

**UNIVERSIDAD DE COSTA RICA
SISTEMA DE ESTUDIOS DE POSGRADO**

INVESTIGACIONES MICOLOGICAS EN COSTA RICA

**Tesis sometida a la consideración
de la Comisión de Estudios de Posgrado en
Biología para optar el grado de**


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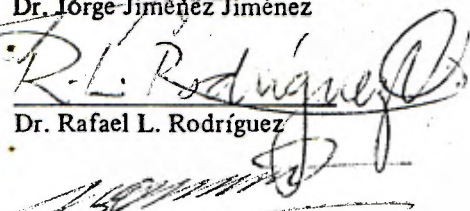
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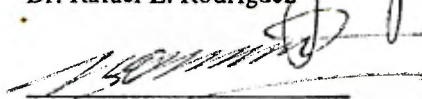
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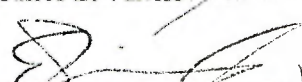
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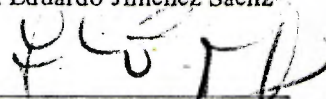

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*A mis padres y
demás seres queridos*

JASR

INTRODUCCION

La investigación micetológica en Costa Rica es relativamente reciente, ya que el estudio de los hongos en forma sistemática y académica se inició en la Escuela de Biología, de la Universidad de Costa Rica, en la década iniciada en 1960. Los tres trabajos aquí consignados y aceptados por el sistema de Estudios de Postgrado de la Universidad de Costa Rica como cumplimiento de requisito de tesis para optar por la Maestría en Biología, constituyen una muestra del esfuerzo y logros obtenidos en ese campo y una contribución al conocimiento universal de la Micología.

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CONTRIBUTION TO THE STUDY OF XYLOPHALLUS XYLOGENUS

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SUMMARY

A new collection of *Xylophallus xylogenus*, made at the same latitude as the type, confirms rotting wood as its natural substrate. The unpleasant odor of its gleba, typical of the phalloids, and its attraction to insects are reported. From study of sections of the fruiting body in different stages of development, we conclude that the gleba is not interrupted from its origin and thus the axial tissue never reaches the volva. The prosenchymatous internal layer of the volva is intimately connected with the "veins" of the gleba and becomes part of its lacunose system. The presence of a pore at the apex of the receptacle in unopened eggs is confirmed. As fruiting bodies mature, the pore becomes wider. The apparent continuity between the axial tissue and the volva in one specimen is assumed to result from swelling of one of the apical "veins" of the gleba due to pressure exerted by elongation of the stalk. When stained with safranin, the hyaline spores show a central zone of red cytoplasm surrounded by a large colorless portion. In material mounted in Amann's lactophenol with cotton blue, the spores mostly have a vacuole at both ends of the long axis; however, spores occasionally have three vacuoles or just one central vacuole. That the only known collections of *X. xylogenus* were made at the same latitude seems to confirm the narrow distribution of the species and its rarity. *Xylophallus xylogenus* grows on wood in rather large colonies with the fruiting bodies joined by stolon-like rhizomorphs.

Xylophallus is a monotypic phalloid genus, based on a species originally described by Montagne in 1855 (11) as *Phallus (Mutinus) xylogenus*—although it had a free cap bearing the gleba—from material collected by Leprieur (No. 840) near Cayenne. Since the receptacle was not adnate to the stalk and was not perforated, Montagne pointed out that the species might merit classification in a separate section under *Phallus*. In 1861, Schlechtendal (12) established *Phallus* section *Xylophallus*, not the generic standing for *Xylophallus* as Ainsworth (1) states. In 1898, Fischer transferred the species to *Mutinus* (4). In 1921, Fischer (5) sectioned fruiting bodies in different stages of development. His interpretations were uncertain because he found an apical perforation of the gleba in some cases and not in others, and he was not sure whether the gleba was continuous over the apex of the

receptacle. He described an axial tissue that reached the apical portion of the gleba in young stages but was later obliterated. In 1923, Fischer (6) still classified the fungus as *Mutinus xylogenus* because the axial tissue initially reaches the volva. He still left open the question as to whether the gleba is a continuous layer from the beginning or whether, in fact, it is initially perforated by the axial tissue. He also suggested *Xylophallus* as a new genus, which he mentioned for the first time in 1930 (7) and finally established in 1933 (8), maintaining that the axial tissue reaches the volva and is later obliterated. Since then, other mycologists have recognized *Xylophallus* (1, 2, 13). Probably by typographic error, Bessey's (2) key to Gasteromycetes called it *Xylophagus*, a genus in the Polyporales (1).

In this paper, the finding of this very uncommon phalloid in Costa Rica is reported and it is redescribed in view of the fragmentary, somewhat confusing, and not widely disseminated literature on it (3, 4, 5, 6, 7, 8, 10, 11, 12). We include some results of our morphological and developmental studies which do not agree with those of earlier workers (6, 11, 12).

MATERIALS AND METHODS

Fruiting bodies of *Xylophallus xylogenus* (Mont.) Fischer were collected in Finca La Selva, Puerto Viejo de Sarapiquí Heredia, Costa Rica, at 250 m in a moist premontane forest (9) on a fallen log covered with moss. The fruiting bodies were fixed in FAA; some were sectioned by hand, while others were embedded in paraffin after dehydration in a TBA series. Serial sections were made 10 μ in thickness and stained with safranin-fast green. Duplicates were placed at the herbaria of the University of Costa Rica (#994), the University of California, Berkeley, and the Royal Botanic Gardens, Kew.

RESULTS

Morphological description

The unopened, fully developed eggs (FIGS. 1a, 12a) are obovoid, averaging 6 mm tall, 5 mm thick in the middle, 2 mm in the basal part, and 3.5 mm at the top. The volva is dark brown in the upper part, paler below. The fruiting bodies occur singly or in colonies of two to five, connected by rhizomorphs on their lower surface which penetrate the wood. Several rhizomorphs 1-5 mm in diam originate from the base of each fruiting body (FIG. 12a). Some penetrate the substrate and others branch out and sometimes form a reticulum on the surface of

the substrate. At dehiscence, the volva is irregularly rent into four or more lobes at the apex (FIGS. 1b, c, 12b); the open volva is 4–5 mm in diam in the middle. The total height of the open mature fruiting body is 8–11 mm (FIGS. 1d, 12b). The length of the stalk free of the volva is 4–6 mm and the length of the receptacle is 3–4 mm (FIG. 1d). The lower part of the stalk is lacunose with transversely widened chambers having prominent edges. The chambers are deeper and better defined near the receptacle. The stipe is yellowish white. The stalk is 1 mm wide where it springs from the volva, 2.5 mm wide

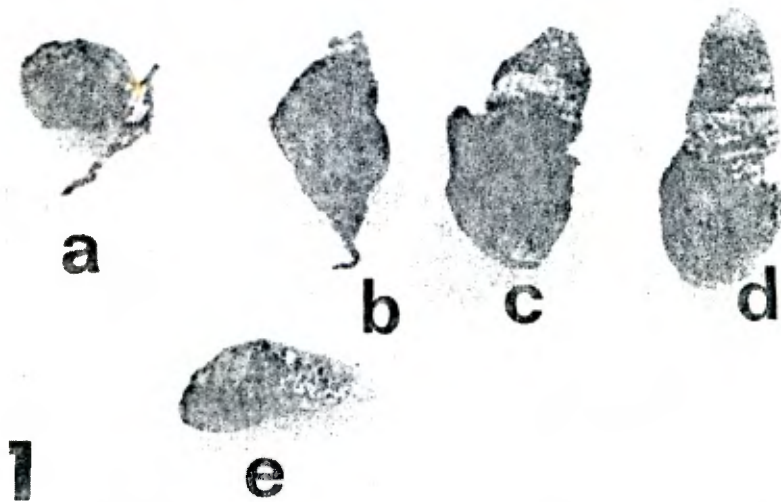
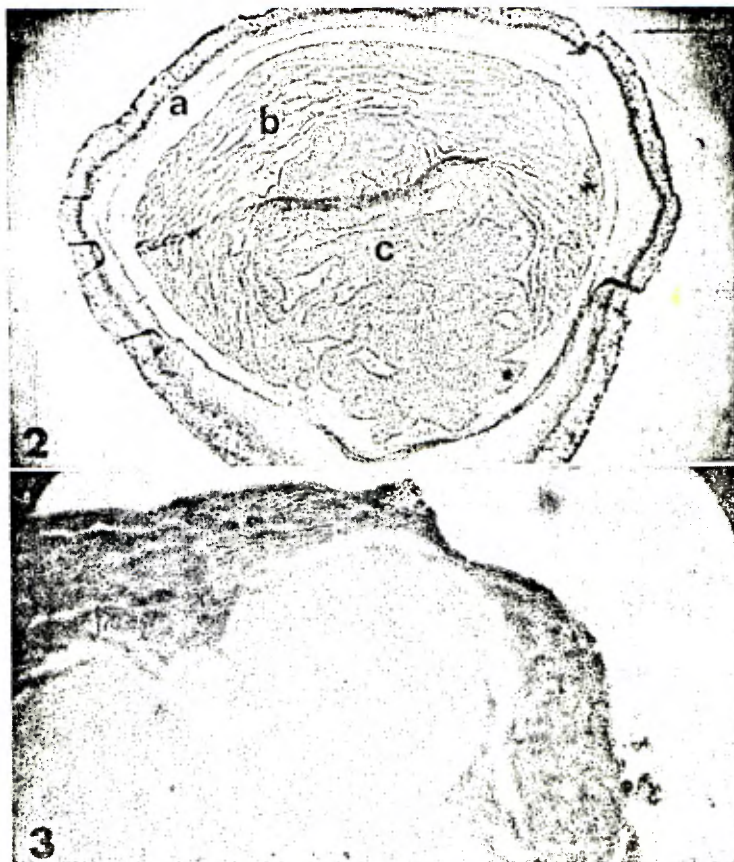


FIG. 1. *Xylophallus xylogenus*. Developmental stages: a. Unopened egg with rhizomorphs; b–d. Fruiting body; e. Fruiting body without volva; $\times 4$.

at the union with the receptacle (FIGS. 1c, e). The receptacle is almost smooth with some slight depressions, umbilicate at the apex, and definitely adnate to the stalk. At the lower part it is approximately 2–3 mm thick and at the apex 1 mm. The lower external edge is irregular and free. The gleba is a dark olive mass with a typical phalloid stink and covers the whole receptacle, including the apex (FIGS. 1c, 12b). Small Diptera were observed to crowd on it, and presumably disseminate the spores. The latter may also be dispersed by rain drops. When fully mature the gleba is sufficiently compact to be removed in large portions with a dissecting needle.

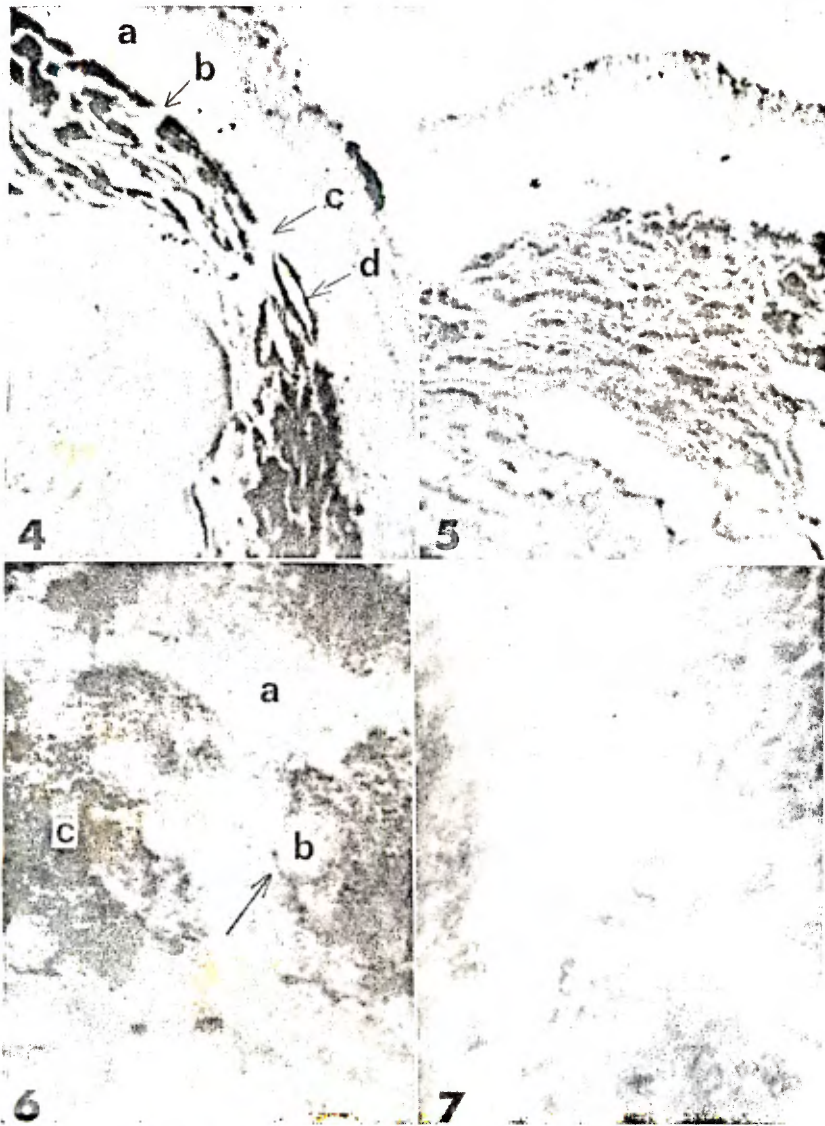
Anatomical description

Frechand sections of the eggs show the stalk to be definitely lacunose, with an axial tissue in the middle, the apex of the receptacle being covered by the gleba. The inner mucilaginous layer of the lower part of



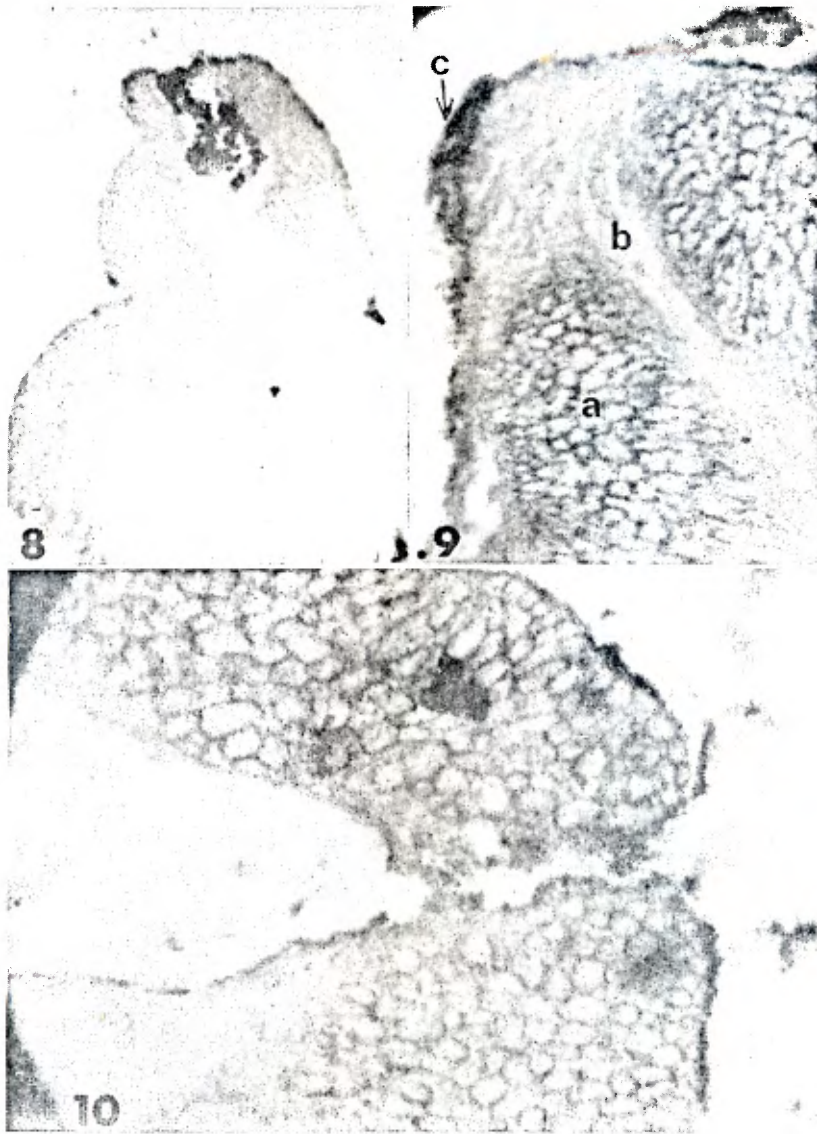
FIGS. 2-3. *Xylophallus xylogenus*. 2. Longitudinal section of immature egg: a. Volva layers; b. Gleba; c. Stalk and receptacle; $\times 130$. 3. Longitudinal section of a mature fruiting body with compressed gleba, $\times 66$.

the volva resembles the axial tissue in consistency and structure. Microtome sections of the immature egg show the volva to be composed of two or three distinct layers (FIGS. 2, 5). The outer layer is pseudoparenchymatous, with large cells having thick brown walls. The middle layer is also of pseudoparenchyma but with smaller cells having thinner



FIGS. 4-7. *Xylophallus xylogenus*. 4. a. Volva; b. "Veins" of gleba connecting with innermost layer of volva; c. "Veins" forming apparent connection between apex of the receptacle and volva, d. Lacunae of gleba; $\times 58$. 5. Lateral view of fruiting body showing volva and "veins" of lacunae, $\times 58$. 6. Gleba section: a. "Veins"; b. Basidium-like round structures; c. Spore masses in lacunae; $\times 500$. 7. Spores, stained, seen under phase contrast, $\times 1,250$.

walls. Although visibly different under the microscope, the layers intergrade gradually and might be considered a single layer. The innermost layer is continuous with "veins" that surround the lacunae of the gleba (FIGS. 4, 5, 6). The immature stalk and receptacle is three-fourths covered by the gleba (FIG. 2). At all ages, the main body of the stipe, including the receptacle, is pseudoparenchymatous. Internally, both stalk and receptacle show an axial prosenchymatous tissue which fills a number of chambers in both. In the mature fruiting body, the gleba is present as a continuous mass over the apex of the receptacle (FIGS. 1c, d, e, 3, 11). In microscopic sections, the gleba presents a lacunose structure, each cavity being delimited by plates or "veins" on both sides of which spores originate (FIGS. 2, 4, 5, 6). As the stalk grows the lacunae of the gleba are compressed, becoming lamellose (FIG. 3). No sections were found in this stage where the axial tissue passes through the gleba. Among the spores are many round green-staining structures 8–16 μ in diam, possibly basidia, and cells that stain light bluish green, possibly immature spores (FIG. 6). In eggs about to open we obtained longitudinal sections of the exact middle that showed the apical pore of the receptacle and the axial tissue that extends from the lower part of the apex of the receptacle under the gleba (FIGS. 9a, b, c). The pore is about 30 μ in diam. This has not been observed by other workers. The structure shown in FIG. 4 was found in only one specimen and may be considered atypical, although it is not easy to section the middle portion of each specimen. However, during development of the stalk the gleba is compressed against the unopened apex of the volva and there is always a thin layer of gleba between the volva and the axial tissue. Therefore, we consider this apparent connection to result from swelling of one of the "veins" or plates that connect the inner layer of the volva with the lacunose mass of the gleba (FIGS. 4, 5). Otherwise, completely developed fruiting bodies would have a glebal layer of uniform thickness throughout as shown in Fischer's FIG. B (8) and our FIG. 2. This is not the case according to our FIG. 3. Dr. D. M. Dring (personal communication) suspects that our FIG. 4 shows the last stage of the process by which the gleba extends over the top of the receptacle. Fischer's FIGS. B–C (8) suggest that no connection should exist at the stage shown in our FIG. 4. Some details of Fischer's FIG. B do not represent a young egg well, especially the relation between the gleba and the innermost volva layer, and the structure of the gleba itself which appears labyrinthine, whereas in our section the glebal cavities are tangentially enlarged and flattened. His FIG. C doesn't show the axial tissue reaching



