CHAPTER 45

BREVILEGNIA Coker and Couch
In, Coker, J. Elisha Mitchell Sci. Soc. 42:212. 1927

Monoecious. Sporangia cylindrical to clavate; renewed sympodially. Spores monomorphic or not swimming; released from the sporangium at the deliquescence of the sporangial wall; in some species, some primary and secondary sporangia discharge spores in an achlyoid fashion; sporangium sometimes disarticulating from the hypha, or portions floating away as the wall disintegrates, and then spores often escaping individually from the clustered, adhering cysts. Gemmae present or absent. Oogonia lateral or terminal, spherical, obpyriform to obovate, sometimes irregular. Oogonial wall unpitted; smooth or with slight to prominent irregularities or ornamentations (sparse) on the outer surface, smooth or irregular on inner surface. Oogonial stalks of various lengths, sometimes glomerulate. Oospore eccentric, single. Antheridial branches, when present, androgynous, monoclinous, or diclinous. Antheridial cells simple; laterally or apically attached.

Type species: *Brevilegnia subclavata* Couch, J. Elisha Mitchell Sci. Soc. 42:229, pls. 39-41; pl. 42, figs. 1-7. 1927.

The genus was first known under the binomials *Thraustotheca unisperma* (Coker and Braxton, 1926) and *T. unisperma* var. *litoralis* (Coker, 1927). At the time, the authors of these two taxa recognized that certain of the characteristics digressed from those known to circumscribe *Thraustotheca*, namely, the depauperate nature of growth and the production of oogonia each with a single oospore. Later, Coker and Couch (Coker, 1927) used these differences as the chief ones on which to base their new name *Brevilegnia*. Experience has since shown that the nature of the mycelium is much too variable to be a useful diagnostic character, but the condition of uniovulate oogonia appears to be quite stable.

In all species in the genus, some primary (first formed) sporangia discharge spores by means of the gradual disintegration of the sporangial wall, a pattern of release generally referred to as thraustothecoid or brevilegnoid. Usually the deliquescence of the sporangium takes place in various regions of the confining wall such that most encysted primary spores float free, leaving only a small clump of cells adhering to the sporangium base. Secondary sporangia are usually brevilegnoid, but some (as in *Brevilegnia bispora*) are achlyoid as well.

It is not uncommon for portions of secondary sporangia to float free, with the spores then eycysting to leave a net-like mass of cysts. Additionally, some spores may remain attached at the site of the sporangium (even though the wall has disintegrated) and then encyst in place. In either instance, dictyucoid sporangia are the result, and distinguishing older specimens of *Brevilegnia* from *Dictyuchus* becomes a difficult matter to resolve. The surest way to separate members of the two genera, of course, is to determine the spore release pattern in the primary sporangia. Those of *Brevilegnia* swell

somewhat as the sporangium wall dissolves, but those of *Dictyuchus* (the ones usually designated as the false-net types) do not. Moreover, in *Brevilegnia*, disarticulation usually is only fragmentary, a portion of the spores adhering in a basal mass at the junction of the sporangium and the hypha. When the primary sporangia of species of *Dictyuchus* disarticulate, they do so in their entirety. The wall of the secondary sporangia of species of *Brevilegnia* and of some representatives of *Dictyuchus* also deliquesce. Again, the distinction between discharge in a *Brevilegnia* fashion and the "false-net" release in *Dictyuchus* is one of the degree of disintegration of the liberated encysted spores. In the former, the sporangium swells, and some portion of the spores float free before the remnant of the sporangium disarticulates. In *Dictyuchus* species, on the contrary, the liberated spore cysts adhere, and the entire sporangium may detach from the subtending hypha.

Salvin (1942a) also commented on spore release in species of *Brevilegnia*. He noted that sporangia of Brevilegnias with uniseriate or biseriate spores discharged in a dictyuchoid manner, but those with spores in more than two rows were thraustothecoid in their release. Although this is a useful guide, it is not entirely dependable. Salvin (1942a:48) also saw a difference between brevilegnoid and thraustothecoid discharge. He wrote that the wall of the sporangia of *Brevilegnia* species was "...thinned and weakened..." to a much greater degree than was the wall in *Thraustotheca* specimens. He also observed -- contrary to what Coker had stated -- that portions of the sporangial wall in the Brevilegnias persisted. This of course accounts for the separation of some groups of spores of deliquescing sporangia, and the retention of other groups.

In 1942(a) Salvin proposed that the genus *Brevilegnia* and *Thraustotheca* be merged, with the former becoming a subgenus of the latter. Based on the remarkable variability of his isolate *Brevilegnia* C-2, Salvin also suggested that *B. unisperma* var. *unisperma*, *B. unisperma* var. *delica*, B. *unisperma* var. *litoralis*, B. *megasperma*, B. *subclavata, B. diclina, B. linearis* (and possibly *B. unisperma* var. *montana*) should be combined into a single species, *Thraustotheca unisperma*. *Brevilegnia* C-2, Salvin found, could be induced to develop characteristics approximating those of each of these species, and he therefore reasoned that they were all one taxon. Later, A. W. Ziegler (1958a:406) also recommended that *Brevilegnia* be reduced to synonymy with *Thraustotheca*. The experimental work performed by Sorenson (1964) on *B. unisperma* var. *delica*, led him to conclude that if other Brevilegnias showed restricted nutritional capacities as had *B. unisperma* var. *delica*, this would constitute another character on which to maintain *Brevilegnia* separate from *Thraustotheca*. Cejp (1959a:263) listed *Thraustotheca*, *pro parte*, as a synonym of *Brevilegnia*, but it is not clear precisely which segments of the former were being considered.

A statistical analysis of morphological variability in five isolates of *Brevilegnia*, grown in three media (Seymour's glucose-glutamate agar, soil extract, and triple distilled water), was made by Headington (1971). He applied Duncan's Multiple Range Test to determine the significance of the mean values for sporangium length, diameters of the hyphae, encysted spores, oogonia, and oospores. Headington also analyzed other

characters such as sporangium and oogonium shape, oogonial wall pits and ornamentations, and frequency of antheridial branch origins. Certain species showed some statistically significant differences in one or more parameters. Generally, however, Headington demonstrated that (1) the least variance in the parameters measured was encountered with cultures propagated on the glucose-glutamate medium, and (2) without exception, isolates developing on this medium had smaller oogonia and oospores than when grown in water culture. Only in the case of antheridial branch origin frequency, among the parameters measured qualitatively, was there any substantial difference in colonies grown in the three media, and then only for *B. bispora* and *B. unisperma* var. *delica* (= *minutandra*). When propagated in soil water, colonies of *B. bispora* produced antheridial branches attendant to 10% of the oogonia, but on glucose-glutamate and in distilled water, no antheridia were formed. The branch frequency in *B. unisperma* var. *delica* colonies was 20% in triple distilled water; there were no antheridial filaments produced by specimens grown in the other two media.

Key to the species of *Brevilegnia*

1. Antheridial branches predominantly or strictly diclinous 2
1. Antheridial branches predominantly or exclusively androgynous or monoclinous, or both types present in varying proportions, or antheridial filaments extremely rarely produced 3
    2. Oogonia predominantly irregular, asymmetrical, or with wall sparsely ornamented; sporangia often clustering at apex of hypha . . . . . *B. diclina* (p. 747)
    2. Oogonia spherical or obpyriform, and smooth-walled; sporangia rarely clustering at apex of hypha . . . . . *B. longicaulis* (p. 749)
3. Sporangia either all filamentous with spores in a single row, or short-clavate to obpyriform 4
3. Sporangium cylindrical, fusiform, or long-clavate; if filamentous, always accompanied by some sporangia with 2-3 rows of spores; never short-clavate to obpyriform 5
    4. Sporangia filamentous, spores uniseriate; glomerulate oogonial stalks lacking . . . . . *B. linearis* (p. 750)
    4. Sporangia short-clavate to obpyriform, spores in more than one row; glomerulate oogonial stalks common . . . . . *B. subclavata* (p. 752)
5. Oogonial wall predominantly irregular or ornamented; lateral hyphal swellings sometimes present . . . . . *B. unisperma* (p. 753)
5. Oogonial wall predominantly smooth, hyphae without lateral swellings 6
    6. Antheridial branches extremely rarely produced, and absent from some cultures; when present,

androgynous . . . . . *B. minutandra* (p. 756)

6. Antheridial branches abundant or sparse, but not absent from cultures; when present exclusively androgynous or monoclinous or a combination of both types 7

7. Oogonia large, predominantly 30–34μm in diameter, or greater; intercalary oogonia commonly produced . . . . . *B. megasperma* (p. 758)

7. Oogonia small, predominantly 18–28μm in diameter, or less; intercalary oogonia absent or rare 8

8. Antheridial branches predominantly androgynous; some primary and secondary sporangia releasing spores in an achlyoid fashion, but primary ones not exclusively achlyoid . . . . . *B. bispora* (p. 760)

8. Antheridial branches predominantly or strictly monoclinous; no primary sporangia releasing spores in an achlyoid fashion; secondary sporangia rarely if ever behaving in an achlyoid manner at discharge 9

