LECANOPTERIS SPINOSA — A NEW ANT-FERN FROM INDONESIA

A.C. JERMY

British Museum (Natural History) London SW7 5BD.

and T.G. WALKER

Dept. Plant Biology, University of Newcastle upon Tyne NE1 7RU

ABSTRACT

Whilst collecting plants in the Latimojong Mnts., Sulawesi (Celebes) the authors found a new species of ant-inhabited fern here described as **Lecanopteris spinosa** sp. nov. An account of the morphology and anatomy is given and comparisons are made with other species variously placed in the genera *Lecanopteris* Reinw. and *Myrmecophila* (Christ) Nakai. On grounds of anatomy and rhizome morphology it is argued that the new species is intermediate between these genera thus supporting Copeland's view that they should be united. The highly developed rhizome structure is discussed in relation to the ants that inhabit it.

INTRODUCTION

In 1824 Reinwardt described a fern which he called *Onychium carnosum,* unaware that Kaulfuss (1820) had already used the generic name for another totally different species. No sooner than the name was published Reinwardt became aware of his mistake and in 1825 published a substitute generic name, *Lecanopteris.* Blume (1828a) elaborated the description emphasizing that the species was distinct from any other *Polypodium* in having a peculiar habit with a swollen rhizome and sori immersed at the reflexed tips of the pinnae segments. Later (1828b) he figured *L.carnosa* together with a variant which he called *L.pumila* although the text description of this new species never appeared.

The genus was upheld by some pteridologists (e.g., Presl 1836, Fee 1852) whilst others (e.g. Mettenius 1856; Hooker & Baker 1868, 1874) still preferred to treat it under a large and variable *Polypodium.* Cesati (1876) described a related species (now *L. deparioides* (Ces.) Bak.) under *Davallia* believing the reflexed leaf tip to be similar to the indusium of that genus. In 1881 however Baker accepted *Lecanopteris* and described a fourth species *(L. incurvata)* from Sumatra placing it here on account of its soral structure alone, as his specimen *(Curtis 24:* K) was without a rhizome. Later collections of what is undoubtedly the same species (e.g. Benkoelen, *Brooks, s.n.* 1920—23; BM) show a typical swollen and naked rhizome.

Christ (1897), whilst not accepting the generic rank, did however accept the taxonomic concept of Baker (et alia) and he went further and grouped together four other species of *Polypodium* which had similar swollen ant-inhabited rhizomes, under the section *Myrmecophila,* a name legally instated at generic rank by Nakai (1929). Whilst the rhizomes of *Myrmecophila* were ant inhabited and often massive they were not naked but covered with distinct clathrate, dark-centred scales. The sori were superficial, although sometimes deeply immersed lying close to the rachis or costa. This taxonomy was maintained although some (e.g. van Alderwelt van Rosenburgh 1909) went further and included *Lecanopteris* as a subsection within · section *Myrmecophila,* when others (e.g. Ching 1940) accepted both as genera. Copeland (1905) maintained *Lecanopteris* (pro gen.) but placed *Myrmecophila* as a section of *Polypodium.* In 1929 he pointed out the affinity of the former to *Microsorium* sect. *Phymatodes* and its relationship to *Myrmecophila* which he proposed (1929: 122) should be united under *Lecanopteris,* a position he maintained in 1947 and 1960.
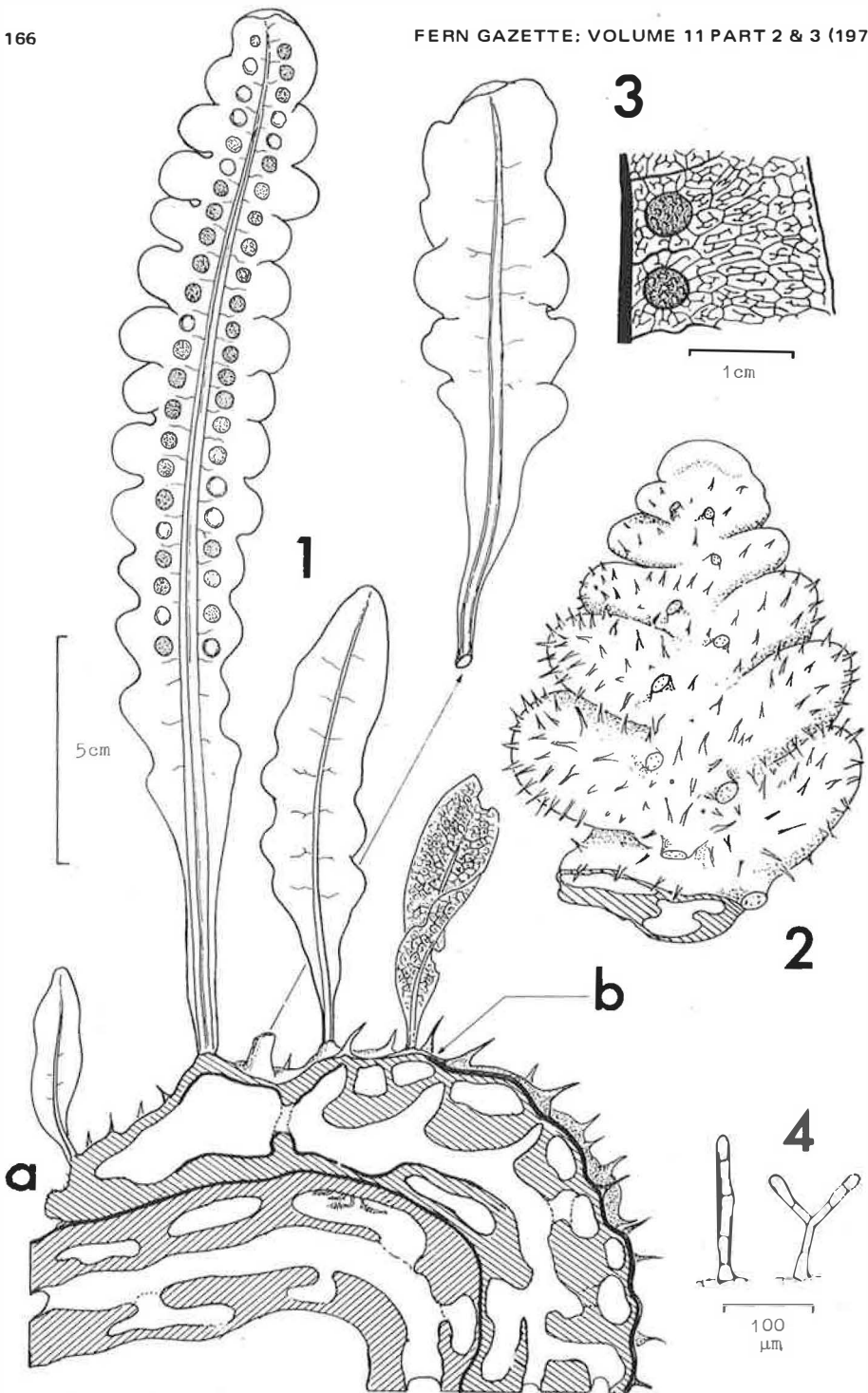
FIGURES 1—4, *Lecanopteris spinosa:* 1, diagrammatic sketch of whole plant, (a, growing point; b, advancing front of black pigment zone); 2, portion of rhizome; 3, enlargement of portion of frond showing venation; 4, hairs from rhizome apex.

