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ASCAL STRUCTURE, ASCOCARP ONTOGENY, AND A NATURAL CLASSIFICATION OF THE THELEBOLACEAE*

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(With Plates 16–19)

Many of the genera placed in the Pseudoascobolaceae by Boudier do not show true relationships and were based on the number of asci and ascospores, and other superficial features. Qualitative microscopic and microchemical characters of the asci and ascospores, combined with characters of ascocarp development, cultural features, and cytological aspects will provide a more natural classification of this group. The genera of the Thelebolaceae are discussed.

Thelebolus stercoreus Tode (*1790*) appears to be the first record of a hyaline-spored coprophilous discomycete. Strangely, however, *Thelebolus* Tode ex Fr., selected later as the type of the family Thelebolaceae, (Eckblad, *1968*) was considered by earlier mycologists to belong in the Gasteromycetes (Persoon, *1801*; Fries, *1822*). Essentially all of the coprophilous discomycetes were placed in the genus *Ascobolus*, Pers. ex Fr. by these authors, with a few remaining in *Peziza* Dill. ex St-Amans. Although the limits of *Ascobolus* were extended dramatically with the addition of many species by several authors, it was Fuckel (*1870*) who first considered *Thelebolus* an ascomycete, and eventually with the work of Heimerl (*1889*) it came to reside among the discomycetes.

Boudier's (*1869*) monumental work, "Mémoire sur les Ascobolés", laid the foundation for most of the subsequent studies of coprophilous discomycetes. He characterized the Ascobolei mainly by their relatively broad asci which protrude above the general level of the hymenium as they ripen. The spores commonly lie in two or three irregular rows in the ascus instead of in a single vertical row as in other discomycetes. He divided the Ascobolei into the "Ascobolei genuini" with pigmented ascospores and the "Ascobolei spurii" with hyaline ascospores. Boudier placed *Angelina* Fr., *Ascobolus*, and *Saccobolus* Boud. in the "Ascobolei genuini" and *Ascophanus* Boud., *Thecotheus* Boud., and *Ryparobius* Boud. in the "Ascobolei spurii." I will focus the remainder of this paper on a discussion of the latter group.

Until recent years the "Ascobolei spurii" of Boudier (*1869*) persisted more or less

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as a natural unit, although going under other names, i.e. Hyalosporae, Saccardo (*1884*); Hyalosporeae, Heimerl (*1889*); Groupe Pseudoascobolés, Boudier (*1885*); Theleboleen, Brefeld (*1891*); Pseudoascoboleae, Rehm (*1895*); and Tribu Pseudoascobolés, Boudier (*1907*). Unaware of Boudier's work, Fuckel (*1870*) placed all of the Ascobolei known to him in the "Bulgariacei" and Karsten (*1871*) restricted *Ascobolus* to the pigmented forms while placing the hyaline-spored species either in *Peziza* (8-spored) or *Pezizula* Karst (multi-spored). As noted by Rifai (*1968*) and Kimbrough (*1970*), a number of workers continue to treat the Ascobolaceae in a broad sense to include both hyaline and pigmented spored taxa. I choose, however, to follow Eckblad (*1968*), and Rifai (*1968*) in recognizing the Thelebolaceae as a distinct family.

Boudier's (*1869*) "Ascobolei spurii" was divided first on spores per ascus, *Ascophanus* with 8 to 16, and *Ryparobius* and *Thecotheus* both multispored. *Thecotheus* was distinguished from *Ryparobius* by much larger thick-walled spores, more cylindric asci, more elongate paraphyses, and larger apothecia. A number of other genera subsequently have been proposed for hyaline-spored species (Table I). Renny (*1874*) proposed *Ascobolus* sect. *Ascozonus* for multispored species with asci that dehisce by a longitudinal apical split. Hansen (*1876*) elevated *Ascozonus* to generic rank. Saccardo (*1884*) proposed *Lasiobolus* for 8-spored species with setose apothecia;

TABLE I. GENERA OF HYALINE-SPORED COPROPHILOUS PEZIZALES

PERSOON, 1801	BOUDIER, 1907	SEAVER, 1928	ECKBLAD, 1968
Hymenothecii	Pseudoascobolei	Pezizaceae	Thelebolaceae
Ascobolus	*Boudierella*		*Ascozonus*
Peziza	*Cubonia*	Sphaerosporae	*Caccobius*
Gasteromycetes	*Thecotheus*	*Cubonia*	*Coprobolus*
Thelebolus	*Ascophanus*		*Coprotus*
	Lasiobolus	Humarieae	*Lasiobolus*
FRIES, 1822	*Ryparobius*	*Ascophanus*	*Thecotheus*
	Ascozonus	*Humarina*	*Thelebolus*
Elvellaceae	*Thelebolus*	*Streptotheca*	*Trichobolus*
Cupulati	*Aphanoascus*	*Ryparobius*	*Leporina*
Ascobolus	Pyronemacées	*Thecotheus*	
Peziza	*Zukalina*		Pyronemaceae
Gasteromycetes	Humariacées	Lachneae	*Cheilymenia*
Thelebolus	*Ciliaria*	*Lasiobolus*	*Coprobia*
BOUDIER, 1869	*Cheilymenia*	*Patella*	*Fimaria*
	Humaria		*Iodophanus*
Ascobolei spurii	*Coprobia*	Pezizeae	*Octospora*
Ascophanus		*Peziza*	
Ryparobius	Pezizacées		Pezizaceae
Thecotheus	*Aleuria*		*Peziza*

