followed by parasexual recombination (see p. 230); by mixing sporangia of two different races, new races with a different pattern of virulence towards potato varieties have been obtained after several cycles of inoculation (Malcolmson, 1970). The parasexual cycle has been experimentally demonstrated for *P. parasitica* using fungicide resistance as a genetic marker (Gu & Ko, 1998).

Within 1–2 days of infection, tissues of resistant hosts undergo necrosis so rapidly that sporulation and further growth of the fungus cannot occur. Such a reaction is sometimes termed **hypersensitivity**, and the function of the *R* genes is to accelerate this host reaction. When potato tubers are inoculated with an avirulent race of *P. infestans*, they respond by secreting antifungal substances called **phytoalexins**. Two of the phytoalexins formed by resistant tubers are rishitin and phytuberin. Rishitin, originally isolated from the potato variety Rishiri, is a bicyclic sesquiterpene. Tomiyama *et al*. (1968) showed that R_1 tuber tissue inoculated with an avirulent race of *P. infestans* produced over 270 times the amount of rishitin than when inoculated with a virulent race. The *R* genes of the potato probably determine the ability of host tissue to recognize and respond to avirulent races of *P. infestans* (Day, 1974). The detailed molecular interactions which determine race specificity are, however, complex and still only incompletely understood at present (Friend, 1991).

Breeding for field resistance

In addition to the major genes for resistance in potato, numerous other genes also exist which, although individually of small effect, may contribute to resistance if present together. Resistance of this kind is known as **general resistance** or **field resistance**, and some potato breeding programmes aim at producing varieties possessing it (Niederhauser, 1991). This is preferable to single-gene resistance because *P. infestans* is less likely to overcome the combined resistance of numerous minor genes simultaneously. Field resistance retards the infection process, e.g. by production of a particularly thick cuticle or by a leaf architecture unfavourable to infection, lowers the number of sporangia produced, and extends the time needed by the pathogen to initiate new infections (Wastie, 1991). Field resistance is equally effective against all physiological races of *P. infestans*, and it reduces the severity of an epidemic and consequently the need to apply fungicides (Erwin & Ribeiro, 1996).

Tomato late blight

P. infestans also causes significant worldwide crop losses of tomato (*Lycopersicon esculentum*) which, like potato, belongs to the Solanaceae. The general principles of control of tomato late blight are similar to those described above for potato, including fungicides used and blight forecasting (Erwin & Ribeiro, 1996). Many strains of *P. infestans* are capable of infecting both tomato and potato. However, since the resistance gene systems are different in these two hosts, correlations between virulence of a given strain on potato and tomato cannot be drawn (Legard *et al*., 1995).

5.4 Peronosporales

The Peronosporales are obligately biotrophic pathogens of a few groups of higher plants and are responsible for diseases mainly of aerial plant organs known collectively as **downy mildews**. The order currently comprises two families, the Peronosporaceae (*Peronospora*, *Plasmopara*, *Bremia*) and Albuginaceae (*Albugo*). There are about 250 species (Kirk *et al*., 2001). DNA sequencing data (Cooke *et al*., 2000; Riethmüller *et al*., 2002) are confusing at present because species of *Phytophthora* (Pythiales) and *Peronospora* (Peronosporales) seem to intergrade in phylogenetic analyses. *Peronospora* seems more closely related to *Phytophthora* than to other members of the Peronosporales such as *Albugo*, which in turn may have affinity with *Pythium*. Considerable rearrangements between the Peronosporales and Pythiales will therefore have to be carried out at some point in the future. However, we prefer to retain the conventional system for the time being because the downy mildews (Peronosporales) represent a

convincing biological entity (Dick, 2001a). The key features distinguishing them from the Pythiales are as follows.

First, they are obligate biotrophs and cannot be grown apart from their living host. The mycelium in the host tissues is coenocytic and intercellular, with haustoria of various types penetrating the cell walls. No member of the Peronosporales has as yet been grown in axenic culture, although some can be propagated in dual culture with callus tissues of their plant hosts. None the less, some species (e.g. *Plasmopara viticola*) can cause cell damage to their hosts which leads to the leakage of cytoplasm (Lafon & Bulit, 1981). This is similar to the rots caused, for example, by *Phytophthora erythroseptica* (Plate 2f) and suggests an incomplete adaptation to the biotrophic habit, tying in with the likely origin of Peronosporales from within the Pythiales (Dick, 2001a).

Second, whereas *Pythium* and *Phytophthora* spp. are typically able to attack a very wide range of host plants, Dick (2001a) has pointed out that Peronosporales parasitize a narrow range of angiosperm families, usually dicotyledons, and especially herbaceous plants which are either highly evolved or accumulate large amounts of secondary metabolites such as essential oils or alkaloids. Any one species of downy mildew is specific to only one or a few related host genera. Dick (2001a, 2002) has speculated that a co-evolution of the downy mildews with herbaceous angiosperms occurred mainly in the Tertiary period, and as several independent events, whereby *Phytophthora* and downy mildews share common ancestors. The Peronosporaceae are relatively recent; *Peronospora*, along with its host plants, may have arisen in the mid to late Tertiary in the vicinity of Armenia and Iran. *Plasmopara* is probably of South American origin and dates back to the early Tertiary, whereas *Bremia lactucae* is a central European species. In contrast, the Albuginaceae (*Albugo*) are more ancient, with a late Cretaceous origin possibly in South America (Dick, 2002).

A third major feature of the Peronosporales is the tendency of their sporangia to germinate directly, rather than by releasing zoospores. Many species have lost the ability to produce zoospores altogether, their sporangia being functional 'conidia' which are disseminated by wind. The sporangiophores are well-differentiated, showing determinate growth and branching patterns which provide characteristic features for identification. The production of directly germinating sporangia on well-defined sporangiophores represents an adaptation to the terrestrial lifestyle and supports the postulated origin of the Peronosporales in the drier Tertiary period (Dick, 2002). The life cycle of Peronosporales is similar to that of *Phytophthora* (see Fig. 5.19). Sporangia infect directly or produce infective zoospores, leading to a new crop of sporangiophores and sporangia, and this asexual cycle spreads the disease during the vegetation period. Sexual reproduction is by means of oospores which are formed within the host tissue and survive adverse conditions after host death.

