended to have a more limited distribution than nepenthebiont or nepenthephil animals, usually occurring

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at only a few sites in a patchy distribution, although a few species such as the bdelloid rotifers, Rhabditis, Scirtothrips dorsalis and Anystis were fairly widespread among the different sites (Table 8). The occurrence of individual species at different sites must be determined by the degree of overlap between the geographical distribution of the animal species and that of Nepenthes, as well as by the degree of overlap between the plant habitat and the habitats normally favoured by the nepenthexene species. Those species which were found at few sites therefore either have a limited geographical distribution, or are rare in the type of habitats in which the plants usually grow. Some species had such a limited distribution that they occurred only at one site. Thus, many of the oribatids (Hermannia, Zetorchestes, Carabodes, Tetracondyla, Rostrozetes and Peloribates) were found only at site 4 (Table 8), although this is probably a reflection of the fact that these species usually occur in small pitchers and that this was the only site where small pitchers were studied. In some cases, a number of the nepenthexene animals found (Monospilus dispar, Lepidocyrtus, Sminthurus, the unidentified ceratopogonid and mycetophilid larvae and Malaconothrus and Liebstadia) appear to be restricted to one site (Table 8) but this is a result of the fact that they were found in only one pitcher. The restriction of Psychodid B to site 3 is probably related to the fact that this was the only site where the habitat of the plants and the animal overlapped, since this species appeared to be breeding primarily in the heavily polluted stream alongside which the Nepenthes plants were growing. Larvae of the unidentified phlaeothripid (Thysanoptera), which were found only in pitchers of N. mirabilis in Macau (Table 8), probably occurred only at this site due to geographical isolation of the species. It is also possible that

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the restriction of Phyllognathopus vigueri to sites 2, 4 and 6 (Table 8) is a result of limited geographical distribution, since this species has been recorded from an enormous range of habitats including pools, springs, subterranean waters and in Bromeliaceous and other plants (Ward and Whipple, 1959), so that it is unlikely that limited habitat overlap is responsible for its limited occurrence in the pitchers.

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GENERAL DISCUSSION

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More than sixty species were found to be associated with Nepenthes plants in Hong Kong but most of these animals were nepenthexene forms and only 10 species of nepenthebiont and nepenthephil animals occurred in the pitchers, and on aerial parts of the plants. The nepenthebiont species included three anoetid mites, one mosquito (Culex sumatranus) and two lepidopterans, while the nepenthephil component of the fauna included one mosquito (Armigeres magnus) and two mites (Bdellodes and Galumna). The status of the phorid Megaselia corkerae is uncertain because, although this species was decribed from the pitcher habitat, it is quite possible that it also breeds in other container habitats in Hong Kong. A number of factors indicate that it is probably nepenthephil rather than nepenthebiont; thus population levels were generally low in the pitchers and relatively few pitchers were occupied. In addition, this species is a detritus feeder and the females would therefore be expected to oviposit preferentially in older pitchers; however, they seem to oviposit indiscriminately in pitchers of any age, which suggests this it is a nepenthephil species which has not fully adapted to the pitcher habitat.

Nepenthes mirabilis in Hong Kong and South China is relatively isolated from other areas where Nepenthes occurs and so the diversity of its fauna is more or less comparable to that of other outlying, isolated species of Nepenthes. Thus N. madagascariensis has 7 nepenthebiont and nepenthephil species associated with it, N. pervillei in the Seychelles has 2 associated species, and N. distillatoria in Sri Lanka has 4 associated species (Beaver, 1983). The Hong Kong fauna appears to be marginally more diverse, but this is probably a result of the fact that the fauna of the three afore-mentioned Nepenthes species has been poorly investigated. In regions closer to the distributional centre of the genus, which is

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presently considered to be the Malay Archipelago (Kurata, 1976), the diversity of the Nepenthes fauna is greatly increased; thus, 39 species have been recorded from Nepenthes in Malaya, 22 in Sumatra and 23 in Borneo (Beaver, 1983). The comparative richness of the Nepenthes fauna in these areas may be a result of the fact that there has been a greater period of time for speciation to occur amongst Nepenthes animals in these areas (since the genus originated here), and also of the fact that in these regions numerous Nepenthes species occur (11 in Malaya, 19 in Sumatra, 28 in Borneo - Beaver, 1983) which cover a wide range of habitats, thereby increasing the pool of potential pitcher inhabitants.

