

CHAPTER 43

THRAUSTOTHECA Humphrey Trans. Amer. Phil. Soc. (N. S.) 17:131. 1893.

Monoecious. Sporangia short, broad, clavate, but very occasionally elongate or fusiform; renewed sympodially. Spores monomorphic; primary ones encysting in the sporangium and being released on the deliquescence of the sporangial wall; laterally biflagellate, reniform planonts released from the cysts on germination. Gemmae present. Oogonia lateral, infrequently terminal, spherical or obpyriform. Oogonial wall pitted; smooth. Oogonial stalks short, stout. Oospores eccentric; one to several in an oogonium. Antheridial branches declinuous; abundant; branched and often very irregular; appearing in some cultures before the oogonial initials are formed. Antheridial cells tubular or clavate; laterally appressed.

Type species: *Thraustotheca clavata* (de Bary) Humphrey, Trans. Amer. Phil. Soc. (N. S.) 17:131. 1893.

Humphrey's genus was based on *Dictyuchus clavatus*, a species which Büsgen (1882:261, pl. 12, figs. 1-8) described and used in his study on sporangium development, but attributed to de Bary under the name *Dictyuchus clavatus* de Bary *sp. nov.* Three additional species have been admitted to the genus -- *Thraustotheca achlyoides* (Coker and Couch, 1923), *T. irregularis* (M. W. Ward, 1939), and *T. primoachlya* (Coker and Couch, 1924) -- of which the first was removed to *Calyptralegnia* (Coker, 1927). Inasmuch as both *T. irregularis* and *T. primoachlya* produce primary sporangia that are achlyoid in their discharge pattern, we are accommodating these species in *Achlya*, and leaving *Thraustotheca* as a monotypic genus. Were one inclined to do so, *A. dubia*, with its thraustothecoid sporangia, might be assigned to *Thraustotheca*, see discussion of that species.

On the basis of data from his extensive physiological study on the influence of pH on watermold growth and reproduction Barbier (1969) concluded that *Thraustotheca* (and perhaps also *Dictyuchus*) should be suppressed. Cejp (1959a), in fact, reduced *Thraustotheca* to synonymous status with *Dictyuchus* Leitgeb, *pro parte*. A brief historical account of *Thraustotheca* appears in a 1952(a) publication by Höhnk.

Thraustotheca clavata (de Bary) Humphrey
Trans. Amer. Phil. Soc. (N. S.) 17:131. 1893.
(Figure 105)

Dictyuchus clavatus de Bary, Bot. Zeitung (Berlin) 46:649, pl. 9, fig. 3. 1888.
(Also in Büsgen, Jahrb. Wiss. Bot. 13:261, pl. 12, figs. 1-8. 1882)

Monoecious. Mycelium extensive, densest near periphery of colony; hyphae stout, much branched distally, and secondary branches often twisted or curled and

irregular. Sporangia generally obpyriform to broadly clavate, sometimes short-fusiform to cylindrical; renewed sympodially or in a cymose manner; 53-421 × 30-106 μm. Spores monomorphic; released passively in encysted stage upon disintegration of sporangial wall, infrequently germinating in an aplanoid fashion; 10-13 μm in diameter. Gemmae usually sparse; small, obpyriform to nearly spherical; terminal or intercalary, single or catenulate. Oogonia lateral, infrequently terminal, rarely sessile; spherical or obpyriform; immature ones occasionally or only infrequently proliferating; (25-) 40-60 (-93) μm in diameter. Oogonial wall pitted under region of attachment of antheridial cells, occasionally faintly pitted elsewhere as well; smooth. Oogonial stalks ($1/4$ -) 1-2 (- $4\frac{1}{2}$) times the diameter of the oogonium, in length; stout; straight or curved, sometimes slightly irregular; unbranched. Oospores eccentric; spherical; (1-) 4-8 (-22) per oogonium, and usually not filling it; (16-) 18-24 (-27) μm in diameter; at germination forming a short, unbranched germ hypha bearing terminally a small, short-clavate to obpyriform sporangium, or forming a new mycelium directly. Antheridial branches declinous; slender or moderately stout; usually sparingly branched, but sometimes profusely branched and gnarled, twisted, and irregular; occasionally extensively developed but not attached to oogonia; persisting. Antheridial cells simple, rarely compound; tubular or slightly clavate, often long, slender, clasping the oogonium, and lobed or branched; persisting; laterally appressed; fertilization tubes often visible, persisting or not.

