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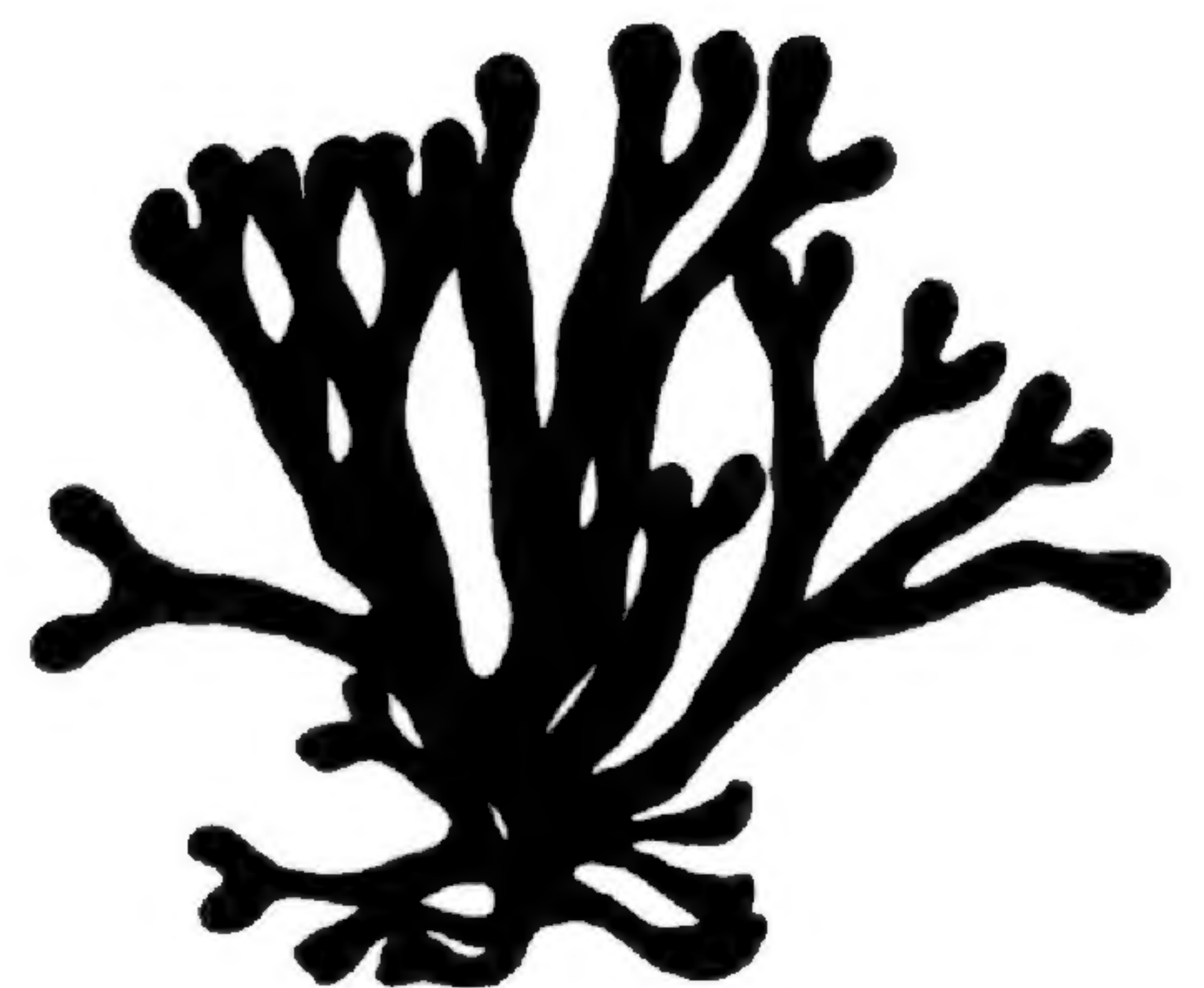
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The Genus *Acervus* (Ascomycetes, Pezizales)