Holttum (1954) placed the two species of section *Myrmecophila* found in Malaya in *Phymatodes* Presl. [*P. sinuosa* (Wall. ex Hook.) J. Sm.; *P. crustacea* (Copel.) Holtt.] on the grounds that they "have all the characters . . . [of *Phymatodes*] apart from the swollen rhizome". They do not however have the characteristic knobbly, branched paraphyses amongst the sporangia as the other species of this genus, e.g. *P. scolopendria* (Burm.) Ching. *Lecanopteris,* with its distinct sori and clathrate scales, Holttum keeps as a separate genus.

    The finding of an ant-fern in Sulawesi with a swollen, naked rhizome but with fronds with the texture and sori of *L. sinuosa* places it intermediate between sections *Lecanopteris* and *Myrmecophila*. Although in the two genera the position of the sori

| TABLE 1: Species of *Lecanopteris* discussed in this paper.	
Rhizome naked; sorus only slightly immersed at pinnae or segment ends which are ± reflexed (= section **Lecanopteris**)	Rhizome with clathrate scales; sorus immersed close to costa of ± simple fronds or close to costule of pinnae (= section **Myrmecophila**)
L. carnosa (Reinw.) Bl.	L. lomarioides (Brause) Baker
L. davallioides v.A.v.R.	(incl. L. crustacea Copel)
L. deparioides (Ces.) Bak.	L. mirabilis (C. Chr.) Ching
(incl. L. curtisii Bak.)	L. sarcopus de Vr. & van Teyss.
L. incurvata Bak.	L. sinuosa (Wall.) Copel.
L. nieuwenhuisii Christ*	(incl. L. pumila Bl. ex Copel.)
L. philippensis v.A.v.R.*	
L spinosa Jermy & T.G. Walker	
* rhizome not seen	

varies and this is correlated with the dissection of the frond, the vascular supply to it and its general structure is similar. The species examined by us are listed under the two sections in Table 1. In all, the maturing fertile sporangia are immersed in a mat of long setae topped by an abortive sporangium which often breaks away leaving a curious cup-shaped head and which, although possibly homologous with the branched paraphyses of other Microsorioid genera, should not be confused with them. The rhizome architecture varies from the more massive irregular growth pattern in *L. crustacea* through *L. spinosa,* both without scales, to the regular *L. sinuosa* with scales; *L. mirabilis* is irregular and expansive with often an almost naked upper surface; according to Copeland (1929) *L. sinuosa* has a Papuan form (not seen by us) with a glabrescent rhizome. Except for *L. davallioides* and *L. nieuwenhuisii,* where we have seen no rhizome material, all the species in section *Lecanopteris* have uniseriate, occasionally branched, trichomes on the epidermis of the young rhizome. In anatomical structure both the rhizome and frond of *L. spinosa* are similar to *L. carnosa* and *L. sinuosa* (cf. Yapp 1902).

