

## CHAPTER 47

### *DICTYUCHUS* Leitgeb Jahrb. Wiss. Bot. 7:374.1869-70

Monoecious or dioecious. Sporangia cylindrical to clavate; renewed sympodially or infrequently in a basipetalous fashion; often disarticulating. Spores monomorphic; encysting within the sporangium, and subsequently emerging individually from the cysts as reniform planonts, leaving the empty sporangium net-like; sporangium wall remaining intact and cysts being angular, or deliquescing, with the adhering cysts becoming rounded. Gemmae rare. Oogonia lateral or terminal; spherical or obpyriform occasionally slightly irregular. Oogonial wall unpitted, or pitted only where antheridial cells are attached; smooth. Oogonial stalks of various lengths. Oospores eccentric; single. Antheridial branches declinous, monoclinal, or androgynous, or originating from hyphae of a male mating strain; often enwrapping the oogonium. Antheridial cells simple, lateral or digitate, often partially enveloping the oogonium.

Type species: *Dictyuchus monosporus* Leitgeb, Jahrb. Wiss. Bot. 7:374, pls. 22, 23. 1869-70.

The genus *Dictyuchus* was established for a single species. According to Leitgeb the antheridial branches of *D. monosporus* arose from filaments other than those bearing oogonia. Since Leitgeb did not explicitly state that sexual reproduction occurred only when compatible strains were mated, there is no proof of dioecism for the entity he named *monosporus*. In this connection, it should be noted that in the discussion of *Dictyuchus* in his 1868 paper Leitgeb stated that net sporangia were produced by both the male and female individuals, and this observation might imply that mating strains were involved in the production of the sexual apparatus. In any case, the name *monosporus* definitely has been applied to a dioecious species (J. N. Couch, 1926b) of the genus. The status of the type species and alleged synonymous forms is discussed more fully in connection with *Dictyuchus monosporus*.

Much taxonomic emphasis in *Dictyuchus* has been placed on the behavior of the sporangium during discharge, specifically whether the wall deliquesces or not. Thus, the concept of a true-net versus a false-net sporangium developed (J. N. Couch, 1931; Coker, 1935; Coker and Matthews, 1937), but has since been questioned (T. W. Johnson, 1951) as an important taxonomic character. Padgett and Seymour (1974) recognized four sporangial types in the genus, namely, achlyoid, false-net, and two types of true-net ones. We do not believe it is any longer necessary to separate species in the genus on sporangium net-type, and with the removal of those species whose primary sporangia are achlyoid (*D. achlyoides* and *D. pseudoachlyoides*), the genus is now a more clearly and compactly defined taxon.

Because the secondary sporangia of some species of *Brevilegnia* tend to produce dictyuroid sporangia, it often is difficult to distinguish them from taxa in *Dictyuchus*. Identifying representatives of the two genera is discussed in the account of *Brevilegnia*.

Key to the species of *Dictyuchus*

- 1. Dioecious; antheridial branches or oogonia, or both, cross-induced . . . . . *D. monosporus* (p. 772)
- 1. Monoecious; antheridial branches and oogonia self-induced . . . . . *D. pseudodictyon* (p. 777)

*Dictyuchus monosporus* Leitgeb  
Jahrb. Wiss. Bot. 7:374, pls. 22, 23. 1869-70  
(Figures 107 B-G, 108)

*Dictyuchus anomalus* Nagai, J. Fac. Agric. Hokkaido Imp. Univ. 32:28, pl. 7, figs. 1-6. 1931.

*Dictyuchus missouriensis* Couch, J. Elisha Mitchell Sci. Soc. 46:227, pl. 15. 1931.

Dioecious; oogonia self- or cross-induced, antheridial branches cross-induced. Mycelium of compatible thalli extensive, diffuse; hyphae slender to moderately stout; sparingly to abundantly branched. Sporangia of compatible thalli similar; usually very abundant; elongate-cylindrical to elongate-narrowly clavate; straight, curved, or slightly irregular; unbranched or branched; often disarticulating; renewed sympodially or in a cymose fashion; 60-780 x 10-40  $\mu\text{m}$ . Spores monomorphic; discharge and behavior dictyucoid, in some sporangia the primary spore cysts remain polygonal and closely appressed after release of the secondary planonts, in others, the primary spore cysts become spherical or slightly oval prior to planont release; sometimes aplanoid; secondary spore cysts 10-17  $\mu\text{m}$  in diameter. Gemmae absent or very rare; when present, obpyriform to short-cylindrical. Oogonia lateral, infrequently intercalary, terminal, or sessile; spherical or obpyriform, infrequently broadly oval or ellipsoidal; (15-) 22-35 (-67)  $\mu\text{m}$  in diameter. Oogonial wall unpitted or extremely rarely very sparsely pitted; smooth. Oogonial stalks ( $1/2$ -) 2-4 $1/2$  (-8) times the diameter of the oogonium, in length; slender, curved, bent, or slightly irregular; unbranched, branched, or forming glomeruli sparingly. Oospores eccentric; spherical, occasionally broadly oval to nearly cylindrical; single in an oogonium, and usually not filling it; (14-) 20-30 (-51)  $\mu\text{m}$  in diameter; at germination producing a slender germ hypha bearing a short, cylindrical, terminal sporangium.

The problem of speciation in the dioecious forms of *Dictyuchus* and those alleged to have solely diclinous antheridial branches is complex and challenging. Questions of identification are further intensified by the fact that Leitgeb did not specifically describe the type species, *D. monosporus*, as a dioecious form.