9. Wall of some oogonia conspicuously thickened, but all oogonia unpitted; gemmae absent . . . . . *B. crassa* (p. 763)

9. Wall of all oogonia thin, some showing pitting; gemmae present . . . . . *B. globosa* (p. 764)

Brevilegnia diclina Harvey
J. Elisha Mitchell Sci. Soc. 42:243, pls. 44, 45. 1927
(Figures 112 A-C, 113 K)

Monoecious. Mycelium dense, moderately extensive; hyphae slender, moderately branched except near periphery of colony where abundantly branched. Sporangia short- or long-cylindrical, or fusiform, occasionally narrowly clavate, infrequently short-filiform; straight, curved, or slightly irregular; renewed sympodially or often in a cymose fashion, infrequently in a basipetalous manner, clustering of sporangia by repeated short, sympodial branching common; 60-327 x 9-41 μm. Spores monomorphic; discharge and behavior brevilegnoid, infrequently to rarely dictyucoid, and in such instances, empty or partially emptied sporangia disintegrating in part; primary spore cysts 8-16 μm in diameter: infrequently, cylindrical cysts are produced, these up to 28 μm long. Gemmae absent. Oogonia lateral, infrequently terminal; spherical, but usually irregular or asymmetrical to sparingly papillate and irregular; immature ones sometimes proliferating; (14-) 20-26 (-33) μm in diameter, including wall ornamentations. Oogonial wall unpitted; generally irregular, or provided with a few short, broad or narrow papillae in addition to being irregular, or having one or two long-conic projections. Oogonial stalks (1-) 1.5–3.5 (-6) times the diameter of the oogonium, in length; usually twisted, contorted or irregular; unbranched or branched, occasionally to infrequently glomerulate, sometimes producing short, lateral,

papilliform evaginations at various points along their length. Oospores eccentric; spherical; one per oogonium, but usually not filling it; (16-) 18–21 (-26) μm in diameter; germination not observed. Antheridial branches frequently present, but sometimes not directly associated with oogonia; diclinous, rarely androgynous; often branched, irregular, or twisted and somewhat contorted; tending to enwrap the oogonia when attached to them; persisting. Antheridial cells sometimes not developed; simple; when present, tubular and irregular; persisting, laterally appressed; fertilization tubes not observed.

Brevilegnia diclina is one of the few species in the Saprolegniaceae where sporangium configuration is useful in species recognition. Because the hyphal extension resulting from sympodial branching is commonly very short the secondary sporangia are often clustered at the ends of hyphae.

The oogonia of *Brevilegnia diclina* are usually irregular or asymmetrical (Fig. 113 K), or distinctly but sparsely ornamented (Fig. 112 B, C). This feature alone, however, does not distinguish the species from *B. unisperma* (Fig. 112 L-N) or *B. linearis* (Fig. 112 G, H). In these latter two taxa, however, the antheridial branches are predominantly androgynous; the diclinous condition clearly prevails in *B. diclina*.

The source of culture water may modify the configuration of the sporangia and antheridial branches in *Brevilegnia diclina*, but does not alter the spore release pattern (T. W. Johnson, 1977d). We have found that colonies propagated in soil extract or pond water produce noticeably twisted and irregular antheridial filaments (Fig. 113 K). In the same media (on hempseed), isolates frequently display greater numbers of clustered sporangia (short sympodial or cymose branching) than do those propagated in distilled water.

Cooper (1929b) investigated some developmental and cytological aspects of *Brevilegnia diclina*. He reported that while fertilization took place in this species, it did so without benefit of fertilization tubes. The spores were multinucleate, Cooper contended, and the sporangium wall underwent dissolution at spore release, rather than bursting open from internal pressure. These observations need confirmation by application of modern techniques. Headington's (1971) study on the statistical significance of variability in this and other species of *Brevilegnia* is summarized in the general remarks on the genus.

The collection identified by Moruzi and Toma (1969) as *Thraustotheca clavata* was in a probability *Brevilegnia diclina*. *See* also foregoing discussion of *Thraustotheca* sp. J. V. Harvey. Date (1976a) did not mention antheridial branches in his report of *B. diclina*; the identification is therefore in doubt.

CONFIRMED RECORDS: -- BRITISH ISLES: Forbes (1935a:233, pl. 9, fig. 5). CZECHOSLOVAKIA: Cejp (1959a:266, fig. 101d-g). GERMANY: Höhnk (1952a:73, *et sqq*.). INDIA: Mar and Khulbe (1984:200, pl. 1, fig. 11); Khulbe and Sati (1979:229). NORWAY: T. W. Johnson (1977d:293, figs. 15-19). UNITED STATES: Beneke

(1948b:135); R. L. Butler (1975: figs. 193-196); Cooper (1929b: p1s. 3 - 5); J. V. Harvey (*loc. cit.*; 1927b: 558); Headington (1971:11); Wolf (1944:41).

RECORDED COLLECTIONS: -- BRITISH ISLES: Cook and Forbes (1933). CENTRAL AMERICA: Wolf (1939b). DENMARK: A. Lund (1978). GERMANY: Höhnk (1956a). INDIA: Date (1976a: 99, figs. 1-6)(?); Khulbe (1983c); Mer *et al. (1980);* Sati and Khulbe (1980). RUMANIA: Moruzi and Toma (1969: 208, pls. 1, 2) (?); SOUTH AMERICA: A. L. Rogers *et al*. (1970). UNITED STATES: Coker (1927); W. B. Cooke (1969); W. B. Cooke and Bartsch (1960); J. V. Harvey (1927c, d; 1930; 1952); T. W. Johnson (1956a); K. B. Raper (1928); Scott (1960b); A. W. Ziegler (1958b). USSR: Meshcheryakova (1974); Mil'ko (1965). WEST INDIES: Scott (1960a).

SPECIMENS EXAMINED: -- NORWAY (3), TWJ. OCEANIA (1), RLS. UNITED STATES (7), TWJ, RLS. Centraalbureau (1).

Brevilegnia longicaulis Johnson
Mycologia 42:244, fig. 1. 1950
(Figure 113 G-J)

Monoecious. Mycelium dense, limited; hyphae slender, abundantly branched. Sporangia clavate or cylindrical; straight or slightly curved to faintly irregular; renewed sympodially; 90-488 x 21-55 μm. Spores monomorphic; discharge and behavior brevilegnoid, rarely dictyucoid and then sporangium is usually partly disintegrated and disarticulating; rarely germinating *in situ*; primary spore cysts 6–11 μm in diameter. Gemmae lacking. Oogonia lateral, rarely terminal; spherical or obpyriform; immature ones occasionally proliferating; (20-) 25–30 (-34) μm in diameter. Oogonial wall unpitted; smooth. Oogonial stalks (1-) 2.5–3.5 (6) times the diameter of the oogonium in length; slender, usually moderately or slightly curved to sinuous and slightly irregular, occasionally strongly curved or bent; unbranched. Oospores eccentric; spherical; one per oogonium and usually not filling it; (20-) 22–26 (-31) μm in diameter; at germination producing a slender, short, irregular germ hypha that bears a small, terminal, brevilegnoid sporangium, or branches to form a new mycelium directly. Antheridial branches usually associated with most oogonia; diclinous, generally relatively long; slender, irregular or moderately contorted; unbranched or very sparingly branched; persisting. Antheridial cells simple; irregularly tubular or clavate; persisting; laterally appressed; fertilization tubes not observed.

Not only does *Brevilegnia longicaulis* appear to be rare (if one may judge from the literature) it has a noticeably disjunct distribution: Western Pacific region and Norway. Perhaps this watermold is more common than the collection records indicate but is simply misidentified or masked in gross culture by more rapidly growing fungi. The species with which *B. longicaulis* is most likely to be confused is *B. megasperma* if attention is not given to antheridial branch origin. In *B. megasperma*, the antheridial filaments are androgynous or monoclinous; they are diclinous only, so far as is known, in *B. longicaulis*.

Like *Brevilegnia diclina, B. longicaulis* has diclinous antheridial branches, but these two species may be distinguished from one another by the configuration of the oogonial wall: always smooth in *B. longicaulis*, predominantly irregular or sparingly papillate or otherwise ornamented in *B. diclina*. The origin of antheridial branches readily separates *B. longicaulis* from *B. linearis*. The differences between *B. longicaulis* and *B. bispora* are recorded in the discussion of the latter species.

The morphological variability of *Brevilegnia longicaulis* was studied experimentally by T. W. Johnson (*loc. cit.*). The amount of culture water and the level of aeration influenced sporangium shape to some extent. Temperature did not have a pronounced effect on morphology of the asexual apparatus in this species. Gemmae could not be induced to form by varying the culture conditions, and although the environment influenced the frequency of antheridial branch development, external conditions did not modify their origin. In the Norwegian isolates of *B. longicaulis* the shape of some sporangia produced by colonies propagated in pond water or soil extract was modified, but oogonium stalk length, antheridial branch origin, and the spore discharge pattern were not changed (T. W. Johnson, 1977d).