Peronosporales cause economically significant diseases, and one of them – *Plasmopara viticola* – has had a major impact on agriculture and plant pathology because it led to the discovery of Bordeaux mixture (see p. 119). Overviews of the Peronosporales have been given by Spencer (1981), Smith *et al*. (1988) and Dick (2002).

5.4.1 *Peronospora* (Peronosporaceae)

Peronospora destructor causes a serious disease of onions and shallots whilst *P. farinosa* causes downy mildew of sugar beet, beetroot and spinach, but can also be found on weeds such as *Atriplex* and *Chenopodium*. *Peronospora tabacina* causes blue mould of tobacco. This name refers to the bluish purple colour of the sporangia, which is actually a feature of many species of *Peronospora*. Crop losses associated with *P. tabacina* can be up to 95%. This species was introduced into Europe in 1958 and has spread rapidly since (Smith *et al*., 1988).

Peronospora parasitica attacks members of the Brassicaceae. Although many specific names have been applied to forms of this fungus on different host genera, it is now customary to regard them all as belonging to a single species (Dickinson & Greenhalgh, 1977; Kluczewski & Lucas, 1983). Turnips, swede, cauliflower, Brussels sprouts and wallflowers (*Cheiranthus*)

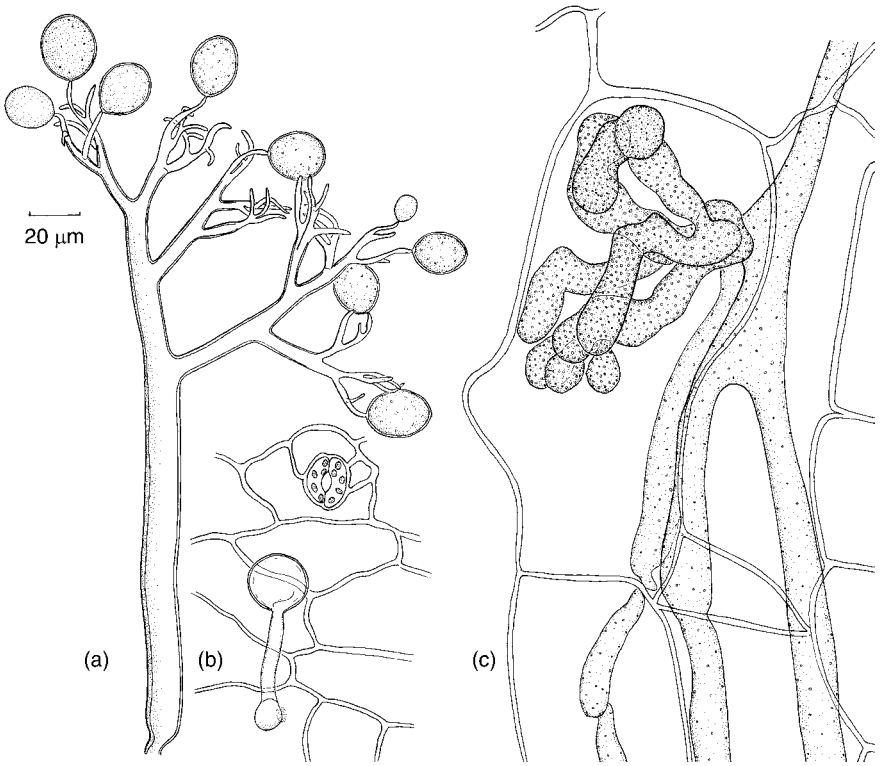

Fig 5.28 *Peronospora parasitica* on *Capsella bursa-pastoris*. (a) Sporangiophore. (b) Sporangium germinating by means of a germ tube. (c) L.S. of host stem showing intercellular mycelium and coarse lobed haustoria.

are commonly attacked, and the fungus is found particularly frequently on shepherd's purse (*Capsella bursa-pastoris*). Diseased plants stand out by their swollen and distorted stems bearing a white 'fur' of sporangiophores (Plate 2g). On leaves the fungus is associated with yellowish patches on the upper surface and the formation of white sporangiophores beneath. Sections of diseased tissue show a coenocytic intercellular mycelium and branched lobed haustoria in certain host cells (Fig. 5.28c; Fraymouth, 1956).

Following penetration of the host cell by *P. parasitica*, reactions are set up between the host protoplasm and the invading fungus. The haustorium becomes ensheathed by a layer of callose which is visible as a thickened collar around the haustorial base in susceptible host plants, whereas the entire haustorium may be coated by thick callose deposits in interactions showing a resistance response (Donofrio & Delaney, 2001). The general appearance of haustoria of *Peronospora* is very similar to that of *Phytophthora* shown in Fig. 5.21; the main body of the haustorium is surrounded by host cytoplasm, the host plasma membrane, an extrahaustorial matrix, the fungus cell wall, and the fungal plasma membrane (Fig. 5.29). Although the haustoria undoubtedly play a major role in the nutrient uptake of the fungus from the host plant, it should be noted that intercellular hyphae are also capable of assimilating nutrients *in planta* (Clark & Spencer-Phillips, 1993; Spencer-Phillips, 1997).

The sporangiophores emerge singly or in groups from stomata. There is a stout main axis which branches dichotomously to bear egg-shaped sporangia at the tips of incurved branches (Fig. 5.28a). Detachment of sporangia is possibly caused by hygroscopic twisting of the sporangiophores related to changes in humidity.