An historical perspective of certain species in the genus is in order. In 1872, Lindstedt described *Dictyuchus magnusii* solely from specimens which he evidently did

not bother to isolate. In any event, its circumscription hardly distinguished it from Leitgeb's species. Another new taxon, *D. carpophorus*, was described by Zopf in 1893. He emphasized its profusely developed antheridial branches that enveloped the oogonia, and essentially ignored other characteristics. Thirty years later, Coker (1923) added to the complexity of identification by his account of the species known to that time. Specimens of *Dictyuchus* that were sexually sterile -- and remained so with prolonged incubation or when mated with one another -- Coker assigned to a new species, *D. sterile*. Because the sporangia in his sterile plants were sometimes deciduous Coker thought them to be nearest *D. monosporus*, a species that had not been reported from the New World up to that time. Coker (1923) believed that Linstedt's *D. magnusii* was probably not a valid species, but seemed to be allied with *D. monosporus*. *Dictyuchus carpophorus*, Coker contended, was only doubtfully distinct from *D. monosporus*, but, like other students of the water molds, he ignored the fact that Zopf unambiguously illustrated *D. carpophorus* as having some monoclinal antheridial branches. At least it may be said that Coker (1923) recognized the possibility of heterothallism (heteroecism) occurring in *Dictyuchus*, an idea not considered either by Pieters (Kauffman, 1915) or Humphrey (1893:132, pl. 20, figs. 112-114) both of whom allegedly collected Leitgeb's species.

In 1926(b), J. N. Couch published his now classical paper on heterothallism in *Dictyuchus*. From a characterization of sexual responses in a number of isolates, he so redefined the concept of sexuality in *D. monosporus* that his view has persisted more than four decades almost without change. As to the contribution of his discoveries to taxonomy within the genus, Couch simply wrote that any distinctions among *D. monosporus*, *D. carpophorus*, *D. sterile*, and *D. magnusii* seemed to be invalidated by the results of his studies. Conceivably it was this conclusion that led Coker and Matthews (1937:52) to list *D. carpophorus* and *D. sterile* as synonyms of *D. monosporus*, together with Nagai's (*loc. cit.*) *D. anomalus*.

We have carried out an extensive series of matings among specimens of *Dictyuchus* collected from widely scattered geographical areas. The pairings (in water cultures) included isolates of two kinds, namely, those in which oogonia and antheridial branches developed only by cross-induction, and ones self-inductive for oogonia but not for antheridial elements. The results of our experimental work demonstrate that there are at least four mating strains in Leitgeb's species.

In the majority of pairings among our isolates both parts of the sexual apparatus were cross-induced, and structurally comparable in all respects (Fig. 107 B-D) to *Dictyuchus monosporus* as that species was defined by J. N. Couch (1926b). In any given pairing of isolates there was a varied number of oogonia attended by cross-induced antheridial filaments: as many as 90% or as few as 5% of the oogonia in any given paired subculture lacked attendant antheridia.

A second mating type appeared in two-member cultures consisting of the antheridial plant of *Dictyuchus monosporus* and an isolate self-induced for oogonia only. The oogonium-bearing strain elicited antheridial branches to develop from the male partner (*D. monosporus*), but these seldom contacted or functioned(?) in the sexual

process. The isolates with self-induced oogonia were in all respects identifiable as Nagai's *D. anomalus* (strain N of J. N. Couch, 1926b). Mycelium of the male *D. monosporus* when paired with *D. anomalus* did not form oogonia, and no antheridial filaments developed in paired mycelia of *D. anomalus* with a female (oogonium-producing) strain of *D. monosporus*.

Antheridial strains of *Dictyuchus monosporus* cross-conjugated with *D. missouriensis* (Fig. 108 A, B), a species self-induced for oogonia. Such compatible matings constitute a third sexual response among our isolates. Moreover, the repeated subculturing of the *D. missouriensis* element (in the preparation of material for pairing experiments) resulted in loss (in some instances) or diminution in frequency of the one characteristic by which this species usually is recognized, namely, the strongly bent neck of the obpyriform oogonium (J. N. Couch, *loc. cit.*, pl. 15, fig. 5, left). Such an oogonium appears as if it is attached to its stalk by a beak-like process.

Finally, a fourth sexual response occurred in matings between the antheridial or oogonial isolates of *Dictyuchus monosporus* and a strain DOH (Fig. 108 E), self-induced only for oogonia. When paired with a potential male isolate of *D. monosporus*, strain DOH induced that isolate to produce functional antheridial branches many of which became associated with the oogonia of DOH (Fig. 108 D). However, when isolate DOH conjugated with a female strain (oogonium potential) of *D. monosporus*, strain DOH produced some monoclinal antheridial branches (Fig. 108 C) as well as cross-induced filaments.

What taxonomic implications emerge from the results of cross-conjugation tests? We believe there are three. In the first place, the name *Dictyuchus monosporus* must be reserved for those individual specimens that without exception conjugate such that oogonia or antheridia, or both, are cross-induced. To be sure, no such concept appears in Leitgeb's account (*loc. cit.*) of this species, but Couch's (1926b) work certainly established precisely this limit. Secondly, *D. anomalus* represents individuals of a strongly female nature readily capable of inducing antheridial filaments in *D. monosporus*. Third, *D. missouriensis*, identical to *D. anomalus* in its "femaleness" and conjugating capabilities, loses in culture the one feature that presumably sets it aside from all others in the genus, namely, the sharp bend at the base of the obpyriform oogonium. In the absence of this feature, the oogonia of *D. missouriensis* are indistinguishable from those of *D. monosporus*. It is pertinent to recall also that *D. missouriensis* has long been grouped with the monoecious species of the genus. However, from both a structural and a physiological standpoint, it, like *D. anomalus*, is only a variant of *D. monosporus*. The reactions elicited by our strain DOH remain unexplained; they do suggest that sexuality in the genus probably is quite complex.

Among our collections of *Dictyuchus* are isolates that either are consistently sterile sexually or for which we have not found a compatible companion. Confronting such isolates, Coker (1923) proposed for them species status as *D. sterile*. There is a question to be resolved of the validity and position of this taxon in the genus.

Whether Coker had in fact collected genetically sterile individuals -- and therefore had justification for proposing that *Dictyuchus sterile* be recognized -- cannot

now be determined, just as we are not certain that many nonconjugating strains we have isolated are truly infertile. The fact remains, however, that sporangium-producing individuals morphologically identical to *D. sterile* are known to conjugate with other asexual individuals to produce functional sex cells. Since the name *sterile* may apply to asexual or potentially sexual water molds, it is ambiguous and must be discarded. The published records of Coker's species are listed among those of unnamed collections of *Dictyuchus*.