FIGS. 8-10. *Xylophallus xylogenus*. 8. Section of old fruiting body free of gleba showing disintegration of axial tissue and particles of foreign matter within the pore, $\times 66$. 9. Section of egg about to open: a. Pseudoparenchyma of receptacle; b. Apical pore with axial tissue; c. Gleba; $\times 300$. 10. Enlargement of receptacle of FIG. 11 to show pore and spore mass within, $\times 210$.

either gleba or volva. Similar structures were found by us in sections of the rhizomorphs or in what we consider to be the younger fruiting bodies, although no gleba was evident. Study of fruiting bodies at proper stages are needed to determine if the gleba is actually formed

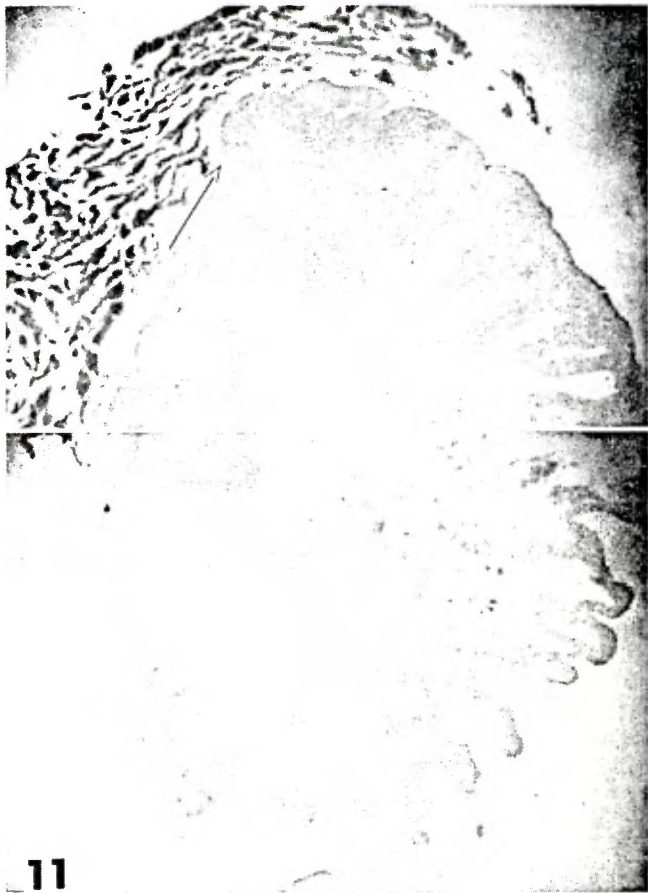


FIG. 11. *Xylophallus xylogenus*. Median longitudinal section of mature fruiting body free of volva, showing gleba above, receptacle and stipe with chambers, axial tissue partially disintegrated, and lateral pore (arrow), $\times 16$.

by a ring that later grows to cover the apex of the receptacle or if the gleba covers the apex of the receptacle from its origin. The axial tissue is a prosenchyma similar to the mucilaginous tissue of the inner layer of the volva. Sections of mature eggs without volva (FIG. 11)

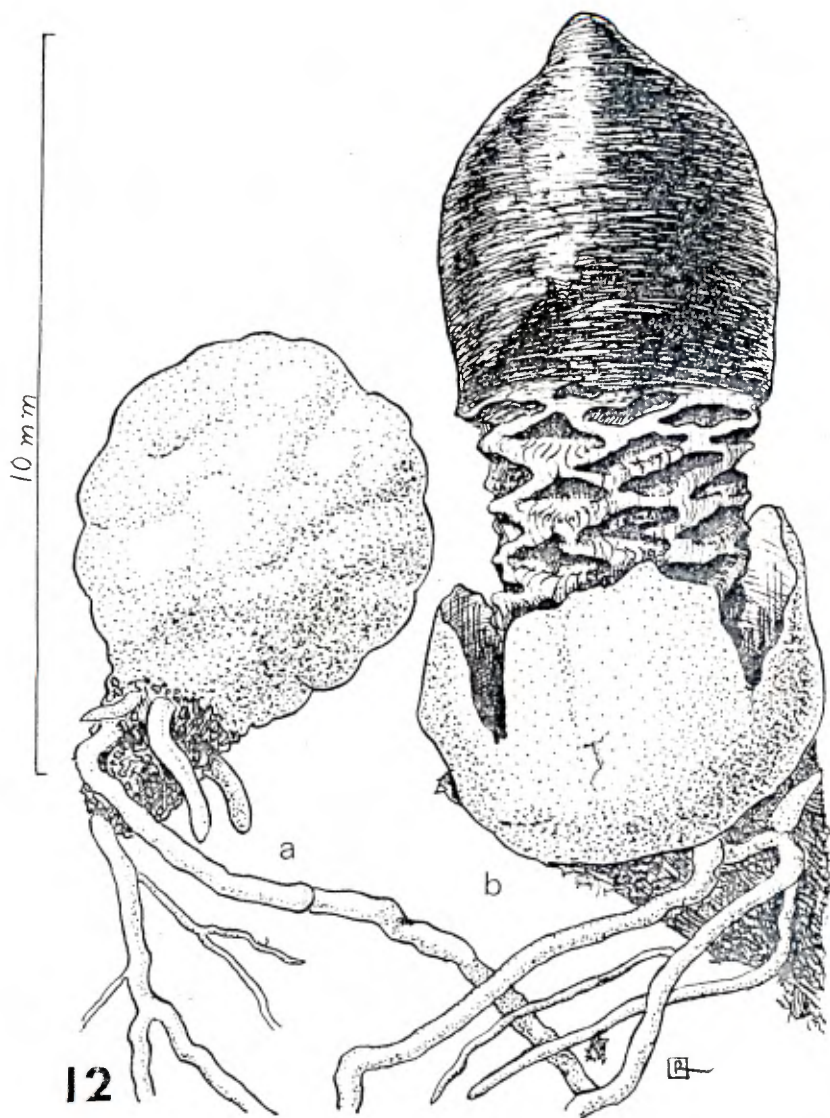


FIG. 12. *Xylophallus xylogenus*. a. Immature fruiting body with rhizomorphs; b. Mature fruiting body showing volva and rhizomorphs, chambered stalk, and gleba; $\times 12$.

show a lateral pore at the apex of the receptacle, and the lower stalk chambers open both outwardly and inwardly while those in the receptacle open only inwardly. The upper part of the receptacle shows, in advanced stages, a distinct pore approximately 100 μ in diam with axial tissue disintegrated. Thus, the pore becomes wider permitting penetration of particles of foreign matter (FIG. 10) clearly differentiated under the microscope. The externally modified receptacle and its slight depression are clearly seen in FIGS. 11 and 12b. The spores are hyaline, narrowly ellipsoid, $4-4.9 \times 1.5-2.8 \mu$. In fixed and stained preparations they are colorless except for a central, red-stained zone (FIG. 7). In fresh preparations mounted in Amann's lactophenol with cotton blue, most spores have two vacuoles near the poles, although one or three vacuoles are also occasionally seen. Since *Xylophallus xylogenus* is epixyloous, its gleba develops on a receptacle externally modified from the stipe, and the gleba covers the apex of the receptacle completely, it merits recognition in a genus separate from *Mutinus*.

ACKNOWLEDGMENTS

The authors wish to acknowledge Dr. Rafael Lucas Rodríguez for his encouragement, assistance in the translation of Fischer's papers, and for the drawing made for this paper; Dr. D. M. Dring for his valuable suggestions and critical review of the manuscript; and Dr. Ralph Emerson for providing a copy of Montagne's paper.

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THE MYXOMYCETES OF COSTA RICA¹

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SUMMARY

This is the first comprehensive paper on the Myxomycetes of Costa Rica encompassing a total of 91 species collected in that country between 1963 and 1967 by the second author and including a few specimens collected by others at approximately the same period of time. No new species are described but a few of those included have been rarely collected before anywhere. Thus, the specimen of Badhamia cinerascens Martin, is the second world collection of that species, and that of Lamproderma muscorum (Lev.) Hagelst. is one of the most typical of the species ever found. Other interesting finds include: Ceratiomyxa morchella Welden, Tubifera bombardia (Berk & Br.) Martin, Comatricha subcaespitosa Peck, the second collection of this species from the tropics, Physarum citrinum Schum. and Physarum dictyosporum Martin, the first collection of

¹Supported in part by United States National Science Foundation grants GB-2738, and GB-6812X1, X2, X3 to C. J. Alexopoulos.

this species outside the United States.

The genus *Diachea* is transferred to the Didymiaceae, following Farr's (1974) suggestion, supported by Blackwell's (1973, 1974) work.

INTRODUCTION

Relatively little is known about the Myxomycetes of Costa Rica. Although a few specimens have been collected in that country from time to time, most mycologists had largely neglected these organisms until Martin and Welden undertook an expedition to Panama and Costa Rica in the summer of 1952 and Welden (1954) published a list of Myxomycetes from these two countries in which he also included specimens which had been collected in Costa Rica by C. W. Dodge. Welden's paper lists 15 species from Costa Rica.

In 1963 a systematic study of the Myxomycetes of Costa Rica was begun by us, the second author being largely responsible for the collection of the specimens and the first largely responsible for their identification. Some specimens collected by Dr. George Carroll in 1962, by Dr. Bernard Lowy in 1964 and by Dr. E. F. Morris in 1966 are also included. A few of the specimens recorded were developed in moist chamber culture on tree bark, dead herbaceous stems, or other debris collected in Costa Rica by Dr. G. C. Carroll in 1964 and subsequently cultured at the University of Texas. The second author has continued collection, identification and moist chamber culture work and a second report will eventually be published elsewhere.

It will be noted that certain common species in such genera as *Licea*, *Calomyxa*, and *Echinostelium*, are absent from our list. These genera consist mainly of species with minute sporophores which are usually not detected in the field. Inasmuch as extensive moist chamber culture work was not undertaken in connection with this project such species were not observed. The classification adopted here is that of Alexopoulos (1973). Names of species are according to Martin and Alexopoulos (1969) and are arranged in alphabetical order under each genus. In the list of species reported below the collection locations are recorded with reference to the map (Figure 1) in which



I. SAN JOSE

1. San Pedro, Sabanilla, Cinco Esquinas, San Ramon de Tres Rios
2. Los Juncales
3. Electriona
4. Rio Claro
5. Villa Colon
6. San Isidro de Coronado
7. Santa Maria de Dota
8. San Marcos de Tarrazu
9. Santa Ana
10. Aserri, Vuelta de Jorco
11. San Isidro del General

II. ALAJUELA

12. Lagunas de San Isidro
13. Carrizal
14. Tacaes
15. Ciudad Quesada
16. San Matéo
17. Orotina
18. Atenas
19. Volcan Poas

III. CARTAGO

20. Orosi

21. El Empalme

22. Turrialba

23. Cerro de la Muerte

IV. HEREDIA

24. La Virgen de Sarapiquí

25. Rio La Hoja

26. Vara Blanca

27. Puerto Viejo de Sarapiquí

V. GUANACASTE

28. El Coto

29. Canas

30. Liberia

31. Santa Cruz

VI. LIMON

32. Siquires

37. Guapiles

VII. PUNTARENAS

33. Coto 47

34. Golfito

35. Palmar Sur

36. San Vito de Java

Figure 1. Map of Costa Rica showing provinces (Roman numerals) and localities (Arabic numerals) where specimens were collected.

the provinces of Costa Rica are designated by Roman numerals and the localities by Arabic numerals in parenthesis. Thus, Ceratiomyxa morchella Welden, for example, is recorded from Sarapiquí of Heredia and from Siquirres of Limón, designated in this paper as IV (27) and VI (32) respectively.

Specimens are deposited in the myxomycete collection of the University of Costa Rica at San José under UCR numbers and in the University of Texas Myxomycete Collection (TEX) under UTM numbers. Of a total of 91 species in this collection, 12 are listed by Welden from Costa Rica. Three of Welden's species, Badhamia decipiens (now Physarum decipiens), Diderma chondrioderma, and Comatricha aequalis are not included in our collection but are listed in this paper for the sake of completeness. This brings the total number of species now reported in the literature from Costa Rica to 94. In the list of species that follows, those preceded by an asterisk (*) have been reported from Costa Rica by Welden (1954). All others are new records for that country². No attempt was made to search the world herbaria for Costa Rican myxomycete specimens. It is probable that a number of additional species could be recorded if that were to be done.

LIST OF SPECIES

Subclass CERATIOMYXOMYCETIDAE Martin
In Ainsworth, Dict. Fungi, ed 5, 497. 1961.

Order C E R A T I O M Y X A L E S Martin, N. Am. Flora
1 (1):5. 1949.

Family CERATIOMYXACEAE Schroet., in Engler & Prantl,
Nat. Pfl. 1 (1):15. 1889.

²Most of the Costa Rica records in Martin and Alexopoulos (1969) refer to specimens in this collection.

Ceratiomyxa Schroet. in Engler & Prantl, Nat. Pfl. 1 (1): 16. 1889.

*1. Ceratiomyxa fruticulosa (Mull.) Macbr., N. Am. Slime-Moulds 18. 1899.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: Widespread and abundant. I (1), UCR-60 (TEX 418), 24 VI 1963; (7), UCR-127 (TEX 422), 9 VIII 1963; (8), UCR-259 (TEX 423), 5 XI 1964; (11), UCR-236 (TEX 424), 16 X 1964. III (21), UCR-66 (TEX 419), 28 VI 1963. IV (25), UCR-91 (TEX - specimen lost), 17 VII 1963. V (28), UCR-90 (TEX 420), UCR-95 (TEX 421), 19 VII 1963. VI, Welden, p. 96. All on dead wood.

COMMENTS: All specimens are typical of the species in the morphology of their fructifications and all but UCR-259 are of the arborescent type. In UCR-259 the fructification is sessile, the branches are very short, and the whole structure approaches the well-known porioides type. UCR-60, 90, and 259 are yellowish; all others are white. UCR-158 is an extensive group of robust, well-developed sporophores. The over-all range of spore dimensions is 6.5-7.5 μ m. Many of the spores are oval to subglobose. In UCR-259 the spores are in the upper part of the over-all size range given above.

2. Ceratiomyxa morchella Welden Mycologia 46:94, 1954.

KNOWN WORLD DISTRIBUTION: Panama, Honduras (TEX), Surinam, Venezuela, Puerto Rico, Florida (TEX).

COSTA RICA: IV (27), UCR-153 (TEX 426), 24 XI 1963. VI (32) UCR-225 (TEX 427), 2 X 1964. Both on dead wood.

Most of the fructifications in UCR-153 are typically morchelloid. The spores are 6-7.5 x 7.5-10.5 μ m. UCR-225, however, consists of one stipitate, morchelloid fructification, 3 sessile, circular somewhat flattened fruiting bodies, and one larger body 4.5 x 1 mm at its widest point which closely resembles the porioides form of C. fruticulosa. Furthermore, in spite of the fact that the range in spore size does not differ appreciably from what is expected, the majority of spores are in the upper limits of the range. It will be recalled that this was also the

case with C. fruticulosa UCR-259 which approached the porioides form.

Specimens like UCR-225 cast some doubt on the validity of C. morchella as a good species, but until many more collections are available for extensive comparative studies, it is thought best to recognize the species. Contrary to C. fruticulosa, C. morchella and C. sphaerosperma have been found only in wet, hot lowlands (100-300 m).

*3. Ceratiomyxa sphaerosperma Boedjin, Misc. Zool. Sumatrana 24:1, 1927.

KNOWN WORLD DISTRIBUTION: Sumatra, Krakatoa, Panama Canal Zone, Dominica, Jamaica, Brazil, ?Spain.

COSTA RICA: IV (27), UCR-319 (TEX 1451), 10 VI 1966. On dead wood. VI, Castilla, C. W. Dodge 9238, 23 VII 1936.

The fructifications are typical of the species. The spores are spherical or subspherical, 6-7 μ m diam.

Subclass MYXOGASTROMYCETIDAE Martin

In Ainsworth, Dict. Fungi, ed. 5. 497. 1961. Emend Ross, Mycologia 65:483. 1973.

Order L I C E A L E S Jahn, in Engler & Prantl, Nat. Pfl., ed. 2, 2:319. 1928.

Family RETICULARIACEAE Rost, Versuch 6. 1873 (as Tribus).

Tubifera J. F. Gmelin, Syst. Nat. 2:1472. 1791.

1. Tubifera bombardata (Berk. et Br.) Martin, Brittonia 13: 210. 1961.

KNOWN WORLD DISTRIBUTION: Ceylon, Malaya, Sumatra, Philippines (TEX 1682), Puerto Rico, Jamaica, Brazil.

COSTA RICA: I (1), UCR-126 (TEX 431), 7 VIII 1963. II (22) UCR-193 (TEX 438), leg.: B. Lowy, 25 VI 1964; (21) UCR-257 (TEX 437), 6 XI 1964. All on dead wood.

The sporangia of UCR-193 are typical and the pseudocapillitial bristles bear the spine-like protuberances; the spores measure 6-6.5 μm and their surfaces are definitely reticulate. UCR-126 and 257 represent an interesting variant. We place them here chiefly because of their long stipes on which the sporangia are borne. The fructifications, up to 5 mm tall, consist of from 7 to 20 sporangia, all on long stalks which are firmly united 2/3 to 3/4 of their length, but are separate at the top. The sporangia are ovate-cylindrical, with membranous peridia which are evanescent at the top. No pseudocapillitium is evident in any of the sporangia examined. Even those in which the peridium is still intact contain no bristles or other material except spores. Martin (1961) in reducing Alwisia to a synonym of Tubifera, noted that a Jamaican specimen at IF and IA lacks bristles. The spores of UCR-257 are definitely reticulate over most of the surface exhibiting a broken reticulation over about 1/4 of the wall. They measure 6.5-7 μm in UCR-126 and 6-6.75 μm in UCR-257. Dr. Martin, who kindly examined UCR-257, concurred with our determination.

2. Tubifera ferruginosa (Batsch) J. F. Gmel, Syst. Man. 2:1472. 1791.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (6), UCR-85 (TEX 429), 9 VII 1963. On dead wood. UCR-109 (TEX 436), 3 VIII 1963. III (21), UCR-63 (TEX 2256), 28 VI 1963. On mossy wood.

All three of these collections might represent sessile phases of T. microsperma except for the size of the spores. Each fructification consists of numerous, crowded, cylindrical sporangia tapering down to a stalk-like base. The fructification as a whole, however, unlike those in UCR-40, 43, and 78 (see next species below) in no case rests on a stalk-like hypothallus. The spores are strongly reticulate over at least one half and up to the entire surface and measure 6-6.5 μm being remarkably uniform in size. Such

specimens are intermediate between T. ferruginosa and T. microsperma and throw doubt on the validity of the characters separating the two species.

3. Tubifera microsperma (Berk. & Curtis) Martin, Mycologia 39:461. 1947.

KNOWN WORLD DISTRIBUTION: North and South America, West Indies, Hawaii, Tropical Asia, Japan.

COSTA RICA: I (1), UCR-40 (TEX 430), 4 VI 1963, on dead wood; (5) UCR-78 (TEX 433), 3 VII 1963, on mossy dead wood. II (12), UCR-43 (TEX 434), 1 VI 1963, on dead wood.