Geographical evidence suggests that the evolution and spread of Nepenthes species has gone on largely independently of the evolution and spread of their associated faunas (Beaver, 1983). Wide-ranging species of Nepenthes therefore tend to have different species of insect and arachnid associated with them in different parts of their range (Beaver, 1983), and this is illustrated by the fact that of 27 species recorded from N. mirabilis, only 6 occur in more than one region (Beaver, 1983). None of the 10 species recorded from N. mirabilis in Hong Kong are associated with N. mirabilis in other regions and only 1 species (C. sumatranus) has been found in Nepenthes pitchers elsewhere. Culex sumatranus has been recorded from unspecified Nepenthes spp. in Viet Nam and Cambodia, as well as from Hong Kong, and it has also been found in Sumatra (Sirivanakarn, 1977), although it has never actually been recorded from pitcher plants in the latter location. As this species is definitely nepenthebiont, this may be due to misidentification since, in the immature stages, this species is virtually indistinguishable from C. curtipalpis (Sirivanakarn, 1977), which has been recorded from Nepenthes pitchers in Sumatra (Brug, 1931).

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Colonization of new areas by Nepenthes species tends to be followed by adaptation of elements of the local fauna to the pitcher plant habitat, rather than by invasion and colonization of the plants by species already associated with Nepenthes elsewhere (Beaver, 1983). This pattern of colonization is clearly visible in Hong Kong where A. magnus, which is not associated with Nepenthes elsewhere in its wide geographical range, is almost exclusively found in Nepenthes pitchers. This species, which is nepenthephil overall since it is regularly found in other habitats, therefore seems to be developing into a nepenthebiont species in the Hong Kong region. There is some overlap between elements of the local fauna in Hong Kong and Nepenthes-breeding species found in other regions; thus Culex shebbearei, Uranotaenia nivipleura, Toxorhynchites splendens and Tripteroides aranoides have all been recorded in Hong Kong (Chau, 1982), although they have never been found breeding in Nepenthes pitchers. The processes of colonization do therefore seem to be very localized with some species developing into pitcher inhabitants in certain areas, while in other areas different species colonize the pitchers, despite a general overlap in the geographical distribution of the faunas involved.

The Nepenthes fauna in most regions is dominated by diptera, both in terms of the number of species present, and also in terms of overall abundance. However in Hong Kong, anoetid mites are the most dominant members of the pitcher communities in terms of the number of individuals and percentage of pitchers occupied and they share co-dominance with diptera in terms of the number of species present (excluding nepenthexene species) Zwickia was the most common Nepenthes associate in Hong Kong, occupying 87% of all pitchers sampled, whereas in Penang, West Malaysia, only 45% of Nepenthes pitchers sampled contained Zwickia mites (Beaver, 1979a).

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This difference in the abundance of individual species may in fact be even greater, since although two species of Zwickia were involved in Penang, the figures for their abundance were presented pooled. The great disparity in the percentage of pitchers occupied by mites of the same genus in two different geographical areas may be attributable to the fact that Zwickia mites in Hong Kong have developed the ability to actively colonize pitchers. It is possible that Zwickia mites in Malaysia are also able to actively colonize pitchers but, if they are totally reliant on other vectors for dispersal, this would explain the observed differences in the relative abundance of the mites in the two areas. Zwickia deutonymphs in Hong Kong were never found on dipteran adults, whereas in Malaysia, deutonymphs were found attached to a phorid adult (Beaver, 1979a), which may indicate that the Malaysian mites are indeed dependent on phoretic transport for dispersal. One other species of anoetid in Hong Kong (Anoetid A) is also capable of active colonization, but the third species, Creutzeria, is apparently totally reliant on other insects for dispersal.

Anoetid mites are particularly successful in colonizing pitchers once dispersal has occurred, because they have evolved haplodiploid sex determination (OConnor, 1982). This means that only one female deutonymph is required to start a colony of mites in a pitcher. Zwickia was much more successful than Anoetid A in terms of abundance and this may be related to the differences between the normal sex ratios of the two species. Thus, the normal ratio of females: males in Zwickia populations was 3:1, whereas for Anoetid A it was 1:1. This means that there is a greater chance that deutonymphs of Zwickia entering the pitchers will be female and capable of starting a colony and therefore this species is likely to be more successful in colonizing pitchers. It is interesting to note in

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this respect, that the percentage of pitchers occupied by Zwickia was approximately 3 times the percentage occupied by Anoetid A (87% versus 32%). The normal sex ratio of Creutzeria mites was not determined as the species occurred so rarely and generally in very low numbers, but this species occupied far fewer pitchers than either Zwickia or Anoetid A. It is possible that this is partially due to differences in the normal sex ratios of the species, but it may also be due to the fact that the mites appear to require very specific environmental conditions, or it may be that total reliance on passive dispersal is much less effective than a combination of active and passive colonization of pitchers.