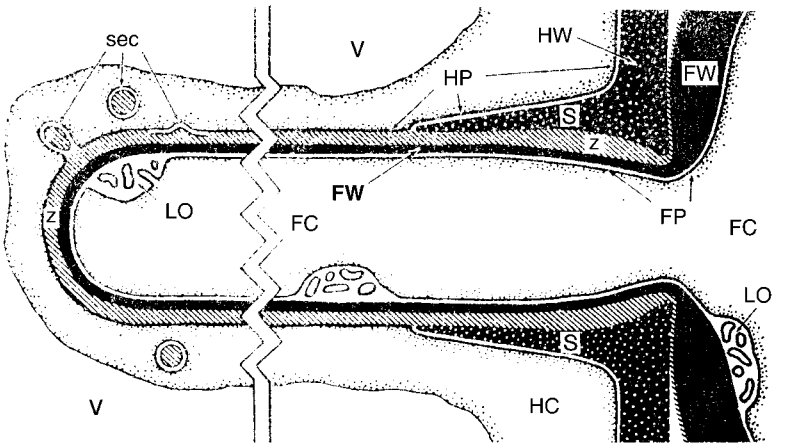

Fig 5.29 *Peronospora manshurica*. Diagram of host–pathogen interface in the haustorial region. Fungal cytoplasm (FC) is bounded by the fungal plasma membrane (FP), lomasomes (LO) and the fungal cell wall (FW) in both the intercellular hyphae (right) and the haustorium (centre). The relative positions of the host cell vacuole (V), host cytoplasm (HC) and host plasmalemma (HP) are indicated. The host cell wall (HW) terminates in a sheath (S). The zone of apposition (Z) separates the haustorium from the host plasmalemma. Invaginations of the host plasmalemma and vesicular host cytoplasm are considered evidence for host secretory activity (sec). After Peyton and Bowen (1963).

In *P. tabacina*, however, it has been suggested that changes in turgor pressure of the sporangiophores occur which parallel changes in the water content of the tobacco leaf. Sporangia may be discharged actively by application of energy at their point of attachment to the sporangiophore. In the Sclerosporaceae (see Section 5.5), violent sporangial discharge also occurs. Upon alighting on a suitable host, sporangia of *P. parasitica* germinate by the formation of a germ tube rather than zoospores. The germ tube penetrates the wall of the epidermis by means of an appressorium (Fig. 5.28b).

Oospores of *P. parasitica*, like those of most other Peronosporales, are embedded in senescent leaf tissues and are found throughout the season. There is evidence that some strains of the fungus are heterothallic whilst others are homothallic (McMeekin, 1960). Both the antheridium and oogonium are at first multinucleate. Nuclear division precedes fertilization, and meiosis occurs in the oogonium and antheridium (Sansome & Sansome, 1974). Fusion between two nuclei is delayed at least until the oospore wall is partly formed.

The wall of the oospore of *P. parasitica* is very tough, and it is difficult to induce germination. In *P. destructor* and some other species, germination occurs by means of a germ tube but in *P. tabacina* zoospores have been described. It is probable that oospores overwinter in soil and give rise to infection in subsequent seasons. Although oospores of *P. destructor* have been germinated after 25 years, it has not proven possible to infect onions from such material. Possibly in this case the disease is carried over by means of systemic infection of volunteer onion bulbs (Smith *et al*., 1988).

Peronospora parasitica and *Arabidopsis thaliana*

The chance discovery of a *P. parasitica* infection in an *Arabidopsis thaliana* weed population in a Zurich garden showing haustoria, sporangia and oospores (Koch & Slusarenko, 1990) opened up the possibility of using this genetically well-characterized 'model plant' to investigate plant–pathogen interactions involving downy mildews. The interaction between *Arabidopsis* and *Peronospora* is governed by a gene-for-gene relationship, i.e. it is a form of major gene resistance based on specific recognition of a pathogen avirulence gene (*avr*) product by the product of a matching host resistance (*R*) gene (e.g. Botella *et al*., 1998). Molecular aspects of the *Arabidopsis* immune response to infections by

P. parasitica and other pathogens have been investigated in some detail. Infection of one leaf triggers a localized reaction, the hypersensitive response, leading to death of the plant cells in the vicinity of infection. Additionally, a systemic response is initiated, i.e. plant organs distal to the infected leaf become resistant against further attack. This phenomenon is called **systemic acquired resistance** and is active against attacks by the same as well as many other pathogens. It is triggered at the site of initial infection by various **elicitor** molecules of pathogen origin, e.g. fatty acids such as arachidonic acid, or by other substances. The signal is transmitted by signalling molecules such as salicylic acid (Lawton *et al*., 1995; Ton *et al*., 2002) which itself has no antimicrobial activity. Salicylic acid-independent signalling events are probably also involved (McDowell *et al*., 2000). Salicylic acid is produced at sites of infection, diffuses through the plant and interacts with a signalling chain, leading to the expression of a set of pathogenesis-related (*PR*) genes. A whole subset of *PR* genes involved in resistance to *P. parasitica* (*RPP* genes) is now known (McDowell *et al*., 2000). The function of many *PR* genes is still obscure; those whose functions are known encode chitinases, β-1,3-glucanases, proteinases, peroxidases or enzymes involved in toxin biosynthesis (Kombrink & Somssich, 1997). By creating mutants of *Arabidopsis* or of crop plants which overexpress their own regulatory genes or *PR* genes, or express introduced genes encoding elicitor molecules of pathogen origin, constitutive resistance against pathogen attack may be generated. This is considered to hold great potential for agriculture (Cao *et al*., 1998; Maleck *et al*., 2002).

Control of *Peronospora*

Downy mildew infections caused by *Peronospora* spp. are controlled mainly by fungicide applications. Metalaxyl is very effective against all downy mildews, but resistance has arisen in several species, and thus this fungicide is now applied in a cocktail with dithiocarbamates (Smith *et al*., 1988). Fosetyl–Al is also now widely used as a foliar spray, root dip or soil amendment (Agrios, 2005).