Coker and Matthews (1937) included Zopf's *Dictyuchus carpophorus* as a synonym of *D. monosporus*, but this is unacceptable for two reasons. Zopf made no mention of the necessity of pairing cultures of *D. carpophorus* to obtain the sexual apparatus. A more cogent reason, however, is the fact that single colonies of Zopf's species evidently produced monoclinal antheridial branches. Such filaments, save in two-member, mated cultures (strain DOH) do not develop in *D. monosporus*.

In the foregoing attempt to resolve problems in the taxonomy of *Dictyuchus monosporus* and its kindred species, the nature of the sporangium at and after spore release is ignored. Traditionally (J. N. Couch, 1931; Coker and Matthews, 1937), species of *Dictyuchus* have been separated initially on the nature of the net of cyst walls remaining after planont emergence, that is, whether the sporangia were true-net or false-net. Sporangium type is by no means consistent among specimens of the same species (T. W. Johnson, 1951; Padgett and Seymour, 1974), and is thus inconsequential taxonomically.

Not all investigators reporting *Dictyuchus monosporus* recorded that identification was based on mating studies. Most published accounts refer to diclinous antheridial branches in *D. monosporus*, but that term is reserved specifically for a condition occurring in monoecious species. The antheridial branches of *D. monosporus* are not diclinous, they are cross-induced. There is no way to sort out which reports of *D. monosporus* were based on compatibility tests and which were not, save in instances where authors (1) clearly stated or implied that two-member cultures were used, or (2) had collected one of the species which appear to be mating strains of *D. monosporus* and are therefore synonymous with it. These instances are listed as confirmed records.

Some reports of *Dictyuchus monosporus* (or its synonymous elements) are the result of misidentifications. The following are prominent in this regard: Cejp (1934:194; based on a mixed culture); Goldsmith (1948:140, pl. 16, figs. 9, 10; based on an obviously mixed culture); Kobayasi and Konno [1971a:13, fig. 4 H-J (androgynous antheridial filaments); 1973:500, fig. 10 G-F (androgynous and monoclinal antheridial branches)]; Rose (1932:51, pl. 5, fig. 41; centric oospores); S. B. Saksena and Rajagopalan [1958:16, figs. 47-51 (a species of *Brevilegnia*); *ibid.*, p. 17, figs. 52-57 (identified as *D. pseudodictyon*, but in all probability was the *missouriensis* element of *D. monosporus*)]; Szwank (1938:14, pl. 5, figs. 3-7; androgynous and diclinous antheridial apparatus).

CONFIRMED RECORDS: -- AFRICA: Alabi (1967: pl. 13, figs. a-c. Figures a and b appear to be nearly identical to illustrations prepared by T. W. Johnson, 1955b, showing the "*D. anomalus*" mating strain of *D. monosporus* to be parasitized by *Rozella*

*achlyae* Shanor). ICELAND: Howard *et al.* (1970: figs. 18, 19); T. W. Johnson (1974b:23, figs. 153-155). INDIA: Dayal and Thakur Ji (1968c:36, figs. 35-42); R. C. Srivastava (1976: pl. 4, fig. B). JAPAN: S. Ito (1936:91, fig. 37.1); Nagai (*loc. cit.*). SOUTH AMERICA: Beneke and Rogers (1962:189, pl. 1, figs. 8, 9); Milanez (1970:30, figs. 12-15). UNITED STATES: Beneke (1948b:108, 119); R. L. Butler (1975: figs. 169-180); J. N. Couch (1926b:854, pls. 35-38; *loc. cit.*); T. W. Johnson (1950b:400); Milanez (1966:96, pl. 10, figs. a-e); Rossy-Valderrama (1955:38, pl. 6, figs. 1-8); W. A. Sherwood (1966b: figs. 1, 2, 8-25, 37); A. W. Ziegler (1948b:26, pl. 6, figs. 2-7).