in *1889*, *Cubonia*, for hyaline, spherical-spored species; and in *1895*, *Boudierella*, for species with spherical, ornamented spores. Heimerl (*1889*) placed *Thelebolus* near *Ryparobius* and *Ascozonus* in the Hyalosporeae, and Boudier (*1907*) added *Aphanoascus* Zukal, but the recognition of this genus is currently in question (van Brummelen, *1967*; Eckblad, *1968*). Heim and Le Gal (*1936*) originally placed *Selenaspora* in the Pseudoascobolaceae, but later Le Gal (*1953*) had some doubt about its taxonomic position. The traditional arrangement of genera of the Pseudoascoboleae is similar to that in the following key.

A CLASSICAL KEY TO THE GENERA OF PSEUDOASCOBOLEAE

1. Apothecia setose . . . . . *Lasiobolus*
1. Apothecia without setae 2
   2. Asci 8-spored. . . . . *Ascophanus*
   2. Asci with more than 8 spores 3
3. Apothecium containing one large ascus . . . . . *Thelebolus*
3. Apothecium with several asci. 4
   4. Asci opening by a vertical slit as far as an annular thickening . . . *Ascozonus*
   4. Asci with a normal operculum. 5
5. Paraphyses abundant, asci elongate . . . . . *Thecotheus*
5. Paraphyses scanty, asci short . . . . . *Rhyparobius*

During a study of the structure and development of *Thelebolus zukalii* Heimerl (Kimbrough, *1966a*), it became apparent that this species differed significantly from the type, *T. stercoreus* Tode ex. Fr. In an attempt to determine the taxonomic position of *T. zukalii*, observations were made on a number of species of other genera of Pseudoascoboleae (Kimbrough, *1966b*). It was concluded that these genera did not show true relationships and that taxa previously ascribed to the Pseudoascoboleae should be founded on qualitative microscopic and microchemical characters, especially those of the asci and ascospores, rather than on quantitative and superficial features such as the number of asci and ascospores. Spore and ascal characteristics combined with those of ascocarp development, cultural features, and cytological aspects will provide, I feel, a more natural classification of this group.

The genus *Thelebolus*, for example, has a very distinct ascus. It is obvious, even when mounted in water, that the ascus of *T. stercoreus* has a peculiar structure. After screening a number of stains (Kimbrough, *1966b*) it was found that the ascal wall layers could be differentially stained, the outer wall with Congo red (Fig. 3), the inner wall with acid fuchsin in lactic acid (Fig. 1). The prominent ring in the *Thelebolus* ascus is part of the outer layer. The outer layer does extend beyond the ring, and at spore liberation the thin single layered apical portion splits irregularly. The ascus of *T. zukalii*, although superficially similar, has a quite different wall structure. The outer layer extends completely around the dome of the large ascus and there is a conspicuous absence of a ring. Both inner and outer wall layers become abruptly thinner near the ascus apex (Fig. 14). Although both develop angiocarpically, other differences between these species are obvious, *T. stercoreus* with small, thick-walled,

eguttulate spores, glabrous, more pigmented ascocarp, and more submerged growing habit; and *T. zukalii* with larger, thin-walled ascospores with deBary bubbles (Fig. 13), setose apothecia (Fig. 12), and less submerged growth habit. This prompted Kimbrough & Korf (*1967*) to transfer *T. zukalii* from *Thelebolus* to *Trichobolus*. Subsequently, species of *Trichobolus* with three or more asci were found, and recently species with 8-spored asci were discovered (Figs. 16–20).

In examining other Pseudoascoboleae, choosing initially the multispored genera, other interesting features of asci and apothecia were noted. Ascal structure in a majority of the species of *Rhyparobius* was basically like that of *T. stercoreus*, i.e. a Congo red-positive layer terminates with a ring around the dome of the ascus, and an inner layer of layers extends the complete length (Fig. 4). Although the species investigated thus far have a wide range of spores per ascus (Figs. 1, 2, 7) and asci per apothecium, (Figs. 2, 10) the basic structural features are identical to those of *T. stercoreus*. All are angiocarpic (Figs. 2, 6) and have asci that tear irregularly at spore liberation (Figs. 5, 11).

Several species previously assigned to *Rhyparobius* display a very obvious ring in the ascus, and consequently several mycologists considered them in *Ascozonus* (*Streptotheca* sensu Seaver, *1928*). A study of *Ascozonus* revealed another set of apothecial and ascal characteristics. The apothecia develop gymnocarpically, with a border of flexuous excipular cells (Fig. 33). A very prominent ring is evident in the ascus wall, and in Congo red this was shown again to be a part of the outer layer (Fig. 31). Unlike the *Thelebolus* ascus, the outer wall extends beyond the ring and almost to the tip (Fig. 32). A small papillate area at the tip is composed of only inner wall material (Fig. 31). Larger, naviculate spores characterize this genus (Fig. 33).