CONFIRMED RECORDS: -- NORWAY: T. W. Johnson (1977d:291, figs, 9-14). OCEANIA: T. W. Johnson (*loc. cit.*). REPUBLIC OF CHINA: Chiou *et al*. (1975:170, pl. 2, fig. 30).

RECORDED COLLECTION: -- NEW ZEALAND: Karling (1966f. Collection site is given in Karling, 1965).

SPECIMENS EXAMINED: -- NORWAY (2), TWJ. OCEANIA (3), TWJ, RLS.

Brevilegnia linearis Coker and Braxton *ex* Coker
J. Elisha Mitchell Sci. Soc. 42:214, pl. 32. 1927
(Figure 112 D-H)

Monoecious. Mycelium dense, limited; hyphae slender, much-branched. Sporangia long, narrow-cylindrical; straight, curved, or irregular; spores in a single row; unbranched or once-branched; renewed sympodially, or in a basipetalous manner; tending to disarticulate; primary ones 120-685 x 8-16 μm. Spores monomorphic; discharge and behavior brevilegnoid, sometimes aplanoid; primary spore cysts 8-20 μm in diameter; elongate or cylindrical spores occasionally produced in some sporangia, these 13-60 x 8-22 μm. Gemmae lacking. Oogonia lateral, infrequently terminal; generally spherical, but occasionally irregular or asymmetrical; sometimes immature ones proliferating; (16-) 18–21 (-27) μm in diameter, including any wall projections. Oogonial wall unpitted; smooth or occasionally slightly irregular, with one to a few low, inconspicuous, broad papillae. Oogonial stalks (1.5-) 2–4.25 (-7) times the diameter of the oogonium in length; slender; irregular or twisted and contorted, often curved or sinuous, sometimes recurved, infrequently loosely and sparingly coiled; unbranched. Oospores eccentric; spherical; one per oogonium, and usually not filling it; (12-) 15–19 (-23) μm in diameter; at germination producing an unbranched or branched germ hypha.

Antheridial branches abundant; predominantly androgynous, rarely diclinous; slender, irregular; unbranched or once-branched; sometimes showing one or more short, lateral, papillate protrusions; persisting. Antheridial cells simple; tubular or clavate and usually slightly irregular; persisting; laterally appressed; fertilization tubes not observed.

Brevilegnia linearis is one of the most readily recognizable species in the genus, and, like *B. diclina*, its sporangia are distinctive. These are long, cylindrical or filiform cells terminating the main hyphae, and containing spores in a single row. When secondary sporangia are produced in a basipetalous manner, these are usually noticeably shorter than the primary ones. The wall of the sporangium disintegrates, as is characteristic of the Brevilegnias, but the spores tend to adhere in long chains, and only slowly disarticulate. Commonly, an entire sporangium will be deciduous. Branching takes place only very infrequently in the sporangia of *B. linearis*, and so far as we are aware, when it does occur, only one lateral branch develops. It is not uncommon to find uniseriate chains of spores floating free from the mycelium in water cultures. (*See also Phragmosporangium*.)

The individual spores of *Brevilegnia linearis* also are distinctive. While many cysts are spherical, there are instances in every water culture where large, long- or short-cylindrical ones occur among the spherical spores in some sporangia (Fig. 112 D). In exceptional instances, the spores may be as large as the oogonia, or slightly larger.

The oogonia and oospores of *Brevilegnia linearis* are generally small. In the specimens at hand, about half of the oogonia were irregular or very sparsely papillate (Fig. 112 G), the remaining being smooth (Fig. 112 F). We judge from Coker's account (*loc. cit*.) of the species that the majority of oogonia in his specimen were smooth also. The irregular oogonia somewhat resemble those of *B. diclina* (Fig. 112 C), but the two species are obviously different in predominant antheridial branch origin. *Brevilegnia unisperma* often has ornamented oogonia, and a few of these (Fig. 112 L) also bear a strong resemblance to the irregular ones of *B. linearis*. The oogonial wall ornamentations in *B. unisperma* are much more abundant and prominent than are those in *B. linearis*.

The ecology of *Brevilegnia linearis* is of some interest. Alabi (1971a) found this watermold to be a "dry season" species in Nigeria, and one of us (RLS) also found it to be seasonally "distributed" in Amazonas, Brazil. In India, on the other hand, Khulbe and Bhargava (1977) reported it as a "low temperature" species.

Coker alone (*loc. cit*.) published the paper in which the original description of *Brevilegnia linearis* appeared, but did not cite his name as author of the species. In 1937, Coker and Matthews attributed the species to the joint authorship of Coker and Braxton.

CONFIRMED RECORDS: -- INDIA: Khulbe (1977:16, pl. 1, figs. 1, 2; 1980c:78, figs. 1, 2); Mer and Khulbe (1984:200, pl. 2, figs 1, 4). UNITED STATES: Coker (*loc. cit*.); A. W. Ziegler (1948b:27, pl. 6, figs. 8-16; 1952: 15, pl. 1, fig. 7; pl. 6, fig. 6).

RECORDED COLLECTIONS: -- AFRICA: Alabi (1967; 1971a, b; 1973). BRITISH ISLES: Sparrow (1957). INDIA: Khulbe 1979, 1980a, d, 1981); Khulbe and Bhargava (1977, 1983); UNITED STATES: T. W. Johnson (1956a); Pendergrass (1948); K. B. Raper (1928); Scott (1960b); A. W. Ziegler (1958b). WEST INDIES: Scott (1960a).

SPECIMENS EXAMINED: -- SOUTH AMERICA (2). RLS. UNITED STATES (2), TWJ.

Brevilegnia subclavata Couch
J. Elisha Mitchell Sci. Soc. 42:229, pls. 39 - 41; pl. 42, figs. 1-7. 1927
(Figure 114 F-I)

Monoecious. Mycelium dense, limited; hyphae slender to moderately stout, moderately branched. Sporangia short, broadly clavate to nearly obpyriform, but short-cylindrical when formed in basipetalous succession; renewed sympodially and also in a cymose or basipetalous manner; 88-159 x 30-100 μm. Spores monomorphic; discharge and behavior brevilegnoid, infrequently aplanoid; spherical or polyhedral and 10-18 μm in diameter, but sometimes elongate and cylindrical and up to 34 μm long. Gemmae lacking. Oogonia lateral, infrequently terminal, very rarely sessile or intercalary, then single; predominantly spherical or obpyriform, sometimes subspherical or slightly irregular; (18-) 20–24 (-27) μm in diameter, including any wall ornamentations. Oogonial wall unpitted (?); smooth, very rarely with one or two prominent, cylindrical or papillate wall ornamentations. Oogonial stalks (1.5 -) 2–4.5 (-6) times the diameter of the oogonium in length; slender; usually curved, bent, or irregular; unbranched, once- or twice-branched, or forming compact glomeruli. Oospores eccentric; spherical; one per oogonium, and usually not filling it; (14-) 16–19 (-25) μm in diameter; germination not observed. Antheridial branches usually present; androgynous; irregular, bent or curved; unbranched or branched; persisting. Antheridial cells simple; tubular or clavate, and usually slightly irregular; persisting; laterally appressed; fertilization tubes not observed.

In common with *Brevilegnia bispora* and *B. minutandra, B. subclavata* produces glomerulate oogonial stalks with some frequency. Unlike *B. minutandra*, however, Couch's species is generously supplied with antheridial branches, and its sporangia are not cylindrical or long-clavate. *Brevilegnia bispora* also has androgynous antheridial filaments, and in this respect does not differ from *B. subclavata*. However, *B. bispora* has an achlyoid spore discharge pattern in some primary and secondary sporangia, and these asexual structures are not short and broadly clavate. In *B. linearis*, androgynous antheridial branches predominate -- just as in *B. subclavata* -- but in the former species the spores are uniseriate. Antheridial branch type is a useful character on which to separate *B. subclavata* (exclusively androgynous) from *B. diclina, B. longicaulis, B. crassa, B. globosa, and B. megasperma*. The antheridial branch origin of *B. unisperma* certainly allies it to *B. subclavata*, but the oogonia of the latter are almost always smooth in contrast to the irregular to ornamented ones in the former.

The production of short-clavate to nearly obpyriform sporangia (Fig. 114 I) make *Brevilegnia subclavata* easily recognized. The glomeruli (Fig. 114 G) produced by this species are noticeably more compact than is usually encountered in *B. minutandra* (compare Figs. 114 G, 115 A, B) where such oogonial stalks are common.

Couch (*loc. cit*.) was unable to induce planonts to emerge from the encysted spores produced by *Brevilegnia subclavata*. In our specimens the vast majority of spores did not excyst or even germinate to form a new hyphal system. We have seen a few excystments from spores floated in a 1:1 mix of bog water and charcoal-filtered distilled water. The secondary planonts are reniform and laterally biflagellate. In ordinary water cultures (charcoal-filtered, distilled or tap water), secondary planonts have not been observed.