I. An Emendation

II. The Apothecial Ontogeny of *Acervus flavidus* with
Comments on *A. epispartius*



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- No. 1. Sylvia A. Earle:** *Hummbrella*, a New Red Alga of Uncertain Taxonomic Position from the Juan Fernandez Islands (June 1969).
- No. 2. I. Mackenzie Lamb:** *Stereocaulon arenarium* (Sav.) M. Lamb, a Hitherto Overlooked Boreal-Arctic Lichen (June 1972).
- No. 3. Sylvia A. Earle and Joyce Redemsky Young:** *Siphonoclathrus*, a New Genus of Chlorophyta (Siphonales: Codiaceae) from Panama (July 1972).
- No. 4. I. Mackenzie Lamb, William A. Weber, H. Martin Jahns, Siegfried Huneck:** *Calathaspis*, a New Genus of the Lichen Family Cladonia-ceae (July 1972).
- No. 5. I. Mackenzie Lamb:** *Stereocaulon sterile* (Sav.) M. Lamb and *Stereocaulon groenlandicum* (Dahl) M. Lamb, Two More Hitherto Overlooked Lichen Species (March 1973).
- No. 6. I. Mackenzie Lamb:** Further Observations on *Verrucaria serpuloides* M. Lamb, the Only Known Permanently Submerged Marine Lichen (April 1973).
- No. 7. Bruce H. Tiffney and Elso S. Barghoorn:** The Fossil Record of the Fungi (June, 1974).
- No. 8. Donald H. Pfister:** The Genus *Acervus* (Ascomycetes, Pezizales). I. An Emendation. II. The Apothecial Ontogeny of *Acervus flavidus* with Comments on *A. epispartius* (May, 1975).
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THE GENUS ACERVUS (ASCOMYCETES, PEZIZALES)¹

DONALD H. PFISTER

I. AN EMENDATION

SUMMARY

An emendation of the genus *Acervus* Kanouse is proposed. The genus, previously monotypic, is considered to be an older name for *Phaedropezia* Le Gal. Two new combinations are made: *Acervus flavidus* and *A. epispartia*. The latter is the older epithet for *A. aurantiacus*, type of the genus *Acervus*. The histories of the two genera are discussed, a key to the recognized species is given, and detailed notes for the species are provided.

Stability in the Pezizalean generic nomenclature and circumscriptions is the result of recent investigations by many workers. In his synthesis of the order, Korf (1972) has summarized the work. Because generic delimitations are now more perfectly defined, it is possible to study and analyze poorly known genera. As a consequence, an occasional merger of genera may be effected. A case in point involves the reexamination of *Acervus* Kanouse and *Phaedropezia* Le Gal. The material studied includes holotypes, all available dried collections referred to either genus, and fresh material from the West Indies.

The monotypic genus *Acervus* was erected by Kanouse (1938) upon a single collection from Michigan which she named *A. aurantiacus* Kanouse. This remained the only known collection until Gamundi (1970) reported the species from Argentina. Kanouse considered the asci to be inoperculate and thus placed the genus in the Dermateaceae. Seaver (1951) treated it in the Helotiaceae and placed it in the tribe Ascotremelleae. From his study of the holotype Korf (1963) concluded that the asci were suboperculate and treated the genus in the Sarcoscyphaceae. Korf (1972, 1973) later reconsidered his position and *Acervus* was placed in the Pyronemataceae sensu Korf. Denison (1972) also treated *Acervus* in the Sarcoscyphaceae though he did not state his reasons. The genus was not accepted by Eckblad (1968) who included it among the genera he considered to be insufficiently known.

Kanouse (1938), Korf (1963) and Gamundi (1970) gave detailed descriptions of *Acervus aurantiacus*. Critical features are: (1) the small size of the ascospores which rarely reach a length greater than 8 μm ; (2) the medullary excipulum which is composed of large diameter, interwoven hyphae with occasional swellings; (3) the ectal excipulum which, though not clearly delimited from the medullary excipulum toward the

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inside, is differentiated into more or less closely packed *textura angularis* toward the outer surface; (4) the bright yellow to orange paraphyses, the pigments of which are soluble in water and alcohol.