    It is seen that *L. spinosa* is intermediate between the two sections as hitherto defined and is further proof in support of Copeland to unite *Myrmecophila* and *Lecanopteris* under the latter. If the degree of organisation and adaption of the rhizome is significant, *L. spinosa* would be the most advanced member of section *Lecanopteris*.

DIAGNOSIS AND DESCRIPTION

Lecanopteris spinosa Jermy & Walker **sp. nov.** (fig 1 et sequ.)

Planta myrmecophila epiphytica. *Rhizoma* glabrum ventricosum 2.5—4 cm crassum, ramis brevibus
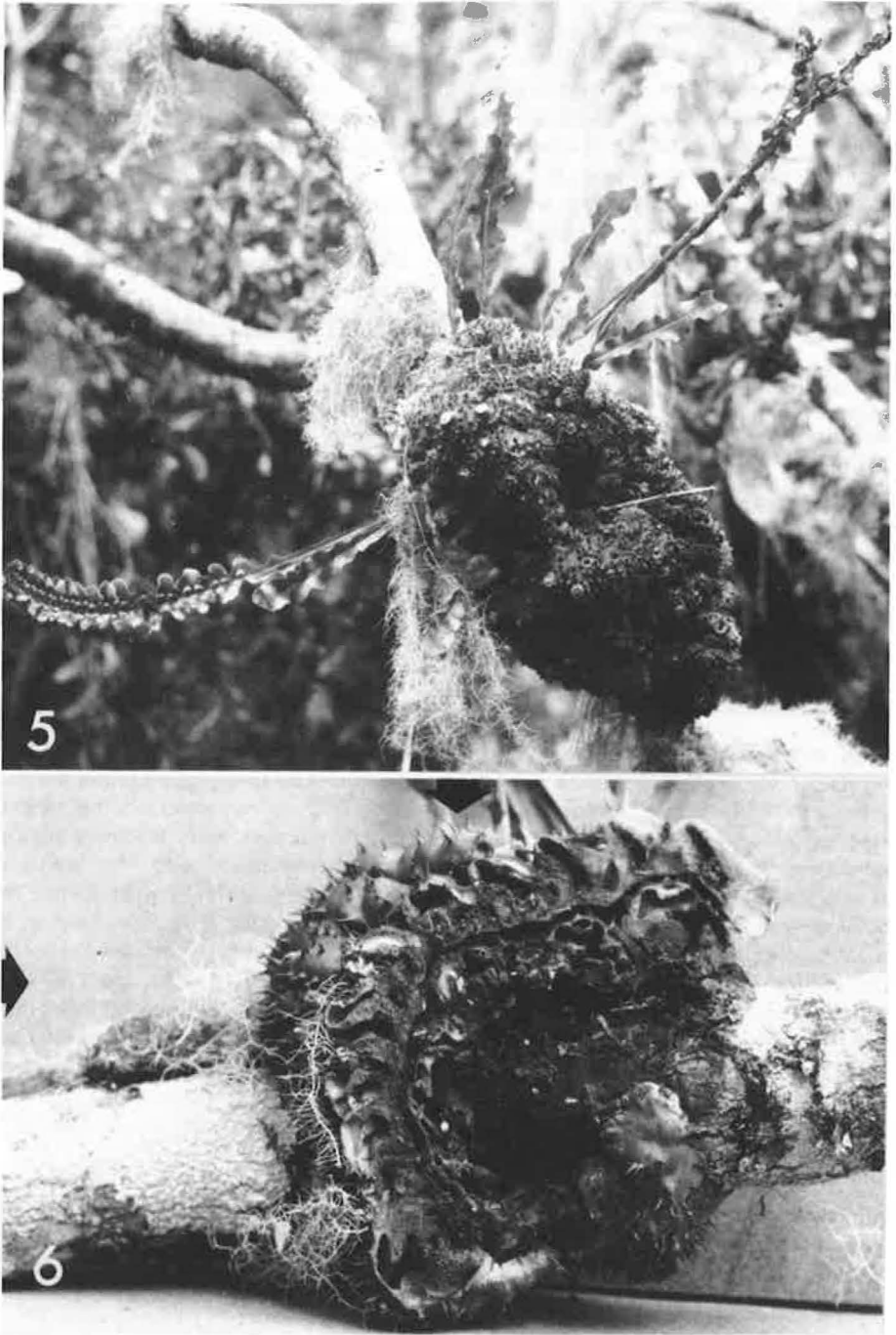
FIGURES 5—6, *Lecanopteris spinosa:* 5, plant in situ x ½; 6, sectioned rhizome showing galleries (arrow intersection indicates ants removing pupae).

lateralibus, porticus ad apicem capiens, initio subviride pruinosum, demum nigrum coriaceum, spinis ad 6 mm conicis attenuatis. *Frondes* exstipitatae, bifariae, usque ad 30 x 5 cm (frondes steriles saepe 6—8 cm longae); rhachis flavovirens; *lamina* frondum sterilium simplex, frondum fertilium pinnatifida lobata, apices loborum rotundatis; venae anastomosantes, areolae venulis liberis clavatis includentibus. *Sori* immersi uniseriati prope rhachidem, sporangia initio sporangibus sterilibus elongatis obtecta at sine paraphysibus ut in speciebus nonnullis *Microsorii*. *Sporae* monoletes (56—) 69—(82.5) μm longae luteolae laeves.