CONFIRMED RECORDS: -- GERMANY: Höhnk (1952a:69, pl. 10). INDIA: Mer and Khulbe (1984:201, pl. 2, fig. 2); Prabhuji (1979:68, pls. 1, 2); Prabhuji and Srivastava (1978a:35); Prabhuji *et al.* (1984a:100, figs. 1–18). UNITED STATES: Beneke (1948b:136); R. L. Butler (1975: figs. 201–204). Couch (*loc. cit*.); Milanez (1966:93).

RECORDED COLLECTIONS: -- CENTRAL AMERICA: Wolf (1939b). GERMANY: Höhnk (1956a, 1958). MEXICO: Céspedes and Castillo (1982). PEOPLE'S REPUBLIC OF CHINA: Yu and Liang (1983). SOUTH AMERICA: Upadhyay (1967). UNITED STATES: Coker (1927); J. V. Harvey (1952); T. W. Johnson (1956a); Sparrow (1952b, 1965). WEST INDIES: Sörgel (1941).

SPECIMENS EXAMINED: -- OCEANIA (1), RLS. UNITED STATES (3), TWJ.

Brevilegnia unisperma (Coker and Braxton) Coker
In, Coker, J. Elisha Mitchell Sci. Soc. 42: 213. 1927
(Figures 112 I–N, 114 A–E, 116 F, G)

Thraustotheca unisperma Coker and Braxton, J. Elisha Mitchell Sci. Soc. 42:140, pl. 11, figs. 1-7; pl. 12. figs. 1-6. 1926.

Thraustotheca unisperma var. *litoralis* Coker and Braxton, J. Elisha Mitchell Sci. Soc. 42:141, pl. 11, figs. 8-13. 1926.

Brevilegnia unisperma var. *litoralis* Coker and Braxton, *in*, Coker, J. Elisha Mitchell Sci. Soc. 42:213. 1927.

Brevilegnia irregularis Rossy-Valderrama, J. Elisha Mitchell Sci. Soc. 72:133. figs. 14–22. 1956.

Monoecious. Mycelium dense, limited; hyphae slender, usually sparingly branched except near periphery of colony where moderately branched, and sometimes gnarled and irregular; hyphae of some isolates producing ovoid, globose, subglobose, or apiculate swellings on short or long lateral branches, the swellings hyaline, containing diffuse cytoplasm, 10–63 μm in diameter. Sporangia cylindrical to long- or short-clavate, occasionally fusiform; usually slightly irregular or curved, infrequently straight; renewed sympodially or often in a cymose fashion, hence clustered at tips of

hyphae; 31-408 x 18-36 μm. Spores monomorphic; discharge and behavior brevilegnoid, occasionally dictyucoid, but sporangium then also fragmenting in a brevilegnoid fashion; primary spore cysts often angular, 10-16 μm in diameter. Gemmae present or absent; when present, sparse, cylindrical to short-obpyriform; single, terminal. Oogonia generally lateral, infrequently terminal, very rarely sessile; spherical, subspherical, obpyriform, or ovoid, occasionally irregular or angular; immature ones rarely proliferating; (14-) 18-24 (-45) μm in diameter, including wall ornamentations. Oogonial wall unpitted; generally sparsely papillate, crenulate, or irregular, the ornamentations usually low and broad, but sometimes long-conic or cylindrical; infrequently to rarely smooth; wall sometimes of uneven thickness. Oogonial stalks (0.5-) 1–2.5 (-5) times the diameter of the oogonium, in length; slender, usually irregular, curved, or twisted, and occasionally provided with one or two short, lateral, cylindrical or papillate outgrowths; unbranched or branched. Oospores eccentric; spherical; one per oogonium, and not filling it; (12-) l4–17 (-23) μm in diameter; at germination producing a short, slender germ hypha bearing a small, clavate, terminal, brevilegnoid sporangium, or becoming branched and the apex of some branches forming a small sporangium. Antheridial branches present or absent; when present, sometimes sparse; monoclinous or androgynous; slender, often irregular and twisted or contorted; unbranched to moderately branched, occasionally or infrequently not attached to any oogonia; occasionally forming a dense growth around the oogonium and its stalk; persisting. Antheridial cells not always produced; when present, irregularly tubular to clavate; persisting; laterally appressed, infrequently apically attached; fertilization tubes not observed.

Brevilegnia unisperma can be identified by the preponderance of irregular (Fig. 112 J) or sparsely papillate (Fig. 114 B, 112 L) oogonia and its rather small oospores. *Brevilegnia diclina* also has some irregular to ornamented oogonia, but its diclinous antheridial branches as well as oospore size separate it readily from *B. unisperma.* Although specimens of *B. linearis* may have some ornamented oogonia, the spores in this species are uniseriate, and there are no monoclinous antheridial filaments (these are common in *B. unisperma*). In *B. bispora* the oogonia generally are smooth, and this feature together with the achlyoid manner of spore release by some of its sporangia distinguishes it from *B. unisperma*.

Attention has been called (T. W. Johnson, 1977d) to the fact that the absence of antheridial branches in *Brevilegnia unisperma* var. *litoralis* was the only character by which it could be distinguished from the variety *unisperma*. Coker and Braxton (*loc. cit*.) found antheridial branches on 25-65% of the oogonia in their specimens of *Thraustotheca unisperma*. By contrast, the isolates of *B. unisperma* examined by Milanez and Beneke (1968) had no oogonia accompanied by antheridial filaments, or up to 50% of them with attendant filaments. Two specimens from the southern Scandinavian peninsula, T. W. Johnson (1977d) reported, had 9-16% and 30-50%, respectively, of the oogonia with attendant antheridial hyphae (among several subcultures). Inasmuch as the oogonia of

the variety *litoralis* are (Coker and Matthews, 1937:55) "… exactly similar in structure and measurements to *B. unisperma...*" we see no justification for retaining the variety.

The discovery of hyphal swellings in isolates clearly identifiable as *Brevilegnia unisperma* removes any major distinction between this species and *B. irregularis.* The oogonia of *B. unisperma* may be irregular on the inner surface (Fig. 112 J) or the entire oogonium may have an irregular configuration. *Brevilegnia irregularis* also has these characteristics (Fig. 116 F, G). When a large number of specimens are examined, we see no distinctions between Rossy-Valderrama's (*loc. cit.*) species and *B. unisperma*; the former is justifiably reduced to synonymy.

Certain reports of *Brevilegnia unisperma* require comment. The specimen isolated by Milanez and Beneke (1968) had the smallest predominating oospore diameter -- 12-14 μm -- recorded for this species. Rose (1932), on the other hand, found the oospores to be rather large: averaging 21 μm in diameter. The configuration of the sexual apparatus in the *Thraustotheca* sp. reported by Richter (1937) suggests that he had collected *B. unisperma*. The two specimens identified by S. B. Saksena and Rajagopalan (1958) as *Dictyuchus missourienis* were probably members of *Brevilegnia* since the sporangium wall deliquesced soon after the spores were formed. This being so, a position for their isolates near *B. unisperma* is clearly supported by the description of their specimens. On the other hand, because the oogonia of their isolates were "beaked" as in *D. missouriensis* (=*monosporus*), the Indian fungi cannot be identified specifically with *B. unisperma*. It seems likely that it was *B. unisperma* that J. V. Harvey (1942) reported as *Calyptralegnia (Thraustotheca) unisperma* var. *litoralis*. The *Brevilegnia* sp. collected once on human hair bait by T. W. Johnson (1974b) was not isolated and remains unidentified; he believed the fungus had affinities with *B. unisperma*. Other Brevilegnias provisionally identified with *B. unisperma* (T. W. Johnson, 1974b) also could not be isolated hence their identity is in considerable doubt.

CONFIRMED RECORDS: -- CENTRAL AMERICA: Headington (1971:10, 11). GERMANY: Höhnk (1952a:71, 73, pl. 11). NORWAY: T. W. Johnson (1977d:288). RUMANIA: Toma (1968:112, pls. 1, 5). SWEDEN: T. W. Johnson (*op. cit.*). UNITED STATES: Beneke (1948b:131, 134); R. L. Butler (1975: figs. 197–200); Coker and Braxton (*locc. citt.*); Milanez (1966:94, pl. 8); Milanez and Beneke (1968:17, pl. 2, figs. 1, 2); Rose (1932:47, pl. 5, figs. 42, 43); Sorenson (1962: pl. 4, figs. C, F); A. W. Ziegler (1952:15, pl. 1, fig. 5; pl. 6, fig. 7).

RECORDED COLLECTIONS: -- AFRICA: Alabi (1967; 1971a, b; 1973). BRITISH ISLES: Apinis (1958, 1964). DENMARK: A. Lund (1978). GERMANY: Höhnk (1956a); Richter (1937: 256, figs. 14, 15) (?). ICELAND: T. W. Johnson (1974b: 22) (?). RUMANIA: Toma (1969, 1971). UNITED STATES: Coker (1927); J. V. (Harvey (1942); T. W. Johnson (1955b); V. D. Matthews (1927); K. B. Raper (1928); A. W. Ziegler (1958b).