Thraustotheca clavata is a very distinctive species, recognizable at once by its obpyriform to clavate sporangia (Fig. 105 F), and its strictly declinous, usually sparingly (but sometimes abundantly) branched antheridial filaments (Fig. 105 E). Deliquescence of the sporangium wall is generally as Coker (1923) described the process. The wall begins to disintegrate near the apex of the sporangium or at some point laterally. Dissolution continues until only a small basal portion of the wall remains; subsequently, those remnants disappear as well. In contrast to certain *Brevilegnia* species, which also have a similar pattern of spore release, the sporangia of *T. clavata* rarely disarticulate from their subtending hyphae.

Thraustotheca clavata is widely distributed geographically, but it is seldom abundant. We have collected it several times in intermittently wet alluvial soils, but never consistently even at sites which previously had yielded the species.

A number of investigators have used *Thraustotheca clavata* in various nontaxonomic studies. Prominent among these are the papers by Heath (1974a; ultrastructure), Liles (1969; factors affecting sporangium development and sporogenesis), R. K. Saksena and Bhargava (1946; cytology), Schrader (1938; nuclear behavior), Shanor (1937; cytology, developmental morphology), Sorenson (1964; nutritional study), and Whiffen (1945; physiology). Weston's (1918) account of developmental morphology in *T. clavata* is a classic of detail and accuracy in observations.

We have collected from two sites on the island of Oahu, Hawaii, a thraustothecoid watermold having some greatly expanded oogonia and lateral,

irregular swellings, (Fig. 106), The enlarged oogonia, producing oospores consistent in size and structure with *Achlya diffusa*, have a noticeably irregular, unpitted wall (Fig. 106 B). The lateral swellings, also having a thin wall that is irregular on the inner surface (Fig. 106 A), usually are only sparsely provided with cytoplasm, and only infrequently contain an oospore (Fig. 106 C). As in *T. clavata*, the antheridial branches in the fungus are declinous (Fig. 107 A).

The presence of hyphal swellings in *Achlya diffusa* and its morphological similarity to *Thraustotheca clavata* suggested to us the intriguing possibility that the Oahu isolates might be natural hybrids between these two species. To test this hypothesis, we made experimental crosses between *A. diffusa* and *T. clavata* using isolates from the same localities where the putative hybrid was found. In addition, crosses also were made among isolates of *Achlya irregularis* from Amazonas and isolates of *A. diffusa* from that locality and from Oahu.

The experimental crosses were made in the following manner in sterile, glass Petri plates (100 x 20 mm). Autoclaved soil was mixed with sterile water, put into a Petri plate, and the plate slanted to provide a slope of soil (W. A. Sherwood, 1966b). Young colonies on hempseed were positioned about 3 cm apart on the surface of the sloped soil; after 3-4 days, the mycelia from the two colonies had grown into contact with one another. The plates were left undisturbed, at room temperature, for several weeks until the soil was dry. With sterilized scissors, a strip of mycelium between the two colonies was severed from the remainder of those colonies. This strip was left intact on the soil, and the other portions of the colonies (including the hempseeds) were removed and discarded. The strip of mycelium remaining on the soil surface in the Petri plate consisted of intermingled hyphae from both test colonies and, presumably, any sexual unions between the test species. The soil was flooded, and again baited, this time with the hempseed halves being placed directly on the strip of mycelium itself. When mycelium appeared on the baits these were transferred to a Petri plate containing fresh, sterile distilled water. These cultures then were examined daily for evidence of spore discharge and hyphal swellings.