If we are to recognize this species, these three collections fit perfectly in that all the fructifications have a conspicuous stalk-like hypothallus and the spores measure 5-6 μm diam.

Dictydiaethalium Rost., Versuch 5, 1873.

1. Dictydiaethalium plumbeum (Schum.) Rost., in Lister, Mycet. 157. 1894.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-59 (TEX 440), 23 VI 1963. IV (25), UCR-92 (TEX 432), 15 VII 1963. V (29), UCR-100 (TEX 439), 19 VII 1963. VII (35), UCR-308 (TEX 1450), 10 XI 1965. UCR-92 on bark; all others on dead wood.

All four collections are typical of the species, but UCR-59 is imperfectly matured. The pseudoaethalia of UCR-92 are dark chocolate-brown whereas in UCR-100 and 308 the color is more yellow-brown. The pseudocapillitial threads are 4-4.5 μm thick. The spores measure 9.5-10.5 μm diam. They are bright yellow in mass, pale yellow by transmitted light, with conspicuously thick, minutely roughened walls.

Lycogala Adans., Fam. Pl. 2:7. 1763.

1. Lycogala epidendrum (L.) Fries, Syst. Myc. 3:80. 1829.

KNOWN WORLD DISTRIBUTION: Cosmopolitan

COSTA RICA: Widespread and abundant. I (1), UCR-97 (TEX 443), 29 VII 1963; UCR-230 (TEX 445), 3 X 1964; (5), UCR-69 (TEX 441), UCR-70 (TEX 442), 3 VII 1963. III (20), UCR-8 (TEX 2255), 20 V 1963; (22), UCR-222 (TEX 444) 1 X 1964. VII (35); San Vito de Java, E. F. Morris #957 (TEX 1991), 13 III 1966. UCR-70 on bark; all others on dead wood.

COMMENTS: All 7 collections of this ubiquitous species are typical, with no more than expected variation in aethalial size, color, and markings. The spores in Nos. 8 and 230 measure 6-7.5 μm whereas those of the other specimens are smaller; 5.5-6.5 μm .

2. Lycogala exiguum Morgan, Jour. Cinc. Soc. Nat. Hist. 15:134. 1893.

KNOWN WORLD DISTRIBUTION: Cosmopolitan, especially in the tropics.

COSTA RICA: VII (35), UCR-311 (TEX-1444), 19 XI 1965.

COMMENTS: This species is usually easily identified by its dark, almost black aethalia and especially by the tessellate pustules on the peridium. The spores of the present specimen are somewhat on the large side, measuring 5.5-6.0+ μm . They are, however, warted rather than reticulate as in L. epidendrum. UCR-97 (see previous species) is close to L. exiguum because of its dark aethalia, its tessellate pustules and its non-reticulate spores. The latter, however, measure over 6 μm in diameter and on that basis we leave it in L. epidendrum. Such intermediate forms tend to confuse the issue and one is unable to draw a clear cut line between the two species.

Family CRIBRARIACEAE Rost. Versuch. 5. 1873.

Cribraria Pers., Neues Mag. Bot. 1:91. 1794.

The genus Cribraria is in great need of thorough revision. None of the existing keys is satisfactory and the characters of so many of the described species overlap that correct identification has become extremely difficult.

Unfortunately, no Cribraria has been grown in laboratory culture and it is impossible, therefore, to study the stability and consequently the validity of the characters used in separating species. In spite of this well-nigh chaotic situation, new species and even varieties continue to be described! The following identifications represent our best judgment, but in view of the above must be considered tentative.

1. Cribraria intricata Schrad., Nov. Grn. Pl. 7. 1797.

KNOWN WORLD DISTRIBUTION: Cosmopolitan

COSTA RICA: I (9), UCR-136 (TEX 2263), 20 IX 1963. II (15), UCR-201 (TEX 849), 24 IX 1964. IV (24), UCR-156 (TEX 2259), UCR-157 (TEX 843), 24 XI 1963; (27), UCR-322 (TEX 2262), 10 VI 1966. All on dead wood.

COMMENTS: Most specimens fit the description given by Martin & Alexopoulos (1969) as well as any Cribraria specimens fit any published description. The sporangia vary from .5 to .75 μ m in diameter and the stalks from 1.5 to 2.5 mm in height. The cup is represented by a thin, membranous, small disc. The nodes are expanded with several free ends. UCR-156 approaches C. splendens because of the strong ribs, but the stalks are longer and the sporangia smaller than is generally true for that species.

2. Cribraria languescens Rex, Proc. Acad. Phila. 43:394. 1891.

KNOWN WORLD DISTRIBUTION: North America, West Indies, Europe, Asia, Africa.

COSTA RICA: I (2), UCR-110 (TEX 838), 3 VII 1963; (1) UCR-196 (TEX 2264), 11 IX 1964; (10) UCR-148 (TEX 840), 4 X 1963. IV (26), UCR-103 (TEX 837), 29 VII 1963. IV (25), UCR-266 (TEX 847), 17 IX 1965. VII (35), UCR-309 (TEX 789), 19 XI 1965. All on dead wood.

COMMENTS: There is considerable variation in these specimens. The diameter of the sporangia varies from .3 to .56 mm, and the stalks are much shorter in UCR-110, 148, and, to a lesser extent, in UCR-266, than usually described for this species. The color of the sporangia also deviates in many instances from the typical. Those of UCR-266,

for example, are very dark. Until we have a better understanding of this genus, all these specimens must be placed in C. languescens.

3. Cribraria microcarpa Schrad., Nov. Gen. Pl. 8. 1797.

KNOWN WORLD DISTRIBUTION: Europe, N. America, West Indies, Colombia, Brazil.

COSTA RICA: I (4), UCR-56 (TEX 841), 21 V 1963. II (14), UCR-131 (TEX 851), 17 VIII 1963. Both on dead wood.

COMMENTS: UCR-56 is a rather typical specimen. UCR-131, on the other hand, exhibits great variation in sporangial diameter and in sporangium:stalk relationship. At first glance the specimen appears to be a mixture of two species, but we believe it is all C. microcarpa.

4. Cribraria minutissima Schw., Trans. Am. Phil. Soc. II, 4:260. 1832.

KNOWN WORLD DISTRIBUTION: U.S.A., West Indies, Uruguay, Brazil, Europe, Hawaii, Asia.

COSTA RICA: V (31), UCR-91 (TEX 852), 18 VI 1964. On dead wood.

COMMENTS: Whether this specimen is indeed C. minutissima or whether it represents an undescribed species is difficult to determine because of the very small number of sporangia at hand, none of which is intact. The overall height of the sporangia does not exceed .37 mm high and the sporangium about .13-.14 μm diam. The cup is represented by a minute membranous disc. The peridial net consists of even threads connected by small, flat, scarcely expanded nodes, and forming mostly pentagonal regular meshes. There are no free ends. The spores measure 6 μm .

5. Cribraria splendens (Schrad.) Pers., Syn. Fung. 191. 1801.

KNOWN WORLD DISTRIBUTION: Europe, N. America, West Indies, Brazil, Asia.

COSTA RICA: I (2), UCR-111 (TEX 790), 3 VII 1963; (7), UCR-122 (TEX 848), 9 VIII 1963; (8) UCR-258 (TEX 2261),

5 XI 1964. IV (24), UCR-155 (TEX 853), 24 XI 1963. All on dead wood.

COMMENTS: All these are probably C. splendens, but in UCR-111 the sporangia are smaller than usual and the nodes are somewhat thickened. UCR-155 is the specimen most typical of the species.

6. Cribraria tenella Schrad., Nov. Gen. Pl. 6. 1797.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-207 (TEX 844), 28 X 1964, UCR-247 (TEX 845), 26 X 1964, UCR-99 (TEX 791), 27 VII 1963; UCR-46b (TEX 2265), 8 VI 1963. III (22), UCR-221 (TEX 846), 1 X 1964. II (14), UCR-132 (TEX 850) 17 VIII 1963. All on dead wood.

COMMENTS: Of the six, UCR-99 is probably the most typical but all deviate in some character from the description. UCR-207 approaches C. languescens. In UCR-132 there are a number of free ends in the peridial net.

7. Cribraria violacea Rex, Proc. Acad. Sci. Phila, 43:393. 1891.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-1145, 16 IV 1971, on dead wood. Locality unknown, TEX-842, summer 1964, leg. G. C. Carroll, on bark. Both developed in moist chamber.

COMMENTS: The color and the minuteness of the sporophores make this species unmistakable.

Dictydium Schrad., Nov. Gen. Pl., 11. 1797.

*1. Dictydium cancellatum (Batsch) Macbride

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: Widely distributed and abundant. I (1), UCR-68 (TEX 824), 2 VII 1963; UCR-48 (TEX 825), 8 VI 1963; (6), UCR-86 (TEX 826), 9 VII 1963. III, (20), Welden, p. 96, UCR-19 (TEX 822), 20 V 1963. II (12), UCR-33 (TEX 823), 1 VI 1963. IV (24), UCR-152 (TEX 827), 24 XI 1963. All on dead wood.

COMMENTS: All specimens are typical and remarkably uniform with only very minor variations. In UCR-33 the sporangia are a trifle smaller and the spores somewhat larger than in the other specimens.

Order E C H I N O S T E L I A L E S Martin, Mycologia
52:127. 1960.

Family CLASTODERMATACEAE Alexopoulos & Brooks, Mycologia
63:926. 1971.

Clastoderma Blytt, Bot. Zeit. 38:343. 1880.

1. Clastoderma debaryanum Blytt, Bot. Zeit. 38:343. 1880.

KNOWN WORLD DISTRIBUTION: Probably cosmopolitan, abundant in the tropics.

COSTA RICA: I (1), UCR-195 (TEX 2254), 11 IX 1964, on bark covered with lava dust. Locality not recorded, UCR-105 (TEX 2173), July 1963, developed in moist chamber on bark from unidentified tree, collected July 1963 and cultured in Austin, Texas. Sporangia formed on filter paper in August 1964 and September 1965.

COMMENTS: Our specimens represent an interesting but not very rare variation from the typical in that the prominent, oval, amber-like swelling which usually divides the two portions of the stipe, is absent from all our sporangia.

Order T R I C H I A L E S Macbride, N. Am. Slime-Moulds,
ed. 2. 237. 1922.

Family TRICHIACEAE Rost., Versuch 14. 1873 (as tribus).

Perichaena Fries, Symb. Gast. 11. 1817.

1. Perichaena chrysosperma (Currey) Lister

KNOWN WORLD DISTRIBUTION: Cosmopolitan

COSTA RICA: II (13), UCR-104 (TEX 830), 30 VII 1963.

COMMENTS: This specimen consists of several typical sporangia and plasmodiocarps on bark. Most plasmodiocarps are doughnut-shaped.

2. Perichaena depressa Lib., Pl. Crypt. 378. 1837.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: Locality unknown, G. C. Carroll #3, (TEX 1452), summer 1964. On plant debris in moist chamber.

COMMENTS: This is a typical specimen.

Arcyria Wiggers, Prim. Fl. Holsat. 109. 1780.

*1. Arcyria cinerea (Bull.) Pers. Syn. Fung. 184. 1801.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: Widely distributed and abundant. I (1) UCR-41 (TEX 807), 4 VI 1963, UCR-113 (TEX 809), 5 VII 1963. II (12), UCR-32 (TEX 810), 1 VI 1963; (14), UCR-129 (TEX 805), UCR-133 (TEX 803), 17 VIII 1963; (15), UCR-197 (TEX 804), 24 IX 1964. V (28), UCR-93 (TEX 808), 19 VII 1963; (31), UCR-192 (TEX 812), 20 VI 1964. VII (34), Welden, p. 96, UCR-303 (TEX 811), UCR-315 (TEX 806), 16 XI 1965. IV (27), TEX 859, G. C. Carroll # CR-2, 11 VI 1962, UCR-326, 10 VI 1966.

COMMENTS: This is an extremely variable species. In color, the sporangia range from ashy gray, almost white, to a decidedly yellowish hue; in shape, from ovate to long cylindrical when mature. The capillitium is usually distinctly spiny. The so-called digitate form was described by Schweinitz in 1832 as a distinct species, A. digitata, but all modern authors agree it is only a variation of A. cinerea particularly common in the tropics. Inasmuch as, in many fruitings, single sporangia are usually mixed with those united on a common stalk, it appears that a single plasmodium may give rise to both forms. It is of interest to note, however, that we have never been able to germinate spores from digitate fruitings whereas we have often obtained cultures by sowing spores from single sporangia on agar. Nevertheless, Mims (personal communication) noted the formation of some digitate fruitings in agar cultures obtained by sowing

spores from single sporangia collected by one of us (C.J.A.) in Hawaii. Thus, we have experimental as well as circumstantial evidence that the two forms (single and digitate) are the same species.

From the specimens at hand, UCR-32, 93, 113, 197, and 303 are cinereous, whereas UCR-41, 129, 133, 192, and 315 show various amounts of a creamy or yellowish color. In all but UCR-315 the sporangia are cylindrical; in UCR-315 they are mostly globose to ovate. They vary in length from .25 mm to 1.5 mm in UCR-315 to as long as 3 mm in UCR-303. These measurements do not include the stalk. UCR-133 and 303 are typically digitate forms with few if any single sporangia present. Most of the other collections are mixed digitate and simplex with only UCR-315 consisting of only single sporangia. This is in accordance with the well known observation that the digitate form is more prevalent in the tropics.

*2. Arcyria denudata (L.) Wettst. Verh. Zool.-Bot. Ges. Wien 35:abh. 535. 1886.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: Widespread and common. I, Welden, p. 97, (1), UCR-21 (TEX 817), 21 V 1963, UCR-27 (TEX 814), 21 V 1963; (5), UCR-72 (TEX 813), UCR-79 (TEX 815), 3 VII 1963; (6), TEX 858, collected by G. C. Carroll # GC-1 12 VI 1962. II (12), UCR-34 (TEX 816), 1 VI 1963; (14), UCR-130 (TEX 818), 17 VIII 1963. III (20), UCR-7 (TEX 820), 20 V 1963. IV (27), UCR-321 (TEX 1449), 10 VI 1966. V (30), UCR-101 (TEX 821), 19 VII 1963. VI, Welden, p. 97. VII (34), E. F. Morris #970 (TEX 1996), 16 III 1966.

COMMENTS: The color of the sporangia in the various collections varies from bright rose in UCR-79 to a light chocolate brown in UCR-72. UCR-79 approaches Hagelsteins' (1929) variety dispersa of A. insignis. The sporangia are bright rose, somewhat smaller than in typical A. denudata and scattered. Nevertheless, we believe that the specimen is better referred to A. denudata. UCR-72 on mossy wood; UCR-7, 21, 27, 34, and 79 on dead wood; UCR-101, 130 and GC #1 on bark.

3. Arcyria incarnata Pers., Obs. Myc. 1:58, 1796.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-178 (TEX 829), 5 VI 1964. V (31), UCR-184 (TEX 828), 20 VI 1964.

COMMENTS: This is much less common than the previous species. Both specimens are typical. UCR-178 on bark, UCR-184 on dead wood.

4. Arcyria insignis Kalch. & Cooke, in Kalchbr., Grevilia 10:143. 1882.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-25 (TEX 857), 22 V 1963. III (22), UCR-219 (TEX 856), 1 X 1964. Both on dead wood.

COMMENTS: The chief differences between this species and A. denudata are color and size of sporangia and size of sporangial groupings. Except in relatively rare instances the two species may be distinguished easily. Both our specimens are typical of A. insignis. Reference has already been made to UCR-79 which we placed in A. denudata. This represents a form intermediate between the two species.

5. Arcyria leiocarpa (Cooke) Martin & Alexop. The Myxomycetes 131. 1969.

KNOWN WORLD DISTRIBUTION: U.S.A., Panama, Colombia, Scotland, Czechoslovakia.

COSTA RICA: II (Finca los Ensaynos de Buena Vista), summer 1964. In moist chamber culture on debris collected by George Carroll.

COMMENTS: Only three sporangia developed in the culture but were typical of this species. Unfortunately, the specimen was overrun with mold and was discarded. There is, therefore, no voucher available.

6. Arcyria magna Rex, Proc. Acad. Phila. 45:364. 1893.

KNOWN WORLD DISTRIBUTION: N. America, Panama, Brazil, Philippines, Thailand.

COSTA RICA: V (31), UCR-187 (TEX 1440), 18 VI 1964.

COMMENTS: The specimen is not typical of the species chiefly because of the small cluster of the sporangia. The fruiting mass is dingy yellow to olivaceous but the spores are dull rose in mass. The capillitium bears cogs, half-rings and spines. Although its distribution is wide in the Western Hemisphere, A. magna is not commonly found. Dr. Marie L. Farr concurs with our identification.

Hemitrichia Rost., Versuch. 14. 1873.

*1. Hemitrichia calyculata (Speg.) Farr, Mycologia 66:887. 1974.

This species is usually reported as H. stipitata (Masse) Macbr. It is under this name that our specimens are filed.

KNOWN WORLD DISTRIBUTION: Cosmopolitan and common. Abundant in the tropics.

COSTA RICA: I, Welden, p. 97; (1), UCR-53 (TEX 1361), 8 VI 1963, UCR-57 (TEX 1358), 24 VI 1963, UCR-204 (TEX 1363), 28 IX 1964; (5), UCR-75 (TEX 1360), UCR-76 (TEX 1359), 3 VII 1963. II (12), UCR-31 (TEX 1426), 1 VI 1963; (15) UCR-203 (TEX 1429), 24 IX 1964. III, Welden, p. 97; (20), UCR-9 (TEX 1423), UCR-10 (TEX 1424), UCR-17 (TEX 1425), 20 V 1963; (22), UCR-231 (TEX 1430), 1 X 1964, E. F. Morris #901 (TEX 1995), 18 II 1966. IV, Welden, p. 97; (24), UCR-160 (TEX 1362), 24 XI 1963. VI, Welden, p. 97. VII, Welden, p. 97; (34), UCR-314b (TEX 1432), 16 XI 1965. All on decaying wood.

COMMENTS: In its typical expression, H. calyculata exhibits a slender, dark brown, almost black, stalk which may reach a length of 2 mm, as in UCR-231, and which terminates abruptly at the base of a shallow cup with sides at an obtuse angle. The capillitial threads are essentially smooth and the spores are bright yellow, unevenly spinulose, and 7.5-9 μ m diam. However, most of these characters vary considerably even in the same collection and this variation has caused Lister (1894, 1911, 1925) and Hagelestein (1944) to consider this species synonymous with H. clavata which it admittedly resembles. Unpublished electron micrographs, however, bring out some

interesting differences in the capillitia of the two species which appear to be, for the most part, constant. Lister and Hagelstein (loc. cit.) believe H. calyculata to be an environmentally induced variant of H. clavata, developed under conditions of high temperature. It is of interest in this connection that H. calyculata is abundant in the tropics as well as in the temperate zones whereas H. clavata is found only in the temperate zones (Martin & Alexop., 1969).

Until experimental cultural studies are conducted to determine the effect of the environment at the time of sporulation on the taxonomic characters of the Myxomycetes, these questions will not receive a definitive answer. Unfortunately, neither H. calyculata nor H. clavata has been grown in laboratory culture.

In the specimens at hand, the stalks vary from light yellow-brown to almost black and from .45 mm or shorter to 2 mm. They terminate abruptly at the base of a more or less shallow cup in most specimens, but some sporangia in UCR-9, 31, 53, and 203 have short stalks which merge with the bases of the rather deep cups approaching the situation in H. clavata. The capillitium is nearly smooth in most specimens but distinctly roughened in UCR-9, 31, and 203. In spite of these variations, it seems best to include all specimens in H. calyculata.

2. Hemitrichia serpula (Scop.) Rost. in Lister Mycet. 179. 1894.

KNOWN WORLD DISTRIBUTION: Cosmopolitan; abundant in the tropics.