Typus Indonesia, Sulawesi, Latimojong Mnts, SW slopes of Mnt. Rantemario, below Buta Jakke above base camp; on *Platea latifolia* Bl. in mixed oak-podocarp forest, at 1950 m alt., 10 November 1969, *A.C. Jermy 7609;* holotypus in BM; isotypi in BO, GH, L.

Paratypus: Loco citato, *T. G. Walker T12179* (in herb Walker).

Plants epiphytic, found on the upper branches (3—6 cm thick) of trees 15—20 m high. Primary rhizome 2.5—4 cm thick, the advancing front somewhat flattened and adpressed to the substrate and budding off lobes which develop into lateral branches 2.5—5 cm long, 1—3 cm thick, and which on maturity swell to press against each other (see fig 2). In all the plants studied the main axis of the rhizome soon orientated itself across the branch and gradually encircled it. When the first complete turn has been achieved the main rhizome continues to grow in the same direction on top of the old dead, leathery rhizome. Thus a "ball" of rhizome would result often three or four stems thick, each growing epiphytically on itself and in which there would be usually only one advancing apex although occasionally a side branch would continue growth for a time. It is possible that such "balls", found up to 25 cm across, could contain more than one plant but this seems unlikely.

Living rhizomes are pale green with a pronounced glaucous bloom on the younger parts which dries as flat, plate-like scales of white wax. Scales absent but the very young epidermis is sparsely covered with simple, very rarely branched, caducous trichomes of four to eight cells uniseriately arranged, the terminal cell of which is not obviously glandular. Epidermis minutely papillate with scattered multicellular spines, 4—6 mm long, narrowly conical, or cylindrical and tapered with a swollen conical base, occasionally consisting of this only, green and flexuous often turning black before the rest of the epidermal tissue. Green rhizome becoming black (see para. on anatomy) as fronds absciss; the tissue eventually dying as the outer layers become horny or leathery. The meristematic tissues of the lateral branches die at this stage and the invaginated apex is often perforated as the tissues shrink (see below).

Fronds, in two ranks on the main rhizome, not normally seen on the lateral branches although some are initiated there; for the most part initiated on the meristematic front of the rhizome which develops, as the leaf ages, into a conical phyllopodium, stipe virtually absent, articulate to rhizome, the fronds falling as the rhizome blackens. Lamina up to 30 x 5 cm (often only 6—8 cm long in sterile fronds), linear-oblanceolate tapering below to form in the lower 2—5 cms a wing along the rachis, apex rounded, often imperfect and emarginate, margin entire in small sterile fronds to undulate or ± regularly lobed $\frac{1}{3}$ to the rachis in fertile fronds (see fig 1); texture coriaceous, dull, pale green, midrib distinct, yellowish green, raised on the adaxial side and with a narrow ridge on the abaxial surface, the veins conspicuous on drying, anastomosing to form areolae with included free veinlets (see fig 3).