The ecology of anoetid mites living in Nepenthes pitchers has never been studied previously due to the difficulties involved in identifying species and counting individuals, so attempts were therefore made in this study to investigate the ecology of the three species found in pitchers of N. mirabilis in Hong Kong. It was found that although all three species occurred in pitchers of all ages, the relative proportions of the three species altered so that there was a definite species succession with pitcher age. This was brought about by changes in the relative abundance of the specific food types preferred by each species. Most of the prey caught by individual pitchers is trapped within the first thirty days after opening, so that young pitchers contain large amounts of carrion which subsequently decomposes into detritus as the pitchers age. Consequently, Zwickia, which is a carrion feeder, was usually found in young pitchers, whereas the detritus feeding Creutzeria and Anoetid A were found in older pitchers where there was some accumulation of detritus. Creutzeria, which lives on the fluid surface, usually occurred in mature pitchers where the accumulation of surface detritus would be greatest,

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while Anoetid A occurred in the base of old pitchers where most of the debris had settled to the bottom.

The food supply in the pitcher environment is very irregular in space as well as time (Beaver, 1979a) and, as a result, nepenthebiont species have adapted to this irregularity by acquiring the ability to survive long periods without food. This is characteristic of nepenthebiont dipteran larvae and in particular of mosquitoes (Beaver, 1983), thus C. sumatranus and A. magnus are both able to delay larval development for at least three months, and it has been shown that several other nepenthebiont species are also able to survive long periods without food, particularly in the last instar (Assem, 1959; Beaver, 1979a; 1983). Although the ability to delay development indefinitely when food is scarce has so far only been demonstrated in Nepenthes diptera, studies on anoetid mites in Hong Kong indicate that this ability is not confined to dipteran larvae, but is a feature of nepenthebiont fauna in general. Thus, Zwickia mites reared under conditions of starvation were able to survive for at least two weeks in a state of arrested development. It is probable that all three anoetid species are able to delay development when food is scarce since, although the average life cycle length of Zwickia and Anoetid A (and therefore presumably also of Creutzeria) is two weeks when food is abundant, only three or four generations of each species developed within the lifespan of individual pitchers, which on average is at least three months.

In general, there is probably a shortage of food for the Nepenthes fauna, and for dipteran larvae in particular, as the great variation in the amount of prey caught by individual pitchers makes it unlikely that ovipositing females are able to adjust the number of eggs laid to the

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amount of food available in a particular pitcher. Adult females of A. magnus and C. sumatranus usually oviposit in newly opened pitchers, so that in this case (as noted with respect to Tripteroides bisquamatus - Assem, 1959) the females are ovipositing before any prey has been caught by the pitchers and before there is any indication of how much food will eventually be available. As a result, it is clearly impossible for the females to adjust the number of eggs laid to a level which can be supported by individual pitchers and, in general, many more larvae hatch from the eggs than can be supported by the available food resources. In the case of Tripteroides bisquamatus, on average, only 21% of the larvae initially present reached the pupal phase (Assem, 1959) and, although the percentage of larval survival was not determined, there also appeared to be a very low survival rate for larvae of C. sumatranus and A. magnus. The number of larvae which actually survive appears to be determined by the amount of food available rather than by the density of the larvae (Assem, 1959), so that pitchers trapping large amounts of prey will support larger populations of larvae.

While the amount of food available ultimately determines the number of larvae which survive, larval behaviour patterns are important in regulating the number of larvae of a particular species to an acceptable level in individual pitchers. Thus, Assem (1959) noted that cannibalism amongst larvae of Tp. bisquamatus was the major factor reducing larval numbers in pitchers and, that the extent of cannibalistic behaviour was related to the amount of food available. Large larvae seem to be more aggressive towards members of their own species, so that many of the large aquatic larvae in Nepenthes pitchers tend to occur as solitary individuals. Beaver (1979a) found that larvae of Pierretia urceola and Nepenthomyia malayana were always solitary due to aggressive behaviour, and he

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speculated that this behaviour was an adaptation to enable the species to survive in the pitcher environment, where the food supply would be inadequate to support the development of more than one larva. Several larvae of smaller aquatic species such as Corethrella calathicola and Lestodiplosis syringopais frequently occurred together in pitchers (Beaver, 1979a), demonstrating that size and food requirement are important factors in determining the number of larvae present in pitchers. In Hong Kong, larvae of A. magnus occur in the pitchers in much smaller numbers than those of C. sumatranus and they are considerably more aggressive and on occasion are also cannibalistic. This must be related to the fact that they are much larger than the larvae of C. sumatranus so that fewer individuals can be supported by the food supply in the pitchers. Larvae of C. sumatranus never exhibited intraspecific aggressive behaviour, which may be due to the fact that larval numbers are usually regulated by the predatory A. magnus larvae, so that aggressive behaviour is not necessary to reduce larval numbers to acceptable levels. Neither A. magnus nor C. sumatranus occurred as solitary individuals and while this is related to the mean size of the two species, it must also be related to their preferred food resources. Thus, most species which Beaver (1979a) noted as being solitary are obligate predators and they therefore have a very limited food supply, whereas larvae of A. magnus and C. sumatranus are only facultative predators and can subsist on a much wider range of food materials, so that numbers do not need to be so drastically limited.