COSTA RICA: III (20), UCR-20 (TEX 1418), 20 V 1963; IV (26), UCR-102 (TEX 1418), 29 VII 1963; El Roble, UCR-108 (TEX 1420), 30 VII 1963. V, near Laguna de Arenal, E. F. Morris #982 (TEX 1998), 22 III 1966. VII (34), UCR-314a (TEX 1431), 16 XI 1965. UCR-20 and 108 on plant debris; UCR-314a and Morris 982 on decaying wood; UCR-102 on bark.

COMMENTS: This easily recognized species is widely distributed and quite constant in its characters. All specimens in our collection are typical except for the diameter of the capillitial threads which tends to be greater than that given in the various monographs, reaching, in most of

our specimens 7.5 μ m. This and other species of Myxomycetes are often parasitized by a fungus (Stilbella sp.) which produces its synnemata on the surface of the fructifications as in our UCR-108.

Metatrichia Ing, Trans. Brit. Mycol. Soc. 47:51. 1964.

1. Metatrichia vesparium (Batsch) Nann.-Brem. K. Ned. Akad. Wet. C. 69:146. 1966.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-227 (TEX 1366), 9 X 1964; (3), UCR-44 (TEX 1364), 8 VI 1963; (9), UCR-268 (TEX 1367), 27 V 1965. II (22), UCR-214 (TEX 1365), 1 X 1964. VII (33), UCR-290 (TEX 1368), 17 XI 1965. All on decaying wood.

COMMENTS: This very common and easily recognized species usually occurs in two forms: 1) as short-stalked or sessile sporangia crowded into large clusters (pseudo-aethalia), as in UCR-44 and 268, and 2) as polycephaloid, long-stalked pseudoaethalia in which the stalks of many sporangia are completely fused as in UCR-214, 227, and 290. One would be tempted to recognize these two forms as distinct varieties were it not for their occurrence side by side in some fruitings and together with a few individual sporangia. UCR-290 is not mature.

Trichia Haller, Hist. Stirp. Helv. 3:114. 1768.

1. Trichia decipiens (Pers.) Macbr., N. Am. Slime Moulds 218. 1899.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I, (Finca La Azucena, Carretera Panamaerica), UCR-297 (TEX 1407), 19 XI 1965. On decaying wood.

COMMENTS: The single specimen in our collection is typical of the species.

2. Trichia favoginea (Batsch) Pers., Neues Mag. Bot. 1:90. 1794.

KNOWN WORLD DISTRIBUTION: Throughout the temperate zone but also known from the tropics.

COSTA RICA: I (8), UCR-254 (TEX 1409), 5 XI 1964, on bark. III (23), UCR-241 (TEX 1408), 17 X 1964, on bark among Bryophytes.

COMMENTS: Although most spores observed exhibit a rather typical complete reticulation, in some spores of both specimens the reticulation is broken or incomplete. It is chiefly on the nature of the reticulation that T. favoginea was formerly separated from T. persimilis until Farr's (1958) study pointed out the great variability of this character and placed T. persimilis and T. affinis in synonymy with T. favoginea. It is possible, of course, that such variation may represent genetic segregation of possible hybrids between two extreme forms, but until experimental evidence to the contrary becomes available, we are accepting Farr's conclusions.

3. Trichia floriformis (Schw.) G. Lister, Jour. Bot. 57: 110. 1919.

KNOWN WORLD DISTRIBUTION: Widely distributed in all continents but Africa from where it has not yet been reported. In the Caribbean area, known only from Puerto Rico and Jamaica.

COSTA RICA: I (7), UCR-119 (TEX 1911), 9 VIII 1963. IV (25) UCR-96 (TEX 1410), 27 VII 1963. Both on bark.

COMMENTS: Trichia floriformis may be recognized by the petaloid dehiscence of the sporangia, the deep red color of the stalks and the capillitium, and the reddish spores. In a general way it resembles T. botrytis to which it is probably most closely related. The latter has not as yet been found in Costa Rica and, indeed, appears to be rare in the tropics. The T. floriformis sporangia of our specimens are black, which is often the case.

4. Trichia scabra Rost., Mon. 258. 1875.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (7), UCR-118 (TEX 1413), 9 VIII 1963. IV (25), UCR-143 (TEX 1414), 9 XI 1963, both on dead wood.

COMMENTS: All spores examined bear a definite reticulation, at least on one hemisphere and often over the entire surface. Some spores appear oval or slightly turbinate and measure 10 x 12.5 μ m.

5. Trichia varia (Pers.) Pers., Neues Mag. Bot. 1:90. 1794.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (11), UCR-234 (TEX 1415), 16 X 1964. IV (25), UCR-167 (TEX 1412), 9 IV 1964, on stroma of ascomycete.

COMMENTS: Both are typical specimens, although some elaters appear to have three rather than two spiral bands. UCR-167 was determined by Dr. Marie L. Farr.

6. Trichia verrucosa Berk., in Hook, f. Tasm. 2:269. 1859.

KNOWN WORLD DISTRIBUTION: Tasmania, New South Wales, Europe, U.S.A., Mexico, Dominica, Jamaica, South America.

COSTA RICA: I (8), UCR-253b (TEX 1417), 5 XI 1964, on bark.

COMMENTS: Although widely distributed this species is not so common as some of the other Trichias. Our collection consists of three clusters of sporangia interspersed among many fine sporangia of Physarum tenerum (UCR-252a). The material is in all ways typical.

Order P H Y S A R A L E S Macbride, N. Am. Slime-Moulds ed. 2. 22. 1922.

Family PHYSARACEAE Rost., Versuch. 9. 1873. (as tribus).

Cienkowskia Rost., Versuch. 9, 1873.

1. Cienkowskia reticulata (Alb. & Schw.) Rost. Mon. 91. 1874.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: III (21), UCR-62 (TEX 1447), 28 VI 1963, on dead wood.

COMMENTS: A collection of many sporophores ranging from .5 mm spheres to 6 mm long, straight or sinuous plasmodiocarps. The peridium is covered with a thick incrustation of yellow lime on which tomato-red glossy spots are scattered. The duplex nature of the capillitium is evident but the spiny branches of the tubules are not so numerous as they are usually.

Physarella Peck, Bull. Torrey Bot. Club 9:61. 1882.

1. Physarella oblonga (Berk. & Curtis) Morgan Jour. Cinc. Soc. Nat. Hist. 19:7. 1896.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-28 (TEX 1437), UCR-38 (TEX 1438), 28 V 1963, UCR-50 (TEX 1439), 8 VI 1963. All on dead wood.

COMMENTS: Of our three specimens only UCR-50 is in good condition, the other two having fruited on decaying wood encrusted with lava dust which crumbles and results in the destruction of most sporangia thereon.

Badhamia Berk., Trans. Linn. Soc. 21:153. 1853.

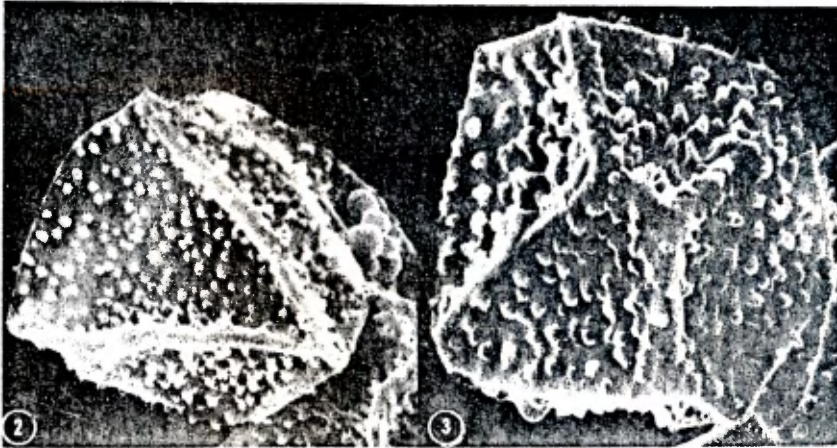
1. Badhamia cinerascens Martin, Jour. Wash. Acad. 22:88. 1932.

KNOWN WORLD DISTRIBUTION: Colombia.

COSTA RICA: III, UCR-13 (TEX 2105), 11 V 1965. On bark. (Authentic specimen).

COMMENTS: This is the second world collection of this species reported in the literature and is the only specimen of a Badhamia from Costa Rica in our collection. Dr. G. W. Martin, who first described this species, concurred with our identification, noting, however, that ". . . the Costa Rican collection is more limy than the type and the spores somewhat smaller, but I can regard neither character as significant . . . Certainly I cannot assign your specimen

to anything but *B. cinerascens*." Figures 2 and 3 are presented as further evidence in support of our identification.



Figures 2-3. Scanning electron micrographs of the spores of *Badhamia cinerascens* Martin.
 Figure 2. Spore of UCR-13, X 4500
 Figure 3. Spore from TYPE in IA, X 5070
 (Magnifications approximate).

Fuligo Hall., Hist. Stirp. Helv. 3:110. 1768.

1. Fuligo megaspora Sturgis, Colo. Coll. Publ. Sci. 12:443. 1913.

KNOWN WORLD DISTRIBUTION: U.S.A., Guatemala, Europe, Congo, Pakistan.

COSTA RICA: IV (25), UCR-168 (TEX 1448), 9 IV 1964. On dead wood.

COMMENTS: A typical well-formed aethalium, 3 cm in length. Most spores measure 18 μ m diam.

*2. Fuligo septica (L.) Wiggers, Prim. Fl. Holsat. 112. 1780.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: Widely distributed and very common. I (5), UCR-81 (TEX 1435), UCR-82 (TEX 1454), UCR-87 (TEX 1456), 8 VII 1963. II (19), UCR-83 (TEX 1455), 7 VII 1963. III, UCR-80 (TEX 1434), 4 VII 1963; IV, Welden, p. 97. V (31), UCR-182 (TEX 1436), 19 VI 1964, UCR-185 (TEX 1457), 20 VI 1964. VII, Welden, p. 97. (34), UCR-318 (TEX 1458), 16 XI 1965. All on wood or bark.

COMMENTS: In UCR-182 the lime of the cortex is white; in all others it is some shade of yellow. Differences in color of the cortex have been used to distinguish among varieties (Martin & Alexopoulos, 1969; Nannenga-Bremekamp, 1973) but the taxonomic significance of aethial color can be determined only by careful culture work and genetic studies under controlled conditions. F. septica is relatively easy to grow in laboratory culture from spores to the plasmodial stage, but cultures sporulate unpredictably and only after a very long time.

Craterium Trent., in Roth, Catalecta Bot. 1:224. 1797.

1. Craterium leucocephalum (Pers.) Ditmar, in Sturm, Deuts. Fl. Pilze 1:21. 1813.

KNOWN WORLD DISTRIBUTION: Cosmopolitan

COSTA RICA: I (1), UCR-171 (TEX 1459), 3 VI 1964; (7) UCR-243 (TEX 1461), 6 XI 1964. II (16), UCR-279 (TEX 1462), 7 VI 1965. V (31), UCR-190 (TEX 1460), 18 VI 1964. VII (34), UCR-301 (TEX 1463), 16 IX 1965; (35), UCR-306 (TEX 1464), 19 XI 1965. UCR-171 on bark; UCR-243, 279, 190, on dead leaves; UCR-301 on living leaves; UCR-306 on dead wood.

COMMENTS: Considerable variation is encountered in this species in the shape and color of the sporangia and their method of dehiscence. In UCR-171, 190, and 279 the sporangia are essentially globose; in UCR-243 they are long goblet-shape; and in UCR-306 they are intermediate. In UCR-243 and 279 the brown base of the sporangium is clearly evident; in the others the sporangia are almost entirely white. The operculum is perfectly developed in UCR-243; in all others dehiscence is irregular. Whether the variations noted are genetically or environmentally controlled is not known.

Physarum Pers., Neues Mag. Bot. 1:88. 1794.

1. Physarum bitectum G. Lister, Mycet. ed. 2. 78. 1911.

KNOWN WORLD DISTRIBUTION: Western Europe, U.S.A., Puerto Rico, Colombia, South Africa, Australia, New Zealand.

COSTA RICA: I (10), UCR-287 (TEX 2113), 15 VII 1965, on dead leaf.

COMMENTS: This species is not commonly reported, but as Martin & Alexopoulos (1969) mention, it may be more widespread than is supposed because it often resembles other species such as P. bivalve and may be misdetermined. Our specimen appears to be typical. Dr. Marie L. Farr concurs with our identification.

2. Physarum bivalve Pers., Ann. Bot. Usteri 15:5. 1795.

KNOWN WORLD DISTRIBUTION: Europe, N. America, Chile, South Africa, Angola, Southeast Asia, Japan, Philippines, Samoa.

COSTA RICA: I (7), UCR-121 (TEX 1465), 9 VIII 1963, on dead wood, UCR-251 (TEX 1467), 6 XI 1964, on dead leaves. V (31), UCR-183 (TEX 1466), 20 VI 1964, on dead leaves.

COMMENTS: UCR-251 is the most typical of the three specimens, consisting both of isolated sporangia and variously shaped plasmodiocarps of different lengths. The most interesting of the three specimens, however, is UCR-183 in which all the sporophores are in the form of bright yellow, clam-shaped sporangia.

3. Physarum bogoriense Racib., Hedwigia 37:52. 18F. 1898.

KNOWN WORLD DISTRIBUTION: Known from all continents but particularly abundant in the tropics and subtropics.

COSTA RICA: I (1), UCR-205 (TEX 1471), 28 IX 1964, on herbaceous stem, UCR-98 (TEX 1469), 29 VII 1963, on mossy bark, UCR-147 (TEX 1470), 18 X 1963, on dead leaf. II (17), Orotima, UCR-281 (TEX 1473), 9 VI 1965, on dead leaf. III (22), UCR-220 (TEX 1472), 1 X 1964, on plant debris. IV, UCR-64 (TEX 1468), 24 VI 1963, on leaf base.

COMMENTS: This distinctive species fruits occasionally on bark or wood but usually on dead leaves and plant debris.

The yellowish or brown outer peridium and the stellate dehiscence make it easy to recognize in the field under a hand lens. Only occasionally encountered in cold climates, it is one of the most abundant species in warm regions.

4. Physarum cinereum (Batsch) Pers., Neues Mag. Bot. 1:89. 1794.

KNOWN WORLD DISTRIBUTION: Cosmopolitan and very common.

COSTA RICA: I (1), UCR-172 (TEX 2233), 3 VI 1964; (7), UCR-244 (TEX 1475), 6 XI 1964, both on living leaves, San Antonio de Belem, UCR-329 (TEX 1487), 3 VII 1966, on dead wood.

COMMENTS: In UCR-244 the sporangia are well formed but the lime is scanty and the peridium is iridescent; the spores measure 7-9 μ m. In UCR-239 the lime is much more abundant and there are two long, branched plasmodiocarps in addition to the few sporangia. One is tempted to place this specimen in the closely allied P. vernum, but the spores are clearly brownish-violaceous rather than dark purplish-brown; it seems better, therefore, to retain it in P. cinereum in spite of its occurrence on wood. UCR-172 is a scanty collection of but a few sporangia. The spores are not well formed and the determination is therefore tentative.

5. Physarum citrinum Schum., Enum. Pl. Saell. 2:201. 1803.

KNOWN WORLD DISTRIBUTION: Cosmopolitan but not common.

COSTA RICA: I (11), UCR-240 (TEX 1474), 16 X 1964, on wood.

COMMENTS: Our specimen, consisting of over 100 sporangia, is typical in some respects, not so in others. The sporangia are .7-1 mm diam.; the stalks are short and calcareous but tend to be more orange than yellow in color; the columella is minute and conical but the capillitial nodes are elongated. The spores are almost smooth and measure 11-12 μ m, which is somewhat larger than described. New species have been described on smaller differences!

6. Physarum compressum Alb. & Schw., Conspl. Fung. 97. 1805.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-30 (TEX 2010), 3 VI 1963, UCR-36 (TEX 1479), 6 VI 1963, UCR-206 (TEX 1484), 28 IX 1964, all on bark; UCR-140 (TEX 1481), 10 VIII 1963, on lizard dung in moist chamber; UCR-169 (TEX 1482), 10 IV 1964, on plant debris; (10), UCR-141 (TEX 1480), 4 X 1963, on dead wood; III (22), E. F. M. #902 (TEX 1994), 18 II 1966, on dead herbaceous stem; III (23), UCR-286 (TEX 1485), 15 VII 1965, on moss.

COMMENTS: This ubiquitous species is a very variable one and several of its forms have been described as new species or have been confused with other Myxomycetes. Typically the sporangia are fan-shaped, as in UCR-286, but plasmodiocarpous fruitings, as in UCR-141 and 200 are not uncommon. Polycephaloid fruitings which resemble *P. nicaraguense* (q. v.) are sometimes produced; UCR-36 is a good example of this variation. Culture studies (Alexopoulos, 1969) have shown that spores taken from various types of fruiting bodies, such as those described above, will yield the typical fan-shaped sporangia when conditions for fruiting are favorable.

*7. Physarum decipiens Curtis, Am. Jour. Sci. II. 6:352. 1848.

KNOWN WORLD DISTRIBUTION: U.S.A., Canada, South America, Western Europe to Greece; Hawaii, Asia, Australia.

COSTA RICA: Heredia (Reported by Welden, 1954 as Badhamia decipiens (Curt.) Berk. No specimen in our collection).

8. Physarum dictyosporum Martin, Brittonia 14:183. 1962.

KNOWN WORLD DISTRIBUTION: U.S.A. (Michigan, Iowa, Kansas, Texas).

COSTA RICA: V (31), UCR-186a (TEX 1486), 20 VI 1964, on dead leaf.

COMMENTS: This is one of the very few species of Physarum with reticulate spores. In our specimen, short plasmodiocarps intermingle with sessile sporangia. The lime in the sporophore is often concentrated in the center forming a rigid pseudocolumella which assumes the shape of the fruiting body. This species, discovered in 1962, has hitherto been known only from four localities in the U.S.A. as noted above.

*9. Physarum didermoides (Pers.) Rost., Mon. 97. 1875.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-1 (TEX 1488), January 1963, UCR-261 (TEX 919), 28 X 1964, UCR-84 (TEX 1492), 9 VII 1963, both on bark; UCR-112 (TEX 1493), 3 VII 1963, on wood covered with moss; UCR-145 (TEX 1517), 18 X 1963, on bark. (4), Rio Claro, UCR-4 (TEX 1489), April 1963, on plant debris. II (19), UCR-165 (TEX 2232), 4 IV 1964, on moss. III, UCR-18 (TEX 1490), 20 V 1963; (22), UCR-213 (TEX 1495), UCR-217 (TEX 1496), UCR-218 (TEX 1497), 1 X 1964, all on bark. VII (34), UCR-300 (TEX 1498), UCR-312 (TEX 1499), 16 XI 1965, on dead leaves.

COMMENTS: All specimens except UCR-145 and 261 are typical of the species. Those two approach P. tessellatum in that the sporangia are somewhat flattened, approximately isodiametric, and crowded together. However, the tessellate crust formed by the contacting sporangia of P. tessellatum is absent in both specimens and we must therefore, consider all as belonging to P. didermoides. It is of interest to note that laboratory cultures of the aberrant forms produced the same type of fructifications. This is another of the relatively few species of Myxomycetes that grow readily in culture from spores.

10. Physarum flavidum (Peck) Peck, Ann. Rep. N. Y. State Mus. 31:55. 1879.

KNOWN WORLD DISTRIBUTION: N. America, Europe, Japan.

COSTA RICA: I (21), UCR-106 (TEX 1501), 26 XII 1963, on mosses and lichens.