Phaedropezia, the more recently established genus, was described by Le Gal (1953). Under this genus she brought together a natural and homogeneous group of species. *Peziza epispartia* Berk. & Br. was listed as the type of the genus since it was considered by Le Gal to be the best known and most adequately studied of the species. *Psilopezia flavida* Berk. & Curt. was placed in the genus and *Phaedropezia genuina* Le Gal was described as a new species. Later *Peziza flavotिंगens* Berk. & Br. also was considered a distinct species of *Phaedropezia* (Le Gal 1959). Patouillard (1913) had considered the asci to be inoperculate in *Peziza epispartia* whereas, in her original account of *Phaedropezia*, Le Gal described and illustrated the asci as suboperculate. Although she did not place the genus in the Sarcoscyphaceae because of the apothecial anatomy and concomitant fragile texture of the apothecia, both Eckblad (1968) and Korf (1970) considered *Phaedropezia* to belong to that family.

Le Gal (1969) argued that *Phaedropezia* was not sarcoscyphaceous. Cytological evidence substantiates her contention (Pfister 1972) since ascospores are uninucleate rather than multinucleate as in the Sarcoscyphaceae. Korf (1972, 1973) placed *Phaedropezia* in the Pyronemataceae.

Comparative studies of the apothecial anatomy of the holotypes of *Acervus aurantiacus* and *Phaedropezia epispartia* show that there is no significant difference between the two specimens. The name *Acervus*, being older, takes precedence over *Phaedropezia*. The genus *Acervus* as now conceived is essentially identical in circumscription to *Phaedropezia*. The excellent accounts by Le Gal, and her insight into the relationships of these species, leave little to add descriptively.

The placement of the genus within the Pezizales remains problematic. As indicated previously, the asci have been interpreted by various investigators as inoperculate, suboperculate, and operculate. In my studies of the genus, I have not observed a true terminal operculum. The asci dehisce by splitting apically, producing a lateral flap. This is not unlike the bilabiate asci of *Caccobius*, *Coprobolus*, *Trichobolus*, *Thelebolus*, and *Ascozonus* all of which have been treated as Pezizales. No apical pad or thickening was observed. This, along with the structure of the apothecium and the uninucleate condition of the ascospore, is considered sufficient to warrant its placement in the Pezizineae. Ascospore discharge is forcible. Le Gal (1969) established the tribe Sowerbyelleae of the Pezizales in which she included *Phaedropezia*, *Caloscypha*, and *Sowerbyella*. She thought that both *Sowerbyella* and *Phaedropezia* would be shown to have the same unique carotenoids which Arpin (1969) found in *Caloscypha*, and believed the apothecial anatomy to be similar in all three genera. Korf (1973) added *Acervus* to this tribe. This grouping is

tentatively accepted here, though not without hesitation. Pigments do differ between *Acervus* and *Caloscypha*, at least in solubility. The pigments in *Acervus* are easily and readily soluble in alcohol and in water to some extent but those in *Caloscypha* are not significantly soluble in either alcohol or in water. Studies of the carotenoids in members of these genera and study of the ontogeny of the apothecia may add needed information which might then allow more precise placement of this genus within the order. Another possible solution to the problem of determining the relationships of *Acervus* was offered by Rifai (1968). He suggested that *Phaedropezia* might require an additional family within the Pezizales. Details of apothecial ontogeny outlined in part 2 of this paper do indicate that *Acervus* might occupy an isolated position in the order. However, erection of a new family is still premature.

ACERVUS Kanouse, *emend.* Pfister

- ≡ *Acervus* Kanouse, Pap. Michigan Acad. Sci. **23**:149. 1938 (1937). TYPE: *Acervus aurantiacus* Kanouse = *Acervus epispartius* (Berk. & Br.) Pfister.
 = *Phaedropezia* Le Gal, Prodr. Flore Mycol. Madagascar **4**:179. 1953. TYPE: *Peziza epispartia* Berk. & Br.

KEY TO THE SPECIES

- Spores 5.8-7.5(9) × 3.2-4 μm, with relatively thin walls, spores blunt, spores regular in outline *Acervus epispartius*
 Spores (7.5)9-13 × 5 × 5-7 μm, with a thick wall, spores regularly ellipsoid to irregular in outline *Acervus flavidus* (cfr. also *Phaedropezia genuina*)

1. *Acervus epispartius* (Berk. & Br.) Pfister, comb. nov.