RECORDED COLLECTIONS: -- AFRICA: Alabi (1971a, b; 1973); Fajola *et al.* (1978); Nolard-Tintigner (1974: fig. 2). AUSTRALIA: Crooks (1937:215, fig. 1 H-L). BRITISH ISLES: Apinis (1960); Barnes and Melville (1932); Cook and Forbes (1933); Forbes (1935a:232); Newton (1971); Park (1974); Sparrow (1936). CZECHOSLOVAKIA: Cejp (1931; 1933: pl. 2, fig. 4; 1959a:257, figs. 97-99; 1959b). DENMARK: A. Lund (1934:31, fig. 13a, b; 1978). EGYPT: El-Hissy *et al.* (1982). FRANCE: Volkonsky (1934). GERMANY: Höhnk (1956a); Leitgeb (*loc. cit.*); Richter (1937:254); Schlösser (1929); Zopf (1890:298). HONG KONG: Yung and Stenton (1964). INDIA: E. J. Butler and Bisby (1931); Chowdhery and Rai [1980:239, pl. 1, figs. 6-8 (?). The collection of *D. missouriensis* reported by these authors is referable to *D. pseudodictyon.*]; Khulbe and Verma (1983; Misra (1982b); Lacy (1955); Mekrani (1980); S. B. Saksena and Rajagopalan (1958:17, figs. 52-57)(?); G. C. Srivastava (1967b); G. C. Srivastava and R. C. Srivastava (1977b, e); Sydow *et al.* (1907). IRAQ: Al-Saadi *et al.* (1979); Muhsin (1977:23, Figs. A, B); Rattan *et al.* (1978:116, figs. 8, 9)(?); JAPAN: Hoshina *et al.* (1958); Indoh (1937:298, pl. 6, figs. 17-21)(?); S. Ito (1936:90, figs. 37.2-37.6)(?); Kobayasi and Ookubo (1952b:183, fig. 11; 1954: 562, fig. 3)(?); Nagai (1931:27, pl. 7, figs. 7-11); Ookubo (1954); Ookubo and Kobayasi (1955); Sawada (1912: pl. 9, figs. 12-16)(?); Shirai *et al.* (1927); Suzuki (1960f, 1961f). LATVIA: Apinis (1929a:232)(?). MIDDLE EUROPE: Migula (1903:72, pl. 2B, fig. 2). NEW ZEALAND: Karling (1966f). PEOPLE'S REPUBLIC OF CHINA: Shen and Siang (1948:196); Yu and Liang (1983). POLAND: Staniak (1971); Stpiczyńska (1962:111, fig. 11); Stpiczyńska-Tober (1965); Zaborowska (1965); Żebrowska (1976a). REPUBLIC OF CHINA: Chiou *et al.* (1975:17 pl. 2, fig. 28); Sawada (1919:53). RUMANIA: Toma (1969, 1970, 1971). SOUTH AMERICA: A. L. Rogers *et al.* (1970:102); Hutchison (1940:10, fig. 9)(?); deLyra and Milanez (1974:10, fig. 7); Upadhyay (1967). UNITED STATES: Beneke and Schmitt (1961); Bretsnyder (1943:14)(?); W. B. Cooke (1970a); W. B. Cooke and Bartsch (1959, 1960); Crane and Vermillion (1966); Fox and Wolf (1977a:101, figs. 1-3)(?); J. V. Harvey (1927c, d); Höhnk (1935a); G. C. Hughes (1959, 1962); T. W. Johnson (1956a); Kauffman (1915); Klich (1980); Klich and Tiffany (1985); V. D. Matthews (1935); Overman (1970: 30); Rossy-Valderrama (1956); Schmitt (1967); Schmitt and Beneke (1962); Scott (1960b); W. A. Sherwood (1969, 1971); Sorenson (1962: pl. 4, fig. E)(?); Sparrow (1952b); TeStrake (1958, 1959); Whiffen (1945); Wolf (1944:40); Wolf and Wolf (1941); A. W. Ziegler (1958b). USSR: Domashova (1971:190, fig. 2)(?); Dudka (1965, 1966); Dudka and Logvinenko (1968: fig. 1.4)(?); Ėrgashev and Kirgizbaeva (1978); Logvinenko (1970, 1971); Logvinenko and Meshcheryakova (1971); Meshcheryakova

(1970, 1974); Mil'ko (1965); Mil'ko and Zakharova (1976). YUGOSLAVIA: Ristanović (1970a, b; 1973).

SPECIMENS EXAMINED: -- AFRICA (12), AUSTRALIA (12), CANADA (1), CENTRAL AMERICA (12), OCEANIA (32), WEST INDIES and U. S. VIRGIN ISLANDS (24), SOUTH AMERICA (8), IRL. ICELAND (6), NORWAY (1), SWEDEN (2), TWJ. UNITED STATES (numerous), RLS, TWJ.

*Dictyuchus pseudodictyon* Coker and Braxton  
In, J. N. Couch, J. Elisha Mitchell Sci. Soc. 46:228. 1931  
(Figures 109, 110)

*Dictyuchus* sp. Coker and Braxton, J. Elisha Mitchell Sci. Soc. 42:144, pl. 15. 1926.

Monoecious. Mycelium at first limited and diffuse, then becoming dense and moderately extensive; hyphae moderately stout; abundantly branched near substratum, sparingly branched in periphery of colony. Sporangia fusiform or clavate, occasionally cylindrical; straight, occasionally curved or bent, rarely branched; renewed sympodially or in a cymose fashion; 70-603 x 10-44  $\mu$ m. Spores monomorphic; discharge and behavior dictyucoid, rarely achlyoid from secondary sporangia; secondary spore cysts 9-15  $\mu$ m in diameter. Gemmae cylindrical, fusiform, or obpyriform, rarely dolioform; terminal or intercalary, single or catenulate. Oogonia lateral, occasionally terminal; commonly clustered on the hyphae; spherical or obpyriform, occasionally subglobose, infrequently ovoid or obovate; rarely proliferating; (21-) 28-36 (-55)  $\mu$ m in diameter. Oogonial wall unpitted or pitted under the region of attachment of the antheridial cells; smooth on outer surface, sometimes faintly irregular on inner surface. Oogonial stalks  $1/2$  -12 times the diameter of the oogonium in length; curved, bent, usually slightly to conspicuously irregular, rarely straight; unbranched; once-branched, or forming a glomerulus. Oospores eccentric; spherical or broadly oval; single in an oogonium, and often nearly filling it; (19-) 26-32 (-36)  $\mu$ m in diameter; at germination forming a short, slender, unbranched germ hypha bearing a small, terminal, dictyucoid sporangium. Antheridial branches androgynous or monoclinal, occasionally to infrequently declinal; irregular or twisted, sparsely to profusely branched and umbratiform, but generally closely applied to and enveloping the oogonium; persisting or deliquescing in part. Antheridial cells simple; usually large, tubular and contorted or irregular; unbranched, branched, or merely lobed; persisting; laterally or apically appressed, but sometimes attached in a digitate fashion; fertilization tubes produced, but often not clearly visible.

In 1951, T. W. Johnson described a species of *Dictyuchus* (identified simply as 521) in which the most pronounced structural feature was a profusely branched, often umbratiform antheridial apparatus. These filaments, commonly so thickly enveloping the oogonia as to obscure them, were predominantly androgynous or monoclinal. In instances where the attendant antheridial filaments were partially deliquesced, the

oogonia appeared to be invested in a pseudoparenchymatous mesh, bringing at once to mind the "Hülapparat" described by Zopf (1893). Significantly, the later-formed oogonia of *Dictyuchus* 521 often were not associated with the profusely developed antheridial apparatus, but were accompanied by a more modestly developed male companion. Such oogonia were quite like those encountered in *D. pseudodictyon*. It was in *Dictyuchus* 521 also, that both false- and true-net sporangia were discovered, thus calling into question the value of the conventional separation of species on this character. Shortly after *Dictyuchus* 521 had been described, T. W. Johnson and collaborators (1951) identified it as a form of *D. pseudodictyon*, a decision which seemed to be amply justified in view of the somewhat transitory nature of the umbratiform antheridial branches.