Thecotheus, the remaining multispored genus recognized by Boudier (*1869*), has a typical operculate ascus with a well formed wall indentation at the operculum (Figs. 43–45). The asci are diffusely amyloid, similar to a number of Ascobolaceae and Pezizaceae, the thickwalled spores have cyanophilous ornaments or perisporic sheath, (Fig. 44) and apothecia show a unique arrangement of excipular cells (Kimbrough, *1969*).

A large number of multispored species have operculate asci (Fig. 42), thin-walled spores with a conspicuous de Bary bubble (Fig. 42), and gymnocarpic apothecia which are white or scarcely pigmented (Fig. 37). Kimbrough & Korf (*1967*) placed these in *Coprotus* Korf & Kimbrough.

Peculiar ascal wall structures were also found in other multispored taxa. *Caccobius* Kimbrough & Korf (*1967*) has a very broad, essentially obclavate, thick-walled ascus (Fig. 34), which in youth has a conspicuous apical plug that stains in Waterman's blue-black ink (Fig. 35). The tip remains hyaline in Congo red (Fig. 36) and tears irregularly at spore liberation. Apothecia develop angiocarpically, with the paraphyses becoming highly branched and forming a pseudo-excipulum over the asci. *Coprobolus* Cain & Kimbrough (*1969*) has an ascus structure similar to *Caccobius* in that there is an apical thickening in youth and an irregular tear at spore liberation. The apothecial structure, however, is very dissimilar from that of *Caccobius* which is pigmented and bears marginal, agglulinated hairs.

TABLE II

MULTISPORED TENDENCY IN COPROPHILOUS DISCOMYCETES

	8-SPORED MULTIASCAL	MULTISPORED MULTIASCAL	MULTISPORED UNIASCAL
1.	*Thelebolus*	*Thelebolus*	*Thelebolus*
	Trichobolus	*Trichobolus*	*Trichobolus*
	Lasiobolus	*Lasiobolus*	*Lasiocolus*
	Coprotus	*Coprotus*	?
	Ascozonus	*Ascozonus*	?
	?	*Caccobius*	?
	?	*Coprobolus*	?
2.	*Thecotheus*	*Thecotheus*	
	Iodophanus		
	Peziza		
3.	*Coprobia*		
	Cheilymenia		
	Fimaria		
	Cubonia		

(1. Thelebolaceae; 2. Pezizaceae; 3. Humariaceae)

Boudier (*1907*) placed *Zukalina* Kuntze in the Pyronemacées but suggested a relationship of it to *Rhyparobius*. I have been unable to examine any material of this genus and can not make a taxonomic judgement at this time.

In searching for possible relationships in the 8-spored Pseudoascoboleae (Kimbrough, *1966b*), a number of very significant observations were made. Most European and American mycologists have followed Boudier (*1869*) or Saccardo (*1889*) in placing essentially all of the hyaline, 8-spored species either in *Ascophanus* or *Lasiobolus*. Boudier (*1907*), however, recognized that *A. granulata* differed in a number of features and transferred it to *Coprobia* Boud. of the Humariacées. Our studies support this transfer, and a number of current workers (Eckblad, *1968*; Rifai, *1968*; Dennis, *1968*; Kimbrough, *1970*), recognize this genus. Very few workers have recognized Chenantais' (*1918*) transfer of *A. cinereus* to the genus *Thecotheus*, but Kimbrough (*1969*) pointed out that a number of species previously assigned to *Ascophanus* actually belong in *Thecotheus*. The morphological and cytochemical features of the asci (Figs. 43–45) ascospores, and excipulum are the same as those of the type, *T. pelletieri* (Cr. & Cr.) Boud.

Van Brummelen (*1962*) showed that a number of taxa transferred by various

authors to *Ascophanus* resemble it only superficially. He transferred some of these to *Fimaria* Vel., which differed greatly from *Ascophanus* in ascal and excipular characters. Observations of numerous other collections of *Ascophanus* or *Ascophanus*-like organisms revealed other taxonomically different groups (Kimbrough, *1966b*). A number of species with brownish, initially cleistocarpous apothecia, possessed asci with the same microscopic and microchemical features as *Thelebolus stercoreus* Tode ex Fr. Although the asci were very numerous, paraphyses much more inflated and sometimes pigmented, and the apothecia expanded much earlier, the basic structure of spores, asci and excipular elements were the same as *Thelebolus* (Figs. 7–11). The lectotype of *Ascophanus, A. subfuscus* (Cr. & Cr.) Boud. (chosen by Seaver, *1928*) falls into this complex.

Ascophanus carneus and other species were characterized by the presence of callosepectic marked spores, diffuse amyloidy of asci, carotenoid pigments in the paraphyses and excipular cells, and an *Oedocephalum* imperfect state in some. These were transferred to *Iodophanus* Korf in the Pezizaceae (Kimbrough & Korf, *1967*). A small number of species of *Peziza* are also coprophilous.