Armigeres and Culex are not normally considered to be predatory genera (although Culex species belonging to the subgenus Lutzia are all predatory - Bates, 1954), but there seems to be a definite tendency for browsing and carrion-feeding pitcher plant mosquitoes to evolve into

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predators. Thus, in addition to A. magnus and C. sumatranus, several of the Nepenthes mosquitoes such as Tp. bambusa (Beaver, 1979a) and Uranotaenia spp. (Grjebine, 1979) are facultative predators. Uranotaenia is another genus not noted for predatory behaviour (Bates, 1954) but the mouthparts of the Nepenthes-breeding Uranotaenia species in Madagascar have become modified to such an extent that they resemble those of the exclusively predatory genus Toxorhynchites (Grjebine, 1979), illustrating this tendency for pitcher plant mosquitoes to become predacious.

As the only aquatic predators in pitchers of N. mirabilis in Hong Kong, both A. magnus and C. sumatranus play an important role in determining the composition of pitcher communities, although A. magnus being more predacious than C. sumatranus, tends to influence the pitcher communities to a greater extent. Larve of Megaselia corkerae and ?Metriocnemus were therefore most abundant in old pitchers from which A. magnus had already emerged; or in pitchers small enough to prevent the entrance of A. magnus females. Culex sumatranus is also preyed upon by A. magnus and was therefore also found to be most abundant in small pitchers lacking A. magnus larvae, although in general, in larger pitchers A. magnus appeared to have little significant effect on the population levels of Culex larvae. Culex sumatranus in turn had little effect on the population levels of M. corkerae, but it appeared to be a significant predator of ?Metriocnemus, leading to the total exclusion of chironomids from pitchers containing mosquito larvae.

In addition to preying on other dipteran larvae in the pitchers, both mosquitoes also feed on protozoa, rotifers, nematodes and oligochaetes and, as a result, these animals were generally restricted to old pitchers lacking the normal culicine fauna. Species diversity in these old pitchers

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was much higher than in young pitchers, both as a result of the absence of the predatory mosquito larvae and also because the number of nepenthexene species increased as conditions in the pitchers began to approximate those found in other container habitats. In young pitchers, the fluid pH is extremely acidic, sometimes being as low as 1.6, and the protease enzymes secreted by the pitchers are very active so that many nepenthexene animals are presumably in danger of being killed by the high acidity and digested. However, pitchers which have been open for more than one month lose the ability to buffer the fluid pH, so that it rises rapidly due to the entrance of rainwater and the accumulation of the alkaline products of digestion, rendering the plant proteases ineffective. As a result, conditions in the pitcher fluid become tolerable for a wider range of animals, most of which are detritus feeders utilizing the accumulations of detritus in the base of old pitchers as food.

Many of the groups of nepenthexene animals found living in old Nepenthes pitchers are characteristically found in temporary aquatic environments where the prime requirement for survival is an ability to tolerate long periods of desiccation. Nematodes, crustacea, rotifers and protozoa are all characteristic of temporary aquatic environments (Rzoska, 1961; Maguire, 1971; Bayly, 1982) and this is probably mostly as a result of their ability to tolerate desiccation in certain stages of their life cycles. Nematodes in particular, are very tolerant of desiccation and specimens which have been dried for more than four years have subsequently been found to be alive (Hyman, 1951). This desiccation tolerance means that although older pitchers are likely to dry out much more frequently than young ones (since they generally contain less fluid and their tissues are more brittle and are therefore more liable to cracking

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and splitting), this is not necessarily a great disadvantage to the nepenthexene fauna since they can remain inactive in intact dried out pitchers until rain refloods them. As a result, these animals are able to thrive for relatively long periods in old pitchers, whereas animals such as diptera and anoetid mites, which are unable to survive long periods of desiccation, must complete their development and colonize new pitchers within the three month life of an average pitcher.

Most of the nepenthexene fauna which is regularly found in old pitchers (nematodes, rotifers, protozoa) occurred more frequently in small pitchers close to the ground, than in large pitchers, which suggests that these nepenthexene animals originate from the damp soil and pools of water surrounding the plants. The relative proximity of the small pitchers to the ground would facilitate active colonization of the pitchers by nematodes, rotifers and protozoa, either via water films or in splash droplets, whereas colonization of larger pitchers is likely to be more difficult and hence less frequent and would probably involve passive dispersal of resistant stages via insects or wind. It may be noted here that Rhabditis has also been found in pitchers of N. gymnamphora in Java and that these nematodes were confined to ground pitchers (Menzel, 1922), which supports the suggestion that they originate from the soil around the plants.