Since the recovery of *Dictyuchus* 521, we have isolated many additional specimens obviously closely akin to it, but showing various degrees in the magnitude of expression of the antheridial branch complex. These individual specimens unquestionably link 521 to *D. pseudodictyon* with the former simply representing one extreme in a wide range of antheridial branch variants differing in abundance of these filaments and frequency of branching (Figs. 109 A, B, H; 110 A, F).

*Dictyuchus pseudodictyon* can be recognized by its predominantly monoclinal (Fig. 109 D) or androgynous (Fig. 109 B, F) antheridial branches, and the tendency of those filaments to envelop the oogonia. In some instances (Fig. 110 C) the antheridial apparatus is well-developed and abundantly branched, but is not directly applied to an oogonium.

The taxonomic relationship between *Dictyuchus pseudodictyon* and *D. carpophorus* remains obscure. See the discussion of the latter and excluded species.

Certain published accounts of *Dictyuchus* species require comment. The isolates identified by T. W. Johnson (1974b) as *D. carpophorus* have been reexamined, and we now are convinced they were representatives of *D. pseudodictyon*. Rajagopalan's (1963) specimen, and the *D. carpophorus* collected by Dayal and Thakur Ji (1968c), Morochkovs'kiĭ *et al.* (1967), and Szwanke (1938) are with reservation allied to *D. pseudodictyon*. Circumstantial evidence suggests that it was *D. pseudodictyon* which Sorokine (1889-90) reported as *D. magnusii*; one of the illustrations in his paper shows androgynous and monoclinal antheridial branches. A figure provided by Kobayashi and Ôkubo (1954: fig. 38) to illustrate their specimen of *D. monosporus* depicts an androgynous antheridial filament. This being so, we suspect that their plant was *D. pseudodictyon*. The sexually reproducing *Dictyuchus* sp. described by J. V. Harvey (1942) was unmistakably *D. pseudodictyon*.

CONFIRMED RECORDS: -- ICELAND: T. W. Johnson (1974b:23 *et seq.*, figs. 156-159). INDIA: Misra (1982a:121, figs. 5, 6). IRAQ: Muhsin (1977:19, figs. A, B); RUMANIA: Toma (1969:219, pls. 5, 8). SOUTH AMERICA: Beneke and Rogers (1962:189). UNITED STATES: Beneke (1948b:121); R. L. Butler (1975: figs. 185-188); Coker and Braxton (*loc. cit.*); J. V. Harvey (1942:36, pl. 8, figs. 8-11); T. W. Johnson

(1951:367, figs. 1-14); W. A. Sherwood (1966b:36); A. W. Ziegler (1952:13, pl. 1, figs. 11, 12; pl. 5, figs. 5-9; pl. 6, figs. 1-3).

RECORDED COLLECTIONS: -- BRITISH ISLES: Apinis (1964). INDIA: Dayal and Thakur Ji (1968c:34, figs. 29-34)(?); Misra (1982b). IRAQ: Rattan *et al.* (1980). POLAND: Szwanke (1938:14, pl. 5, figs. 3-7)(?). RUMANIA: Toma (1970, 1971). SOUTH AMERICA: Upadhyay (1967). UNITED STATES: Beneke and Schmitt (1961); J. N. Couch (1931); Galler-Rimm (1982); G. C. Hughes (1959, 1962); Klich (1980); Klich and Tiffany (1985); Poitras (1955); Rajagopalan (1963:121, fig. 2 I-L); A. W. Ziegler (1958b). USSR: Morochkovs'kiĭ *et al.* (1967: 125, fig. 109)(?).

SPECIMENS EXAMINED: -- AFRICA (1), AUSTRALIA (3), CENTRAL AMERICA (5), OCEANIA (5), SOUTH AMERICA (12), WEST INDIES (12), RLS. ICELAND (7), NORWAY (4), TWJ. UNITED STATES (37), TWJ, RLS.

### *Dictyuchus* sp.

Citations marked with an asterisk (\*) report the occurrence of unidentified *Dictyuchus* specimens on fish or fish eggs. References to Coker's *D. sterile* are included in the following listings as are unconfirmable reports of the collection of *D. carpophorus*.

AFRICA: El-Hissy (1974: pl. 1, fig. b); Kobayasi and Konno (1977); Nolard-Tintigner (1974\*: fig. 7). AUSTRALIA: Crooks (1937:215). BRITISH ISLES: R. A. Couch (1951: 101, pls. 17, 18. Multiple oospores; possibly a mixed culture.); Dick (1963, 1966); Dick and Newby (1961); Forbes (1935b); Hallett and Dick (1981); Murray (1885\*); O'Sullivan (1965); Perrott (1960); R. E. Roberts (1963); Willoughby (1962, 1974); Willoughby and Collins (1966). CENTRAL AMERICA: Liles (1969); Sörgel (1941). DENMARK: A. Lund (1934). EGYPT: El-Hissy *et al.* (1982). FRANCE: Vey (1976a\*: fig. 1; 1976b\*, 1977: figs. 1-3; on crayfish.). GERMANY: Bock (1956); Höhnk (1935a, 1956a, 1958); Minden (1916); Remy (1950); Richter (1937: 255). INDIA: Chaudhuri *et al.* (1947); Dayal and Tandon (1962, 1963); Dayal and Thakur Ji (1965, 1966), Khulbe and Verma (1983); Mekrani (1980); Mer *et al.* (1980); Mer and Khulbe (1984:201); Misra (1982b); Prabhuji and Srivastava (1977); Sati and Khulbe (1980); G. C. Srivastava (1976b); G. C. Srivastava and R. C. Srivastava (1977e\*); R. C. Srivastava (1976\*: pl. 6, fig. B); R. C. Srivastava and G. C. Srivastava (1978a\*); Thakur Ji and Dayal (1966). IRAQ: Muhsin (1977:27, figs. A-E); Rattan *et al.* (1978). JAPAN: S. Ito (1936:91); S. Ito and Nagai (1931); T. Ito (1942:127; 1944); Kobayasi and Konno (1969:730, fig. 4 F-H); Kobayasi *et al.* (1977); Nagai (1931:28, pl. 6, figs. 11-13); Okane (1978, 1981, 1986); Suzuki (1960b, c; 1961b, h; 1962b, 1981); Suzuki and Hatakeyama (1961); Suzuki and Nimura (1961b). LATVIA: Apinis (1929a). NEPAL: S. C. Singh (1968a:12, fig. 3). NETHERLANDS: Beverwijk (1948). OCEANIA: Kobayasi and Konno (1971b:381, fig. 4 A-C). PEOPLE'S REPUBLIC OF CHINA: Yu and Liang (1983). PHILIPPINES: Dogma (1975). POLAND: Szwanke (1938:13, pl. 5, figs. 1, 2). REPUBLIC OF CHINA: Chien (1981\*); Chiou *et al.* (1975: 169, pl. 2, fig. 27); Chung (1973); Liu and Volz (1977); Volz *et al.* (1974: fig. 1). SOUTH AMERICA: Karling (1984); Sörgel (*op. cit.*). SWITZERLAND: Tiesenhausen (1912:289 *et*