Sori in one row close to and either side of the rachis usually in the upper $\frac{2}{3}$ of the leaf only; circular on flat immersed receptacles which cause projections on the upper surface; sporangia protected in the early stages by long-stalked abortive sporangia which overtop them and whose heads touch one another to form a compact layer (see fig 25). Spores monolete, pale yellow (56—) 69 (—82.5) μm long (in a sample of 50), sporoderm smooth under the SEM with only the occasional papilla in the region of the suture.
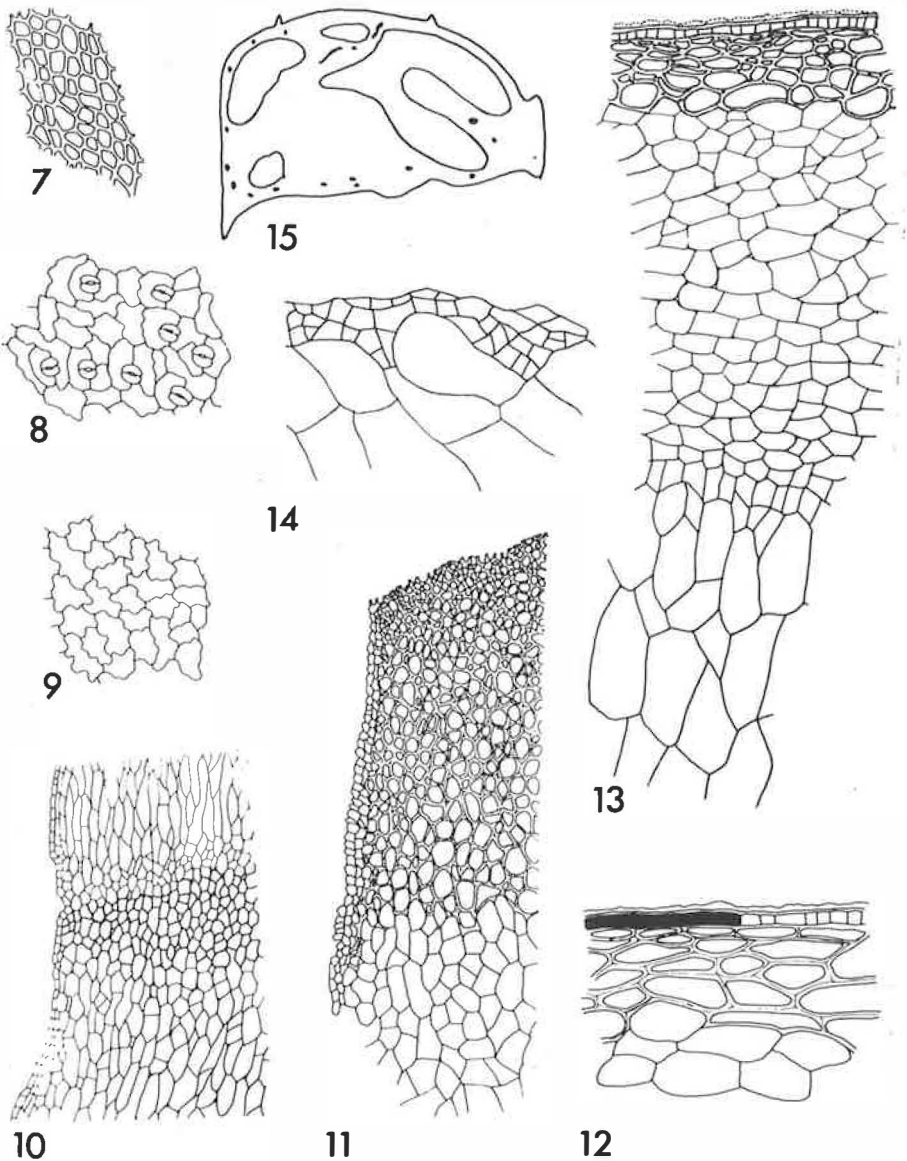
FIGURES 7—15, *Lecanopteris spinosa* anatomy: 7, epldermis of rhizome (x 65); 8, lower epidermis of frond (x 65); 9, upper epidermis of frond (x 65); 10, LS young dehiscence region of frond base (x 45); 11, LS old frond base (x 45); 12, LS old rhizome at junction of green and black areas (x 65); 13, LS young rhizome, boundary between lower water storage tissue and upper parenchyma arrowed (x 55); 14, delimiting region arrowed in fig 13 at later stage just prior to breakdown of water storage tissue of rhizome (x 70); 15, TS rhizome showing galleries (cross hatched) and vascular system.

ANATOMY

1. The root

The roots are short, black and wiry and cling to the substrate and when developed in the chambers produce copious root-hairs. The xylem is diarch and there is a particularly well defined pericycle (fig 26). Abutting onto the endodermis is a ring of cells with heavily thickened walls about seven cells in depth, except opposite the protoxylem points where it is interrupted. This is identical to the root structure of *L. carnosa* as described by Yapp (1902).

2. The rhizome

In the young parts the spines, which are such a conspicuous and permanent feature of this plant are green and flexible when young, consisting of cells with living contents and having lignified walls. As they age the cells lose their contents (fig 24) and the spines become rigid. They first blacken at the tip and then ultimately throughout, this blackening frequently preceding that of the rhizome discussed later.

The rhizome epidermis consists of thick walled cells and is devoid of stomata (fig 7). Overlying the cuticle is a very thick transparent, wax, becoming white on drying seen under the SEM as irregular flakes which harden to the surface when the rhizome blackens. As in some other species of *Lecanopteris* e.g. *L. carnosa,* the rhizome blackens with age and a curious feature in *L spinosa* is that frequently the boundary between green and black areas is absolutely sharp as if drawn by a pen. Although, as ageing occurs, there is a gradual browning of the underlying tissues, the black appearance is entirely caused by the deposition of dense melanic substances in the epidermal layer only (fig 12).

Immediately beneath the epidermis there is a layer a few cells deep which is lignified and internal to this is parenchyma. In the centre of the young parts of the rhizome the parenchyma forms a very distinctive water storage tissue which can be distinguished by the naked eye by its lighter colour. In this tissue the cells are much larger than those of the surrounding parenchyma, are elongated vertically and have a glistening translucent appearance due to their high water content. It is the breakdown of this tissue which leads to the formation of the cavities.