The small size of rosette pitchers and their proximity to ground level also facilitates their colonization by other nepenthexene forms such as oribatid mites. Oribatid mites have been found in pitchers of other Nepenthes species (Hirst, 1928; Willmann, 1931; Thienemann, 1932; Erber, 1979), but in all these cases the mites found were dead and in varying stages of digestion, so that they were assumed to be part of the

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pitcher prey. However, living oribatids of several different genera have been found occupying pitchers of Sarracenia (Swales, 1972), demonstrating that it is possible for oribatids to live in the pitcher environment. Generally only one or two individuals of each genus were discovered living in the pitchers and only adult stages were present (Swales, 1972), which indicates that the mites were accidental inhabitants which nonetheless were able to survive in the pitchers (although not apparently to reproduce). Several genera of oribatid mites were also found living in Nepenthes pitchers in Hong Kong and, as in Sarracenia pitchers, the number of mites of each species found in individual pitchers was usually small, indicating that the pitchers are not a natural habitat. However, on several occasions nymphs were also found, indicating that some of the species may reproduce in the pitchers. Most of the oribatid mites found in the pitchers are probably heliotropic species which normally crawl around on the plants and surrounding vegetation. Small pitchers were more frequently occupied than large ones because less active movement would be required to enter them and, as they are frequently buried amongst vegetation, they would be more easily entered accidentally than large pitchers standing upright, well above ground level.

As already noted, there tends to be little overlap between the nepenthebiont and nepenthephil faunas of Nepenthes species in different regions, but there seems to be some similarity between the nepenthexene faunas of different areas. The oribatid mites Rostrozetes, Oppia, Scheloribates and Liebstadia have all been found in Nepenthes pitchers in Java and Sumatra (Willmann, 1931; Thienemann, 1932), as well as in N. mirabilis in Hong Kong and, although the specimens found in Java and Sumatra were all dead, it is quite likely that they had been living in the pitchers

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prior to death and digestion. Rhabditis, which is a nepenthexene pitcher inhabitant in Hong Kong, has also been found in pitchers of N. gymnamphora in Java (Menzel, 1922). Unfortunately specific identifications are not available for Rhabditis or the Hong Kong oribatids, so that it is not certain whether the same or different species are involved, although it is probable that they are different. Thus, Difflugia has been found in N. gymnamphora in Java (Oye, 1921) and in N. ampullaria in Singapore (Ghosh, 1928), but different species were involved in the two areas. These similarities in the nepenthexene faunas of different regions must be due to overlap between the habitats of wide-ranging nepenthexene genera and those often preferred by Nepenthes. Thus, fairly cosmopolitan genera, which normally inhabit waterlogged soil and boggy areas in general, are likely to be associated with Nepenthes over various parts of its range.

Nepenthes is a tropical genus and most species are confined to purely tropical regions. Nepenthes mirabilis however, is very widespread, occurring in both tropical and subtropical zones and it must therefore be tolerant of a much wider range of climatic conditions than the majority of Nepenthes species. Nevertheless, it is primarily adapted to tropical conditions so that the low temperatures and low rainfall in the winter months in Hong Kong adversely affect growth of the plants. Maximum plant growth and pitcher production takes place in the summer months in Hong Kong, when the highest temperatures and rainfall are recorded. In the winter, growth of the plants is substantially reduced and very few new pitchers are produced, resulting in a reduction in the number of new habitat units available for colonization by the pitcher fauna. This probably has little effect on the pitcher fauna however, since most of the nepenthebiont and nepenthephil inhabitants are also adversely affected by low temperatures, so that most Zwickia mites were killed by temperatures

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lower than 12°C, while development of the larvae of A. magnus and C. sumatranus was suspended when temperatures dropped below 12°C. As a result, it is unlikely that many adults emerge to colonize new pitchers during prolonged cold periods. Megaselia corkerae is more tolerant of low temperatures than A. magnus and C. sumatranus so that the winter months were the major breeding season for this species. For much of the year M. corkerae was restricted to old pitchers by the feeding activities of the predatory mosquito larvae, but in the winter, when the population levels of the mosquitoes were very low and when most of the surviving larvae were quiescent and non-feeding, the phorid was able to breed in pitchers of all ages. As a result, in spite of the decrease in the number of new pitchers available for colonization, overall a far greater number of pitchers were available for colonization by this species than at other times of the year.

While it is unlikely that A. magnus and C. sumatranus are adversely affected by the reduction in the number of habitat units available for colonization in the winter, the decrease in the average length of life of pitchers produced in the winter may have a substantial negative effect on the populations of both species. Under optimum temperature conditions (approximately 25°C), development of both species from egg to adult is completed within one month, which is well within the average lifespan of a pitcher. However, in the winter, development of the larvae may be delayed by low temperatures and, if there are prolonged cold spells, it is quite likely that development may be delayed to such an extent that the pitchers desiccate and die before the larvae can pupate and emerge. As a result, population levels in the winter may be greatly reduced, both because of the death of weaker individuals and also because of the

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inability of the larvae to complete their development within the shortened lifespan of the pitchers.