- ≡ *Peziza epispartia* Berk. & Br., J. Linn. Soc., Bot. **14**:103. 1873.
 ≡ *Phialea epispartia* (Berk. & Br.) Pat., Bull. Soc. Mycol. France **29**:221. 1913.
 ≡ *Phaedropezia epispartia* (Berk. & Br.) Le Gal, Prodr. Flore Mycol. Madagascar **4**:181. 1953.
 = *Peziza flavotिंगens* Berk. & Br., J. Linn. Soc., Bot. **14**:104. 1873.
 ≡ *Humaria flavotिंगens* (Berk. & Br.) Sacc., Syll. Fung. **8**:129. 1889.
 ≡ *Phaedropezia flavotिंगens* (Berk. & Br.) Le Gal, Bull. Jard. Bot. État **29**:96. 1959.
 = *Peziza radiculosa* Berk. & Br., J. Linn. Soc., Bot. **14**:103. 1873.
 ≡ *Sarcoscypha radiculosa* (Berk. & Br.) Sacc., Syll. Fung. **8**:155. 1889.
 = *Peziza microspora* Berk. & Curt. in Berk., Grevillea **3**:150. 1875.
 ≡ *Humaria microspora* (Berk. & Curt. in Berk.) Sacc., Syll. Fung. **8**:131. 1889.
 = *Acervus aurantiacus* Kanouse, Pap. Michigan Acad. Sci. **23**:149. 1938 (1937).

Acervus epispartius has been fully described by several authors (Kanouse 1937, Le Gal 1953, Korf 1963). The specific epithet was misspelled by Cooke in the *Mycographia* where it appeared as *Peziza episparticus*.

Three epithets in the synonymy date from the same publication and

were based on collections made at Peradeniya, Ceylon during November 1867. These sister collections are the holotypes of *Peziza epispartia*, *P. flavotingens*, and *P. radiculosa*. Le Gal (1953) recognized *Phaedropezia epispartia* as one taxon synonymizing *Peziza radiculosa* with it. However, she originally questionably synonymized *Peziza flavotingens* with *Phaedropezia flavida*. Later Le Gal (1959) proposed the combination *Phaedropezia flavotingens* since, in her opinion, two colored plates by Mme M. Goossens-Fontana (Le Gal 1960) showed color differences sufficiently different to warrant creation of the new taxon. Unfortunately, the holotype specimen of *Peziza flavotingens* is immature. This was indicated by the original description (Berkeley 1875), in which it was stated "Fruit scarcely mature." Le Gal (1959) commented that one of the Goossens-Fontana drawings agreed with Cooke's illustration (plate 10, fig. 38) of *Peziza flavotingens* in his *Mycographia*. This plate by Cooke shows apothecia with yellow hymenia attached to the substrate by yellow mycelia. The asci were drawn with four spores and show some granular cytoplasm, possibly another indication that the specimen was immature. One must regard the precise color of Cooke's plates as questionable since he was drawing not from living specimens, but from dried material, written descriptions, and field notes. In addition, my study of the Goossens-Fontana specimen, identified by Le Gal as *Phaedropezia flavotingens*, does not show significant microscopic differences to distinguish it from *Acervus flavidus*. I take a broad view of the significance of color variations and assume the existence of natural differences between specimens of one species depending on substrate, age, and environmental conditions. I refer *Phaedropezia flavotingens* sensu Le Gal to *Acervus flavidus*.

Interestingly, *Peziza microspora*, another synonym of *Acervus epispartius*, has been reported from North America on two occasions. The type collection itself was from South Carolina, and a second collection was from Pennsylvania (in NY). The Pennsylvania specimen was listed by Seaver (1928) as *Humaria microspora* and was treated as a doubtful member of the genus *Humaria*. The packet shows that it was determined by Phillips. The type collection of *Acervus aurantiacus* from Michigan represents the most northerly station yet reported for this species. Thus, though *Acervus* is primarily tropical it may also occasionally be found in the temperate areas of North America. I am not aware of any report of this species from temperate Europe or Asia. This species was reported from India (Uppal et al. 1935) under the name *Peziza epispartia*. The specimen on which this record is based was not examined in the present study.