COMMENTS: Although it appears to be widely distributed, this is not a common species. Our specimen--the first on record south of the United States in the Western hemisphere--is typical in all respects except the capillitial nodes which are not white-calcareous but translucent and amber-like. It may be that the sporangia are not properly matured, but the uniformity of the spores argues against that hypothesis. Experimental culture work would answer this question, but unfortunately we were unable to obtain cultures from this specimen.

11. Physarum globuliferum (Bull.) Pers. Syn. Fung. 175. 1801.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (2), UCR-11 (TEX 1502), X 1962, on dead wood. V (31), UCR-179 (TEX 1573), 20 X 1964, on plant debris. VII (36), E.F.M. #956 (TEX 1993), 12 III 1966, on bark.

COMMENTS: The first two collections are scanty, consisting of but a dozen fragile sporophores each. The E. F. Morris specimen is somewhat more ample. All appear typical, but the sporophores of UCR-11 lack columellae.

12. Physarum javanicum Racib., Hedwigia 37:53. 1898.

KNOWN WORLD DISTRIBUTION: Java, Africa, Florida, California, Jamaica, Trinidad, Colombia, England.

COSTA RICA: I (1), UCR-194 (TEX 1503), 11 IX 1964, on lava dust on dead wood.

COMMENTS: This is another scanty collection of about a dozen sporophores. The sporangia are not turbinate but vertically compressed and conspicuously umbilicate above. The lava dust is crumbling and the specimen is virtually destroyed.

13. Physarum ?leucopus Lk. Ges. Nat. Freunde Berlin Mag. 3:27. 1809.

KNOWN WORLD DISTRIBUTION: Cosmopolitan but apparently rare in the tropics.

COSTA RICA: II (18), UCR-278 (TEX 2192), 8 VI 1965, on dead leaf.

COMMENTS: Dr. Marie L. Farr confirmed our identifications but reaffirmed our reservations. We quote from her commentary: "Appears to fit except for cylindrical columellae present in some sporangia. Also characteristic whitish color of hypothallus absent; some sporangia have irregular pseudocolumella." Farr also questioned the identity of her own specimen from Dominica (Farr, 1969), but decided that both the Dominica and Costa Rica specimens fit in P. leucopus better than in any other species.

14. Physarum melleum (Berk. & Br.) Massee

KNOWN WORLD DISTRIBUTION: Cosmopolitan; common in the tropics.

COSTA RICA: I (1), UCR-142 (TEX 1504), 11 XI 1963; (7), UCR-242 (TEX 1506), 6 XI 1964. II (16), UCR-273 (TEX 2108), 7 VI 1965; (17), UCR-283 (TEX 1507), 9 VI 1965. V (31), UCR-175 (TEX 2117), 20 VI 1964, UCR-177 (TEX 1505), 20 VI 1964.

COMMENTS: Physarum melleum is a variable species in several of its taxonomically important characters such as color of the sporophore, length of stalk, size of columella and presence of a pseudocolumella. These variations are represented in the specimens at hand. The stalk in UCR-142, 242, and 175 is pure white in most sporangia although it has a tendency to become cream-colored in some sporophores of UCR-175; it is of a light cream color in UCR-177 and more yellow in UCR-273 and 283; it may be described as relatively long in all specimens except UCR-242 in which it is medium to short. The peridium is bright yellow from an abundance of lime in UCR-142, 273 and 283, but gray or white in the other specimens. The whole sporophore is grayish white in UCR-175. The columella is small in most specimens, but conspicuous and yellow in UCR-142 and quite conspicuous and pure white in UCR-175. The capillitium is abundant with angular, white nodes in all specimens but UCR-273 in which it is less abundant and has yellowish nodes. The spores are uniformly light violet-brown and very minutely warted in all specimens. They vary in size from 7.5 to 9 μ m in diameter. In spite of the variation, this species is one of the easiest to recognize in the genus.

15. Physarum murinum A. Lister Mycet. 41. 1894.

KNOWN WORLD DISTRIBUTION: Western Europe, U.S.A.

COSTA RICA: IV (24), UCR-151 (TEX 1969), 21 XI 1963, on decaying wood.

COMMENTS: This appears to be the only report of P. murinum from the tropics. Both Dr. G. W. Martin and Dr. Marie L. Farr, who examined our specimen, agree with our identification in spite of some characters which deviate from the typical.

16. Physarum nicaraguense Macbr. Bull. Nat. Hist. Univ. of Iowa 2:382. 1893.

KNOWN WORLD DISTRIBUTION: Nicaragua, West Indies, Ceylon, India, Japan, Philippines, Caroline Islands.

COSTA RICA: I (2), UCR-14 (TEX 1511), 18 V 1963, UCR-16 (TEX 1512), 18 V 1963; (10), UCR-139 (TEX 1508), 4 X 1963. III (22), UCR-216 (TEX 1441), 1 X 1964. VII (Orotina), UCR-285 (TEX 1442), 9 VI 1965. All on bark.

COMMENTS: Physarum nicaraguense appears to be a strictly tropical species. Its occurrence in Costa Rica was expected in view of the fact that Nicaragua is its type locality. We find it to be a well-defined species, apt to be confused only with some aberrant forms of Physarum compressum (q. v. See also comments in Martin and Alexopoulos, 1969, p. 315).

17. Physarum notabile Macbr. N. Am. Slime-Moulds ed. 2. 80. 1922.

KNOWN WORLD DISTRIBUTION: U.S.A. and Canada, West Indies, Europe, ?New Zealand.

COSTA RICA: I (7), UCR-124 (TEX 2005), 9 VIII 1963. II (19), UCR-164 (TEX 1510), 4 IV 1964. Both on bark.

COMMENTS: UCR-124 does not agree perfectly with the description of this species but cannot be placed elsewhere with more certainty. Dr. Marie L. Farr agrees with this view. UCR-164 is more typical.

18. Physarum nucleatum Rex, Proc. Acad. Phila. 43:389. 1891.

KNOWN WORLD DISTRIBUTION: Throughout the U.S.A. and south to Nicaragua, England, Rumania, South Africa, Hawaii, Japan, the tropics in general.

COSTA RICA: VI (32), UCR-224 (TEX 1575), 2 X 1964, on moss.

COMMENTS: An ample and typical collection. Pseudocolumellae are present but are not prominent.

19. Physarum nutans Pers., Ann. Bot. Usteri 15:6. 1795.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (7), UCR-137 (TEX 1925), 9 VIII 1963, UCR-128 (TEX 2001), 9 VIII 1963; (1), UCR-58 (TEX 2000), 24 VI 1963; (8), UCR-255 (TEX 2003), 5 XI 1964; (23), UCR-202 (TEX 2004), 24 IX 1964, UCR-209 (TEX 918), 26 IX 1964. IV (24), UCR-154 (TEX 2002), 24 XI 1963. UCR-58, 128, 154, and 255 are on bark; UCR-202 is on mossy wood; the others are on dead wood.

COMMENTS: Physarum nutans, a very common species throughout the world, closely resembles P. viride in all characters except color, being gray or white instead of yellow or orange (See Martin & Alexopoulos, 1969). Color differences within the same species have been recorded for Physarella oblonga, Physarum tenerum, Arcyria cinerea and other species of Myxomycetes, and are usually not recognized as separate taxa unless and until experimental evidence indicates the differences hold up under different conditions of culture and are not merely due to changes in the environment. No such evidence has been obtained for the P. nutans/viride complex, chiefly because neither species has been grown in laboratory culture after repeated attempts. All our specimens appear to be typical of P. nutans as this taxon is presently circumscribed.

20. Physarum polycephalum Schw., Schr. Natur. Ges. Leipzig 1:63. 1822.

KNOWN WORLD DISTRIBUTION: Common in the U.S.A., West Indies, Brazil, Uruguay, Angola, France, Rumania, Borneo, Japan.

COSTA RICA: I (1), UCR-26 (TEX 1983), UCR-115 (TEX 1987), UCR-116 (TEX 1980), UCR-117 (TEX 1984), all four collected on 5 VII 1963; (11), UCR-233 (TEX 446), 16 X 1964. III (Cartago), UCR-163 (TEX 1981), 16 X 1964. IV (24), UCR-6 (TEX 1421); (27), UCR-324 (TEX 1422), 10 VI 1966. VII (33), UCR-292 (TEX 1982), 17 XI 1965; (Monte Verde), E.F.M. #858 (TEX 1992), 9 II 1966. Cocos Island, W. A. Weber # M-194 (TEX 1207), Jan-Mch 1964. The habitats of our specimens are as follows: On herbaceous material: UCR-233, 292, 324; on bark: UCR-6 and TEX 1207; on dead wood: UCR-26, 115; on dead leaf: UCR-325; on lichen and moss: E.F.M. #858; on debris in moist chamber: UCR-163,

324; collected as plasmodia and fruited on filter paper:
UCR-116, 117.

COMMENTS: Physarum polycephalum exists in two forms and at least two colors in nature. One form is polycephaloid; the other is simple. The latter has been called Physarum obrusseum (Berk & Curtis) Rost. and Physarum polycephalum Schw. var. obrusseum (Berk. & Curtis) G. Lister. Experimental evidence (Alexopoulos, 1969) supports the view that these are but variants of P. polycephalum Schw. which do not deserve separate designations. In color, P. polycephalum sporangia are either yellow to orange or gray to white. The color and type of fructification in our specimens are as follows: Obrusseum type, gray: UCR-6, 117, 324; yellow: TEX 1207; yellowish gray: UCR-116. Polycephaloid type, gray: UCR-292, 325, E.F.M. #858; yellow: UCR-115; yellowish gray: UCR-26. The sporangia of UCR-163 are not well matured and were still black when collected.

21. Physarum pulcherripes Peck, Bull. Buffalo Soc. Nat. Sci. 1:64, July, 1873.

KNOWN WORLD DISTRIBUTION: U.S.A., Panama, Jamaica, Dominica, Trinidad, Ireland, Japan.

COSTA RICA: VII (34), UCR-317 (TEX 2015), 16 IX 1965, on dead wood.

COMMENTS: The identification of this specimen is uncertain. It was first determined by us as Physarum psittacinum. Ditmar and Dr. G. W. Martin agreed that it was probably that although both he and we noted it did not fit the description of that species perfectly. Later, Dr. Marie L. Farr redetermined this specimen as P. pulcherripes noting "Columella absent and lime nodes more as in P. psittacinum, but stipes decidedly limy." Thus, the specimen appears to be intermediate between the two species. We are at present filing it under P. pulcherripes.

22. Physarum rigidum (G. Lister) G. Lister, Mycet., ed. 3. 36. 1925.

KNOWN WORLD DISTRIBUTION: Japan, Philippines, Hawaii, U.S.A. (Texas), West Indies, Brazil, Uruguay.

COSTA RICA: I (23), UCR-210 (TEX 2114), 26 XI 1964; (11), UCR-239 (TEX 1220), 16 X 1964.

COMMENTS: Physarum rigidum was first described as a variety of P. viride whose capillitium often consists of rod-like, rigid tubes containing lime granules. Although the capillitium of our specimens lacks these rigid tubes, it does consist of sparingly branched threads arising vertically from the base of the sporangium and bearing long, orange-yellow nodes. In this respect our specimen approaches P. viride (q. v.) but in its limeless peridia it strongly resembles P. flavicomum where we had originally placed it. The capillitium of P. flavicomum is intermediate between those of P. viride and P. rigidum. It is obvious that what might be called the P. viride/rigidum/flavicomum complex requires much experimental study before the relationships can be untangled. We are basing the identification of our specimens on the conclusions reached by Henney & Henney (1968) who attempted unsuccessfully to cross clones derived from UCR-239 with clones of P. flavicomum. Unfortunately, no one has succeeded in growing P. viride in laboratory culture.

23. Physarum stellatum (Masse) Martin, Mycologia 39:461, 1947.

KNOWN WORLD DISTRIBUTION: North and South America, West Indies, Africa, Hawaii, Philippines, Indonesia, Asia.

COSTA RICA: III (22), UCR-223 (TEX 2012), IX 1964. VII (33), UCR-291 (TEX 2011), 17 XI 1965; (35), UCR-305 (TEX 2013), 19 XI 1965. All on wood.

COMMENTS: The pseudocolumella, characteristically present in this species, is conspicuously present in the first two specimens, not so in the third which is in poor condition. All other characters are typical in all three.

*24. Physarum tenerum Rex Proc. Acad. Phila. 42:192. 1890.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-49 (TEX 2008), 8 VI 1963, UCR-54 (TEX 2007), 11 VI 1963, UCR-37 (TEX 2009) 3 VI 1963, UCR-58 (TEX 2107), 24 VI 1963; (8) UCR-253a (TEX 1416), 5 XI 1964. IV (El Roble), UCR-94 (TEX 2006), 30 VII 1963; IV (Heredia), UCR-61 (TEX 2106), 24 VI 1963. All on bark except UCR-94 on a fungus sporophore.

COMMENTS: This is another species of Physarum with two color forms: yellow and gray to white. The colors of our specimens are as follows: Yellow form - UCR-253a, 94, 58, 61; white form - UCR-37, 49.

25. Physarum ?vernum Somm., in Fries, Syst. Myc. 3:146. 1829.

KNOWN WORLD DISTRIBUTION: Western Europe and the British Isles, Rhodesia, Angola, India, Japan, Hawaii, South Australia, New Zealand, Mexico, Cuba.

COSTA RICA: II (16), UCR-177 (TEX 2014), 7 VII 1965, on bark.

COMMENTS: Physarum vernum resembles both P. cinereum and P. sessile, but is usually more plasmodiocarpous than the former and has larger spores than the latter. Our specimen consists of three plasmodiocarps 1.5 to 2 mm long and about 0.4 mm in diameter. The spores measure 8-10 μ m. The sporophores are heavily encrusted with lime. The capillitial nodes are rather large and angular. Obviously the specimen is intermediate between P. vernum and P. cinereum, but we believe it to be closer to the former. Dr. Marie L. Farr concurs.

26. Physarum viride (Bull.) Pers., Ann. Bot. Usteri 15:6. 1795.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-149 (TEX 2110), 18 X 1963, UCR-238 (TEX 2111), 16 X 1963; (7), UCR-123 (TEX 2112), 9 VIII 1963. V (31), UCR-180 (TEX 2109), 20 VI 1964. All on dead wood.

COMMENTS: Except for its similarity in structure to P. nutans (q. v.) this is a well-defined species which may generally be easily recognized by the petaloid dehiscence of the peridium with patches left clinging to the capillitial mass. All our specimens are typical.

Family DIDYMIACEAE Rost., Versuch. 12, 1873.

Diachea Fries, Syst. Orb. Veg. 143. 1825.

Fries first described Diachea in 1825 as a member of his Trichiacei but three years later in his Systema he transferred it to the Stemonitei where it remained until Rostafinski (1874) placed it in the family Spumariaceae of his Calcareae (now order Physarales). (See Martin & Alexopoulos, 1969, p. 176). In this decision Rostafinski was followed by Cooke (1877) and partly by Zopf (1885) who placed Diachea in the Didymiaceae. Masee (1892) continued to regard Diachea as one of the Didymiaceae. All these authors obviously emphasized the presence of lime (a physaraceous character) more than the type of capillitium and peridium which, in Diachea, resemble those of the Stemonitales.

Lister, in all three editions of his monograph The Mycetozoa, placed Diachea in the Physaraceae, but mentions (1911, 1925) that "this genus forms a connecting link between the Calcarineae and the Stemonitaceae." Morgan (1894) in the meantime, had transferred it back to the Stemonitaceae emphasizing its resemblance to Lamproderma except for the limy stalk and columella. The European monographers continued to classify this genus in the Physarales, both Schinz (1920) and Krzemieniewska (1960) including it however, in the Physaraceae, following Lister. American monographers, on the other hand (Macbride, 1899, 1922; Macbride & Martin, 1934; Martin, 1949; Martin & Alexopoulos, 1969; Alexopoulos, 1973) followed Morgan, the one exception being Hagelstein (1944) who used Lister's classification throughout, patterned, with few modifications, after Rostafinski.

By 1973, the basis for classification of the Myxomycetes was placing more emphasis on the development of the sporophore (deBary, 1859; Ross, 1957, 1960, 1961, 1973; Alexopoulos, 1969, 1973) rather than on the characters of the mature fructification alone as had been done until recent years. In that year (1973) Blackwell examined the stalk structure of the mature sporophore of Diachea leucopodia with the electron microscope and concluded that the development is "nonstemonitaceous" (subhypothallic) and

that ". . . Diachea (is) misplaced in the Stemonitomycetidae." Shortly thereafter, Farr (1974) on the basis of other features, also suggested that "Diachea seems . . . more naturally and compatibly placed in the Physarales, family Didymiaceae, rather than in the Stemonitaceae." With these conclusions we concur and, therefore, classify Diachea in the Didymiaceae, recognizing, at the same time, that there is merit in considering the erection of a new family for this intermediate genus.

1. Diachea bulbillosa (Berk. & Br.) A. Lister, in Penzig, Myxom. Buit. 45. 1898.

KNOWN WORLD DISTRIBUTION: Southern and Eastern Asia, Eastern Canada, U.S.A., Central America, West Indies, Colombia.

COSTA RICA: V (31), UCR-176 (TEX 1369), 20 VI 1964. VI (37), E. F. Morris # 907 (TEX 1990), 20 II 1966. Both on living leaves.

COMMENTS: A recently described taxon from Dominica, W. I. (D. silvaepluvialis Farr, 1969) differs from this species chiefly in the brown sheathlike covering over the calcareous stipe. All specimens hitherto described as D. bulbillosa should be reexamined for this character. In our specimens all stalks are white and our identifications were checked by Dr. Farr herself.

2. Diachea leucopodia (Bull.) Rost., Mon. 190. 1874.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (7), UCR-120 (TEX 1370), 9 VIII 1963, UCR-263 (TEX 1371), 6 XI 1964. IV (27), UCR-320 (TEX 1372), 10 VI 1966. All three on living leaves. VII (38), E. F. Morris # 846 (TEX 1997), 8 II 1966, on dead grass culms.

COMMENTS: All specimens are typical. The species is hard to confuse with any other.

Diderma Pers., Neues Mag. Bot. 1:89. 1794.

*1. Diderma chondrioderma (deBary & Rost.) G. Lister, in Lister, Mycet. ed. 3. 258. 1925.

KNOWN WORLD DISTRIBUTION: Great Britain, Poland, Rumania, U.S.A., Galapagos Islands, Ceylon, Malaya, Japan.

COSTA RICA: V (?), Welden, p. 98.

COMMENTS: We have no specimen from Costa Rica in our collections.

2. Diderma effusum (Schw.) Morgan, Jour. Cinc. Soc. Nat. Hist. 16:155. 1896.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: V (31), UCR-181 (TEX 2194), 19 VI 1964. On leaf.

COMMENTS: This is a typical specimen of a very common and widely distributed species.

3. Diderma hemisphaericum (Bull.) Hornem., Fl. Dan. 33:3. 1829.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-173 (TEX 2115), 3 VI 1964. II (16), Carretera panamericana (La Azucena), UCR 298 (TEX 2116), 19 XI 1965. UCR-275b (TEX 1405), 7 VI 1965.

COMMENTS: All three specimens of this easily recognized species are typical.

4. Diderma sauteri (Rost.) Macbr., N. Am. Slime-Moulds. 103. 1899.

KNOWN WORLD DISTRIBUTION: Scotland, Austria, Rumania, Eastern North America.

COSTA RICA: I (1), UCR-235 (TEX-specimen misplaced).

COMMENTS: Martin & Alexopoulos (1969) state that this is a very rare species. Our specimen, if indeed it belongs here, is the first one reported from the tropics. It has a calcareous peridium on the basis of which Dr. G. W. Martin disagreed with our identification without, however, assigning our specimen to another known species. Later, Dr. Marie L. Farr expressed the opinion that our

identification was probably correct. We place this specimen tentatively in D. sauteri for lack of a better suggestion. The specimen deposited in the Texas herbarium has been misplaced; the one in the University of Costa Rica herbarium is available.