In some cases, for example where the plants grow in extremely exposed areas or at relatively high altitudes, prolonged cold periods could result in the virtual elimination of many elements of the pitcher fauna. If this happens then presumably the eliminated species are subsequently replaced by recolonization of the pitchers from other less drastically affected sites. The frequency of interpatch movement is likely to be low, as pointed out by Beaver (1983), since there is a regular supply of new pitchers for colonization at each site, reducing the need for the pitcher fauna to move from site to site searching for new pitchers to colonize. However, a certain amount of interpatch movement must occur because otherwise it is likely that the faunas of different sites would differ substantially, both as a result of different animals colonizing the plants initially and as a result of the speciation of genetically isolated populations. It was found that the nepenthebiont and nepenthephil pitcher fauna of all sites (except those on Lantau island) were very similar, indicating that when N. mirabilis first spread into the region, the local fauna colonizing the pitchers followed the spread of the plants throughout the area. The only exceptions were the sites on Lantau island where the number of plants was so small that it is possible that these sites have been overlooked by some of the colonizing fauna. A certain amount of interpatch colonization must also have gone on ever since the initial spread of the plants, because there is no evidence that any of the populations at different sites are diverging, so that some breeding contact must be maintained between sites.

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In general, most sites within Hong Kong are fairly close together, which would tend to increase the frequency of interpatch movement by the Nepenthes diptera. The dipterans must have some means of locating the plants and it is possible that the characteristic strong smell of the flowers, which carries over long distances, may play some part, although this would not explain how new patches of immature plants developing from seed are initially colonized. Within established sites, spread of the plants seems to be accomplished largely by vegetative propagation, since very few seedlings were found in these areas. This may be a result of the fact that the seedlings are unable to compete with the mature plants, or it may be that lepidopteran larvae feeding on the fruits destroy most of the seeds, so that few viable seeds are released. The lepidopteran which fed on the fruits was only found at one site but other sites were not investigated thoroughly so it is possible that this species is fairly widespread and causes substantial harm.

Although the spread of plants in established habitats is not dependent on the production of seeds, the dispersal of Nepenthes plants throughout a region is totally dependent on the production of viable seed which can be transported to new areas via wind or water. The purely tropical Nepenthes species, N. gracilis, produces seed which is apparently viable for very short periods of time (Garrard, 1955; Lim and Prakash, 1973), but since climatic conditions vary little throughout the year in regions where this species grows, there is no particular advanta to be gained by having seeds which are capable of germinating over long periods of time. In Hong Kong, however, the seeds of N. mirabilis were viable for a much longer period and this may be a reflection of the fact that the plants are growing in a much more unstable environment, where

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there is definite survival value in the seeds being viable for longer periods, so that some at least may germinate when conditions are favourable. Since most plants in Hong Kong flowered in June, July and August, the bulk of annual seed production also took place in these months. As the maximum percentage of germination was obtained from seeds stored for two months, this means that the maximum viability of most of the seeds produced in Hong Kong coincides with the period when the climate is also at its most favourable for growth. With seeds stored for longer periods, the time required for germination to take place was greatly increased, thus seeds stored for four months required a further four months for germination. As a result, these seeds would avoid germinating in the winter when the chances of the seedlings surviving would be very low. The pattern of germination of seeds of N. mirabilis in Hong Kong therefore seems to be specifically adapted to the climatic conditions found in the region. It would be interesting to see whether seeds of N. mirabilis growing in tropical areas also exhibit the same patterns of germination, as this would indicate whether the germination characteristics of the seeds are determined purely genetically or whether climatic factors are responsible for imposing particular germination patterns on the seeds.

The results of this study on the ecology of the Nepenthes community in Hong Kong reinforces many of the conclusions which Beaver (1979a; 1979b; 1983) has reached in his study of Nepenthes pitcher faunas, while at the same time adding some new information to our knowledge of Nepenthes pitcher faunas in general. Thus, many new animals have been added to the list of pitcher inhabitants, including numerous genera of oribatid mites which have never previously been considered to be part of the pitcher

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fauna. The ecology of anoetid mites living in the pitchers has also been studied for the first time and this revealed, amongst other things, that some species are capable of active colonization of pitchers, a factor which greatly increases their dominance of the pitcher communities. Such factors as age and size of the pitchers were also shown to have marked effects on the composition of the pitcher communities, therefore in any further work on pitcher faunas, both these factors must be taken into account when sampling pitchers or designing experiments.