One of the largest segregates of *Ascophanus* is *Coprotus*, with 18 species found thus far in North America. As was mentioned earlier with the multispored forms, the asci are operculate (Fig. 38) with uniform wall thickness, spores contain de Bary bubbles (Fig. 40) and apothecia are nonpigmented and gymnocarpic (Fig. 37). The spores per ascus may range from 4 to 256 and asci per apothecium vary from 5 or 6 to several hundred.

In recent examinations of 8-spored, setose species believed to be *Lasiobolus*, a number of features appeared in some which were atypical for that genus. Apothecial hairs were uniformly tapered, with a number of septa (Fig. 17) as opposed to those of *Lasiobolus* which are typically barrel-shaped at the base and nonseptate (Figs. 25–29). The two-layered ascus wall becomes considerably thinner at the apex, (Fig. 18) stains uniformly with Congo red, and dehisces by an irregular tear at spore liberation, (Fig. 19). This is evidently a species of *Trichobolus* with numerous 8-spored asci. Its spores with de Bary bubbles are similar to those of *Coprotus*, *Lasiobolus*, and other species of *Trichobolus*.

Lasiobolus was emended by Kimbrough and Korf (*1967*) to include not only 8-spored species but also the multispored *L. cainii* (Fig. 26). Recently, however, a beautiful uniascal species of *Lasiobolus* was discovered near Gainesville, Florida. Its superficial appearance is similar to that of *T. zukalii* (Fig. 21), but the asci were definitely operculate (Fig. 22) with a chemically differentiated area of dehiscence (Fig. 23) and the hairs are of the bulbous, nonseptate type (Fig. 25). Thus, this makes a total of three genera, *Thelebolus*, *Trichobolus*, and *Lasiobolus*, with species that range from those with uniascal apothecia and multispored asci, to those with numerous 8-spored asci.

If one examines closely a large number of coprophilous taxa distributed among the discomycetes, pyrenomycetes, and loculoascomycetes, he is impressed with the variety of ways these fungi have adapted to this peculiar environment. One of the most striking features is a tendency toward an increased spore number per ascus

accompanied by a decrease in asci per ascocarp. However, in the Sporomiaceae, instead of increased spores per ascus, there is an increase in the number of cells in each of the eight ascospores. The tendency toward increased spores and reduced number of asci is evident to some degree in all genera of the Thelebolaceae. Table II compares these tendencies in the Thelebolaceae and coprophilous genera of Pezizaceae and Humariaceae. All of the Thelebolaceae, with the possible exception of *Thelebolus* spp., have been found only on dung. Those species of *Thelebolus* collected elsewhere were likely on stercoroid soil. Also, *Thecotheus pelletieri* is the only non-Thelebolaceae found thus far with multispored asci. The recent discovery of wood inhabiting species of *Thecotheus* (Pfister, *1971*) enables us now to say that all genera of Pezizaceae with coprophilous species also have lignicolous species. The coprophilous genera of Humariaceae (= Aleuriaceae Arpin, *1969*) very likely have soil inhabiting species as well.

Within the Thelebolaceae we see a number of modifications in the apothecium which have accompanied the reduced ascus number. *Thelebolus*, *Trichobolus*, and *Lasiobolus* are all angiocarpic, or according to van Brummelen (*1967*), cleistohymenial. Apothecia in the uniascal species of these genera remain closed until spore liberation. Those with few asci open in the telohymenial phase, while those with numerous 8-spored asci open during the prohymenial phase. Species of *Coprotus* examined thus far are gymnocarpic, or eugymnohymenial with an excipulum (terminology of van Brummelen, *1967*). In multispored species the excipular growth exceeds that of the hymenium, making the development appear pseudo-angiocarpic. Although not studied in culture, *Caccobius* and *Coprobolus* appear to be cleistohymenial while *Ascozonus* appears gymnohymenial. With few exceptions an increase in spores per ascus is accompanied by a decrease in spore size. Although paraphyses are somewhat variable in 8-spored species of these genera, with a reduction in asci per apothecium the paraphyses are more highly branched and filamentous. It appears that the earlier the apothecium expands the more inflated the paraphyses become. The best example of this is found in *Thelebolus* where in uniascal *T. stercoreus* there is a thin layer of highly branched, filamentous paraphyses, in multiascal *T. crustaceus* slightly inflated paraphyses, and in *T. subfuscus*, greatly inflated and sometimes pigmented paraphyses. In *Coprotus*, however, the 8-spored species have highly variable paraphyses and thus this correlation does not hold.

Preliminary results indicate that the cytological aspects of a number of the Thelebolaceae may enable us to better understand relationships within this family and to other confused taxa. Contrary to Berthet (*1964*) and Eckblad (*1968*), who state that the mycelia of the Pezizales are coenocytic, we have found in research currently underway in my laboratory that the mycelium and vegetative cells in species of *Thelebolus*, *Trichobolus*, *Lasiobolus*, and *Coprotus* are consistently uninucleate. A very reduced ascogenous system has already been reported for *Thelebolus* (Ramlow, *1906*) and *Trichobolus* (Kimbrough, *1966a*). A similar system is present in the uniascal *Lasiobolus* mentioned earlier. We also have some evidence that there is a modified crozier system present in the 8-spored, multiascal genera. For example, in *Coprotus*

lacteus (Ck. & Phil.) Kimbrough the crozier system is of the "aporhynque type", even though the ascal base would lead one to suspect the typical crozier system was at work. We anticipate that a great amount of taxonomically useful information will come from similar cytological and developmental studies.