5. Diderma testaceum (Schrad.) Pers. Syn. Fung. 167. 1801.

KNOWN WORLD DISTRIBUTION: N. America, Jamaica, Dominican Republic, Chile, Europe, Japan, Ceylon, India.

COSTA RICA: VII (34), UCR-304 (TEX 1399), 16 XI 1965.
On leaf fragment.

COMMENTS: The glossy peridium and the large columella are unmistakable characters of this ubiquitous species. Our sporangia are pure white.

Didymium Schrad., Nov. Gen. Pl. 20. 1797.

*1. Didymium clavus (Alb. & Schw.) Rab. Deuts. Krypt. Fl. 1:280. 1844.

KNOWN WORLD DISTRIBUTION: Europe, U.S.A., West Indies, Ceylon.

COSTA RICA: I (1), UCR-74 (TEX 2234), 4 VII 1963, UCR-198 (TEX 2238), 16 IX 1964. III (23), UCR-272 (TEX 2236), 10 VI 1965. VII (34), UCR-313 (TEX 2237), 16 XI 1965. All on dead wood, those of UCR-74 and 198 covered with lava dust.

COMMENTS: The sporangia of UCR-272 are the most typical being decidedly umbilicate above and much depressed. The others tend to be more subglobose, approaching those of D. minus.

2. Didymium crustaceum Fries, Syst. Myc. 3:124. 1829.

KNOWN WORLD DISTRIBUTION: Great Britain, Central Europe, Canada, U.S.A., West Indies, South America, Angola, India.

COSTA RICA: III (23), UCR-199 (TEX 2239), 26 IX 1964, on mossy bark.

COMMENTS: Our specimen consists of two small sporangial

clusters and two single sporangia. All are sessile with very limy peridia.

3. Didymium difforme (Pers.) S. F. Gray, Nat. Arr. Brit. Pl. 1:571. 1821.

KNOWN WORLD DISTRIBUTION: Europe, temperate N. America, W. Indies, S. America, Japan.

COSTA RICA: I (7), UCR-250 (TEX 2240), UCR-252 (TEX 2193), both on 6 XI 1964; (10), UCR-258 (TEX 2241), 15 VII 1965. Caretera Panamericana (La Azucena), UCR-299 (TEX 2242), 19 XI 1965. All on dead leaves.

COMMENTS: This is a widely distributed, probably cosmopolitan species and, therefore, quite variable, sometimes approaching Diderma testaceum in its general appearance (See Martin & Alexopoulos, 1969, p. 384).

4. Didymium iridis (Ditmar) Fr., Syst. Mycol. 3:120. 1829.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1) UCR-5 (TEX 2243), January 1963, on dead wood, UCR-332 (TEX 2235), 2 XI 1967, on seeds of Ricinus communis in moist chamber, (La Palma) E. F. Morris # 992 (TEX 1985), 27 II 1966, on dead herbaceous plant; (9), UCR-271 (TEX 2246), 1 VI 1965, on dead leaves. II (16), UCR-280 (TEX 2247), 7 VI 1965, on dead leaf; (19), UCR-166 (TEX 2244), 4 IV 1964, on moss. V (31), UCR-189 (TEX 2245), 18 VI 1964, on dead leaves. VI (37), G. C. Carroll (TEX 414, m. ch. cult. # Co-27), 18 IX 1964, on decaying wood in moist chamber.

COMMENTS: This species closely resembles D. nigripes differing from it chiefly in having a white rather than dark columella, a character that appears to be constant under a variety of environmental conditions. D. iridis is one of the best known of all myxomycete species, having been collected all over the globe. It grows and sporulates easily in laboratory culture on artificial media and its genetics have been intensively studied by Collins and his associates who found both homothallic and heterothallic strains. Its spore development has been recently investigated by Aldrich (1974).

5. Didymium minus (A. Lister) Morgan, Jour. Cinc. Soc. Nat. Hist. 16:145. 1894.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (7), UCR-249 (TEX 2188), 6 XI 1964.
Carretera Panamericana, (La Azucena), UCR-295 (TEX 2248),
19 XI 1965. Both on dead leaves.

COMMENTS: UCR-295 is moldy and less typical in its general appearance than UCR-249. The latter is quite typical except for its spores which are somewhat smaller (7-7.5 μ m) than described for this species (8-11 μ m).

6. Didymium nigripes (Link) Fries, Syst. Myc. 3:119. 1829.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (9), UCR-269 (TEX 2189), 1 VI 1965. VII (34), UCR-302 (TEX 2190), 16 XI 1965. Both on dead leaves.

COMMENTS: See comments under D. iridis to which this species appears to be most closely related.

7. Didymium squamulosum (Alb. & Schw.) Fries, Symb. Gast. 19. 1818.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-150 (TEX 2249), 22 X 1963, on living leaves, UCR-226 (TEX 2250), 9 X 1964, on dead leaves; (7), UCR-262 (TEX 2251), 6 XI 1964, on herbaceous stem; (9), UCR-270 (TEX 2252), 1 VI 1965, on dead leaves.
Carretera Panamericana (La Azucena), UCR-296 (TEX 2253),
19 XI 1965, on plant debris.

COMMENTS: All specimens are typical of this unmistakable species. This is one of the relatively few Myxomycetes which can be cultured easily in the laboratory.

Subclass STEMONITOMYCETIDAE Ross, Mycologia 65:483. 1973.

Order S T E M O N I T A L E S Macbride, N. Am. Slime-Moulds, ed. 2. 122. 1922.

Family STEMONITACEAE Rost., Versuch. 6. 1873 (as Tribus).

Stemonitis Roth, Mag. Bot. Rommer & Usteri I (2):25. 1787.

1. Stemonitis axifera (Bull.) Macbr., N. Am. Slime-Moulds 120. 1889.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-22 (TEX 1373), 21 V 1963, UCR-47 (TEX 1375), 8 VI 1963; (8), UCR-265 (TEX 1377), 5 XI 1964. II (12), UCR-35b (TEX 1374), 1 VI 1963. III (21), UCR-65 (TEX 1376), 28 VI 1963; (22), UCR-232 (TEX 1387), 1 X 1964. All on dead wood.

COMMENTS: Stalk length varies greatly in this species. In UCR-22, for example, the stalks are 0.45-1.5 mm high, whereas in UCR-47 they are 3-4 mm. UCR-265 exhibits the membranous expansions in the capillitium, supposedly characteristic of S. flavogenita, and larger surface net meshes than usually found in S. axifera, but the spores place it in the latter species.

2. Stemonitis flavogenita Jahn, Verh. Bot. Ver. Brand. 45:165. 1904.

KNOWN WORLD DISTRIBUTION: U.S.A., West Indies, Panama, Brazil, Europe, Asia, Africa.

COSTA RICA: VII (35), UCR-310 (TEX 1379), 19 XI 1965; (34), E. F. Morris #971 (TEX 1999), 16 III 1966. Both on decaying wood.

COMMENTS: Both specimens agree as closely as can be expected with the description of this variable species.

3. Stemonitis fusca Roth, Mag. Bot. Romer & Usteri I (2): 26. 1787.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-88 (TEX 1381), 7 VII 1963. II (12), UCR-35a (TEX 1380), 1 VI 1963. VI (37), Coll. by G. C. Carroll (TEX 224), 18 IX 1964. III (20), UCR-15 (TEX 388), 20 V 1963; (22), E. F. Morris #897 (TEX 1989), 18 II 1966. VII (34), UCR-316 (TEX 1484), 16 XI 1965. All on dead wood.

COMMENTS: UCR-35a probably represents the variety papillosa. The spores are not reticulate but papillate, the papillae clearly evident only under the oil immersion objective, particularly with phase contrast optics.

4. Stemonitis herbatica Peck, Ann. Rpt. N. Y. State Mus. 26:75. 1874.

KNOWN WORLD DISTRIBUTION: N. America, Jamaica, Brazil, Europe, Africa, Fiji.

COSTA RICA: VI (32), UCR-1481 (No specimen in TEX), 1 VI 1972, on both mossy dead wood and living grass. VII (33), UCR-294 (TEX 1378), 17 XI 1965, on herbaceous stem.

COMMENTS: Both our specimens are typical of the species.

5. Stemonitis splendens Rost. Mon. 195. 1874.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-23 (TEX 1385), 21 V 1963, on wood, UCR-52 (TEX 1386), 8 VI 1963, on bark (?).

COMMENTS: In UCR-23 the sporangia are partly agglutinated.

Lamproderma Rost., Versuch. 7. 1873.

1. Lamproderma arcyronema Rost., Mon. 208. 1874.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-45 (TEX 1400), UCR-46a (TEX 2191), 8 VI 1963; (7), UCR-248 (TEX 1402), 6 XI 1964; (11), UCR-237 (TEX 1401), 16 X 1964. II (14), UCR-134 (TEX 1396), 17 VIII 1963. VII (34) E. F. Morris #968 (TEX 1988), 16 III 1966. All on dead wood.

COMMENTS: The stalks of UCR-237 are somewhat shorter than usual, constituting about 1/2 to 3/5 of the total height of each sporophore.

2. Lamproderma muscorum (Lev.) Hagest., Mycologia 27:88. 1935.

KNOWN WORLD DISTRIBUTION: Colombia.

COSTA RICA: II (16), UCR-274 (TEX 1433), 7 VI 1965, on dead leaf. Det. by G. W. Martin.

COMMENTS: Martin & Alexopoulos (1969) say of this particular collection: "A very fine collection . . . from Costa Rica . . . appears to be the closest approach to what Lévêillé described that we have seen."

3. Lamproderma scintillans (Berk. & Br.) Morgan.

KNOWN WORLD DISTRIBUTION: Southern Canada, U.S.A., West Indies, Panama, S. America, Galapagos, Great Britain, Germany, Southern and Eastern Asia, Hawaii.

COSTA RICA: I (1), UCR-29 (TEX 1397), 31 V 1963; (9), UCR-135 (TEX 1403), 20 IX 1963. II (16), UCR-275a (TEX 1404), 7 VI 1965; (17), UCR-282 (TEX 1406), 9 VI 1965. All on dead leaves.

COMMENTS: The sporangia of this species are described by Lister (1925) as "steel blue, red or bronze, brilliantly iridescent." This variation in color is sometimes noted in a single sporangial group presumably developed from a single plasmodium, as in our UCR-29 in which both blue and bronze sporangia are found on the same small leaf fragment. In UCR-275a, except for a few blue sporangia on the margin of the leaf, all are bright golden in color. So are those of UCR-282 in which the peridium still persists. In UCR-135 most sporangia are not fully mature. The majority are violet-blue.

One might be tempted to conclude from a study of our specimens that the bronze or golden color is that of the fully and properly matured sporangia and that the violet and blue tints represent earlier stages in sporangial development. This is another case where extended experimental studies in artificial culture would be most helpful. The species has been grown in the laboratory by Alexopoulos (TEX 268, culture) and by Kalyandasundaram (1974), but it is difficult to maintain in culture and no experimental studies have been conducted.

Comatricha Preuss, *Linnaea* 24:140. 1851.

*1. Comatricha aequalis Peck. Ann. Rpt. N. Y. State Mus. 31:42. 1879.

KNOWN WORLD DISTRIBUTION: U.S.A., Costa Rica, Jamaica, Europe.

COSTA RICA: VII (?), Welden, p. 97.

COMMENTS: We have no specimen from Costa Rica in our collections.

2. Comatricha elegans (Racib.) Lister, Guide Brit. Mycet., ed. 3. 31. 1909.

KNOWN WORLD DISTRIBUTION: Europe, U.S.A., West Indies, Brazil, Argentina, S. Asia, Japan.

COSTA RICA: I (1), UCR-39 (TEX 1389), 4 VI 1963. On wood.

COMMENTS: A small collection consisting of about two dozen sporangia. The columella divides at the base of each sporangium into a number of strong branches and the whole configuration of the sporangia is typical for the species. C. lurida is distinguished from C. elegans by its columella which reaches into the sporangium and then divides. Whether this character is constant under various environmental conditions remains to be determined by experimental work when someone succeeds in growing these two species in artificial culture.

3. Comatricha subcaespitosa Peck, Ann. Rpt. N. Y. State Mus. 43:71. 1890.

KNOWN WORLD DISTRIBUTION: Eastern and Central U.S.A. and Canada, California, England, Switzerland, Dominica.

COSTA RICA: V (31), UCR-188 (TEX 1356), 18 VI 1964, on wood. Det. by Dr. G. W. Martin.

COMMENTS: Until Farr (1969) reported it from Dominica, this species was believed to be confined to the temperate regions. Our collection seems to be the second to be reported from the tropics.

4. Comatricha tenerrima (M. A. Curt.) G. Lister, Guide Brit. Mycet., ed. 4. 39. 1919.

KNOWN WORLD DISTRIBUTION: Europe, Quebec, U.S.A., Antigua, Brazil, Jamaica, Japan.

COSTA RICA: IV (E1 Roble), UCR-105 (TEX 1390), 30 VII 1963, on wood.

COMMENTS: The sporangia have shed most of their spores and are pale brown in color. They appear cylindrical to fusoid but not so much fusoid as in typical C. tenerrima. The capillitium, too, is not exactly typical, lacking the uniformity expected of this species, some of its branches being somewhat heavier than others. The stalks are long, from 2/3 to 3/4 the height of the sporophores. They are dark brown in color and appear fibrous at their origin from the hypothallus. Dr. Marie Farr concurs with our identification.

*5. Comatricha typhoides (Bull.) Rost., in Lister, Mycet. 120. 1894.

KNOWN WORLD DISTRIBUTION: Cosmopolitan.

COSTA RICA: I (1), UCR-42 (TEX 1391), 4 VI 1963, UCR-77 (TEX 1392), 5 VII 1963; (8), UCR-256 (TEX 1395), 5 XI 1964. II (14), UCR-138 (TEX 1394), 17 VIII 1963. VII, Welden, p. 97. All on wood.

COMMENTS: The sporangia of UCR-42 are hard and aberrant for the most part, but the spores are typical. Spore markings of C. typhoides appear to be remarkably constant even when sporangia are developed under adverse conditions as Wollman's (1966) experimental work has amply demonstrated. This makes this species particularly easy to recognize. No other Comatricha has spores resembling those of C. typhoides. The delicate peridium is present on some sporangia in all specimens cited above.

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Ecology, anatomy and redescription of *Laternea pusilla*

by

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Abstract: *Laternea pusilla*, found on rotting logs in Costa Rica (Central America) is redescribed. The receptacle is formed by 2, 3, or 4 arms instead of just 2 as originally reported. Comparative ecological observations of the species during several months, in its natural habitat and at different altitudes and environments are presented.

Anatomical studies show that the receptacle of *L. pusilla* originates from primordial tissue above the rhizomorph. Initially the receptacle forms a chambered unit which branches into 2, 3, or 4 arms, similarly chambered. The branches finally encompass the gleba, which is swept up and left suspended underneath the arch of the receptacle arms. As the fruiting body develops, the outer chambers of the arms are disrupted and form the crests of the mature body, while the upper inner chambers give rise to the trabecular structure that holds the lantern and the suspended gleba.

Laternea is shown to be the valid name for the genus rather than *Colonnaria* Raf., which is either a synonym of *Clathrus* or a third genus. *Colonnaria pereximia* L. D. Gómez, on the basis of the variability of *Laternea pusilla* as to the number of arms of the receptacle, is considered synonymous with the latter.

The genus *Laternea* was established by Turpin (1822) to contain *Laternea triscapa*, and Berkeley and Curtis (1869) described *L. pusilla* based on two sporophores found in Cuba and now in the Kew Gardens Herbarium. Patouillard (1903) reported the finding of *L. pusilla* in Martinique and Guadeloupe, although his species description is questionable. Linder (1928) reviewed the genus and concluded that it should be considered monotypic, valid only for *L. triscapa* and that many species erroneously included in the genus should be transferred to the genus *Clathrus*. Many species have nevertheless been included in the genus *Laternea*, confusing the taxonomy of the genus and that of the Phallales (Fischer, 1886, 1891, 1893, 1900). Dennis (1953) made a more detailed description of *L. pusilla* from material collected four years earlier in Jamaica. More recently Gómez (1974)

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reported a new Clathraceous species as *Colonnaria pereximia* L. D. Gómez, from specimens which were originally classified by the author as *Laternea pusilla*. Dr. D. M. Dring (personal communication) agrees with the latter point of view. Rafinesque's (1808) original description of *Colonnaria* is unacceptable because it is poor and questionable; it runs as follows: "*Colonnaria (urceolata & truncata . . .)* divided into four pillars united at the top, which bear the seeds in the margin." This description could be applied to several genera of the family clathraceae, and Cunningham's (1931) rejection of Rafinesque's description is clearly justified; Ainsworth (1963) considers *Colonnaria* a *nomen dubium*. Fischer (1933) based *Colonnaria* on *Clathrus columnatus* Bosc (1811) = *Laternea columnata* (Bosc) Nees v. Esenbeck (1858) = *Colonnaria columnata* (Bosc) E. Fischer. Dr. D. M. Dring (personal communication) indicates that he "normally does not separate *Colonnaria* [as based on *C. columnatus* Bosc] from *Clathrus* . . . because it often has branched arms and there is no specialized glebiferous tissue." In my opinion, this is the proper interpretation. However, "if *P. columnatus* is separated from *Clathrus*, then its name should be *Colonnaria* for reasons of priority", rather than *Linderia* Cunningham [as in Dring, 1973]. Santesson (1943) adopting the latter point of view, clearly illustrated and described *Colonnaria* as having smooth arms and the specific gleba tissue commonly becoming " . . . entirely mucilaginous and disappeared with the spore mass, so finally there is nothing to indicate its earlier existence." This is not the case in *L. pusilla*, in which the specific glebiferous tissue or "lantern" remains after spore dispersal, except when it has been eaten by predators. Zeller (1949) recognized *Clathrus*, *Colonnaria* and *Laternea* as three separate genera. On the basis of the above information Gómez's specimens and mine should be classified as *Laternea*.

The purpose of this paper is to describe the anatomy and development of the fruiting body and to redescribe the species to complement earlier descriptions. (Berkeley & Curtis, 1869; Patouillard, 1903; Dennis, 1953), and also to communicate for the first time the culture and ecological observation of a phalloid during several months in a seminatural environment.

MATERIAL AND METHODS

A log covered with moss, bearing abundant mycelium and two sporophores of *L. pusilla* Berk. & Curt, was collected in a wet low montane forest at 2300 m in July 1973, near El Cedral, San José, Costa Rica. The original log was cut in two, leaving abundant mycelium in both parts. One part, Log # 1, was transferred to a moist shady environment, similar to its natural habitat, at 1235 m and observed daily for several months. The other part, Log # 2, was placed under a mango tree (*Mangifera indica*) at 975 m in a more windy and sunny environment. No special treatment was given to this log. Log # 1 was exposed to a humid medium either by rain or by daily watering. After two months Log # 1 was protected with a fine porous cloth, and insecticide (Bayer Baygon spray) applied around and under the log. After six months Log # 1 was moved to the same locality as # 2 but placed in a shady spot protected from sun and wind and watered daily. Completely developed fruiting bodies were obtained from Log # 1 and freeze-dried. Fruiting bodies in different stages of development were fixed in FAA and embedded in parafine after dehydration in a TBA series. Longitudinal and serial cross sections 10 μ m thick were made and stained with safranin-fast green. About a year later

two additional specimens, GL 904, JASR & MNC 1858 11-8-75, Cartago, Costa Rica, were collected at 1200 m from a similar substrate. Initially the more mature fruiting body appeared to be a new species since it had four arms which were not fused at one point but forming two arches, each supporting part of the gleba. The arches were connected by a short bridge 5 mm in length (Fig. 4). The other unopened fruiting body from the same mycelium was placed in a moist chamber to obtain, three days later, a three-armed receptacle.