The water storage tissue is of short duration, rarely being found intact more than about two centimetres behind the apex of the main stem of the branches. This agrees with the situation as described for *L. carnosa* by Yapp but although he described some of the anatomical details their possible importance in the formation of the cavities appears to have eluded him as he believed that only very young plants (which he did not possess) would provide the answer.

The innermost one or two layers of the parenchyma bordering onto the water storage tissue are not especially prominent at first, being thin walled and tending to be aligned with their long axes in the same plane as the cells of the water storage tissue (arrowed in fig 13). Later on, however, these parenchyma cells divide to form a very conspicuous delimiting layer from which finger-like processes project between the outermost cells of the water storage tissue (fig 14). This later stage is illustrated by Yapp (1902). The cells of this delimiting layer become rapidly and progressively more suberized and when this process has reached a certain stage the water storage tissue also develops a very small amount of suberization. At this point the delimiting layer apparently cuts off the once more or less intimate contact between the water storage tissue and the ground parenchyma of the rhizome, with the subsequent disintegration of the water storage tissue and the resultant space forming a chamber lined by a layer
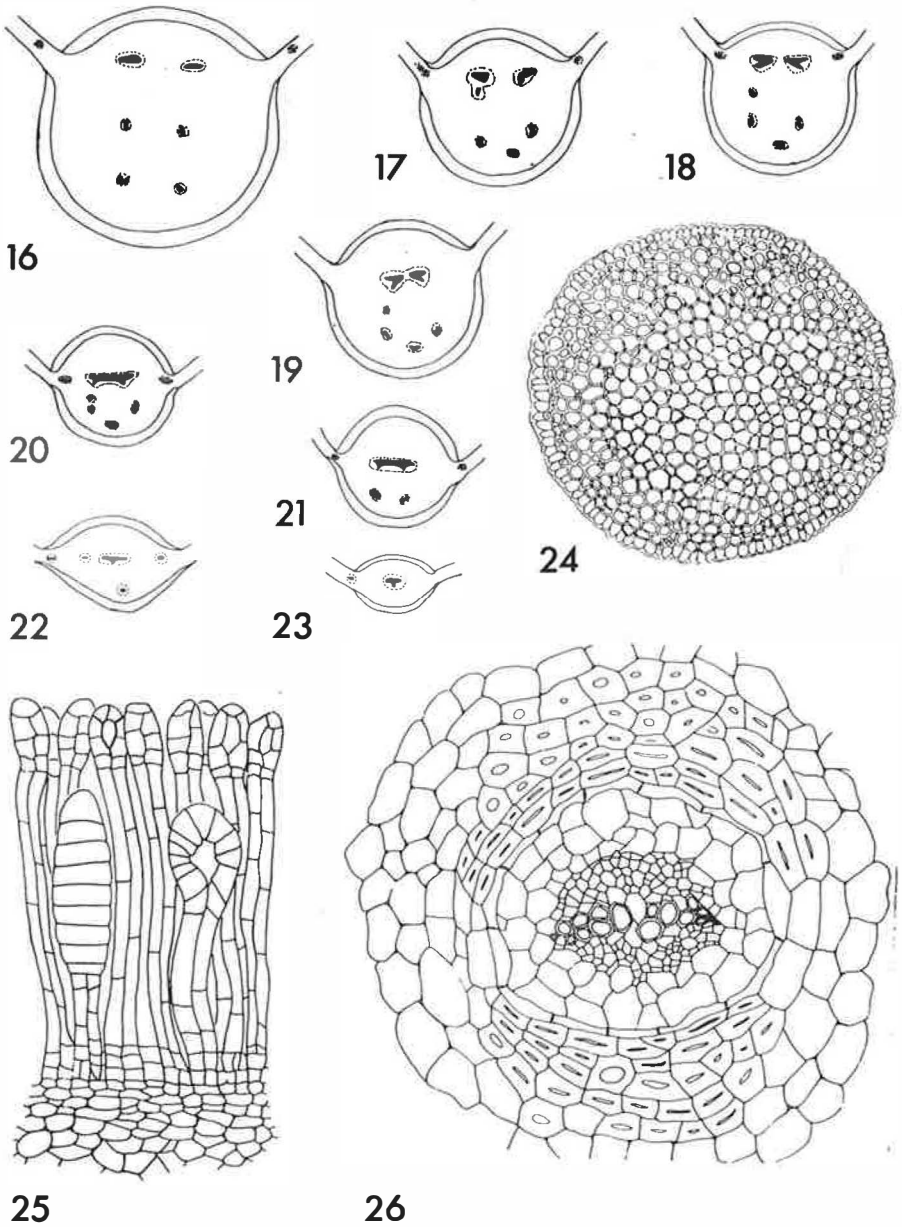
FIGURES 16—26, *Lecanopteris spinosa* anatomy: 16—23, TS rachis from base towards apex, xylem as solid black, endodermis as broken line (x 5.75); 24, TS mature spine of rhizome (x 55); 25, LS young sorus (x 90); 26, TS stele and inner cortex of root (x 400).

of dark suberized cells. If a young apex is sectioned the development of the delimiting layer, its progressive suberization and the breakdown of the water storage tissue can be seen as a continuous process occurring over a distance of 0.5—1 cm. Hence the chambers or galleries are constantly being extended, keeping pace with the elongation of the rhizome.