*sqq.* As described, unidentifiable as a *Dictyuchus*.). UNITED STATES: Beneke and Schmitt (1961. Stated that fungus represented a new species with oospores in the hyphae; no name, description, or illustrations.); Clausz (1970, 1974); Coker (1923:151, pl. 52; 1927); Coker and Braxton (1926); W. B. Cooke (1976a). W. B. Cooke and Matsuura (1969); Farr and Paterson (1974); Haenseler *et al.* (1923:44, pl. 2, figs. 7-9); J. V. Harvey (1925a, b; 1927b; 1930; 1942; 1952); Hidalgo-Quimio (1965); Höhnk (1935a); Humphrey (1893: pl. 14, fig. 16); T.W. Johnson (1950b); Klich (1980); Kuehn (1960); C. E. Miller (1965); Overman (1970: 30); Padgett (1978a); Padgett and Heitman (1981); Rose (1932: 50, pl. 5, fig. 40); Rudolfs and Trajkovich (1924); Scott (1960b); Slifkin (1964, 1967a); Sparrow (1965); W. N. Tiffney (1936\*: 23; 1939\*); Wagner-Merner (1980); M. W. Ward (1939); Weston (1919: pl. 23); A. W. Ziegler (1952). USSR: Florinskaya (1969\*: 116, fig. 11; 1971); Kirgizbaeva *et al.* (1975). WEST INDIES: Sörgel (*op. cit.*); Sparrow and Dogma (1973). YUGOSLAVIA: Ristanović (1973).

#### IMPERFECTLY KNOWN SPECIES OF *Dictyuchus*

*Dictyuchus variabilis* (Indoh) Chiou and Chang  
Bot. Bull. Acad. Sin. 17:45, pl. 4. 1976

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

Mycelium dense, depauperate; hyphae delicate, branched. Sporangia clavate to long-cylindrical; unbranched; renewed sympodially or in a cymose fashion; 200-500 x 20-30  $\mu\text{m}$ . Spores monomorphic; discharge and behavior dictyucoid, but in favorable conditions achlyoid from a few primary sporangia, rarely brevilegnoid. Gemmae rare; terminal or intercalary, single or catenulate. Oogonia lateral or terminal, spherical, rarely subspherical; 20-30  $\mu\text{m}$  in diameter. Oogonial wall unpitted(?); smooth. Oogonial stalks short or long; twisted, irregular; simple, branched, or forming a glomerulus. Oospores eccentric; spherical; single, and filling the oogonium; diameter unreported; at germination forming a slender, unbranched germ hypha bearing terminally a small, clavate sporangium. Antheridial branches androgynous; together with the antheridial cells enveloping and wrapping about the oogonium; slender, irregular; unbranched or branched?. (Adapted from Chiou and Chang *loc. cit.*)

*Dictyuchus variabilis* is based on Indoh's *Brevilegnia variabilis* which T.W. Johnson (1974a) suspected would prove to be a species of *Dictyuchus*. In light of the observations by Chiou and Chang (*loc. cit.*) that view may have been premature.

The androgynous antheridial branches of *Dictyuchus variabilis* are, as Chiou and Chang (*loc. cit.*) illustrate them, precisely like ones found (T. W. Johnson, 1974a) in some isolates of *Brevilegnia bispora*. That *D. variabilis* may produce achlyoid sporangia allies it to Indoh's species, and also to *Achlya pseudoachlyoides* (formerly in *Dictyuchus*) Chiou and Chang themselves saw the similarities between *D. variabilis* and the latter species. The paucity of brevilegnoid sporangia in the Taiwan fungus would seem to support the

removal of Indoh's species from *Brevilegnia* and an assignment to *Dictyuchus*. There is, to be sure, very little resemblance in the antheridial branch configuration among Indoh's species (Indoh, *loc. cit.*, fig. 2) and the specimens Chiou and Chang (*loc. cit.*, pl. 4, fig. 2) identify as *D. variabilis*.

As there are no longer any specimens of *Dictyuchus variabilis* available (Liu Chih-hui, communication) the apparent discrepancies between Indoh's species and the Taiwan watermold cannot be resolved. Detailed characterization of additional collections might establish the taxonomic status of both Indoh's fungus and the material from Taiwan.

## EXCLUDED TAXA

*Dictyuchus achlyoides* Coker and Alexander  
In, Coker, J. Elisha Mitchell Sci. Soc. 42:218, pl. 36. 1927

Transferred to the genus *Achlya*.

*Dictyuchus carpophorus* Zopf  
Beitr. Physiol. Morphol. Niederer Organismen 3:49 *et sqq.*, pls. 2, 3, 1893.