SPECIMENS EXAMINED. **Argentina:** suelo bajo *Eucaliptus*, Buenos Aires, Parque Pereyra, Iraola. 20 abril 1970, P. Merlo (LPS). **Ceylon:** holotype of *Peziza radiculosa*, Peradeniya, Nov. 1867 (κ); holotype of *Peziza epispartium*, Peradeniya, Nov. 1867, (κ); holotype of *Peziza flavotingens*, Peradeniya, Nov. 1867 (κ). **Congo:** Panzi,

Chemin herbeuse 650 m. dec. 1949, Mme M. Goossens-Fontana (5105) (BR); sol, Panzi-Kivu alt. 1650 m, nov. 1955, Mme M. Goossens-Fontana (5526) (BR); arbre mort, Panzi-Kivu alt. 1650 m, mai 1953, Mme Goossens-Fontana (5285) (BR); bois mort, Panzi-Kivu, mai 1952, Mme Goossens-Fontana (5248) (BR); groupés sur tronc mort dans champs. de cultures indigens, Binga, 5 junio 1928, Mlle Goossens (765) (BR). **Madagascar:** Terrestre, Institut Pasteur, 11(2) fev. 44, M. Bourguet (PC). **Malaya:** on bare earth by an old termite nest in forest, Pahang, Tembeling, 10 Nov. 1930, E. J. H. Corner (BPI); Pahang, Tembeling, 15 Nov. 1930, E. J. H. Corner (1269) (BPI); Pahang, Tembeling, 8 Nov. 1930, E. J. H. Corner (24166) (BPI). **U.S.A.:** part of holotype of *Acervus aurantiacus* on soil around roots of an elm tree in a bog, South Lyons, Michigan, 6 October 1936, Alexander H. Smith (5044) (MICH); on loose decaying rubbish, Fairmont Park, Philadelphia, Pa., Sept. 1882, W. C. Stevenson, Jr. (477) (NY); holotype of *Peziza microspora* on damp, rotten wood near the ground, South Carolina (K). **Vietnam:** sur la terre, dans les plantations de café, Chi-Né, Tonkin, avril 1911, Mr. Duport (531) (FH-Herb. Patouillard).

2. *Acervus flavidus* (Berk. & Curt. in Berk.) Pfister, comb. nov.

≡ *Psilopezia flavida* Berk. & Curt. in Berk., Grevillea 4:1. 1875.

≡ *Phaedropezia flavida* (Berk. & Curt. in Berk.) Le Gal, Prodr. Flore Madagascar 4:185. 1953.

A description of this species was given by Le Gal (1953). The original placement in *Psilopezia* by Berkeley and Curtis (Berkeley 1875) probably was based on the more or less broad attachment of the apothecia to the substrate. As previously pointed out (Pfister 1973) this species is not a *Psilopezia*.

Massee (1896) said "I should place the present species in the genus *Mollisia*." Such placement is untenable and apparently was based on Massee's belief that the asci were inoperculate.

I have collected this species on several occasions in the West Indies and have reported a collection of it from Dominica under the name *Phaedropezia flavotिंगens* (Pfister 1972). The ascospores were found to be uninucleate.

Fresh apothecia of this species, when placed in FAA, release bright yellow pigments. These pigments may also leach from dried apothecia when rehydrated in water. References to similar soluble pigments were made by Kanouse (1937), Korf (1963) and Gamundi (1970) in their descriptions of *Acervus aurantiacus*.

In fresh material the substrate surrounding the apothecia is bound loosely together with yellow mycelium to form a common mass. A mass similar to this may have been the structure which was described by Kanouse (1938) as the sclerotiform base of *Acervus aurantiacus*. In her description, however, she stated, "arising from a black, tough, rubbery sclerotiform base composed of thin-walled mycelium intermingled with débris." Korf (1963) could find no evidence of this structure and I have found that the mycelial-substrate mass does not withstand drying.