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EXPLANATION TO PLATES 16–19

PLATE 16

Figs. 1–8. Species of *Thelebolus*. — 1. An ascus of *T. stercoreus* stained in acid fuchsin with the outer wall and ring at apex (arrow) remaining hyaline. × 300. — 2. Young cleistohymenial ascocarp of *T. polysporus*. × 300. — 3. An ascus of *T. stercoreus* in Congo red showing unstained apex and small bacilloid spores within. × 300. — 4. An ascus of *T. crustaceus* with hyaline apex in Congo red. × 500. — 5. An empty ascus of *Thelebolus obscura* showing irregular tear after spore liberation. × 500. — 6. A young cleistohymenial ascocarp of *T. crustaceus* showing young asci and filamentous paraphyses. × 250. — 7. An ascus of *T. microsporus* showing faint apical ring in Congo red. × 1000. — 8. A typical clavate paraphysis of *T. microsporus*. × 1000. (Figs. 1, 3, 4, 5 after Kimbrough, *1966b*).

PLATE 17

Figs. 9–11. *Thelebolus microsporus*. — 9. Mature apothecia on dung. × 50. — 10. An apothecial section with pigmented excipulum, encrusted paraphyses and numerous asci. X 400. — 11. A partially empty ascus with apical tear. × 800.

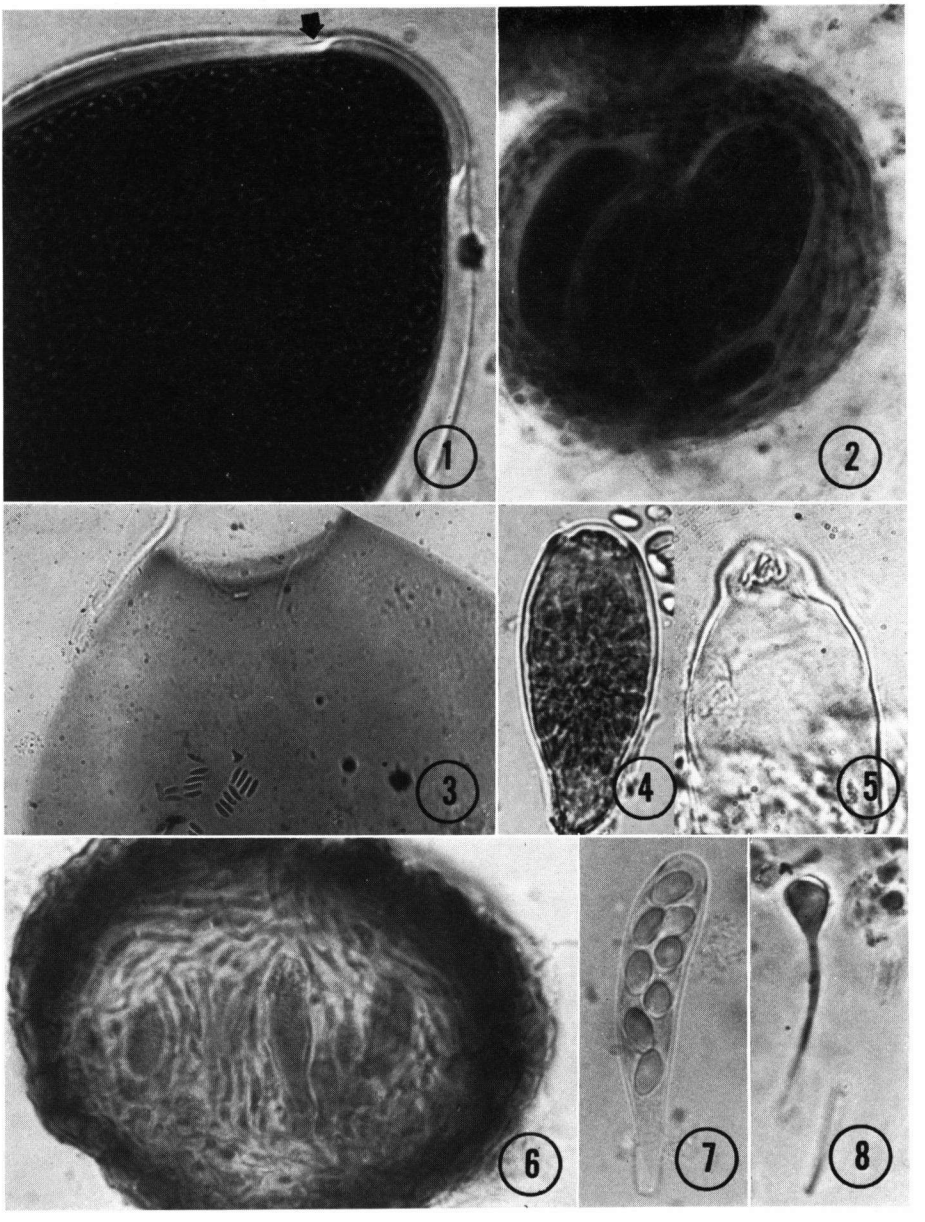
Figs. 12–20. Species of *Trichobolus*. — 12. A mature apothecium of *T. zukalii*. × 25. — 13. Mature ascospores of *T. zukalii* with conspicuous de Bary bubbles. × 1000. — 14. An almost empty ascus of *T. zukalii* showing manner of dehiscence at spore liberation. × 250. — 15. Septate, thick-walled base of hair of *T. zukalii*. × 1000. — 16. Ectal excipulum of an 8-spored species of *Trichobolus*. × 1200. — 17. Sharp. septate hair of an 8-spored *Trichobolus*. × 600. — 18. Ascus of 8-spored *Trichobolus* showing thinner apical region (arrows). × 1200. — 19. Apex of ascus of 8-spored *Trichobolus* showing manner of dehiscence at spore liberation. × 1200. — 20. Paraphyses of 8-spored *Trichobolus*. × 1200. (Figs. 12–15 after Kimbrough, *1966a*).