Nowhere in the literature is there a complete, concise description of *Dictyuchus carpophorus*. Zopf's account (*loc. cit.*) shows primarily his preoccupation with the manner in which the antheridial branches (and cells) of his fungus enveloped the oogonium (Zopf, *loc. cit.*, pl. 2, figs. 2-4, 7; see also our Figure 110 F of *D. pseudodictyon*), a structure he called the "Hüllapparat." Zopf evidently believed that the enveloping filaments of *D. carpophorus* were in a physiological sense not homologous to antheridial branches, and they did not serve a male function. Zopf saw in the "Hüllapparat" of *D. carpophorus* an homology with the fructifications of representatives of *Podosphaera*. The illustration he provided leave no question that he observed the sexual apparatus of a watermold. If the specimen had been properly isolated, it was a *Dictyuchus*.

Coker (1923:157) reckoned that *Dictyuchus carpophorus* was "...doubtfully distinct from *D. monosporus*." Later, J. N. Couch (1926b) was to confirm this view by reducing Zopf's species to synonymy with Leitgeb's. In 1951 and again in 1974(b), T. W. Johnson directed attention to the fact that Zopf (*loc. cit.*, pl. 2, fig. 1) had illustrated monoclinal as well as diclinal antheridial branches for his species, and thus *D. carpophorus* could not be equated with *D. monosporus*. Provisionally, Johnson reinstated *D. carpophorus*, illustrated specimens of it from Iceland, yet understood the species to have a close alliance with *D. pseudodictyon*. At the time, the limits of *D. pseudodictyon* were in question (T. W. Johnson, 1974b) because of an earlier account (T. W. Johnson, 1951) of an isolate (521) that was equated with *D. pseudodictyon* (T.W. Johnson *et al.*, 1951).

We have examined numerous isolates of *Dictyuchus* with well-developed, abundantly branched antheridial filaments, and have attempted to evaluate them in conjunction with Zopf's account of *D. carpophorus*. Although (1) some aspects of *D.*

*carpophorus* -- as Zopf illustrated it -- were given in recognizable detail, and (2) the "species" closely resembles *D. pseudodictyon*, we believe that Zopf's taxon cannot be retained. Zopf called attention to the presence of short, somewhat irregular and branched or lobed lateral extensions from the hyphae of *D. carpophorus*. These short filaments, as illustrated (Zopf, *loc. cit.*, pl. 2, fig. 1), recall a like condition in *Saprolegnia glomerata* (Fig. 96 I). Such hyphae have not appeared in any of our cultures of *Dictyuchus* species. In our analysis of *D. carpophorus*, we are troubled also by the very irregular, lobed and branched, seemingly abnormal sporangium-like elements reported by Zopf (*loc. cit.*, pl. 3, figs. 16, 17). No such elements occur in any of our dictyucoid water molds save very rarely in rather foul, gross cultures prior to isolation. Even from Zopf's very detailed account of his species (and the clear accompanying illustrations), no measurements are given such that the ranges of size of oogonia and oospores can be determined. Moreover, the precise origin of most of the antheridial branches depicted by Zopf is not shown. In sum, *D. carpophorus* is not as precisely defined and circumscribed as the original account of it would at first suggest. While it is altogether likely that *D. carpophorus* Zopf is what would now be recognized as *D. pseudodictyon*, we have no convincing proof for this assumption. Nothing would be contributed to an understanding of speciation in *Dictyuchus* by retaining Zopf's species and attempting to accommodate it into some taxonomic scheme.

Certain reports of *Dictyuchus carpophorus* and *D. monosporus* deserve comment. Szwanké's (1938:14, pl. 5, figs. 3-7) *D. monosporus* had diclinous, androgynous, and monoclinal antheridial filaments, and thus could not have been that species. At best guess he had collected *D. pseudodictyon*. The same may be said for the report of *D. carpophorus* by Morochkovs'kiĭ *et al.* (1967:125, fig. 109), though we are much less certain on this point. Dayal and Thakur Ji (1968c:34, figs. 29-34) recovered a *Dictyuchus* - they identified it as Zopf's species - with diclinous antheridial branches. Their account, too, recalls *D. pseudodictyon*, as does that by Rattan *et al.* (1978:114, figs. 6, 7). The Iceland specimens of *D. carpophorus* studied by T.W. Johnson (1974b:23, figs. 156-159) were variants of *D. pseudodictyon* with somewhat sparser antheridial branches than is usual in this species. Padgett and Seymour (1974: fig. 6) illustrate sporangia of *D. carpophorus* we now know their fungus to have been *D. pseudodictyon*. Kono's (1984:89, fig. 2 F-T) collection of *D. carpophorus*; from the Republic of China (Taiwan) may be referable to the Coker and Braxton species as well.

*Dictyuchus clavatus* de Bary  
Bot. Zeitung (Berlin) 46:649, pl. 9, fig. 3. 1888

*Dictyuchus clavatus* was first described by Büsgen (1882:261, pl. 12, figs. 1-8) but with de Bary given as the author of the species. It is *Thraustotheca clavata*. Sawada's report (1912: pl. 10, figs. 15-22) of *D. clavatus*, was later corrected (Sawada, 1919) as a record of *T. clavata*.

*Dictyuchus lucknowensis* Rai and Misra

The rather poor illustrations suggest that this was a species of *Brevilegnia*, and its achlyoid sporangia predict for it a position with *B. bispora*. Misra (1982b) reported collecting this species in India.

*Dictyuchus magnusii* Lindstedt  
Synopsis der Saprolegnieen..., p. 18, pl. 1. 1872

Lindstedt's species is excluded on the grounds that it is a *nomen ambiguum*. Two features of *Dictyuchus magnusii* remain in dispute, namely, whether it (1) was monoecious or dioecious and (2) had centric or eccentric oospores.