Although our knowledge of pitcher communities has greatly increased over the past five years, the surface has barely been scratched and detailed study of the communities living in the many species of Nepenthes at the distributional centre of the genus, would no doubt reveal much more than the isolated studies of one or two species carried out to date. In addition, the composition of pitcher communities is easily altered and manipulated so that experimental studies on the relationships between the animals in the communities and between the communities and the plants themselves should be possible. As the pitchers are small and numerous and contain relatively simple communities which are amenable to experimentation, they could also be used for investigations into ecological processes such as dispersal, colonization and species interactions and could greatly increase our knowledge of community ecology in general.

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APPENDIX I

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Table A

Standard errors of the mean monthly number of dipteran larvae present in pitchers. (Refer to Fig. 13).

	Culex		Armigeres		Megaselia	
Month	mean	SE	mean	SE	mean	SE
December	1.7	1.0	0.7	0.3	0.14	0.1
January	3.9	2.6	0.4	0.1	0.16	0.2
February	0.1	0.08	0.7	0.5	0	0
March	0.1	0.09	0.2	0.1	0.33	0.2
April	0.3	0.3	1.1	0.7	0.09	0.1
May	0.1	0.03	0.7	0.2	0.07	0.04
June	2.2	1.5	0.9	0.3	0	0
July	0.2	0.2	0.4	0.2	0.02	0.02
August	0.4	0.2	0.6	0.3	0	0
September	0.8	0.5	1.3	0.4	0	0
October	1.7	0.3	1.5	0.3	0.03	0.02
November	2.2	1.9	0.9	0.4	0.02	0.01
December	0.3	0.1	0.8	0.3	0.28	0.2
January	0.2	0.1	1.3	0.3	0.11	0.1
February	0	0	0.01	0	0.74	0.4
March	1.0	0.6	0.2	0.1	1.14	0.7

(Interspecific correlation coefficients:-

Culex/Armigeres	r =	0.0964	not significant
Culex/Megaselia	r =	- 0.1337	not significant
Armigeres/Megaselia	r =	- 0.6011	$P<0.02$)

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Table B.

Standard errors for the mean values of the number of dipteran pupae per pitcher. (Refer to Fig. 19).

Pitcher age class	Culex		Armigeres		Megaselia	
	Mean	SE	Mean	SE	Mean	SE
1	0	0	0	0	0	0
2	0	0	0.32	0.2	0	0
3	0.48	0.2	1.24	0.5	0.12	0.1
4	0.56	0.3	1.12	0.4	0	0
5	0.44	0.2	0.92	0.5	0.04	0.04
6	0.74	0.3	0.17	0.1	0.48	0.4
7	0.68	0.6	0.16	0.1	0.47	0.3
8	0.20	0.2	0.20	0.1	0.33	0.3
9	0	0	0.22	0.2	0.11	0.1

SE = Standard Error

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APPENDIX II

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TABLE A.

Distribution and abundance of pitcher inhabitants in Hong Kong and Macau

(Abundance values are the percentages of pitchers occupied at each site).

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TABLE A

	site number										
	1	2	3	4	5	6	7	8	9	10	11
No. of pitchers sampled	23	108	29	178	14	62	62	35	14	3	25
Species											
Protozoa											
Rhizopoda	5	3	3	2	0	10	7	3	0	0	4
Flagellata	18	7	21	20	7	37	32	20	0	0	27
Ciliata	9	26	10	20	0	15	23	9	14	0	19
Algae											
Bacillariophyta	0	0	10	4	0	5	3	0	0	0	0
Platyhelminthes											
?Catenula	0	5	0	1	0	0	0	0	0	0	0
Oligochaeta											
Pristina foreli Piguet	0	0	0	0	0	4	0	0	0	0	0
Rotifera											
Bdelloidea	0	16	7	11	0	10	11	6	7	50	8

	site number										
	1	2	3	4	5	6	7	8	9	10	11
Species											
Nematoda											
Rhabditis sp.	0	1	7	7	0	3	0	6	14	0	8
Crustacea											
Phyllognathopus vigueri Maupas	0	8	0	1	0	2	0	0	0	0	4
Monospilus dispar Sars	0	0	0	0	0	2	0	0	0	0	0
Insecta											
Collembola											
Paronellidae											
species A	0	0	0	0	0	2	0	3	0	0	0
species B	5	0	0	0	0	0	2	9	14	0	0
Entomobryidae											
Lepidocyrtus sp.	0	0	0	0	0	0	2	0	0	0	0
?genus ?sp.	0	0	0	0	7	0	3	0	0	0	0

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TABLE A - continued

Species	site number 1	2	3	4	5	6	7	8	9	10	11
Trombidiformes											
Bdellidae											
Bdellodes sp.	23	3	14	3	7	16	27	11	7	0	0
Anystidae											
Anystis sp.	9	2	3	3	21	2	3	9	0	0	0
Cheyletidae											
Hemicheyletia sp.	0	1	0	0	0	2	2	0	0	0	0
Cunaxidae											
Cunaxoides sp.	0	1	7	0	0	0	0	0	0	0	0
Hydrachnellae											
Anisitsiellidae											
?genus ?sp.	0	0	0	0	0	3	2	0	0	0	0