The breeding of cultivars with resistance against *Peronospora* spp. has been successful in certain crops, e.g. in lucerne (*Medicago sativa*) against *P. trifoliorum* (Stuteville, 1981). In tobacco plants attacked by *P. tabacina*, this strategy is a useful component of integrated control but is not sufficient on its own to afford complete control (Schiltz, 1981). In the tobacco–*P. tabacina* system, a disease warning system is also in operation in Europe; subscribing tobacco growers are informed of the occurrence of the pathogen, so that preventative measures can be taken (Smith *et al*., 1988). This is profitable because tobacco is a high-value crop.

Because downy mildews infect aerial plant parts and produce air-borne propagules in large numbers, crop sanitation measures are generally not very effective. However, in the case of *P. destructor* which overwinters systemically in volunteer onion bulbs, removal of volunteers is essential. In *P. viciae* on peas and beans, deep ploughing of the crop residue is important as the pathogen survives on infected haulms (Smith *et al*., 1988).

5.4.2 *Plasmopara* (Peronosporaceae)

Although downy mildews caused by species of *Plasmopara* are rarely serious in temperate climates, *P. viticola* is potentially a very destructive pathogen of the grapevine. The disease, which was endemic in North America and not particularly destructive on the local vines, was introduced into France during the nineteenth century with disastrous results on the French vines which had never been exposed to the disease and were highly susceptible. Large (1940) has vividly recounted the moment when Alexis Millardet, walking past a heavily infected vineyard in 1882, noticed that vines close to the road appeared healthy and had been sprayed with a mixture of lime and copper sulphate to discourage passers-by from pilfering fruit. This led to the discovery of Bordeaux mixture, one of the world's first fungicides and still effective against *P. viticola* and other foliar pathogens belonging to the Oomycota.

Plasmopara nivea is occasionally reported in Britain on umbelliferous crops such as carrot

and parsnip, and it is also found on *Aegopodium podagraria*. *Plasmopara pygmaea* is found on yellowish patches on the leaves of *Anemone nemorosa* (Fig. 5.30b), whilst *P. pusilla* is similarly associated with *Geranium pratense* (Fig. 5.30a). The haustoria of *Plasmopara* are knob-like, the sporangiophores are branched monopodially and the sporangia are hyaline (Fig. 5.30). Two types of sporangial germination have been reported. In *P. pygmaea* there are no zoospores but the entire sporangium detaches and later produces a germ-tube. In other species the sporangia germinate by means of zoospores which encyst and penetrate the host stomata. Oospore germination in *P. viticola* is also by means of zoospores.

Because the grapevine is such a high-value crop, the fungicide market is lucrative. Bordeaux mixtures are still used today, and similar fungicide applications to those described for *Peronospora* are made. Resistance to metalaxyl has been observed in *P. viticola*. Disease forecasting systems are being developed (Lafon & Bulit, 1981; Smith *et al*., 1988). Breeding for resistant cultivars is being carried out, but because of the long generation times of the crop, this will be a prolonged effort.

5.4.3 *Bremia* (Peronosporaceae)

Bremia lactucae causes downy mildew of lettuce (*Lactuca sativa*) and strains of it can be found on 36 genera of the Asteraceae including *Sonchus* and *Senecio* (Crute & Dixon, 1981). Cross-inoculation experiments using sporangia from these hosts have failed to result in infection of lettuce and it seems that the fungus exists as a number of host-specific strains (*formae speciales*). Although wild species of *Lactuca* can carry strains capable of infecting lettuce, these hosts are not sufficiently common to provide a serious source of infection. The disease can be troublesome both in lettuce grown in the open and under frames,

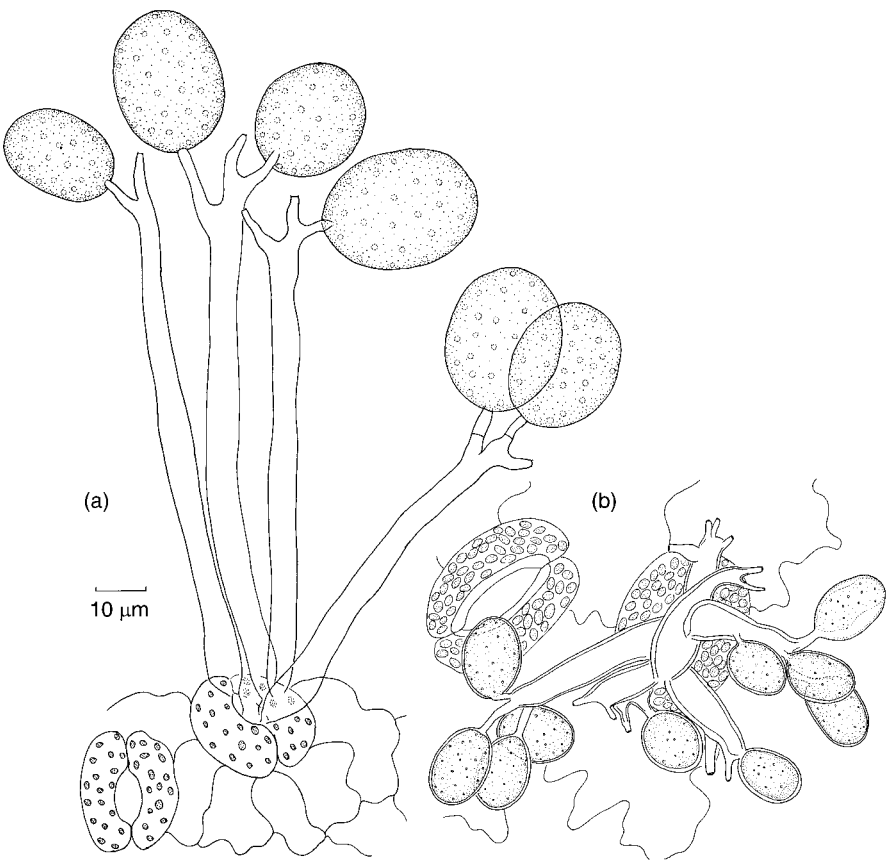

Fig 5.30 *Plasmopara*. (a) Sporangiophores of *P. pusilla* on *Geranium pratense*. (b) Sporangiophores of *P. pygmaea* on *Anemone nemorosa*.