PLATE 18

Figs. 21–30. Species of *Lasiobolus*. — 21. Setose, uniascal ascocarp of *Lasiobolus monascus*. × 100. — 22. Empty ascus of *L. monascus* showing operculum and filamentous paraphyses. × 160. — 23. Apical portion of ascus showing chemically differentiated area of dehiscence. × 1200. — 24. Ascal wall of *L. monascus* in Congo red showing thinner area of outer wall (arrows). × 1200. — 25. Pointed, nonseptate, barrel-shaped hair of *L. monascus*. × 1200. — 26. An ascus of *L. cainii* with thinner areas for dehiscence (arrows). × 440. — 27. An apothecium of *L. lasioboloides*. × 120. — 28. Ascus apices of *L. lasioboloides* in Congo red showing operculum in one and hyaline area of dehiscence in others (arrows). × 1000. — 29. Barrel-shaped nonseptate base of hair of *L. ciliatus*. × 1000. — 30. The epidermoideae excipulum in *L. ciliatus*. × 1000. (Fig. 26 after Kimbrough & Korf, *1967*).

PLATE 19

Figs. 31–45. Species of *Ascozonus*, *Caccobius*, *Coprotus* and *Thecotheus*. — 31. An ascus of *Ascozonus cunicularius* in Congo red, showing prominent ring in outer wall and unstained nippled tip (arrow). × 1200. — 32. An ascus of *A. cunicularius* in acid fuchsin showing thicker inner wall. × 1200. — 33. A mature ascus of *A. cunicularius* with naviculate spores within and surrounded with flexuous excipular cells. × 1000. — 34. Young ascus of *Caccobius miniusculus* with extremely thick walls. × 750. — 35. Young ascus of *C. miniusculus* showing apical plug in blue-black ink (arrow). × 1000. — 36. Mature ascus of *C. miniusculus* with small eguttulate spores and hyaline apical plug in Congo red. × 1000. — 37. Apothecia of *Coprotus lacteus* on dung. × 5. — 38. Operculate ascus of *C. lacteus*. × 1000. — 39. An apothecial section showing excipulum and asci. × 500. — 40. An ascus of *C. lacteus* with 8 spores containing de Bary bubbles. × 