Duplicates were deposited in the herbaria of the University of Costa Rica (JASR & MNC 1572) and the Royal Botanic Gardens, Kew, England.

OBSERVATIONS

Morphology: *L. pusilla* presented abundant white mycelium forming several branched rhizomorphs that traversed the rotting wood (Fig. 5), its natural substrate. Unopened "eggs" are obovoid, 1 cm wide and 1.5 cm tall and occur singly or in clusters connected at their base by rhizomorphs under the moss mat. In younger eggs the delicate outer portion of the peridium splits in flakes that fall at maturity (Fig. 1), although in some cases they may remain adherent. The peridium is whitish with a mucilaginous layer 2-3 mm thick. During development the receptacle ruptures the peridium which remains as the volva, and emerges as a spongy structure composed of 2, 3, or 4 arms united at the apex (Figs. 1, 4) and free at the base, where they are weakly joined to the volva above the rhizomorph. The total height of the open, mature fruiting body ranges from 2 to 4.5 cm. Hand cross sections of the arms show them to be composed of pseudoparenchyma, with cells having a thick wall. The arms are 2-3 chambered, pale red, cylindric, pitted and almost smooth in the lower half. Longitudinal sections show the arms to be composed of cavities irregularly distributed. In some mature fruiting bodies there are vestiges of internal crests below the apex, which joined the arms during early stages of development. At maturity the gleba is located under the apical portion of the receptacle on a differentiated structure or "lantern" which is longitudinally furrowed and connected to the arms by trabecula-like structures that might be considered as internal crests of the arms (Figs. 2, 4); the "lantern" is hollow with open ends and of a deeper color. This structure may well be named an internal or hanging pileus. In my opinion, the lantern originates from the upper internal chambers of the receptacle which are protected from dehydration during development because they are covered by the gleba, while the same chambers at the lower internal part of the receptacle are disrupted and dehydrated as the receptacle develops its branches, leaving just vestiges of their presence.

The gleba is dark olive, almost black, with the characteristic unpleasant odor of phalloids. Spores are 3-4 x 2 μm smooth, bacilloid, and greenish.

Anatomy: Longitudinal microtome serial sections of immature eggs, 3 mm in diameter, show the volva to be composed of two layers (Figs. 6, 7). The outer layers, 80-160 μm wide, usually form flakes that split at maturity (Fig. 1). They are composed of prosenchymatous tissue of loosely interwoven hyphae; the internal layer is 300-500 μm wide and composed of the same kind of tissue, although of thinner and clearer hyphae (Fig. 6). The gleba, surrounded by primordial tissue is labyrinthian and occupies four-fifths of the section (Figs. 6, 7). At this stage there is no evidence of any other structure in this series. Series of excentric longitudinal sections of another egg 5 mm wide show the base of the rhizomorph to be 1 mm

wide and composed of prosenchymatous tissue; immediately above it, the first stages of the receptacle can be clearly seen arising from the primordial tissue (Figs. 10, 11). At a still later stage, several vertical elongate chambers may be seen at the base of the receptacle, which eventually branches into 2, 3, or 4 arms. The outer chambers of each arm are evidently disrupted to form the crest of the mature fruiting body, while the upper inner chambers give rise to the trabecular structures that hold the "lantern" with the suspended gleba (Figs. 1, 8, 9). Later the arms encompass the gleba, forcing it upward and leaving it suspended underneath the arch of the receptacle (Figs. 1, 3, 4). A fourth series of longitudinal sections shows a heart-shaped gleba, with the apparently immature "lantern" in its notch, and opposite peridial sutures (Figs. 10, 11). It is certainly surprising to note that the "lantern" develops after the gleba.

Ecology: The presence of 2, 3, to 4 arms in the receptacle was confirmed in both natural and semi-natural situations. The ratio of individuals with 2 arms to those with 3 was 1:5. The activity of predators and climatic changes, particularly variations in relative humidity, may account for the low number of fruiting bodies usually found in nature. On the other hand, protection of Log #1 with cloth and insecticide, besides the constant humid environment, accounted for the large number of fruiting bodies obtained in a semi-natural situation (16 fruiting bodies in 5 months). Log #2, lacking moisture, in a windy environment and unprotected from predators failed to produce fruiting bodies. It was found that predators are attracted by the odor of the gleba and rupture the peridium before the eggs open

naturally. They eat the receptacle and the gleba, leaving the volva like an empty shell. Fruiting bodies obtained in dry periods of the rainy season were in general smaller. When Log #1 was moved to the same locality as Log #2, and kept moist for more than a month, only two eggs were obtained, but neither reached maturity. They were apparently affected by the low relative humidity and higher temperature of the new habitat. Although Log #1 produced a fairly large number of fruiting bodies before protection, most of them never reached maturity because of predator action.

DISCUSSION

Apparently *L. pusilla* requires a very high relative humidity, low temperature (16-20 C) and a shady place to grow and fructify. This explains why all collections are obtained during the rainy season. In nature these conditions are provided by the moist low planes of the forest and by the mosses that usually cover the logs. Altitude may not be an important factor. I have found the species from 1600 to 2300 m. Under the conditions of this study sporophores were obtained at 1200 m. Here receptacles with three arms were more characteristic than those with two. Fruiting bodies with four arms may be found, although they are less common than those with two or three arms. It was also observed that sporophores are originated at different times of the year, whenever environmental conditions are appropriate. These conclusions can apparently be applied to all other phalloids that are found in similar habitats. Since the same mycelium can, as the present experiments show, give rise to 2-, 3-, or 4- armed, otherwise similar fruiting bodies, the distinction between *L. pusilla* with two arms and *L. pereximia* with three, loses significance. In my opinion *L. pereximia* (*C. pereximia* Gómez) is a synonym of *L. pusilla*. Dring, as stated earlier, agrees with this view.

This work also demonstrated that it is not possible to accept new species descriptions of Clathraceae based on only one or two fruiting bodies.

RESUMEN

Se redescubre *Laternea pusilla* encontrada en madera en descomposición en Costa Rica (América Central). El receptáculo está formado por 2, 3, o 4 brazos en vez de 2 como se comunicó originalmente. Se informa sobre observaciones ecológicas comparativas de la especie, realizadas durante varios meses en su habitat natural, así como en diferentes altitudes y medios.

Los estudios anatómicos muestran que el receptáculo de *L. pusilla* se origina del tejido primordial, por encima del rizomorfo. En su origen, el receptáculo es una estructura con cámaras que se ramifica luego en 2, 3, o 4 brazos igualmente con cámaras. Las ramas finalmente rodean la gleba, la levantan y finalmente la dejan suspendida por debajo del arco que forman los brazos del receptáculo. Conforme el cuerpo fructífero se desarrolla, las paredes de las cámaras externas de los brazos se rompen y originan las crestas del cuerpo fructífero adulto, mientras que las cámaras internas superiores dan origen a las trabéculas que sostienen o suspenden la "linterna" y la gleba.

Se considera *Laternea* Turpin el nombre válido para el género, más que *Colonnaria* Raf., que parece ser aplicable más bien a *Clathrus* Mich. & Pers. *Colonnaria pereximia* Gómez se estima sinónimo de *L. pusilla*, con base en la variabilidad de esta especie en cuanto al número de brazos del receptáculo.

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Figs. 1-4. *Laternea pusilla*.

- Fig. 1.** Eggs developing in the natural substrate. Note unopened eggs with exoperidium flakes and two-armed receptacle in which the external chambers have not broken yet to form the crests. The gleba is being swept up with elongation of the arms.
- Fig. 2.** The fruiting body shown in fig. 1 has reached here its full development; the crests are now formed and the "lantern" is held in place by trabecular-like structures.
- Fig. 3.** A three-armed receptacle seen from above. Note crests, the junction of the arms at the top, and the gleba below.
- Fig. 4.** A four-armed recetacle. Gleba, rhizomorphs and volva are shown. Figs. 2 and 4 show freeze-dried specimens.



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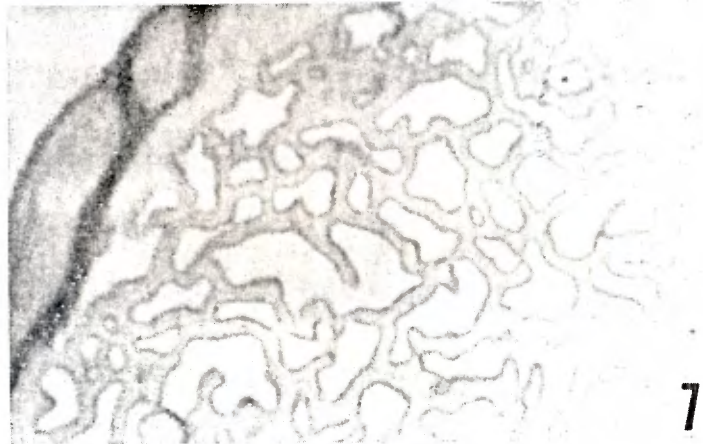
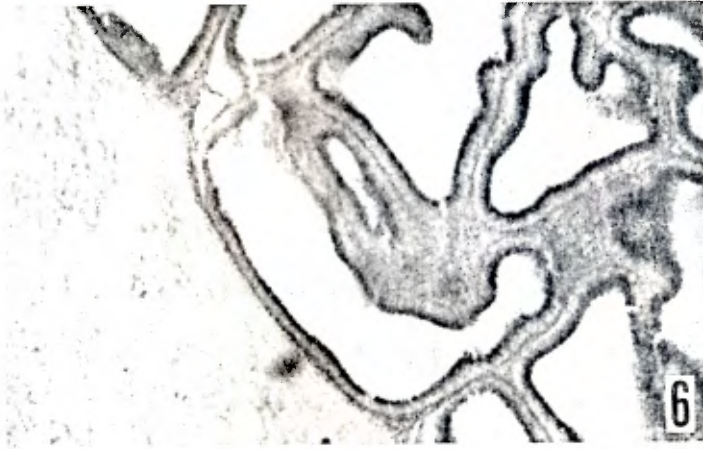
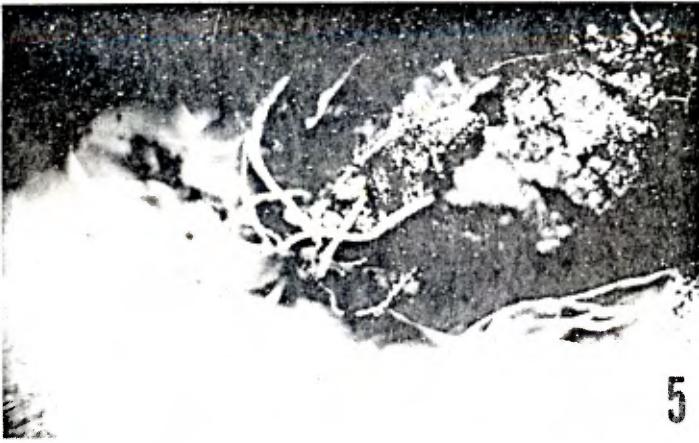
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Figs. 5-7. *Laternea pusilla*.

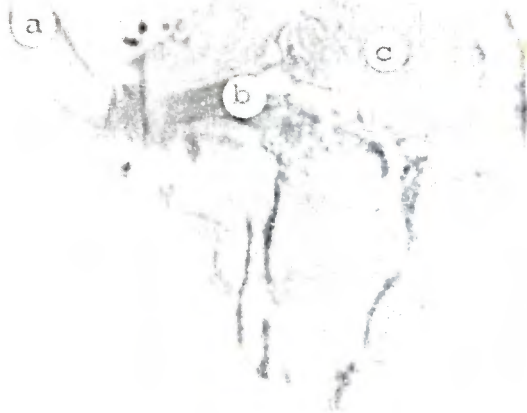
- Fig. 5. Rhizomorphs emerging from the natural substrate.
- Fig. 6. Cross-section of fruiting body showing internal layer of the peridium; primordial and hymenial tissue in the labyrinthine gleba.
- Fig. 7. Section of fruiting body showing the two peridium layers.



Figs. 8-9. *Laternea pusilla*.

Fig. 8 Longitudinal section of fruiting body, showing: a, rhizomorph; b, origin of the chambered recetacle branched at the apex; and c, gleba divided in three parts.

Fig. 9. Detail of fig. 8 showing: a, the prosenchymatous tissue of rhizomorph; and b, chambers of the undeveloped recetacle.



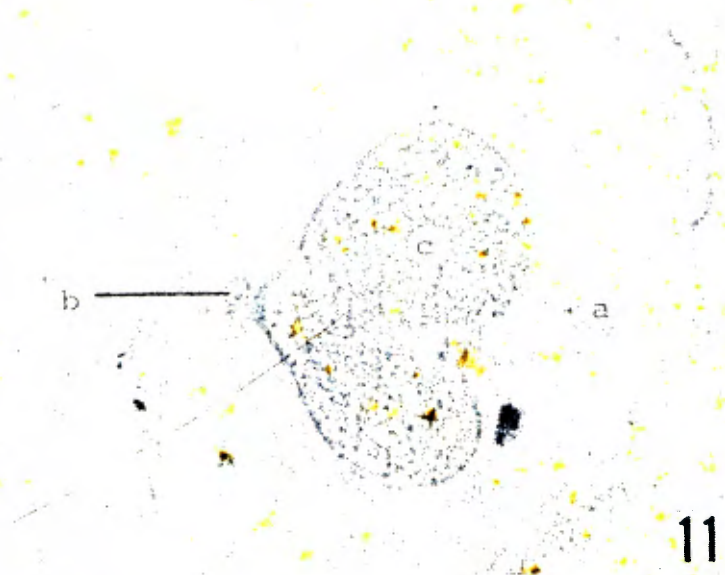
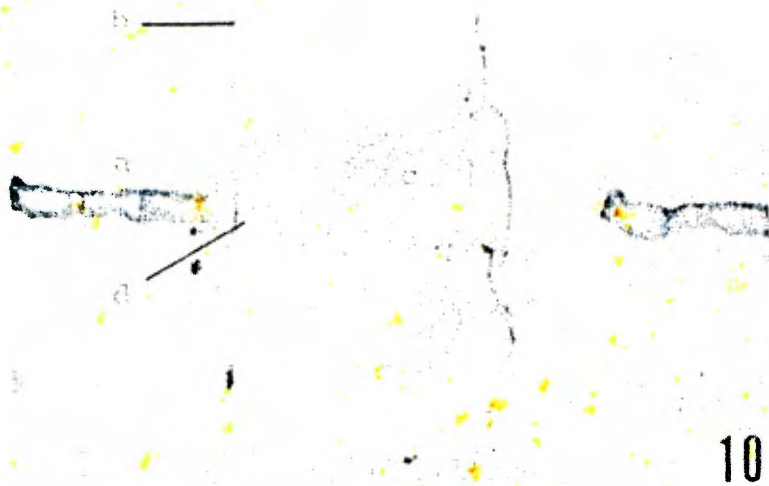
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Figs. 10-11. *Laternea pusilla*.

- Fig. 10. Longitudinal section showing: a, rhizomorph; b, peridium; c, heart-shaped gleba; d, early stages of receptacle development.
- Fig. 11. Longitudinal section of another egg, showing: a, two opposite peridial sutures; b, formation of first chambers of the receptacle; and c, gleba.



Chapter 17

Patterns of Distribution of the Central American Ichthyofauna

WILLIAM A. BUSSING

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1. Introduction

In a previous paper dealing with the biogeography of the ichthyofauna of the San Juan Province of Central America, I analyzed the vicariant patterns of distribution, in light of paleogeologic knowledge in order to determine the origin of historical faunal elements and the barriers responsible for these patterns. Some general conclusions reached at that time were that: (1) an ancient South American Element dispersed into Central America during Late Cretaceous or Paleocene times; (2) Central America was later isolated from South America during most of the Tertiary; (3) land masses south of the Nicaraguan Depression remained emergent throughout the Tertiary; and that (4) the two continents were reunited by the closure of the Bolivar seaway in Pliocene time.

The intent of the present study is to: (1) determine the generalized patterns of distribution of the entire Central American fresh-water ichthyofauna, (2) identify the assem-

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blages of fishes which presently share similar distributions, and (3) review briefly the causes of some of these basic patterns and their disjunct component parts.

2. Methodology

Generalized patterns of distribution were determined for monophyletic groups (usually genera or, in some cases infrageneric categories) and where the constituent species of several distinct genera coincided in forming disjunct populations, these too were noted. Finally all genera were assigned to three basic patterns, each formed of two or more disjunct units. These were subsequently identified as the Old Southern, New Southern, and Northern Elements as in Bussing (1976). It was noted that several widespread characid genera could be divided into species that conformed to an Old Southern distribution and others that were possibly New Southern in nature. Thus, for the purposes of this study, some genera were provisionally divided into two species groups corresponding to the Old and New Southern Elements.

3. Patterns of Distribution

At first glance Central American fish distributions seem to present a mosaic of disarray. If monophyletic groups such as genera are grouped according to overall similarity of pattern, assemblages of unrelated genera with similar disjunct patterns begin to appear. These vicariant clusters or so-called centers of endemism can often be explained in terms of the barriers responsible for these subdivisions. For this purpose, fresh-water fish distributions are eminently more conservative of past distributions because of the inherent physiological nature of these organisms. Fresh-water fishes are far less vagile than other vertebrates, plants, and even most fresh-water invertebrates.

3.1. Old Southern Element

Many genera comprising this element have widespread distributions throughout Middle America as well as northern Mexico, some extending to or beyond the southern United States (Figs. 1 and 2). Many of these genera are Central American endemics (Fig. 3), while others have representatives in South America (Figs. 2 and 4). Nearly all genera range from western Panama to southern Mexico and the greatest number of species is found along the broad Atlantic versant, especially in three cardinal centers of endemism in Central America: (1) between the Río Papaloapam, Mexico and Río Motagua, Guatemala; (2) northeastern Honduras to northern Costa Rica; and (3) eastern Costa Rica to the Canal Zone, Panama. Each of these three centers corresponds to an ichthyological province, the Usumacinta, San Juan and Isthmian (Fig. 5). Many genera of this element also have representative species or populations on the Pacific versant generally between Acapulco, Mexico and the Río Lempa, El Salvador and between Punta Mala, Costa Rica and western Panama. Again, these two regions of endemism correspond to two Pacific versant fish provinces, the Chiapas-Nicaraguan and Isthmian Provinces respectively (Fig. 5).

On the Atlantic versant of Mexico, Rosen (1978) has identified two areas of endemism based on fish distribution: the Río Pánuco basin and the Río Grande, the latter of which in turn is part of a much larger region extending to the southeastern United States. These Atlantic slope centers of endemism and two other centers on the Pacific slope of Mexico are included in Fig. 1.