SPECIMENS EXAMINED: -- AFRICA (2), CENTRAL AMERICA (3), INDIA (1), WEST INDIES (1), RLS. ICELAND (1), NORWAY (1), SWEDEN (1), TWJ. Centraalbureau (1).

Brevilegnia minutandra Höhnk
Veröff. Inst. Meeresf., Bremerhaven 1:127. 1952
(Fig. 115 A-K)

Brevilegnia unisperma var. *montana* Coker and Braxton *ex* Coker, J. Elisha Mitchell Sci. Soc. 42:213, pl. 30, figs. 1-9. 1927.
Brevilegnia unisperma var. *delica* Coker and Alexander *ex* Coker, J. Elisha Mitchell Sci. Soc. 42:214, pl. 31. 1927.
Dictyuchus missouriensis var. *moruzii* Toma, Rev. Roumaine Biol., Sér. Bot. 15:253, pls. 4, 6. 1970.
Brevilegnia montana (Coker and Braxton) Johnson, Mycologia 69:289, figs. 1-8. 1977.

Monoecious. Mycelium diffuse and extensive; hyphae slender, branched. Sporangia sparse or abundant; cylindrical, fusiform or clavate; spores commonly in 1-3 rows; straight, curved, or slightly irregular; renewed sympodially or in a cymose manner; 60 μm–2.4 mm x 12-42 μm. Spores monomorphic; discharge and behavior brevilegnoid, infrequently dictyucoid then sporangium disarticulating and in part disintegrating, extremely rarely achlyoid then only in very old cultures and discharged spore mass not compact; primary spore cysts 7-18 μm in diameter; cylindrical protoplasmic segments up to 85 μm long in some sporangia. Gemmae absent or very sparse; cylindrical, clavate, or obpyriform, and occasionally with one or two short, lateral lobes; terminal or intercalary, single or catenulate. Oogonia lateral or terminal, occasionally sessile, infrequently or rarely intercalary and catenulate; in some colonies, arising in clusters on the hyphae; predominantly spherical, ovate, or broadly apiculate, occasionally broadly fusiform, or dacryoid, or pyriform to obpyriform, infrequently irregular or cylindrical, rarely lunate or turbinate; spherical ones (10-) 16–20 (-28) μm in diameter, nonspherical ones 16-35 x 11-21 μm; germination not observed. Oogonial wall unpitted; smooth. Oogonial stalks short or long; (0.1-) 2–4 (-7) times the diameter of the oogonium, in length; slender, slightly irregular; unbranched or branched and frequently producing extensive or compact glomeruli, or sympodially branched with the new hyphal tip often closely adherent to the oogonial wall. Antheridial branches extremely rarely produced, and usually absent in most colonies; when present, androgynous and then extremely short, and originating very close to the basal septum of the oogonium and often appearing to be a short sympodial branch from the oogonial stalk; persisting. Antheridial cells extremely rarely produced; when present, short, cylindrical, very inconspicuous; persisting (?); laterally appressed; fertilization tubes not observed.

Chiefly there are two characteristics by which this species can be recognized. First, many of the oogonia -- indeed, the majority in some individuals -- are ovate to broadly apiculate or fusiform (Fig. 115 F, G, I) and relatively small. While other species of *Brevilegnia* may produce oogonia of these shapes, they are by no means as common as is found in *B. minutandra*. Secondly, there is a noticeable abundance of glomerulate

oogonial stalks (Fig. 115 A) that are usually quite extensive but sometimes may be very compact (T. W. Johnson *et al*. 1973: figs. 13, 17, 23, 27). To be sure, *B. bispora* may produce such oogonia and glomeruli, but in this species, there are commonly achlyoid primary and secondary sporangia (extremely rare in *B. minutandra*, and lacking in most individuals) and the antheridial branches are far more abundant and prominent than in *B. minutandra*.

Considerable difficulty (leading to indecision) has been encountered in the identification of specimens making up the *Brevilegnia bispora-B. parvispora-B. minutandra* galaxy (T. W. Johnson, 1974a, 1977d; T. W. Johnson *et al*., 1973). The reason for the problems in identity results not from a paucity of specimens, but from the scanty or variable expression by some isolates of characteristics critical for taxonomic decisions. We have reexamined previously characterized isolates (T. W. Johnson, 1977d; T. W. Johnson, *et al*., 1973), and studied additional ones in an effort to resolve the troublesome taxonomy in this group of Brevilegnias.

In their account of *Brevilegnia unisperma* var. *montana*, a rather common fungus in Iceland, T. W. Johnson and his associates (1973) commented that the variety probably was worthy of specific rank. Subsequently (T. W. Johnson, 1977d), that status was proposed, yet with the recognition that Höhnk's *B. minutandra* was possibly nothing more than a variant of *B. montana*. Having studied much additional living material, we are now satisfied that the two should be consolidated, with the name *minutandra* having priority.

The merger of *Brevilegnia minutandra* and *B. montana* turns solely on one character, namely, the presence or absence of an antheridial apparatus. According to Höhnk (1952a:77, pl. 13), *B. minutandra* produced antheridial branches attendant to about 15% of the oogonia. When present, the antheridial filaments were so short as to appear hypogynous (Höhnk, 1952a: pl. 13, fig. 3) or hemihypogynous. *Brevilegnia montana*, on the other hand, had never been observed to have antheridial filaments. One of the conspicuous characteristics of *B. montana* is the production of sympodially branched oogonial stalks (Fig. 115 B–E); T. W. Johnson, *et al*., 1973: fig. 14; T. W. Johnson, 1977d: fig. 5). When these lateral filaments first emerge from the oogonial stalk they can be mistaken for antheridial branches (*see* T. W. Johnson *et al*., 1973: fig. 25). We have discovered in newly isolated specimens that such short sympodial branches terminate -- although quite rarely -- in an antheridial cell delimited from the antheridial branch, but not then emptying itself (as would occur in fertilization). Some isolates at hand have sympodially branched oogonial stalks but no visible antheridial cells, while others have such cells. Moreover, a specimen exhibiting antheridial cells may, when subcultured, produce no visible antheridial apparatus. These observations convince us that presence or absence of antheridia is not a reliable character on which to separate *B. minutandra* and *B. montana*. The concept of the latter (and its predecessor, *B. unisperma* var. *montana*) thus is modified to admit to the taxon individuals that extremely rarely produce an antheridial apparatus. Recognition is thereby facilitated.

We are persuaded from the illustrations of sporangium behavior in

Dictyuchus missouriensis var. *moruzii* that the fungus so named was a species of *Brevilegnia* (Toma, *loc. cit*., pl. 4, fig. 1a-c). The oogonia are depicted in glomeruli, and several are illustrated which show a sympodial branching pattern of the oogonial stalks; both of these features are characteristic of *B. minutandra*. There were no antheridial branches in Toma's specimens, but the absence of such filaments is not unusual in *B. minutandra.*

The consolidation of *Brevilegnia unisperma* var. *delica* with *B. montana* (=*minutandra*) was justified adequately by T. W. Johnson (1977d), and the merger of *B. montana* with *B. minutandra* does not invalidate that taxonomic change. However, it may be recalled that T. W. Johnson (1956a) found eight representatives of the variety *delica* to have predominantly dictyucoid spore release, and only secondary ones with brevilegnoid discharge. He suggested that perhaps a transfer of the variety *delica* to *Dictyuchus* was in order. We are not of that opinion since the dictyucoid sporangia in Johnson's isolates fragmented as the spores emerged from their cysts, hence the sporangia were in fact basically brevilegnoid.

CONFIRMED RECORDS: -- GERMANY: Höhnk (*loc. cit*.; 1952a:77, pl. 13). ICELAND: T. W. Johnson, *et al*. (1973:13, 16 *et sqq*., figs. 1-26). INDIA: Headington (1971:11). NORWAY: T. W. Johnson, Jr. (1977d:289, figs. 1-8). RUMANIA: Toma (*loc. cit.*). SWEDEN: T. W. Johnson (*op. cit.*). UNITED STATES: Beneke (1948b:132, 133); Coker (*locc. citt.);* T. W. Johnson (1956a:190).

RECORDED COLLECTIONS: -- MEXICO: Céspedes and Castillo (1982).

SPECIMENS EXAMINED: -- AFRICA (2), UNITED STATES (8), RLS. ICELAND (9), NORWAY (8), SWEDEN (4), TWJ.

Brevilegnia megasperma Harvey
J. Elisha Mitchell Sci. Soc. 45:322, pls. 32, 33. 1930
(Figures 114 J-L, 116 A-E)

Brevilegnia megasperma var. *brevicaulis* Rossy-Valderrama, J. Elisha Mitchell Sci. Soc. 72:133, figs. 23-29. 1956.