and in market gardens there may be sufficient overlap in the growing of lettuce for the disease to be carried over from one sowing to the next. The damage to the crop caused by *Bremia* may not in itself be severe, but infected plants are prone to secondary infection by the more serious grey mould, *Botrytis cinerea*. Systemic infections can occur. The intercellular mycelium is coarse, and the haustoria are sac-shaped, often several of them being present in each host cell (Fig. 5.31d). The sporangiophores emerge singly or in small groups through the stomata and branch dichotomously. The tip of each branch expands to form a cup-shaped disc bearing short cylindrical

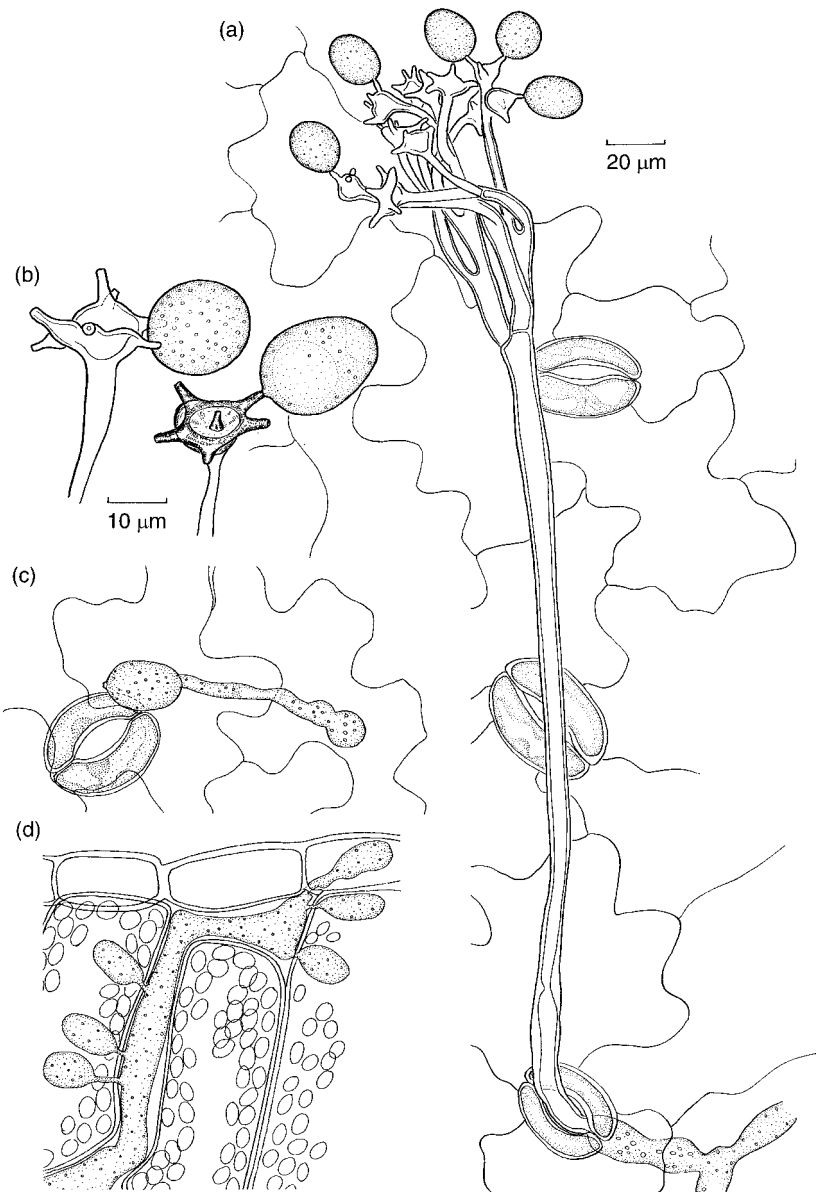

Fig 5.31 *Bremia lactucae* from *Senecio vulgaris*. (a) Sporangiophore protruding through a stoma. (b) Sporangiophore apex. (c) Sporangium germinating by means of a germ tube which has produced an appressorium at its apex. (d) Cells of epidermis and palisade mesophyll, showing intercellular mycelium and haustoria. (a,c,d) to same scale.

sterigmata at the margin and occasionally in the centre, and from these the hyaline sporangia arise (Figs. 5.31a,b). Germination of the sporangia is usually by means of a germ tube which forms an appressorium to penetrate epidermal cells (Fig. 5.31c), or it enters through a stoma. Zoospore formation has been reported but not confirmed. Sexual reproduction is usually heterothallic, although homothallic strains also exist. The oospores are formed in leaf tissue and remain viable for 12 months (Michelmore & Ingram, 1980; Morgan, 1983).

Chemical control of *B. lactucae* on lettuce is certainly possible although not necessarily desirable; hence, intensive efforts for major gene resistance breeding have been made. Integrated control based on resistant cultivars and fungicide applications using metalaxyl and dithiocarbamates is successful (Crute, 1984). However, resistance against metalaxyl arose in Britain as early as 1983. Fosetyl–Al is not as effective as metalaxyl (Smith *et al*., 1988).