From two separate crossing experiments between *Achlya diffusa* and *Thraustotheca clavata* two isolates identical to the putative "natural" hybrids (Oahu) were obtained. The remaining crosses yielded both *A. diffusa* and *T. clavata*, or only one or the other of these two species. Approximately 10% of the crossings did not yield any water molds. In crosses between *A. diffusa* and *A. irregularis* only the former was recovered.

The results of these preliminary crossing experiments provide circumstantial evidence for hybridization between *Achlya diffusa* and *Thraustotheca clavata*. The progeny from these crosses, however, gradually lost -- through subculturing over a nine-month period -- the ability to form hyphal swellings. The Oahu isolates, however, have continued to produce swellings after three years in culture, but these cells become successively fewer following each transfer. Because nothing is known of the genetics of these isolates and the putative hybrids, we are unable to identify the Oahu specimens precisely, but believe it is premature to describe them formally.

The following reports of *Thraustotheca clavata* are likely based on misidentifications, but cannot in any case be confirmed as this species: Florinskaya (1969:116, fig. 12), Moruzi and Toma (1969; probably *Brevilegnia declina*), Sawada (1912:73, pl. 10, figs. 15-22; 1919:54), Shipman [1977: fig. 16 (centric oospores); 1979].

CONFIRMED RECORDS: -- AFRICA: Alabi (1967:81, pl. 10, figs. d, e; 1972: fig. 1C). BRITISH ISLES: O'Sullivan (1965: figs. I-7--I-9-12); CZECHOSLOVAKIA: Cejp (1959a:277, fig. 107). GERMANY: Höhnk (1952a:63, pl. 8); Richter (1937:255, fig. 13); Schrader (1938:128, 131, 139, figs. 1-58). ICELAND: T. W. Johnson (1974b:25, figs. 163-166). INDIA: Chaudhuri and Lotus (1936:330); Chaudhuri *et al.* (1947:20, fig. 4); Khulbe (1977:25, pl. 3, figs. 1-6; pl. 11, figs. 1-3; 1980c:80; 1987:57, pl. 1, figs. 20, 21); Mer and Khulbe (1984:205, pl. 2, fig. 5). JAPAN: S. Ito (1936:88, fig. 36); Kobayasi and Konno (1971a:15, fig. 5 H-J); Konno (1984:90, fig. 2J-L); Nagai (1933:136, fig. 1). MIDDLE EUROPE: Migula (1903:73 pl. 2B, 5H-J). OCEANIA: Kobayasi and Konno (1971b:381, fig. 4D-G). PEOPLE'S REPUBLIC OF CHINA: Ou (1940:433). REPUBLIC OF CHINA: Chiou *et al.* (1975:169, pl. 2, figs. 24-26). UNITED STATES: Beneke (1948b:125); R. L. Butler (1975: figs. 157-160); Coker (1923:148, pl. 51); Coker and Couch (1924: p. 38, figs. 1-3); Coker and Hyman (1912:88 *et seq.*, pl. 63); Milanez (1966:113, pl. 14); Shanor (1937: p1s. 12, 13); F. T. Wolf (1944:39, pl. 4, fig. 30); A. W. Ziegler (1948b:26, pl. 5, figs. 9, 10; 1952:15, pl. 1, figs. 2, 3; pl. 6, fig. 4). USSR: Shkorbatov (1927:81).