Species	site number 1	2	3	4	5	6	7	8	9	10	11
Sarcoptiformes											
Acaridae											
Tyrophagus putrescentiae Schrank complex	0	5	7	2	0	3	3	0	0	0	0
Glycphagidae											
Blomia sp.	0	0	0	1	0	0	3	0	0	0	0
Anoetidae											
Zwickia sp.	91	86	93	90	93	77	97	83	0	0	77
Creutzeria sp.	5	15	38	25	64	2	2	24	14	0	8
Anoetid A	5	36	52	44	86	13	2	20	7	0	23
Oribatei											
Malaconothridae											
Malaconothrus sp.	0	0	0	1	0	0	0	0	0	0	0
Trimalconothrus sp.	0	3	0	0	0	0	0	0	0	0	0

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TABLE A - continued

Species	site number 1	2	3	4	5	6	7	8	9	10	11
Sminthuridae											
Sminthurus sp.	0	0	0	0	0	2	0	0	0	0	0
Thysanoptera											
Scirtothrips dorsalis Hood	0	2	10	5	0	2	2	6	0	0	0
Phlaeothripidae											
?genus ?sp.	0	0	0	0	0	0	0	0	0	0	4
Diptera											
Culicidae											
Culex sumatranus Brug	77	36	48	57	79	31	42	63	71	0	62
Armigeres magnus (Theobald)	56	61	72	49	86	53	55	77	7	0	69
Ceratopogonidae											
?genus ?sp.	0	0	0	0	0	2	0	0	0	0	0
Chironomidae											
?*Metriocnemus*	0	2	0	4	0	2	2	0	0	0	0

Species	site number 1	2	3	4	5	6	7	8	9	10	11
Phoridae											
Megaselia corkerae Disney	27	21	28	12	7	10	21	14	0	0	12
Psychodidae											
?genus sp. A	0	0	7	0	0	2	0	0	0	0	0
?genus sp. B	0	0	7	0	0	0	0	0	0	0	0
Mycetophilidae											
?genus ?sp.	0	0	0	0	0	2	0	0	0	0	0
Acari											
Mesostigmata											
Parasitidae											
Pergamasus sp.	0	2	0	2	0	0	0	0	0	0	0
Uropodidae											
Deraiophorus sp.	0	0	0	6	0	0	0	0	0	0	0
Oplitis sp.	0	0	3	1	0	0	0	6	0	0	0

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TABLE A - continued

Species	site number 1	2	3	4	5	6	7	8	9	10	11
Hermanniidae											
Hermannia sp.	0	0	0	3	0	0	0	0	0	0	0
Liodidae											
Neoliodes sp.	0	0	0	6	0	2	0	0	0	0	0
Zetorchestidae											
Zetorchestes sp.	0	0	0	4	0	0	0	0	0	0	0
Oppiidae											
Oppia sp.	0	0	0	2	0	2	0	0	0	0	0
Carabodidae											
Carabodes sp.	0	0	0	12	0	0	0	0	0	0	0
Otocepheidae											
Tetracondyla sp.	0	0	0	2	0	0	0	0	0	0	0

Species	site number 1	2	3	4	5	6	7	8	9	10	11
Oribatellidae											
Paralemellobates sp.	0	1	0	4	0	3	0	0	0	0	0
Scheloribatidae											
Scheloribates sp.	0	1	7	2	0	2	0	0	0	0	0
Liebstadia sp.	0	0	0	1	0	0	0	0	0	0	0
Oribatulidae											
Zygoribatula sp.	0	11	10	2	0	2	6	3	0	0	0
Phauloppia sp.	5	0	31	0	0	0	2	0	0	0	0
Mochlozetidae											
Podoribates sp.	0	0	0	6	14	0	0	0	0	0	0
Haplozetidae											
Rostrozetes sp.	0	0	0	5	0	0	0	0	0	0	0
Peloribates sp.	0	0	0	9	0	0	0	0	0	0	0

[illegible]

TABLE A - continued

Species	site number 1	2	3	4	5	6	7	8	9	10	11
Galumnidae											
Galumna sp.	9	14	10	27	0	2	0	6	0	0	12
Phthiracaridae											
Hoplophthiracarus sp.	0	2	0	2	0	0	0	0	0	0	0

Species	site number 1	2	3	4	5	6	7	8	9	10	11
Arachnida											
Theridiidae											
Coleosoma sp.	4	2	10	0	0	0	0	0	0	0	0
Argyrodes sp.	0	3	1	0	0	0	0	0	0	0	0

British Museum (Natural History)