5.4.4 *Albugo* (Albuginaceae)

This family has only a single genus, *Albugo*, with about 40–50 species of biotrophic parasites of flowering plants which cause diseases known as white blisters or white rusts. The commonest British species is *A. candida* causing white blisters of crucifers such as cabbage, turnip, swede, horseradish, etc. (Plate 2h). It is particularly frequent on shepherd's purse (*Capsella bursa-pastoris*). There is some degree of physiological specialization in the races of this fungus on different host genera. *Albugo candida* can infect *Arabidopsis thaliana*, and the host defence response is governed by resistance genes involved in the recognition of the pathogen (Holub *et al*., 1995). The principle is similar to, although not as well researched as, the *Arabidopsis–Peronospora* interaction described earlier (p. 116). It is also now possible to establish callus cultures of mustard plants (*Brassica juncea*) containing balanced infections of *A. candida* (Nath *et al*., 2001). This experimental system should facilitate studies of the physiology of host–pathogen interactions. A less common species is *A. tragopogonis*, causing white blisters of salsify (*Tragopogon porrifolius*), goatbeard (*T. pratensis*) and *Senecio squalidus*.

In *A. candida* on shepherd's purse, diseased plants may be detected by the distorted stems and the shining white raised blisters on the stem, leaves and pods before the host epidermis is ruptured (Plate 2h). Later, when the epidermis has burst open, a white powdery pustule is visible. The distortion is possibly associated with altered auxin levels. The host plant may be infected simultaneously with *Peronospora parasitica*, but the two fungi are easily distinguishable microscopically both in the structure of the sporangiophores and by their different haustoria. In *Albugo*, the mycelium in the host tissues is intercellular with only small spherical haustoria (Fig. 5.32) which contrast sharply with the coarsely lobed haustoria of *P. parasitica*. The fine structure of *A. candida* haustoria has been described by Coffey (1975) and Soylu *et al*. (2003). They are spherical or somewhat flattened and about 4 μm in diameter, connected to the intercellular mycelium by a narrow stalk about 0.5 μm wide. Inside the plasma membrane of the haustorium, lomasomes, i.e. tubules and vesicles apparently formed by invagination of the plasma membrane, are more numerous than in the intercellular hyphae. The cytoplasm of the haustorial head is densely packed with mitochondria, ribosomes, endoplasmic reticulum and occasional lipid droplets, but nuclei have not been observed. Since nuclei of *Albugo* are about 2.5 μm in diameter, they may be unable to traverse the constriction which links the haustorium to the intercellular hypha. Nuclei may (e.g. *Peronospora pisi*) or may not be present in the haustoria of other Oomycota. The base of the haustorium of *A. candida* is surrounded by a collar-like sheath which is an extension of the host cell wall, but this wall does not normally extend to the main body of the haustorium. Between the haustorium and the host plasma membrane is an encapsulation. Host cytoplasm reacts to infection by an increase in the number of ribosomes and Golgi complexes. In the vicinity of the haustorium the host cytoplasm contains numerous vesicular and tubular elements not found in uninfected cells. These structures have been interpreted

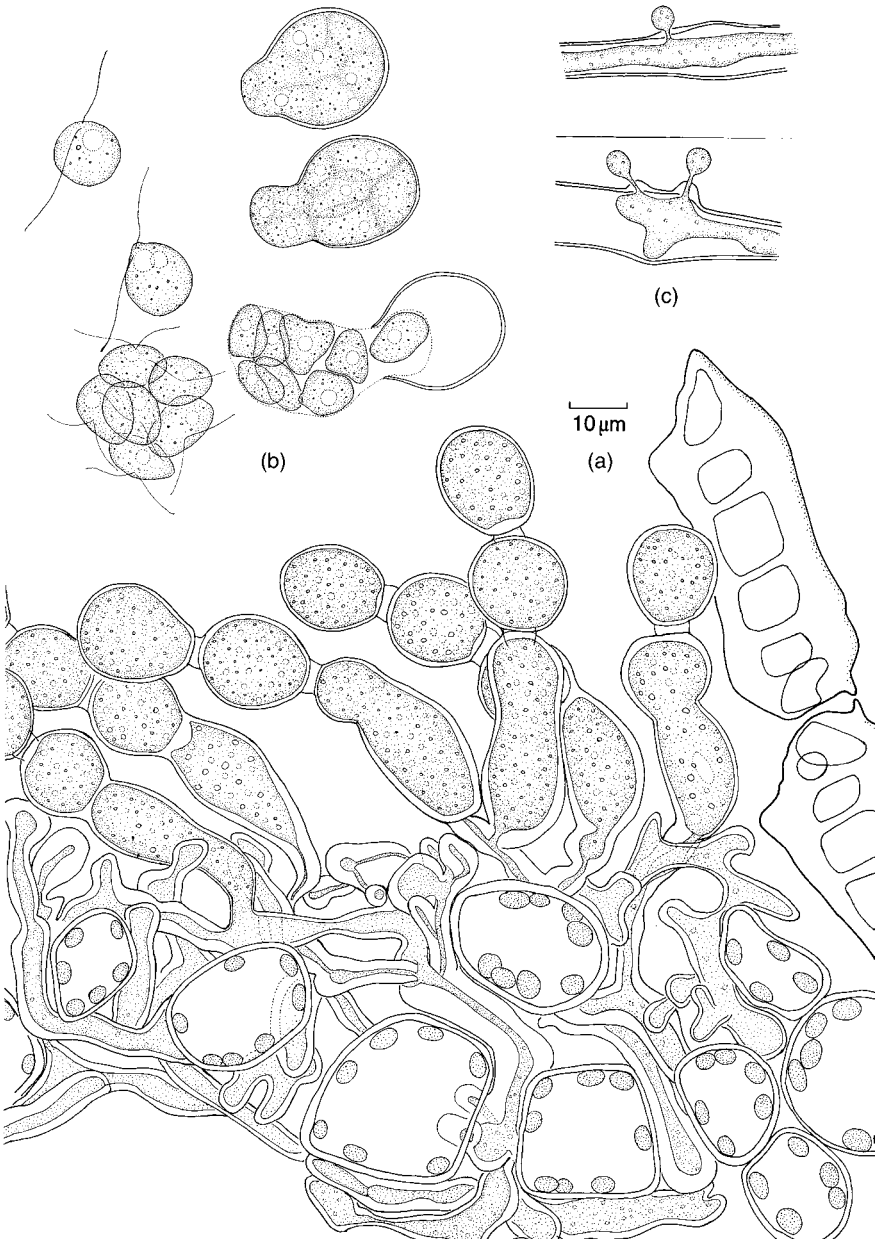

Fig 5.32 *Albugo candida* on *Capsella bursa-pastoris*. (a) Mycelium, sporangiophores and chains of sporangia formed beneath the ruptured epidermis (right). (b) Germination of sporangia showing the release of eight biflagellate zoospores. The stages illustrated took place within 2 min. (c) Haustoria.

as evidence of secretory processes induced in the host cell by the presence of the pathogen.