SPECIMENS EXAMINED. **Congo:** sur detritus de palmiers, Binga, oct. 1944, Mme Goossens-Fontana (3042) (BR). **Guadeloupe:** on debris, Les Mamelles, Parc Tropicale,

5 Jan. 1974, D. H. Pfister (806), M. Sherwood, S. Carpenter (FH); on debris under leaf litter, Les Mamelles, Parc Tropicale, 19 July 1973, D. H. Pfister (536), W. Sarriera, M. Halmos (FH). **Madagascar:** sur l'humus, Ankarafantsika, 1 jan. 1938, R. Decary (PG). **Peru:** on dead sticks, leaves, etc. on the ground in the forest, Iquitos, 10 April 1948, E. J. H. Corner (1202) (BPI). **Puerto Rico:** on soil and debris on bank, Mayagüez Zoo, Mayagüez, 27 Aug. 1972, D. H. Pfister (419) and C. Pfister (FH). **U.S.A.:** holotype of *Psilopezia flavida* Alabama, Peters (κ). **Venezuela:** on unidentified plant debris, mountains above El Rosario, Edo. Miranda, 1 July 1971, K. P. Dumont (VE-1067), J. H. Haines, C. Blanco (NY).

UNSTUDIED SPECIES

Phaedropezia genuina Le Gal, Prodr. Flore Mycol. Madagascar 4:190. 1953.

The holotype of this species is, according to Le Gal (1953), a single poorly preserved specimen. Since I have not seen this specimen and have no firsthand knowledge of it, no new combination is proposed. Le Gal (1953) maintained that smaller size of the apothecia, yellower color, and spore size of $8.5-12 \times 4-5 \mu\text{m}$ sufficiently distinguished *P. genuina* from the other species. The spore size approaches that of *Acervus flavidus*. The report by Cash (1956) of this species from Chile is based, according to my study of her specimen, on an inoperculate Discomycete, probably referable to the genus *Hymenoscyphus*. Its asci have a definite J + apical pore.

2. THE APOTHECIAL ONTOGENY OF ACERVUS FLAVIDUS WITH COMMENTS ON A. EPISPARTIUS

SUMMARY

The ascocarps of *Acervus flavidus* are demonstrated to be cleistohymenial. They open during the prothymenial phase by the formation of a distal flap which turns back to expose the hymenium. No gametangia were seen. A similar type of development has been observed in *Acervus epispartius*. It is suggested that this ontogenetic feature is a useful generic character in *Acervus* and that with future studies the proper supergeneric relationship of *Acervus* might be discovered.

INTRODUCTION

Few members of the Pezizales have been rigorously analyzed in regard to the ontogeny of their apothecia. The Ascobolaceae and certain other coprophilous Discomycetes are exceptions (van Brummelen 1967, 1972, Kimbrough 1972, Kish 1974, Jain and Morgan-Jones 1973). Such studies potentially may elucidate relationships among species within genera and among genera. Van Brummelen (1967) has successfully applied ontogenetic information to his sectional classification of the genera *Ascobolus* and *Saccobolus*. In so doing he developed a set of terminologies, employed here, which are outgrowths and refinements of the work of Corner (1929 a,b; 1930 a,b,c). Van Brummelen's system involves the recognition of

two features: (1) the presence or absence of a layer covering the apothecial initials; and (2) if covered, the stage at which the hymenium is exposed. The burden imposed by such a set of characters is great, since apothecial primordia must be seen, as well as juvenile and mature apothecia.

The subject of this study, *Acervus flavidus* (Berk. & Curt. in Berk.) Pfist., has never been discussed ontogenetically. Material of *A. flavidus* was collected in the field where initial observations were made. Since spore germination was never obtained, the fungus has not been cultivated.

MATERIALS AND METHODS

The ascocarps and primordia used in this study were collected in Guadeloupe, F.W.I. Voucher specimens, DHP 538, 806, and 611 are deposited in the general mycological collection of the Farlow Herbarium (FH). Material was killed and fixed in FAA (Sass 1958) in the field.

Pencil drawings were made by Cathleen K. Pfister from killed and fixed material. This material was then infiltrated with paraffin using the tertiary butyl alcohol method (Jensen 1962). Serial sections were made at approximately 10 μm .