According to Lindstedt (*loc. cit.*, p. 16 *Dictyuchus magnusii* could be considered "trioecious", because there were separate hyphae bearing, respectively, sporangia, oogonia, and antheridial branches. We find nowhere in Lindstedt's paper a statement proving that two member cultures were necessary for sex cell formation. Lindstedt's (1872:59, 61) own designation of *Achlya prolifera* as a dioecious species, and *A. racemosa* (among others) as a monoecious species says much about his concept of sexuality in *D. magnusii*. We are troubled by Lindstedt's applications of these terms since they suggest to us that he equated the conditions "dioecious" and "diclinous" - which, of course, is incorrect. Accounts of *D. magnusii* subsequent to the original description refer to the antheridial filaments -- if they are mentioned at all -- as diclinous (Humphrey, 1893; A. Lund, 1934) or even androgynous and monoclinous (Sorokine, 1899-90:142, pl. 12, figs. 174-179). We submit that Lindstedt did not in fact know precisely what sexual expression existed in his material since he seems not to have made isolations.

If, as Coker (1923) surmised, *Dictyuchus magnusii* differed insignificantly from *D. monosporus*, then Lindstedt's species must have had eccentric oospores. The figures of oospores that Lindstedt provided might easily be interpreted as depicting centric oospores. Humphrey (1893:132, pl. 20, figs. 112-114) so described them in a water mold he identified as *D. magnusii*, and Pieters (unpublished notes, cited in Coker, 1923) did likewise. It appears that A. Lund (1934) was uncertain of the oospore type in the Danish material he identified as Lindstedt's species. Both Fischer (1892:363) and Minden (1912:568) described the oospores of *D. magnusii* as centric. If it is true that *D. magnusii* had centric oospores, then it is this character that would give it validity and separate it from *D. monosporus* and all other species in the genus, not its sexual proclivities.

There are additional reports of *Dictyuchus magnusii* that we are unable to relate either to Lindstedt's species or to *D. monosporus*. These accounts are by El-Hissy (1974: pl. 1, figs. c-e), El-Hissy *et al.* (1982), J. V. Harvey (1930), Höhnk (1935a), A. Lund (1978), Migula (1903:72), Naumov (1954:64), Rattan *et al.* (1980), Sawada (1912:52, pl. 7, fig. 8; lists *D. magnusii* as a synonym of *Achlya prolifera* but this disposition of Lindstedt's species is not followed in his 1919 publication), and Sorokine (1899-90:142, pl. 12, figs. 174-179).

*Dictyuchus missouriensis* var. *moruzzi* Toma  
Rev. Roumaine Biol., Sér. Bot. 15:253, pls. 4, 6. 1970

This is a species of *Brevilegnia*, and is synonymous with *B. minutandra*.

*Dictyuchus polysporus* Lindstedt  
Synopsis der Saprolegnieen . . . , p. 19, pls. 2, 3. 1872

Apinis (1930a:224, pl. 3) placed Lindstedt's species in *Protoachlya*; we so treat it here. It was A. Fischer's (1892:364) view that *Dictyuchus polysporus* was based on a mixed collection of a *Dictyuchus* and a *Saprolegnia*, and Coker (1923:157) was not "...convinced of its validity." Migula's report (1903:72) of Lindstedt's species cannot now be evaluated.

*Dictyuchus pseudoachlyoides* Beneke  
J. Elisha Mitchell Sci. Soc. 64:263, pl. 30, 1948

Transferred to *Achlya*.

*Dictyuchus sterile* Coker  
Saprolegniaceae, p. 151, pl. 52. 1923

According to Coker (*loc. cit.*, p. 152) plants of this species maintained sexual sterility in cultures for a decade on various media. He thought the taxon might represent one member of a dioecious watermold, but was unable to demonstrate compatibility in various pairings in two-member cultures. Coker was impressed by the deciduous nature of the sporangia in *Dictyuchus sterile*, but this is manifested commonly in the dioecious *D. monosporus* as well.

There is, of course, no way to be sure that Coker's watermolds were strictly (and permanently) asexual nor can they be alleged to be mating strains of *D. monosporus* based on available evidence from the literature. The name *sterile* is thus ambiguous in its application, and for this reason should be excluded. As early as 1934, A. Lund stated that in view of Couch's work on heterothallism in *Dictyuchus*, it was not possible to retain *D. sterile* as a synonym of *D. monosporus*.

We are merging the published records of the collection of *Dictyuchus sterile* with those of unidentified species of the genus. A sexually sterile plant identified as Coker's species was used in the excellent ultrastructural studies carried out by Heath and Greenwood (1970 a-c), Heath, Greenwood, and Griffiths (1970), and Heath, Gay, and Greenwood (1971).

*Dictyuchus* sp. Coker and Braxton  
J. Elisha Mitchell Sci. Soc. 42:144, pl. 15. 1926

This “homothallic strain” was later identified by Coker and Braxton as *Dictyuchus pseudodictyon* (J. N. Couch, 1931).

*Dictyuchus* sp. Kobayasi and Konno  
J. Jap. Bot. 46:13, fig. 4 K-N. 1971

If, as Kobayasi and Konno illustrated them, the oospores of this unnamed watermold were subcentric, it cannot be retained in *Dictyuchus*. One figure in their paper (Kobayasi and Konno, *loc. cit.*, fig. N) shows a hyphal segment strongly reminiscent of a filament infected by *Dictyomorpha dioica* (Mullins, 1961) or perhaps by Cornu’s *Woronina polycistis*. If this were true, it would account for the one characteristic singled out by Kobayasi and Konno as the most distinctive one for the unnamed species, namely, that of its irregular sporangia.

*Dictyuchus* sp. Scott  
Virginia J. Sci. (N. S.) 11:21. 1960

Scott had but one collection (in Haiti) of the fungus identified as *Dictyuchus* sp. The irregularly roughened oogonia and the spore release behavior of some sporangia in that watermold suggest to us *Brevilegnia*, not *Dictyuchus*. To identify Scott’s unnamed isolate as *B. diclina* would seem plausible.

*Dictyuchus* 521 Johnson  
Mycologia 43:367, figs. 1-14. 1951

Subsequently identified (T. W. Johnson *et al.*, 1951) as a specimen of *Dictyuchus pseudodictyon*.