The intercellular mycelium aggregates beneath the host epidermis to form a palisade of cylindrical or skittle-shaped sporangiophores which give rise to chains of spherical sporangia in basipetal succession – i.e. new sporangia are formed at the base of the chain. The pressure of the developing chains of sporangia raises the host epidermis and finally ruptures it.

The sporangia are then visible externally as a white powdery mass dispersed by the wind. Sporangia reaching a suitable host leaf will germinate within a few hours in films of water to form biflagellate zoospores of the principal type, about eight per sporangium (Fig. 5.32b). After swimming for a time, a zoospore encysts and then forms a germ tube which penetrates the host epidermis. The asexual disease cycle may be completed within 10 days. Infections may be localized or systemic. Gametangia are formed in the intercellular spaces of infected stems and leaves. Both the antheridium and the oogonium are multinucleate at their inception, and during development two further nuclear divisions occur so that the oogonium may contain over 200 nuclei. However, there is only one functional male and one functional female nucleus. In the oogonium all the nuclei except one migrate to the periphery and are included in the periplasm. Following nuclear fusion a thin membrane first develops around the oospore. Division of the zygote nucleus takes place and is repeated, so that at maturity the oospore may contain as many as 32 diploid nuclei. Sansome and Sansome (1974) reported that meiosis occurs within the gametangia. They also suggested that *A. candida* is heterothallic. The high incidence of oospores of *Albugo* in *Capsella* stems simultaneously infected with *Peronospora parasitica* may result from some stimulus towards self-fertilization in *Albugo* produced by *Peronospora*, a situation analogous to the *Trichoderma*-induced sexual reproduction in heterothallic species of *Phytophthora* (see p. 95).

The mature oospore is surrounded by a brown exospore, thrown into warty folds (Fig. 5.33a). Germination of the oospores takes place only after a resting period of several months. Under suitable conditions the outer wall of the oospore bursts and the endospore is extruded as a thin, spherical vesicle, which may be sessile or formed at the end of a wide cylindrical tube. Within the thin vesicle 40–60 zoospores are differentiated and are released on its breakdown (Figs. 5.33b,c).

The cytology of oospore development in some other species of *Albugo* differs from that of *A. candida*. In *A. bliti*, a pathogen of *Portulaca* in North America and Europe, the oogonia and antheridia are also multinucleate and two nuclear divisions take place during their development. Numerous male nuclei fuse with numerous female nuclei and the fusion nuclei

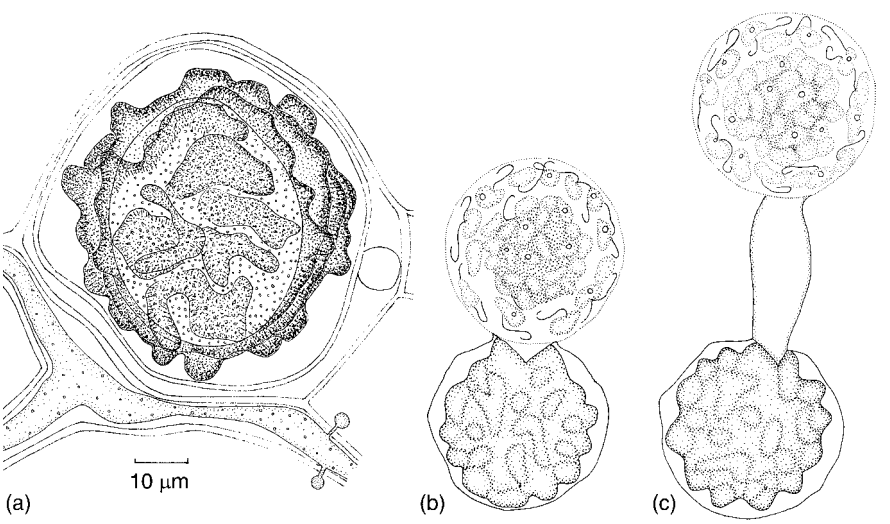

Fig 5.33 *Albugo candida* oospores. (a) Oogonium and oospore from *Capsella* leaf. (b,c) Two methods of oospore germination (after Vanterpool, 1959).

pass the winter without further change. In *A. tragopogonis*, a multinucleate oospore develops and again there are two nuclear divisions involved in the development of the oogonium and antheridium, but finally there is a single nuclear fusion between one male and one female nucleus. This fusion nucleus undergoes repeated divisions so that the overwintering oospore is multinucleate.

Albugo candida alone or in combination with co-infecting *Peronospora parasitica* can occasionally cause significant crop losses in cabbage cultivation. Fungicide treatment is possible, with copper-based or dithiocarbamate-type fungicides commonly used (Smith *et al*., 1988).