1000 — 41. An ascus of *C. sexdecimsporus*. × 1000. — 42. An ascus apex of *C. winteri* showing oblique operculum with thinner wall areas (arrows). × 1000. — 43. An ascus apex of *Thecotheus pelletieri* showing indentations in ascus wall (arrows). × 1000. — 44. Young ascus of *T. cinereus* showing thick inner wall with indentation. × 1000. — 45. Mature ascus of *T. cinereus* with well delimited operculum. × 1000. (Figs. 31–33 after Kimbrough, *1966b*; Figs. 34–36 after Kimbrough & Korf, *1967*; Figs. 37–42 after Kimbrough, Luck-Allen, & Cain, in press; Figs. 43–45 after Kimbrough, 1969).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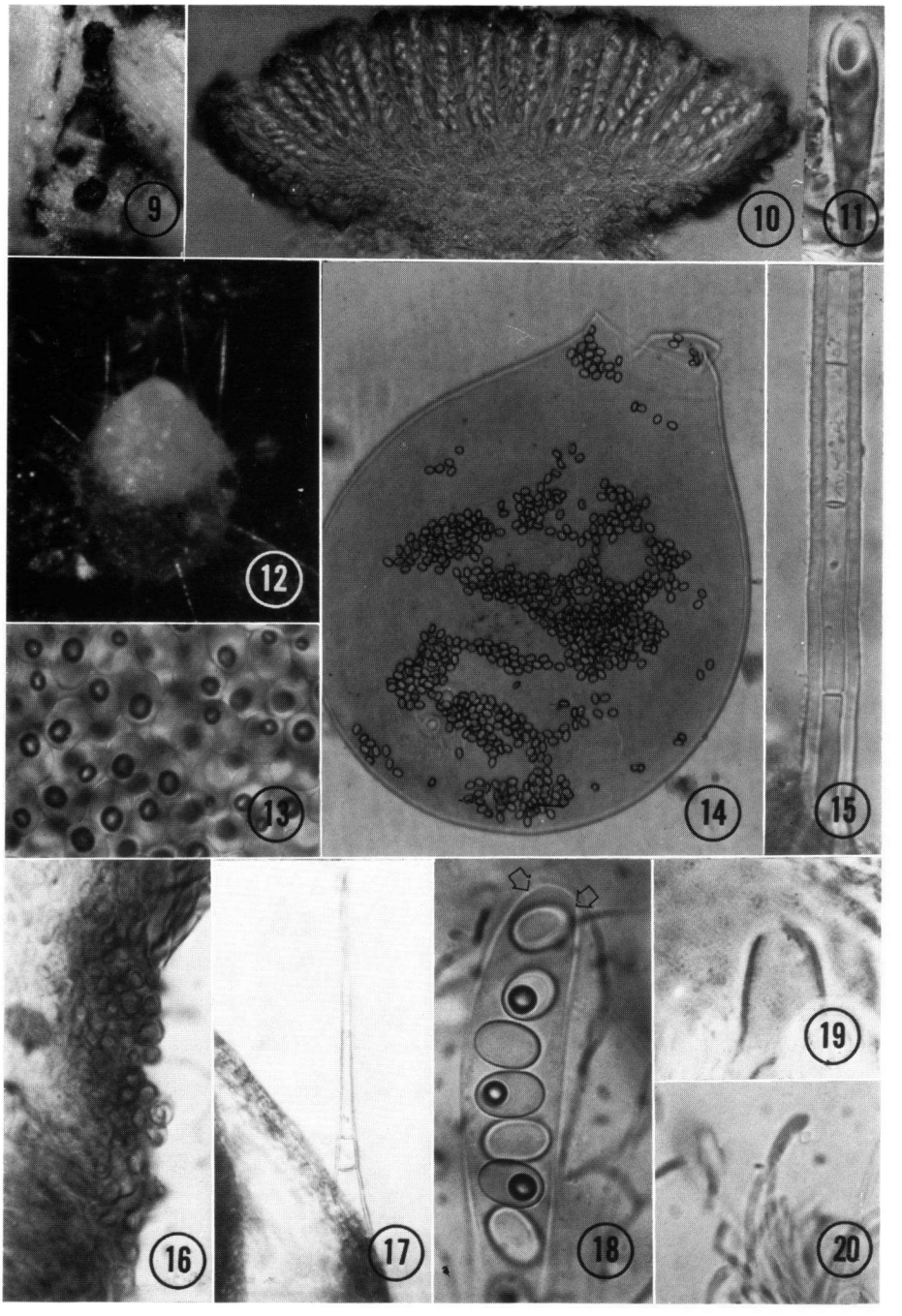
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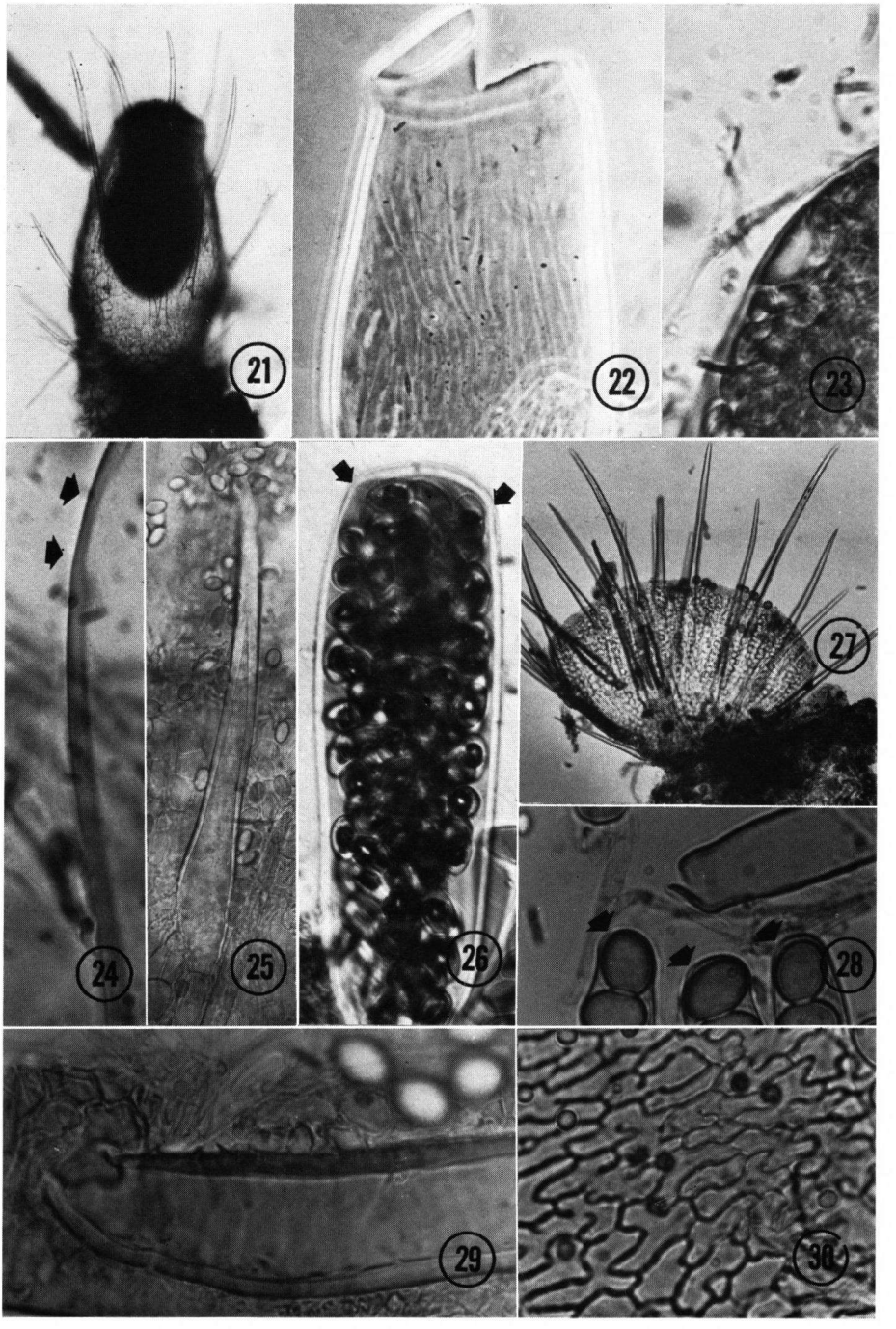
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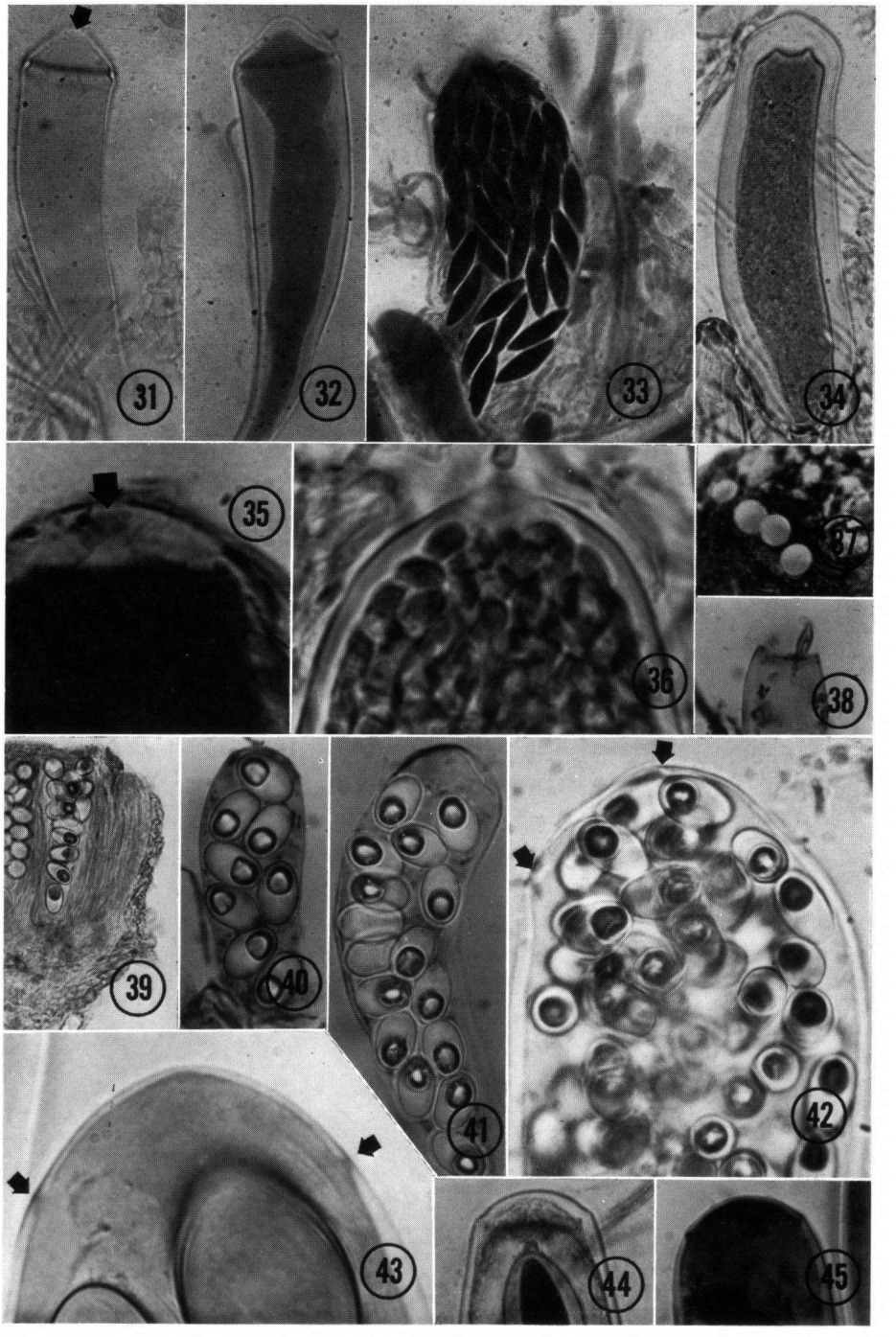
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