RECORDED COLLECTIONS: -- AFRICA: Alabi (1971a, b; 1973); El-Hissy (1974). AUSTRALIA: Cookson (1937). BRITISH ISLES: Apinis (1964); Barnes and Melville (1932); Cook and Morgan (1934); Dick (1962, 1963, 1966); Dick and Newby (1961); Hunter (1975); J. R. Raper (1950b); Sparrow (1936, 1957); Willoughby (1965); Willoughby and Collins (1966). DENMARK: A. Lund (1978). GERMANY: Bock (1956); Höhnk (1956a, 1958); Remy 1950). INDIA: Khulbe (1979, 1981, 1983c); Khulbe and Bhargava (1977, 1983); Mer *et al.* (1980); Sati and Khulbe (1980). JAPAN: Suzuki (1960f, 1961f, 1962b). LATVIA: Apinis (1929a). NEW ZEALAND: Karling (1966f). OKINAWA: Ookubo and Kobayasi (1955). RUMANIA: Toma (1971). TOBAGO AND TRINIDAD: Karling (1987). UNITED STATES: Coker (1927); Coker and Braxton (1926); W. B. Cooke (1969); J. N. Couch (1927); J. V. Harvey (1925b, 1930); G. C. Hughes (1959, 1962); V. D. Matthews (1927, 1935); Poitras (1955); Scott (1960b); Slifkin (1964); Sparrow (1933, 1952b); Whiffen (1945); A. W. Ziegler (1958b). USSR: Dudka (1965); Florinskaya (1971); Logvinenko and Meschcheryakova (1971); Mil'ko and Belyakova (1968). WEST INDIES: Coker (1927); J. N. Couch (1927).

SPECIMENS EXAMINED: -- CENTRAL AMERICA (8), OCEANIA (7), SOUTH AMERICA (4), RLS. ICELAND (5), UNITED STATES (39), TWJ, RLS. WEST INDIES (8), RLS.

Thraustotheca sp.

AUSTRALIA: Karling (1988). BRITISH ISLES: Hallett and Dick (1981); O'Sullivan (1965); Willoughby *et al.* (1984: pl. 1, figs. 5-8). CENTRAL AMERICA: Liles

(1969); Sörgel (1941). DENMARK: A. Lund (1934, 1978). GERMANY: Höhnk (1958). JAPAN: Suzuki and Hatakeyama (1960). PHILIPPINES: Dogma (1975). SOUTH AMERICA: Beneke and Rogers (1962: pl. 1, figs. 10-12); Milanez (1970: 33); A. L. Rogers *et al.* (1970); Sörgel (1941). UNITED STATES: Overman (1970: 38; identified as *T. primoachlya*, from asexual stage only.)(?); Sorenson (1962). WEST INDIES: Sörgel (1941); Sparrow and Dogma (1973).

EXCLUDED TAXA

Thraustotheca achlyoides Coker and Couch
J. Elisha Mitchell Sci. Soc. 39:112, pl. 8. 1923.

Transferred by Coker and Couch (1927) to *Calyptralegnia*.

Thraustotheca irregularis Coker and Ward
In, M. W. Ward, J. Elisha Mitchell Sci. Soc. 55:348, pl. 31. 1939.

Transferred to *Achlya*.

Thraustotheca primoachlya Coker and Couch,
J. Elisha Mitchell Sci. Soc. 40:198, pls. 39, 40. 1924

Transferred to *Achlya*.

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

Transferred to *Brevilegnia* (Coker, 1927).

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

Transferred to *Brevilegnia* (Coker, 1927).

Thraustotheca sp. Harvey
Proc. Oklahoma Acad. Sci. 7:136. 1927 (1928).

In a paper published in the same year as the description of *Thraustotheca* sp. appeared, J. V. Harvey (1927c:135) stated that this was a new species. No further report of the taxon appeared subsequent to 1927, and it may be assumed that Harvey reconsidered his decision. In any event, the name *Thraustotheca* sp. again appeared in 1944, when F. T. Wolf remarked that the fungus so identified was *Brevilegnia diclina*. We are unable to determine whether Harvey was in fact aware that in the same year (1927)

in which he published the description of *Thraustotheca* sp. Coker (1927) established the genus *Brevilegnia*.

As there are no illustrations of Harvey's *Thraustotheca* sp., it is impossible to place his fungus with certainty in *Brevilegnia*. The description of the sporangia recalls the characteristics of those in *B. diclina*, as does the roughened oogonial wall. In *B. diclina*, androgynous (monoclinous *sensu* Harvey) antheridial branches are rare. Harvey described *Thraustotheca* sp. as having both diclinous and androgynous filaments, and if the latter were common (J. V. Harvey, 1927d, does not so state), then an affinity with *B. diclina* is less certain.