Sections were processed as follows: paraffin was removed in xylene, transferred to absolute ethyl alcohol, stained from 15-30 minutes in a 0.5% solution of Congo Red (C.I. No. 22120) in commercial ammonia, counter stained with a saturated solution of orange G (C.I. No. 16230) in clove oil, and returned to xylene. Wall material was stained bright, clear red while cytoplasm was stained orange.

RESULTS

Ontogenetically the ascocarp of *Acervus flavidus* is cleistohymenial, opening at the prohymenial stage. The critical developmental stages are shown in figure 1 (A-C). In the earliest stage observed, the archihymenial stage, the primordium was a stout, subcylindrical mass of mycelium attached to the substrate by yellow mycelium. Examination of ascocarp sections, 8-12 μm thick, at this stage showed no differentiated gametangia. It was composed of undifferentiated, interwoven hyphae which were 7-10 μm in diameter. Toward the base of the young ascocarp the hyphae were more loosely arranged than they were distally. The hyphae tended to become parallel in orientation to one another in the distal portion. Sometimes the hyphae anastomose.

The opening of the ascocarp takes place during the prohymenial phase when a fissure develops which cuts out a more or less circular flap at the distal portion of the ascocarp (fig. 1A). This phenomenon has been observed on several occasions in field collections and was noted in the field by Corner (notes with specimens in BPI) for *A. epispartius*. It thus