Monoecious. Mycelium dense, limited; hyphae slender or stout, moderately to abundantly branched. Sporangia clavate, fusiform, or naviculate; straight or slightly irregular, infrequently to rarely branched; renewed sympodially, sometimes in a cymose fashion; 78-310 x 14-29 μm. Spores monomorphic; discharge and behavior brevilegnoid, occasionally dictyucoid in secondary sporangia and then sporangium is usually partially disintegrated, rarely aplanoid; primary spore cysts 9-14 μm in diameter. Gemmae abundant; cylindrical or clavate, and usually slightly irregular, occasionally lobed or once-branched; terminal or intercalary, single or catenulate. Oogonia lateral, infrequently terminal, usually clustered along segments of the hyphae, occasionally to infrequently intercalary, then single or catenulate, rarely sessile; generally spherical or obpyriform, occasionally obovate; obpyriform to narrowly

dolioform or slightly irregular when intercalary; immature ones rarely proliferating; (21-) 30–34 (-55) μm in diameter. Oogonial wall unpitted; predominantly smooth, rarely with one to a few low, inconspicuous, scattered papillae. Oogonial stalks (0.1-) 1.5–3 (-6.5) times the diameter of the oogonium, in length; slender; usually curved or sinuous and irregular; occasionally to infrequently branched, and tending to form glomeruli. Oospores eccentric; spherical, occasionally ovate to cylindrical in intercalary oogonia; one per oogonium, and usually not filling it; (16-) 24–28 (-33) μm in diameter; germination not observed. Antheridial branches usually absent, but when present, sparse; usually monoclinous, infrequently androgynous, very rarely diclinous; slender; usually irregular or twisted; unbranched or very sparingly branched; persisting. Antheridial cells simple; clavate and slightly irregular; persisting; laterally or apically appressed; fertilization tubes not observed.

The predominating size of the oogonia and oospores of *Brevilegnia megasperma* is larger than that of other species in the genus, except for *B. globosa*. In the latter, however, the oogonial stalks are consistently short, and the oogonial wall presumably is pitted. Although oogonium and oospore diameters in *B. crassa* are slightly smaller than those of *B. megasperma*, the two species could be misidentified if only a few measurements are made. *Brevilegnia crassa* has at least some thick-walled oogonia, but there is none in *B. megasperma*.

In our specimens of *Brevilegnia megasperma* the antheridial branches were sparse, and most oogonia were without such filaments. This characteristic agrees with J. V. Harvey's (*loc. cit*.) delineation of the species. However, when antheridial filaments were present in our isolates they were usually monoclinous and only infrequently androgynous. According to J. V. Harvey (*loc. cit*.), the antheridial apparatus in *B. megasperma* was hypogynous; the illustrations accompanying the description do not convey clearly such an origin. In their compilation of *Brevilegnia* species Coker and Matthews (1937) referred to the antheridial apparatus of *B. megasperma* as androgynous and originating near the oogonium. Other features of our isolates agree well with those described for the species by Harvey.

The disposition of Rossy-Valderrama's (*loc. cit*.) *Brevilegnia megasperma* var. *brevicaulis* is troublesome. We have had available two slides (preserved material) of the type specimen, and take most of the following account from the results of a reexamination of this material.

As the varietal name implies, Rossy-Valderrama's fungus was separated from Harvey's *Brevilegnia megasperma* largely on the basis of shorter oogonial stalks in the variety of *brevicaulis* than in *B. megasperma*. Nevertheless the type material does not display a preponderance of short-stalked oogonia; rather, there are both short- and long-stalked ones, and not uncommonly, glomerulate ones as well. In his account of *B. megasperma* Harvey (*loc. cit*., pl. 33, figs. 1, 10) depicted sparsely branched glomeruli, but did not mention in the description that this condition was present in his species. On the basis of relative stalk length, therefore, we can see no substantial difference between *B. megasperma* and the variety.

Rossy-Valderrama described the antheridial branch origin of *Brevilegnia megasperma* var. *brevicaulis* as generally monoclinous, and only infrequently androgynous or hypogynous. The preserved specimens, however, show so few antheridial branches that it is difficult to say which of the three types predominate. Our Norwegian material of *B. megasperma* had androgynous antheridial filaments generally, but again, any antheridial hyphae were scarce. We found no hypogynous cells either in our specimens or the type material. The Norwegian plants, like Rossy-Valderrama's, had oogonial stalks of a variety of lengths and degrees of branching. The very slight differences in oospore and oogonium diameters between *B. megasperma* and the variety *brevicaulis* are insignificant taxonomically.

In their overall aspect, *Brevilegnia megasperma* var. *brevicaulis* and *B. megasperma* are in very close agreement. This is particularly true for the production and shape of gemmae, sporangium and oogonium shape, and the nature of the oogonial stalks. Accordingly, we believe the variety is not distinct enough from the species to be retained.

CONFIRMED RECORDS: -- NORWAY: T. W. Johnson (1977d:295, figs. 20-28). UNITED STATES: Beneke (1948b:130); Harvey (*loc. cit.*); Rossy-Valderrama (*loc. cit.*; 1955:47, pl. 11, figs. 1-6; pl. 12); Sorenson (1962: pl. 5, figs. A-C).

RECORDED COLLECTIONS: -- SOUTH AMERICA: Upadhyay (1967). UNITED STATES: J. V. Harvey (1942).

SPECIMENS EXAMINED: -- NORWAY (2), TWJ. UNITED STATES (4), TWJ, RLS, C. R. Rossy-Valderrama (preserved type).

Brevilegnia bispora Couch
J. Elisha Mitchell Sci. Soc. 42:228, pls. 37, 38. 1927
(Figures 113 A-F, 115 L-Q)

Brevilegnia parvispora Höhnk, Veröff. Inst. Meeresf., Bremerhaven, 1:127. 1952.

Monoecious. Mycelium dense, moderately extensive; hyphae stout or slender, generally much-branched. Sporangia cylindrical, fusiform, or naviculate; occasionally curved or slightly irregular; renewed sympodially, or in a basipetalous or cymose fashion; 47-311 x 16-53 μm. Spores monomorphic; discharge and behavior in primary sporangia achlyoid and brevilegnoid; discharge and behavior in secondary ones brevilegnoid or occasionally dictyucoid, but if the latter, sporangia disintegrate in part in a brevilegnoid manner; behavior rarely aplanoid; primary spore cysts 8-18 μm in diameter. Gemmae cylindrical, fusiform, or short-clavate to obpyriform; terminal or intercalary, single or catenulate. Oogonia lateral or terminal, occasionally catenulate; spherical, obpyriform, or occasionally ovate, rarely apiculate, or slightly irregular to sparsely papillate; spherical ones (15-) 18–24 (-37) μm in diameter, ovate and obpyriform ones (18-) 27–35 (-41) x (16-) 21–29 (-38) μm. Oogonial wall unpitted; smooth. Oogonial stalks extremely variable in length, 0.5-14 times the diameter of the

oogonium, in length; slender or stout, generally moderately irregular, curved, or twisted, sometimes very stout, extremely irregular and gnarled, and with one to a few short, lateral protrusions; occasionally loosely coiled in addition to being twisted and irregular; unbranched or occasionally sympodially branched or glomerulate. Oospores eccentric; one per oogonium, and nearly filling it or not; (12-) 18–22 (-33) μm in diameter; at germination forming a short, slender, unbranched germ hypha bearing a small, brevilegnoid sporangium, or branching and producing a new mycelium directly. Antheridial branches usually present and abundant, predominantly androgynous, infrequently to rarely monoclinous, very rarely diclinous but then in very old cultures; slender, often irregular and twisted; when arising near the oogonium, short and curved; unbranched or branched; persisting. Antheridial cells simple; tubular, clavate, or noticeably irregular and lobed or once-branched; sometimes as large as the oogonium, or larger; persisting; laterally appressed; fertilization tubes sometimes present, but not persisting.

The generic position of this species is debatable, and future studies may show that it must be assigned to *Achlya* because of its spore release patterns. We retain Couch's species in *Brevilegnia* for two reasons. First, although primary sporangia that discharge spores in an achlyoid manner were present in every isolate we have studied, some primary ones that discharge in a brevilegnoid fashion always also occurred. In some isolates the secondary sporangia were exclusively brevilegnoid in behavior, and in others predominantly so, and then accompanied by sporangia behaving in an aplanoid or dictyucoid manner. The spore discharge in our specimens, therefore, was not consistently of one type. Secondly, the first sporangium to be formed on a germ hypha from an oospore is (in our experience) always of the brevilegnoid type, and this strengthens an affinity with *Brevilegnia*. *Brevilegnia bispora* has a counterpart in *Achlya dubia*, a species in which the primary sporangia are of two types with respect to spore release.