The apices of young rhizome lobes or of the lateral branches are frequently invaginated and have the appearance of a "pore". On dying the parenchymatous cells at the base of this pore shrink and break down thus linking the chamber with the exterior. It is through such natural openings that ants gain entrance to the galleries. The cells lining these openings are similar to those in the galleries suggesting that the opening has been formed in much the same way as the galleries themselves.

In actively growing portions of the rhizome there is a "lip" on the leading edge which consists of young dividing cells forming the meristem. It is in this region that the leaf primordia and the spines arise (marked a in fig 1). This extends along the growing margin and no single apical cell was detected, although it would be exceedingly difficult to find if it did exist without microtoming a considerable number of sections. Toward the sides as the rhizome matures, or in the lateral branches of limited growth, the edges tend to be more or less rounded, the parenchyma comprising the bulk of the rhizome being fully expanded and enclosed in a layer of lignified cells on both upper and lower surfaces and bounded by the epidermis. Further back in the blackened areas, all the cells become orange-yellow and spongy in texture.

The rhizome is permeated with a network of vascular strands which are embedded in the parenchyma above and below the galleries (see fig 15) but which are absent from the water storage tissue where this is present. The individual strands are very similar in structure to the vascular supply of the root (fig 26) except that immediately outside the endodermis there is at most a single layer of thickened cells.

The pattern of the galleries tends to be rather more complex in this species than in most others of *Lecanopteris*. Here they tend to be on three levels with a major gallery running along the entire length of the rhizome and giving off frequent chambers above and below which interconnect with one another. The layout is not so clear as in some other species such as *L. carnosa* and *L. deparioides* where the rhizome can be likened to a series of flasks joined together, each bearing a frond and having one or more chambers within. In *L. spinosa* the fronds tend to be somewhat sparse and the rhizome not organised into units joined together, other than the lateral branches. According to the position of the cut, at any part of an opened rhizome there may be seen three lines of chambers or else large irregular spaces where all the chambers meet (see fig 1). Thus there is a continuous network of galleries and chambers throughout the plant as in all of the Asiatic ant-ferns. This is in contrast to the New World species of *Solanopteris,* described in detail recently by Hagemann (1969) and Wagner (1972), in which the rhizome is dimorphic and the inflated areas are produced on short shoots.

3. The frond
The upper surface of the lamina is devoid of stomata unlike the lower epidermis which is richly provided with them (figs 8—9) the mean length of the guard cells being $46 \mu m$ (range 41—52 μm in a sample of 50). The photosynthetic region consists of several layers of cells which are densely filled with chloroplasts and form a spongy mesophyll. Yapp (1902) reports the presence in *L. carnosa* of a single layer of large colourless cells immediately beneath the upper epidermis which possibly forms a hypodermal water reservoir but in *L. spinosa* the situation is somewhat variable, even in the same section. In some areas the layer is clearly present, containing conspicuous cells which

completely lack chloroplasts, whilst in other areas these cells are less obvious and contain some chloroplasts, although fewer in number than in the spongy mesophyll.

The fronds are initiated at the edge of the rhizome and are completely naked throughout life. Each is borne on a prominent cone-shaped leaf base (phyllopodium) and there is a well-defined dehiscence region present from the beginning which results in the old fronds being shed cleanly. This region consists of a layer of rather irregularly shaped, but more or less isodiametric cells some 12 rows deep, which contrast with the more elongated cells on either side, i.e. in the base of the stipe and in the top of the phyllopodium. The cell walls of the dehiscence layer, with the exception of the uppermost 2 or 3 rows, start to thicken early in development and can be seen even when the young frond has just unfurled (fig 10). Lignification proceeds and ultimately a layer some 20 or more cells thick caps an old leaf base from which the frond has been shed (fig 11). Dehiscence occurs by tearing along the uppermost two or three rows of unlignified cells, and their torn remains may be seen in section. This behaviour contrasts with that reported by Phillips & White (1967) for representatives of several genera belonging to the Polypodiaceae in which a specialised dehiscence layer was by no means so conspicuous.

Six or seven vascular strands are present in the leaf base and traverse the dehiscence layer into the bottom of the rachis, where they become orientated into two vertical rows (fig 16). The upper two strands nearest the adaxial side of the rachis tend to be more conspicuous than the others and are elongated transversely. They approach one another more closely at successive levels up the rachis and quickly fuse to form a very prominent trace which then persists through the remaining length of the rachis. This behaviour is in contrast to that of the other strands which gradually decrease in number by a process of fusion and finally disappear near the tip, leaving only the conspicuous trace noted above (figs 16—23).