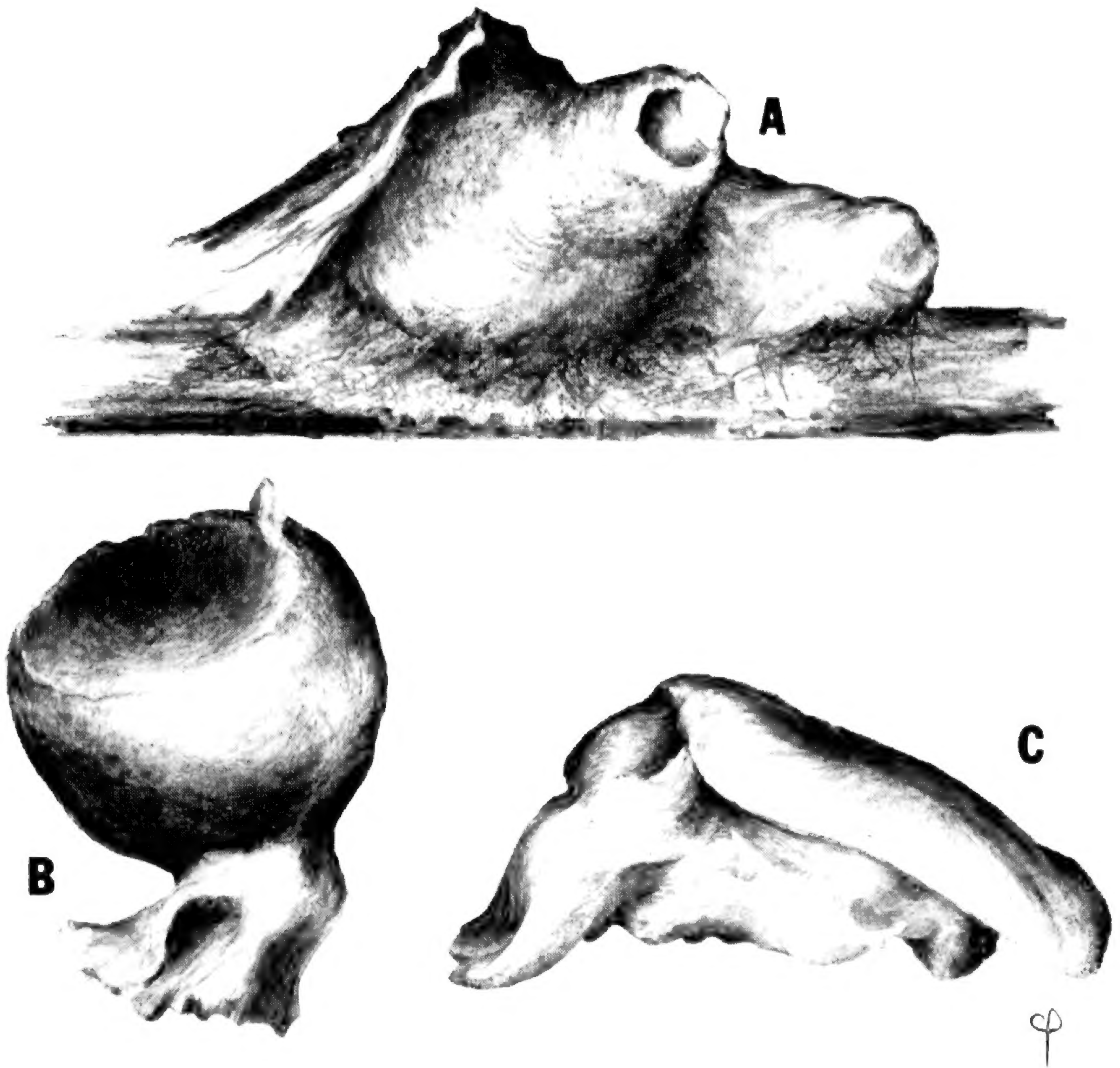


FIG. 1 (A-C). Developmental phases of *Acervus flavidus* (approx. 5x). A. Two juvenile ascocarps. The ascocarp on the right shows the late archymenial phase or early prohymental phase. The ascocarp on the left shows the prohymental phase after rupture of the distal portion to form a semi-circular flap (drawn from DHP 611). B. Ascocarp at mesohymenial phase (drawn from DHP 806). C. Ascocarps at telohymenial phase situated on a mycelial mat (drawn from DHP 806).

seems to occur commonly and regularly. The flap remains attached to one side of the disc where it can be seen through most of the successive developmental stages (fig. 1B). The flap is composed of hyphae which, in section, appear to form a pseudoparenchyma of small diameter cells. At the time of rupture short paraphyses are present which form a discrete hymenium. The ascocarp at this stage is composed of large diameter cylindrical cells or wide hyphae interspersed with thinner hyphae.

Distal rupture and separation of the flap from surrounding tissue resulted from an increase in marginal growth. In section the margins of ascocarps at prohymental and mesohymenial phases were composed of loosely interwoven flexuous hyphae. This is the region of active growth and from this zone arise all successive paraphyses and the excipular tissue.

Ultimately the apothecium reaches a diameter of up to 1.5 cm and is

either slightly concave, flat, or convex. At times it appears to be subsessile; a short thick base develops through the aggregation of mycelium and debris from the substrate. On such a mass one or more apothecia may be situated as in figure 1C. By the telohymenial phase the flap generally has been lost.

DISCUSSION

The development of *Acervus flavidus* as outlined here is unique. Other members of the Pezizales have been shown to be cleistohymenial and to open during the prohymenial phase but none have been described as having the discrete flap of tissue which is characteristic of *Acervus*. The mechanism is particularly effective since the flap does not interfere with spore discharge, yet the hymenium is covered during a critical early stage of development when the apothecium is likely to dry out. Spores are forcibly discharged. Although I have not observed it, Corner noted puffing in one of his Malaysian collections according to field notes accompanying specimens in BPL.

Following van Brummelen's (1967) successful use of ontogenetic features in the sectional taxonomy of the Ascobolaceae, such characters have been used increasingly as taxonomic criteria. The coprophilous Discomycetes in particular have been well studied. However, few studies have been done on terrestrial members. This is the case partly because ontogenetic studies are not always possible since, for the majority of the Pezizales, adequate material can only be collected in nature and cannot be produced in culture. Still, ontogenetic information is a valuable classificatory tool and as van Brummelen (1973) suggested, it may be particularly significant at the supraspecific level.

In *Acervus* I believe the ontogeny is essentially identical in both recognized species and I consider this developmental character to be useful at the generic level. As previously stated, the taxonomic position of *Acervus* is in doubt. I retain it as did Korf (1972, 1973) in Sowerbyelleae, the position assigned *Phaedropezia* by Le Gal (1969). Until ontogenetic information for the other genera of the tribe can be obtained, the significance of this unique mode of development in *Acervus* cannot be evaluated above the generic level. Nonetheless, ontogenetic information may prove to be of use in determining the legitimacy of the tribe.

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