Brevilegnia bispora is a variable species in other characters as well as spore discharge pattern as T.W. Johnson (1974a) discovered in some collections from Iceland. He was unable to identify all of the isolates but we think now that he had simply encountered individuals of *B. bispora* displaying some extremes of variability. In particular Johnson found that isolates alleged to be representative of Couch's species seemed to differ from one another in the nature of the oogonial stalks and the antheridial cells. The oogonial branches were extremely variable as to length (T.W. Johnson, 1974a: figs. 33, 36) and in their general aspect. Often the stalks were stout, twisted, and contorted in some isolates, but in others slender and only indistinctly to moderately irregular. Branching also proved to be variable, with the oogonial stalks either unbranched (Fig. 113 E), sympodially branched (Fig. 113 D), or simply glomerulate (Fig. 115 N). The antheridial cells were tubular, barely irregular structures in some isolates (Fig. 113 F), while in others they were large, conspicuously irregular and lobed (Fig. 115 L, M; *see* also T.W. Johnson, 1974a: figs. 14-16, 23, 34-36). The antheridial filaments, like the oogonial stalks, could be unbranched, relatively

isodiametric hyphae, or branched, stout or slender, irregular and contorted filaments. In some cases, individuals in the Iceland collections of *B. bispora* differed from one another in the predominant sizes of oogonia and oospores, but the discrepancies were minor, and isolates intergrading with those having small oogonia and oospores and those having larger cells occurred rather frequently.

It has been demonstrated (T.W. Johnson, 1974a) that modifications can be culturally induced in some isolates of *Brevilegnia parvispora* in the general aspect of the oogonial stalks, the antheridial branches, and the antheridial cells. Manipulation of the culture environment (the "type" of water used, in particular) did not induce changes in antheridial branch origin or sizes of the oospores and oogonia, or diminish glomeruli or modify quantitatively the production of brevilegnoid primary sporangia.

Although T.W. Johnson (1977d) retained *Brevilegnia parvispora* (Höhnk, *loc. cit*.) provisionally, we believe it is properly to be consolidated with *B. bispora*. There are, to be sure, some differences between *B. parvispora sensu* Höhnk, and *B. bispora* (T. W. Johnson 1974a, 1977d). The predominant oospore diameter in *B. parvispora* as Höhnk described the species was smaller than is usual for Couch's species, but we have uncovered variants with intermediate sizes. The oogonial stalks and antheridial branches in specimens identified as *B. parvispora* (*sensu* Höhnk) are somewhat more slender and delicate than those in *B. bispora*, but in part the general aspect of these hyphal branches is modified by culture conditions. In such features as the type of spore release, antheridial branch origin, oogonium shape (T. W. Johnson, 1974a), and presence of glomerate stalks *B. parvispora* and *B. bispora* are alike. The characteristics of the several isolates we have examined demonstrate that recognizable distinctions between these two taxa are not to be found.

It is likely that *Dictyuchus lucknowensis* (J. N. Rai and Misra, 1978) is a variant of *Brevilegnia bispora* but short of reexamining living material of this species from India, there is no way to be definitive on this point. The dictyucoid sporangium illustrated by Rai and Misra recalls similar ones found occasionally in some cultures of Couch's species. On the other hand, the alleged absence of androgynous antheridial branches in *D. lucknowensis* does not ally it well with *B. bispora*. The formation of achlyoid sporangia by the fungus from India definitely brings to mind the asexual apparatus of *Achlya pseudoachlyoides*, but in this instance again the absence of androgynous antheridial filaments in the Indian watermold implies a less demonstrable affiliation.

Those oogonia of *Brevilegnia bispora* that are unaccompanied by antheridial branches resemble certain ones in *B. minutandra*. In *B. bispora*, however, an antheridial apparatus is displayed prominently (associated with most oogonia) while in *B. minutandra*, the very rarely produced antheridial branches are small and inconspicuous. That *B. bispora* forms some achlyoid sporangia while *B. minutandra* does not further serves to distinguish these two species from each other. The achlyoid sporangia and predominantly androgynous antheridial branches of *B. bispora* separates it readily from *B. longicaulis* (a species with diclinous antheridial branches). Unlike the oogonia of *B. bispora* those of *B. unisperma* generally are irregular or sparsely but prominently ornamented.

In sum, *Brevilegnia bispora* can be recognized by a combination of characteristics: some achlyoid primary sporangia, oogonia on stalks that are sender or stout and often very irregular (or that may be glomerulate), and androgynous antheridial branches sometimes terminating in very large and irregular antheridial cells.

The isolates described by T.W. Johnson (1974a, 1977d), and T.W. Johnson *et al.* (1973) as *Brevilegnia parvispora* were misidentified. These specimens were representatives of *B. bispora*.

CONFIRMED RECORDS: -- AFRICA: Alabi (1967:81, pl. 10, figs. f, g; 1972: fig. 1D). GERMANY: Höhnk (*loc. cit*.; 1952a:66, 67, pl. 9). ICELAND: T.W. Johnson (1974a:8 *et sqq*., figs. 1–43); T.W. Johnson *et al*. (1973:20 *et sqq*., figs. 31–39). INDIA: Pabhuji *et al.* (1984a:100, 102, figs. 19–25). SWEDEN: T.W. Johnson (1977d:296, figs. 29-37). UNITED STATES: R. L. Butler (1975: figs. 189–192); J. N. Couch (*loc. cit.)*.

RECORDED COLLECTIONS: -- AFRICA: Alabi (1971a, b; 1973). BRITISH ISLES: Dick (1962, 1963, 1966); Dick and Newby (1961). DENMARK: A. Lund (1978). GERMANY: Höhnk (1956a)(?). INDIA: Misra (1982a, b). UNITED STATES: Coker (1927).

SPECIMENS EXAMINED: -- AUSTRALIA (3), OCEANIA (2), RLS. ICELAND (20), SWEDEN (3), TWJ. UNITED STATES (2), RLS.

Brevilegnia crassa Rossy-Valderrama
J. Elisha Mitchell Sci. Soc. 72:130, figs. 1-13. 1956
(Figure 116 H-M)

Monoecious. Mycelium dense, moderately extensive; hyphae slender, branched. Sporangia cylindrical or fusiform, straight, curved, or slightly irregular; renewed sympodially or in a cymose fashion; 216-266 x 8-28 μm; spores only in one or two rows. Spores monomorphic; discharge and behavior brevilegnoid, in some secondary sporangia dictyucoid in which cases the sporangium usually also disintegrates in part; primary spore cysts 8–16 μm in diameter. Gemmae absent. Oogonial lateral, occasionally intercalary, infrequently terminal; spherical or obpyriform, occasionally subglobse or slightly irregular; immature ones infrequently proliferating; (2l-) 24–28 (-53) μm in diameter. Oogonial wall unpitted; smooth; variable in thickness from 1.5-18 μm; at least some oogonia in each culture thick-walled, some thin-walled; those with a thin wall becoming more abundant as colony ages. Oogonial stalks (0.5-) 1–2 (-3.5) times the diameter of the oogonium, in length; slender; straight, bent, curved, or sinuous, and often slightly irregular in outline; unbranched. Oospores eccentric; spherical, infrequently broadly oval; one per oogonium, and usually nearly filling it; (11-) 19–22 (-27) μm in diameter; germination not observed. Antheridial branches generally monoclinous, occasionally to infrequently androgynous or diclinous; slender, irregular; unbranched to very sparingly branched; persisting. Antheridial cells tubular to clavate, and often slightly irregular; persisting; laterally appressed; fertilization tubes not observed.

In the specimens we have examined of this unusual species, 80-90% of the first-formed oogonia were noticeably thick-walled. As the colonies aged, however, fewer of the later-formed oogonia exhibited this feature, and the wall was relatively thin (Fig. 116 L) in most oogonia. We have found that isolates do not lose entirely the thick-walled condition through repeated subculture, but certainly this characteristic diminishes in frequency with time.

The nature of the thickened oogonial wall in *Brevilegnia crassa* is not known. Such walls do not collapse as does the envelope surrounding some oogonia of *Aplanopsis terrestris*. Some oogonia of *B. crassa* are invested with a very irregular, hyaline "veil", but this structure does not persist in culture. Transmission electron photomicrographs of the veil reveal only a thin, irregular, electron-dense margin. Since the thick-walled oogonia of *Brevilegnia crassa* have not withstood preparative TEM methods, we are unable to compare and contrast the veil and the wall.

Much further study is necessary to determine if the thick-wall feature of the oogonia in this species is stable enough to have taxonomic application. Should this characteristic prove to be inconstant and is eliminated by culture manipulation, a merger of *Brevilegnia crassa* with *B. unisperma* would have merit.

CONFIRMED RECORD: -- UNITED STATES: Rossy-Valderrama (*loc. cit*.).

SPECIMENS EXAMINED: -- OCEANIA (1), RLS. CENTRAL AMERICA (1), TWJ. UNITED STATES (1), C. R. Rossy-Valderrama (preserved type). WEST INDIES (1), RLS.

Brevilegnia globosa Ziegler
Mycologia 50:405, figs. 9-16. 1958

"Mycelium moderately dense, reaching a diameter of 14 mm on hempseed. Zoosporangia very abundant in both old and young cultures, long, cylindrical, variable, emerging as in the genera *Brevilegnia, Thraustotheca*, and *Dictyuchus*. Gemmae ovoid, terminal, often intercalary. Oogonia plentiful, spherical; lateral on stalks 0.5-2 times the diameter of oogonium in length; 22–31 μm [*sic*] mostly 29 μm in diameter. Oospores eccentric, spherical, single, 22–33 μm [*sic*], predominantly 28 μm; not filling the oogonium. Antheridial branches monoclinous; usually slightly contorted; antheridial cells apically appressed. Mature oospore germinating after 3 months by a germ tube with a terminal zoosporangium; spore behavior as in *Brevilegnia*." (A. W. Ziegler *loc. cit*.)