The sori are produced in a single row on either side of the rachis and are deeply impressed (fig 1). The base of the sorus is richly supplied by vascular tissue which is delimited from the other tissues of the lamina by a single continuous layer of very thick walled cells on the under side only and abutting on to the endodermis. One might speculate as to whether or not this is a device whereby the supplies carried in the vascular strands are diverted to supplying the sorus rather than the underlying tissues of the lamina. There is no mention of this structure in Yapp's account of *L. carnosa* and we failed to find it in our sections of *L. sinuosa* and *L. deparioides*.

ANT-FERN RELATIONSHIP

The rhizome galleries of *L. spinosa* were inhabited by a species of *Crematogaster*. Specimens have been deposited in the Department of Entomology, British Museum (Natural History). It is possible that other genera or species of ants were commensal in the rhizome but we have no evidence of this; Gomez (1974) found at least three genera coexisting in *Solanopteris brunei* (Werkle ex Christ) Wagner. Ants gain access to the chambers through the apical cavities of the lateral branches and we have no evidence that the ants eat their way into the chambers as do *Azteca* sp. into *Solanopteris* (Gomez, l.c.) although they may physically remove dead cells and other detritus that accumulates in the aperture. A full discussion on the evolution of the interaction of *Iridomyrmex myrmecodiae* with *Lecanopteris sinuosa* and other mymecophytes in Sarawak is given by Janzen (1974). The following observations are given in support of his ideas.

The affect of the plant on the ant

Apart from shelter ants may absorb moisture from the living tissue either directly or indirectly. The outer epidermis of *L. spinosa* is hard and impervious to water but rain water could perculate through open phyllopodia or apical "pores" and become absorbed on the spongy dead parenchyma thus maintaining a moist atmosphere within the chambers. To what extent the *Lecanopteris* attracts other arthropods which in turn are captured by *Crematogaster*, by being a source of food or shelter was not observed but little evidence of such is seen on dried material now before us. On analysis, the heaps of debris found rarely at the ends of the galleries consisted mainly of heads (and leg and mouth-parts) of *Crematogaster* and no other specifically recognisable remains except coleopteran (?) larva/castes and elytra and many fragments of insect wing and limbs.

That the fern offers food in the way of highly nutritious spores or young or abortive sporangia has been suggested by several workers (Holttum 1954a, b,; Janzen 1974). Certainly in many cases the whole sorus is removed, presumably by some grazing animal and often the lamina beneath the sorus is also eaten away. As Holttum (1954b) reports for *L. sinuosa*, the paraphysis-like abortive sporangia are full of globules that have the appearance of oil bodies, although we found these difficult to stain with Sudan blue/red. In all the species of *Lecanopteris* studied by us most of the abortive sporangial heads had been lost at the time of sporangial dehiscence leaving a characteristic broken cell at the top of the seta. This may be due to natural fall off or to grazing by ants but it must be admitted that this type of "paraphysis" is seen in many *Microsorium* species not associated with ants. We have not investigated the chemistry of the rhizome tissue and it is possible that the large parenchymatous cells described above contain sugars similar to those in *Solanopteris* (Gomez, l.c.). Ants are certainly found in the green succulent rhizome.

The effect of the ant on the plant

Holttum speculates that in return for shelter provided by the plant the ants bring in mineral substances from the ground and also some nitrogen in their excreta. No evidence of the former was found in *L. spinosa* and no mineral carton was seen associated with the species as is often the case with other myrmecophytes, e.g. *Hydnophytum* and *Myrmecodia* (Janzen 1974). Fern roots were seen to penetrate the cavities, usually through broken down phyllopodia, and once inside developed copious root hairs; whether they absorb anything other than water has yet to be proved.

Another hypothesis is that frequently put forward, and with good evidence, in connection with some flowering plants which also show an association with ants, namely that the ants protect the plant from attack by insects. Our limited observations suggest that first, the ants tended to flee rather than attack when the plant was touched and second, fronds and sori showed signs of being eaten presumably by a herbivorous insect other than the ants themselves. In *L. spinosa* and in the genus as a whole the young fleshy parts of the rhizome are devoid of scales or very poorly furnished with them whilst at the same time occupying an exposed position in the tree canopy. Certain parallels exist between this situation and that discussed in some detail by Janzen (1966) for the "swollen thorn" acacias of Central America. It is certain that in cultivation, slugs will seek out *Lecanopteris* rhizomes in preference to other fern species. This was demonstrated at Newcastle when 39 sporelings of *L. mirabilis* were raised, in the absence of ants, dispersed among several propagating frames and intermixed at random among several hundred sporelings belonging to a large number of genera. In every case the *Lecanopteris* sporelings were irrevocably damaged by slugs

whilst those of the surrounding species had hardly been affected. It is unlikely however that slugs would be predators in nature but the observation establishes the palatability of the rhizome tissue which in nature is untouched.

Although the rhizome is green, little or no CO_2 exchange can take place through the waxy cuticle. The presence of actively respiring ants in the chambers of the green rhizome could then be an advantage.

ACKNOWLEDGEMENTS

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