5.5 Sclerosporaceae

This family comprises the downy mildews of grasses and cereals. Although it is well defined as a biological group, its phylogenetic position is unclear, recent ribosomal DNA-based studies placing its members among the Peronosporales (Riethmüller *et al*., 2002). For reasons of their distinctly different biological features, we consider them briefly here. The principal genera are *Sclerospora*, with sporangia capable of germinating by releasing zoospores, and *Peronosclerospora*, whose sporangia show direct germination by germ tubes and are thus, functionally speaking, 'conidia'. Sporangia or conidia are produced on repeatedly branching aerial structures which resemble those of *Peronospora* spp. In *Peronosclerospora*, the conidiophores project through stomata of the host and branch at their apices to produce up to 20 finger-like tapering extensions which expand to form conidia (Figs. 5.34a–c). The conidia are oval and hyaline. Unlike those of other Oomycota, conidia of Sclerosporaceae are projected actively by a sudden rounding-off of the conidiophore tip and conidial base, and this is visible as a

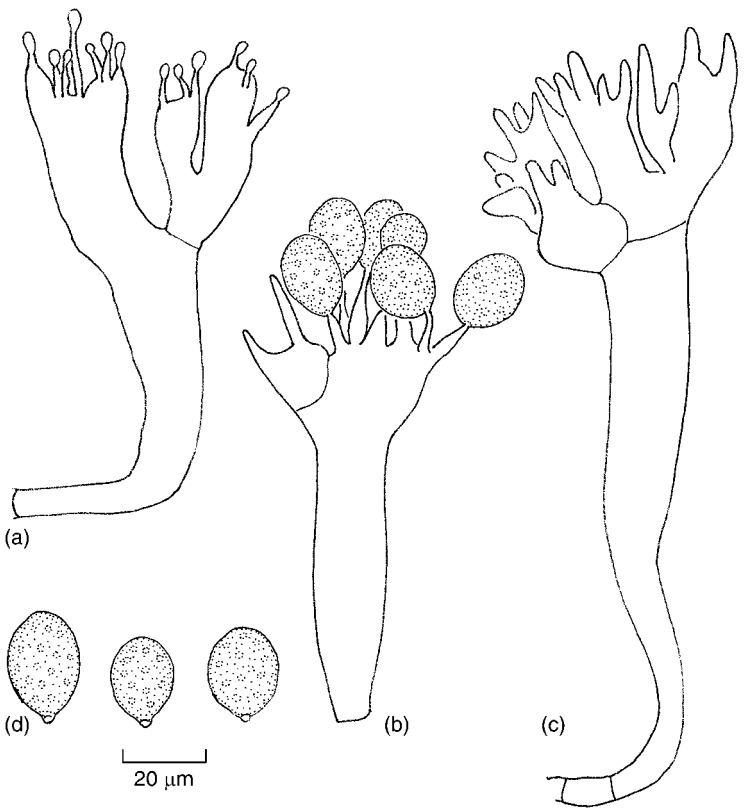

Fig 5.34 *Peronosclerospora sorghi*. (a) Immature conidiophore showing conidium initials. (b) Mature conidiophore from which two conidia have become detached. (c) Old conidiophore; all conidia have become detached. (d) Discharged conidia. Note the small basal projection. Drawn from material kindly provided by K. Mathur.

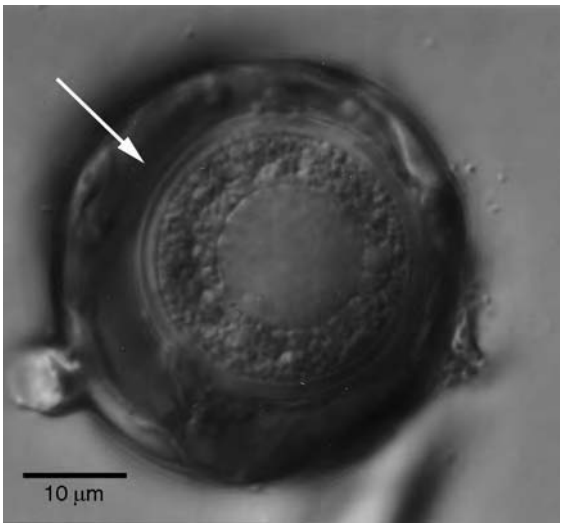

Fig 5.35 Oospore of *Peronosclerospora sorghi*. Note the thickened oogonial wall (arrow), within which the spherical oospore with its wall and ooplast is clearly visible.

small projection at the base of discharged conidia (Fig. 5.34d). Oospores of Sclerosporaceae are distinctive in being surrounded by a thickened oogonial wall (Fig. 5.35), and this feature may enhance the longevity of the oospore. The most important species are *Sclerospora graminicola* infecting pearl millet (*Pennisetum americanum*), and *Peronosclerospora sorghi* pathogenic on sorghum and maize. Because of their similar biological features and great economic importance, these two species are often considered together. Thorough reviews have been written by R. J. Williams (1984) and Jeger *et al*. (1998).

Downy mildews of grasses cause serious crop losses especially in dry subtropical and tropical zones in Africa, their putative centre of evolution, as well as Asia and, to a lesser extent, North and South America. The thick-walled oospores can survive on plant debris and in the soil for up to 10 years, and infections are usually initiated from oospores which germinate directly by means of a germ tube. The plant root may be the initial route of entry, although both *S. graminicola* and *P. sorghi* may also become seed-borne. Later infections are through the shoot surface, either by direct penetration of the epidermis by means of appressoria, or through stomata. Infections of host plants are obligately biotrophic and can become systemic if they reach the apical meristem. Sporangia or conidia are formed only on freshly infected living host tissues under moist conditions, and infections are therefore polycyclic only when sufficient moisture is available. In dry regions, infections may be carried exclusively by oospores, confining the pathogen to one disease cycle per growing season. Oospore production is buffered against environmental extremes by taking place within the tissue of aerial host organs. Like sporangia or conidia, oospores can be blown about by wind.

Control of downy mildew of grasses is difficult. Metalaxyl gives good control both as a seed dressing and as a foliar spray but may not always be available. Numerous cultivars of sorghum and pearl millet show resistance against downy mildews, but this is usually based on one or a few major genes and can therefore be overcome by the pathogens if single cultivars are grown in large coherent areas. On small-scale farms, it may be possible to remove individual infected plants prior to the onset of sporulation (Gilijamse *et al*., 1997).