This species, known only from a single collection, has certain features which appear to set it apart from other members of the genus. It is the only species that seems to be consistently provided with short-stalked oogonia -- shorter even than those produced by Rossy-Valderrama's (1956) *Brevilegnia megasperma* var. *brevicaulis*. Chiefly, however, the distinctive feature of *B. globosa* is its pitted oogonia (under the area of

attachment of the antheridial cells). This characteristic is not mentioned in the description, but is illustrated unmistakably (A. W. Ziegler, *loc. cit*., figs. 11, 12). No other species in the genus is known to have pitted oogonia.

Brevilegnia globosa shares with *B. crassa* the characteristic of monoclinous antheridial branches, but the two differ in other respects (oogonial wall thickness, principally). *Brevilegnia linearis* usually has smooth oogonia, as does Ziegler's species, but generally has androgynous antheridial filaments considerably longer oogonial stalks, and primary sporangia with uniseriate spores. The general configuration of the sexual apparatus in *B. subclavata* (long-stalked oogonia, androgynous antheridial branches) serve to distinguish this species from *B. globosa*.

Brevilegnia globosa is alleged to have some sporangia capable of achlyoid discharge (A. W. Ziegler, *loc. cit*.) but whether this type of spore release occurs in primary or secondary ones is not known. It will be noted in the original description that the upper limit to the range of oospore diameter is larger than the upper limit of oogonial size. Oogonial diameter cited in the Latin diagnosis does not agree with that given in the English description (A. W. Ziegler, *loc. cit*.).

CONFIRMED RECORD: -- UNITED STATES: A. W. Ziegler (*loc. cit*.).

Brevilegnia sp.

AFRICA: Fajola *et al.* (1978). BRITISH ISLES: Dick (1963); Dick and Newby (1961); O'Sullivan (1965); Sparrow (1957): possibly a species of *Brevilegniella*; (*see* Dick, 1961). DENMARK: A. Lund (1978). GERMANY: Remy (1950). INDIA: Prabhuji (1979). JAPAN: Hoshina *et al*. (1960:73, fig. 10. Oogonia provided with 1-2 oospores, hence not brevilegnoid; possibly a mixed culture.) MEXICO: Céspedes and Castillo (1982). PEOPLE'S REPUBLIC OF CHINA: Yu and Liang (1983). PHILIPPINES: Dogma (1975). REPUBLIC OF CHINA: Chiou, *et al*. (1975: 170, pl. 2, fig. 29). UNITED STATES: Sparrow (1965). WEST INDIES: Sparrow and Dogma (1973).

IMPERFECTLY KNOWN SPECIES OF *BREVILEGNIA*

Brevilegnia 3519 Johnson, Howard, and Padgett
Acta Bot. Islandica 2:21, figs. 27-30. 1973

Monoecious. Mycelium limited, sparse; hyphae slender, sparingly branched; hyaline, stalked, lateral swellings generally present but scattered on most hyphae, broadly obovate, ovate, or obpyriform, sometimes apiculate, usually slightly irregular in outline, infrequently catenulate, 20-38 x 18–32 μm, not cut off from the hypha by a septum. Sporangia cylindrical to clavate, occasionally fusiform; straight, curved, or irregular; renewed sympodially; 105-281 x l6-30 μm. Spores monomorphic; discharge and behavior brevilegnoid, infrequently dictyucoid and the sporangium wall disintegrating in part; primary spore cysts 8-11 μm in diameter. Gemmae lacking (?).

Oogonia lateral, rarely terminal or sessile; spherical, broadly ovoid to broadly obpyriform, occasionally fusiform or apiculate; spherical ones (16-) 18 - 21(-23) µm in diameter, nonspherical ones (22-) 24–29 (-33) x (15-) 18–22 (-27) µm. Oogonial wall unpitted; smooth. Oogonial stalks (0.5-) 2–4 (-6.5) times the diameter of the oogonium, in length; slender, irregular, curved, twisted, occasionally once-coiled; unbranched, branched sympodially, or branching to form a glomerulus. Antheridial apparatus not observed.

The ovate, fusiform, or broadly apiculate oogonia of this unnamed species are similar to those of *Brevilegnia minutandra*. The resemblance between the two species is strengthened by the fact that there are no antheridial branches in *Brevilegnia* 3519, a situation encountered in some isolates of *B. minutandra*.

Brevilegnia 3519 differs from all other species in the genus -- with the possible exception of *B. unisperma* -- by its production of short-stalked, hyaline, lateral swellings (T. W. Johnson, *et al*., *loc. cit*.). These lateral protrusions are usually slightly larger than oogonia, and are consistently irregular in general configuration. Because the hyphal swellings are hyaline, conspicuously vacuolate, and not cut off from the subtending stalk by a septum, it is unlikely that they are gemmae. None has been seen to geminate or to develop into some other recognizable structure. Sessile oogonia are associated with some of these lateral protuberances (T.W. Johnson, *et al., loc. cit.,* fig. 30) suggesting that the swellings might be aborted oogonia. Unlike the hyphal swellings produced by *B. unisperma* those formed in this unnamed *Brevilegnia* are predominantly on short, sometimes stout stalks.

Until additional specimens of this unusual watermold are examined, it cannot be properly identified.

CONFIRMED RECORD: -- ICELAND: T. W. Johnson, *et al.* (*loc. cit*.).
MATERIAL EXAMINED: -- ICELAND (1), TWJ.

Brevilegnia C-2 Salvin
Mycologia 34:39 *et sqq.,* figs. 1, 2. 1942

It was with this unnamed species that Salvin demonstrated a very high degree of variability in sporangium shape, number of rows of spores in those sporangia, gemma production, and the general aspect of the antheridial branches. Salvin was unable to identify the fungus, and, in fact, did not give a formal, concise description of the major characters (for example, size of oogonia and oospores, and origin of antheridial filaments). From the illustrations provided by Salvin it appears that *Brevilegnia* C-2 had irregular oogonia and diclinous antheridial branches, characteristics that would ally it with *B. diclina*.

EXCLUDED TAXA

Brevilegnia gracilis van Eek
Phytopathol. Z. 11:260, pl. 2. 1938

As a part of a reinvestigation of pansy root rot in the Netherlands van Eek discovered two fungi which he described as new species of *Brevilegnia: B. gracilis*, and *B. macrospora*. Not only are the two species almost identical in their characteristics, they also are not members of *Brevilegnia*.

To be sure, the descriptions and illustrations of *Brevilegnia gracilis* and *B. macrospora* suggest that the fungi had brevilegnoid spore discharge; the oogonial apparatus in each, however, was clearly of some pythiaceous form. As had Sorenson (1968; *see also* his comments, 1964) we examined specimens of these two species deposited in the Centraalbureau, Baarn. The isolates did not produce sporangia, but the narrow diameters of the hyphae coupled with the nature of the oogonia and oospores confirm that the fungi are pythiaceous. We concur in Sorenson's decision (1968) to remove van Eek's species from the genus. Even van Eek (*loc. cit*.) recognized that the hyphae were smaller in diameter than those typical of the Brevilegnias.

Bhargava (1945a-c) used *Brevilegnia gracilis* as one of the watermolds analyzed for nutritional requirements. Unlike the true watermolds that Bhargava studied, *B. gracilis* reduced the sulfate ion and utilized nitrate nitrogen. Thus, this one species did not conform to the usual -- and very consistent -- nutritional pattern exhibited by members of the family. The removal of *B. gracilis* from the Saprolegniaceae restores the nutritional integrity of the group.

Brevilegnia macrospora van Eek
Phytopathol. Z. 11:258, pl. 1. 1938

Doubtless a species of *Pythium*, probably described from a mixed culture. *See* discussion of the previous species.

Brevilegnia parthenospora Howard
In, Dissertation, Duke University, p. 204, figs. 218-225. 1968

This binomial is a *nomen nudum*. The specimens on which the name was based, and additional ones subsequently collected, were identified by T.W. Johnson, *et al*. (1973) as *Brevilegnia unisperma* var. *montana*. This variety has now been consolidated with *B. minutandra*.

Brevilegnia subterranea
Beih. Bot. Centralbl. (Abt. B) 61. 1941.

This species name is cited by Sörgel (1941) for a collection made in the West Indies. No author is recorded for the species, and no such taxon has been described in *Brevilegnia* so far as we are aware.

Brevilegnia variabilis Indoh
Mag. Nat. Hist., Tokyo 38:87, figs. 1, 2. 1941

See Dictyuchus variabilis. This species, as *Brevilegnia variabilis*, was reported by Sparrow and Dogma (197a) from Hispaniola, but there are no illustrations or descriptive notes accompanying this record. A subculture of the Hispaniola isolate, provided by the late F. K. Sparrow, is a variant of *Dictyuchus pseudodictyon*.