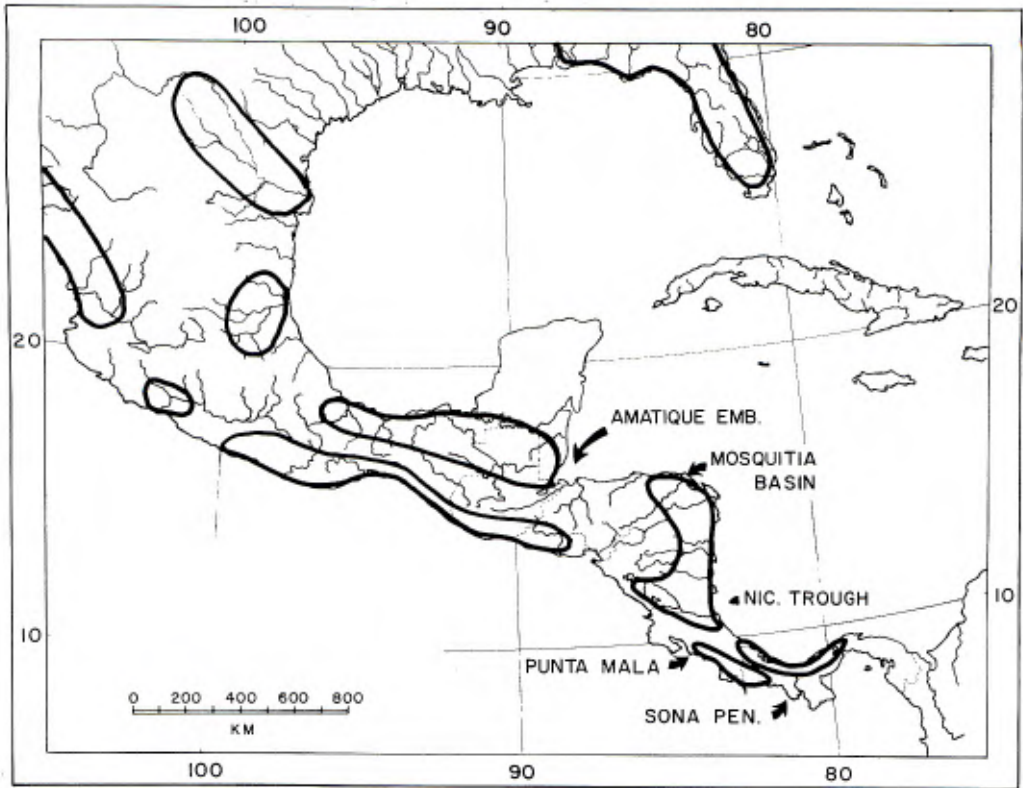


Figure 1. Principal regions of endemism of the Old Southern Element in North and Middle America.

Although most genera of this Element are either endemic to the area or have most representatives there, some justification must be provided in order to include several other variations of the basic Old Southern Pattern. Extremes range from ubiquitous genera or species complexes to relict endemics with a small extant range.

Members of the genus *Poecilia* (subgenus *Poecilia*) and of the *Astyanax fasciatus* species complex are in a class by themselves. The species of *Poecilia* range from the southeastern United States to Argentina and are especially abundant near the coast, often represented by permanent brackish water populations; populations are also found in the highlands of Central America. Several species of the *Astyanax fasciatus* complex extend between the Río Grande drainage of the southern United States and throughout South America as far south as Argentina; species are present in Central America in nearly all habitats between 1000-m elevation and brackish tidal streams. Thus, although these ubiquitous forms have ranges as extensive as, or more so than, many fishes of marine affinities, their fresh-water breeding habits and deep penetration into headwater streams has permitted the formation of numerous geographic races and species throughout their ranges. The subdivision of these two genera generally conforms to the Old Southern pattern, although in *Poecilia* the primary distributions have been partially obscured by subsequent sympatry between congeners. Another wide-ranging group, the species comprising the genus *Cichlasoma*, covers much of South America, exhibits greatest species diversity in Central America, and its *Herichthys* species complex reaches the Río Grande system of the United States. The genus *Poeciliopsis* extends along the Pacific versant from south-

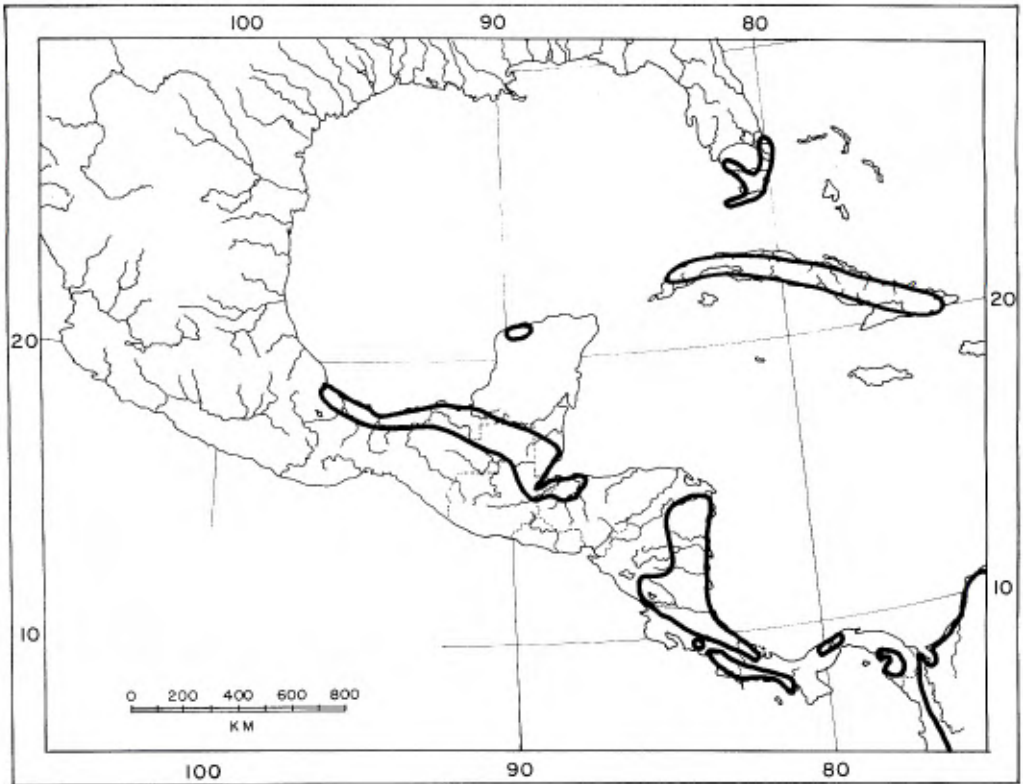


Figure 2. Distribution of the species of the Old Southern cyprinodontid genus *Rivulus* in North and Middle America.

western United States to Colombia, only one species, *P. gracilis*, occurring on the Atlantic slope. These four genera are considered part of the Old Southern Element because of their far northern distributions, as well as their similar patterns of subdivision into species populations.

Several other Old Southern groups are restricted to northern Central America and the southern United States: *Cyprinodon*, *Floridichthys*, *Heterandria* and *Profundulus*, and the closely related *Fundulus*.

Two genera (*Carlana* and *Bramocharax*) are represented by disjunct populations in the Río San Juan drainages of Nicaragua and Costa Rica. *Bramocharax* is also found in Guatemala, but the monotypic *Carlana* has not been taken elsewhere. These isolated species apparently represent relict populations of formerly more widespread genera and since their distribution patterns conform in part to the Old Southern pattern and not at all to the New Southern pattern, they are included in the former element.

I am assigning two other poeciliid genera (*Priapichthys* and *Neoheterandria*) to this element, although their distributions extend from the Río San Juan southward and into northwestern South America. Five characid genera extend throughout Central America and are also well represented in South America. It will be shown that some, perhaps all, of these genera contain species groups which represent both Old and New Southern Elements.

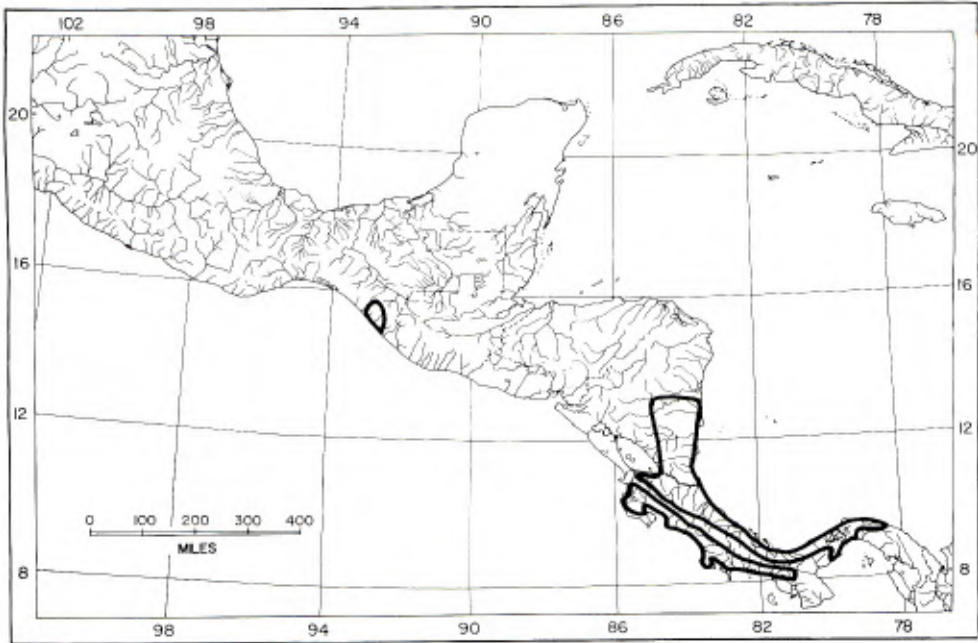


Figure 3. Distribution of the species of the Old Southern poeciliid genus *Brachyrhaphis* in Middle America.



Figure 4. Distribution of the species of the characid *Brycon* in Middle America. Northern populations are considered of Old Southern Origin, whereas isthmian species could be of New Southern lineage.

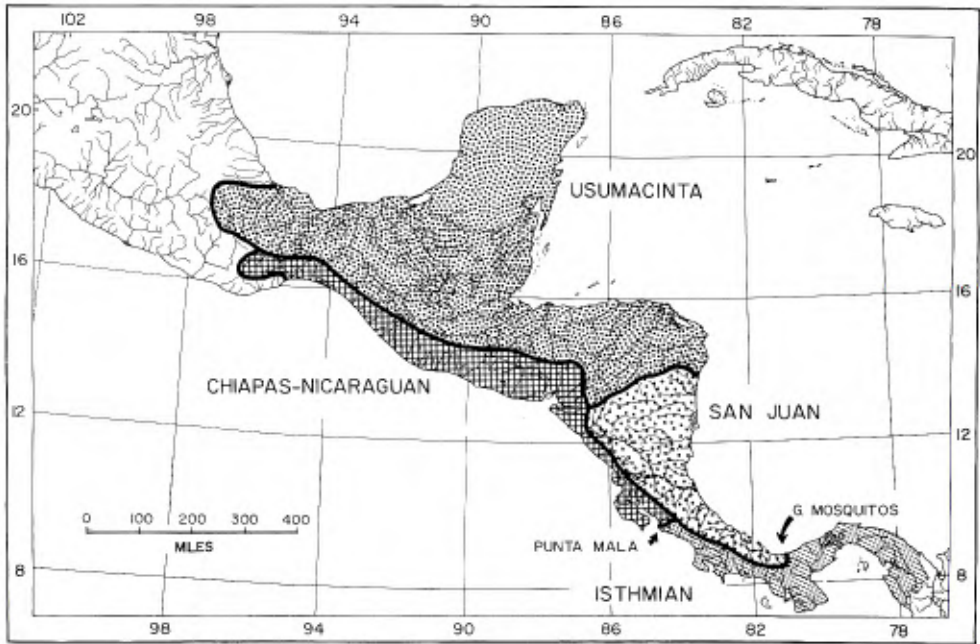


Figure 5. Major ichthyological provinces of Middle America.

Representatives of nine families including 39 genera and approximately 221 species make up the fresh-water fish fauna of this element. Eighteen genera are endemic and five exhibit their principal diversity in the general area. The average number of species per genus is 5.7. On the basis of geological evidence, this element reached Central America from the south in late Cretaceous or early Tertiary times.

3.2. New Southern Element

All genera belonging to this element are restricted to the Isthmian fish province. They do not extend north of Punta Mala, Costa Rica, which marks the boundary of the Chiapas–Nicaraguan Province on the Pacific side, nor do they overcome the Golfo de Mosquitos filter barrier on the Atlantic versant of Panama (Fig. 5). All genera but one are also found in neighboring northwestern Colombia and many Panamanian populations are conspecific with populations found in the Río Atrato and San Juan drainages of Colombia (Eigenmann, 1920a, 1922; Dahl, 1971).

The distributions of the members of this element vary primarily with regard to their degree of northwestward extension on the Pacific versant of lower Central America. Four basic patterns are recognized, all of which include representative populations on the Atlantic slope of Panama (Fig. 6).

The first pattern is shown by genera reaching only as far as the Río Tuira or Bayano basins on the Pacific slope: *Characidium*, *Creagrutus*, *Eretmobrycon*, *Phanagoniates*, *Aparioidon*, *Gasteropelecus*, *Apterotonus*, *Trachycorystes*, *Ageneiosus*, *Pimelodus*, *Hoplosternum*, *Ancistrus*, *Astroblepus*, *Chaetostoma*, *Crossoloricaria*, *Dasylicaria*, *Lasiancistrus*, *Leptoancistrus*, and *Geophagus*. Only four of these genera are represented on the Atlantic versant of central or eastern Panama.

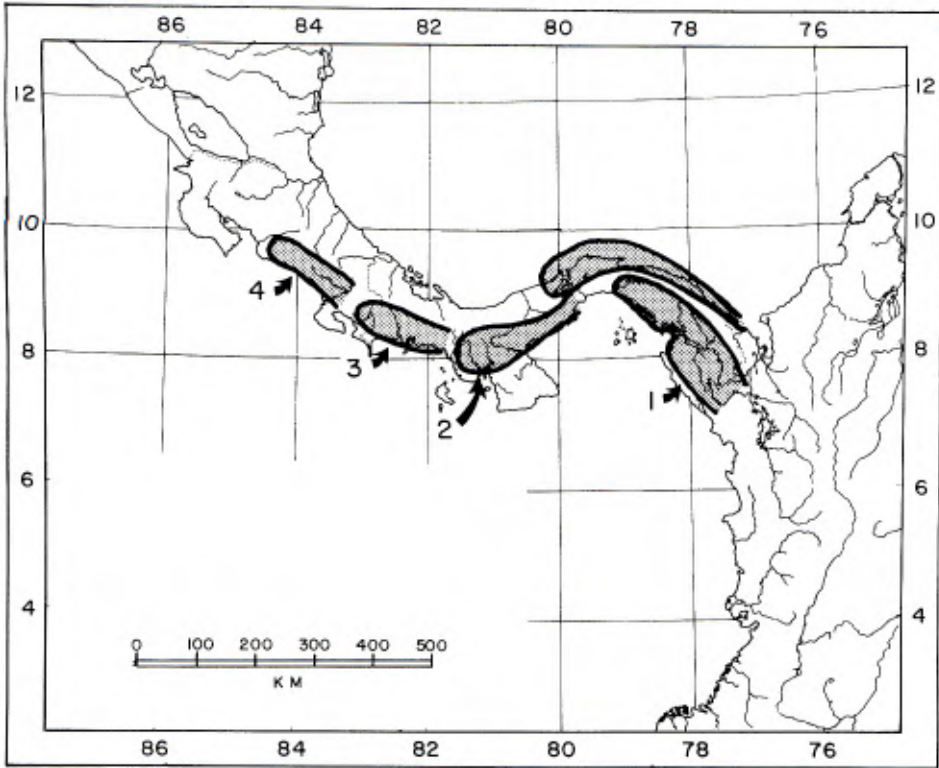


Figure 6. Principal patterns of distribution of species of the New Southern Element.

A second group of genera reach the vicinity of the Soná Peninsula on the Pacific slope of western Panama: *Gephyrocharax*, *Hemibrycon*, *Ctenolucius*, *Eigenmannia*, *Sternopygus*, *Imparales*, and *Sturiosoma*. Only *Gephyrocharax* and *Imparales* also have reached the Atlantic versant in central Panama.

A third category contains the genera *Curimata*, *Hoplias*, *Rineloricaria* and *Aequidens*, which are found in the Río Coto drainage at the southeastern extreme of Costa Rica, but do not reach the Río Térraba basin just to the north. All but *Curimata* have disjunct Atlantic slope populations in central or eastern Panama.

Finally, a fourth group of seven genera reach the Río Térraba drainage, some extending along the Pacific versant to the Punta Mala, Costa Rica filter barrier: *Cheirodon*, *Pterobrycon*, *Piabucina*, *Nannorhamdia*, *Pimelodella*, *Pygidium* and *Hypostomus*. All but *Pterobrycon* and *Nannorhamdia* are also represented on the Atlantic slope of central or eastern Panama.

Most genera of this element are represented by one or two species that have continuous distributions throughout the Isthmian Province, often continuing at the species level into Colombia. Exceptions include *Gephyrocharax*, *Cheirodon* (Fig. 7), and *Piabucina*, which appear to have subdivided *in situ*, yielding several species each. Other exceptions include disjunct populations of *Nannorhamdia* and *Pterobrycon* (Fig. 8) in southeastern Costa Rica, which are widely separated from their congeners in the Río Atrato drainage of Colombia. The genus *Imparales* of central and eastern Panama is otherwise known only from the Orinoco drainage of Venezuela.

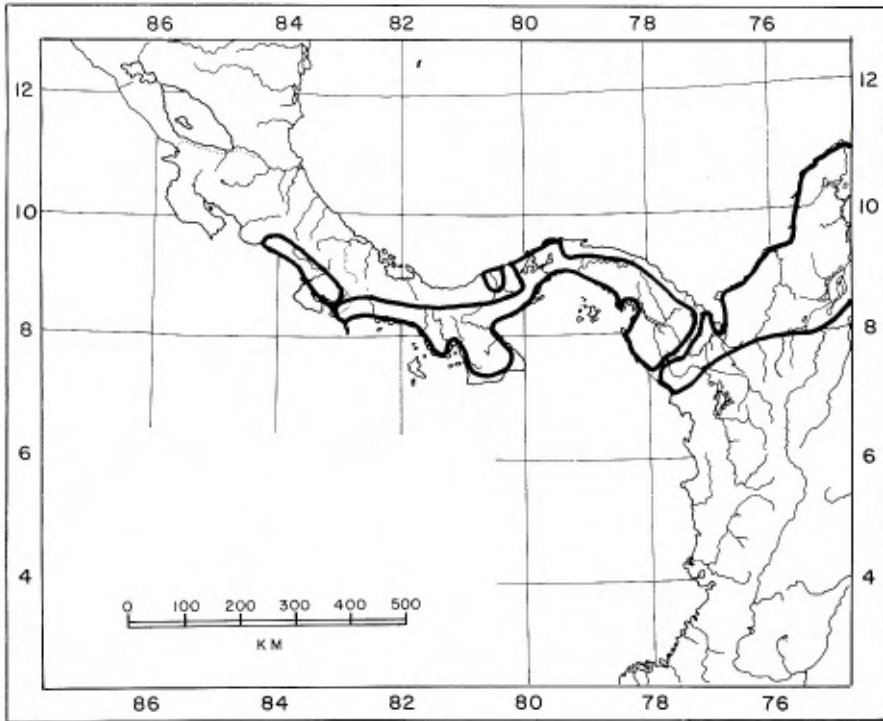


Figure 7. Distribution of the species of the New Southern characid genus *Cheirodon* in Central America, after data from Fink and Weitzman (1974).

Members of this element probably reached Central America sometime in the Pliocene. The assemblage consists of 16 families, 43 genera, and 66 species. Only the recently described *Eretmobrycon* (Fink, 1976) represents an endemic genus. The average number of species per genus is only 1.5.

3.3. Genera Containing Both Southern Elements

If we are consistent in our method of analysis, as many as five characid genera should be separated into species groups in order to be allocated to different historical elements. Four of these genera range throughout Central America, one reaches the United States; the other, *Bryconamericus*, extends only to northern Nicaragua. All are well represented in Colombia and are among the most speciose characid genera in South America.

Certainly in the case of the *Astyanax fasciatus* species complex containing perhaps six valid species ranging from the United States border to the southern limit of Central America, on the one hand, and *Astyanax orthodus* (*Astyanax bimaculatus* complex) of Colombia, Panama and Costa Rica, on the other (Fig. 9), we are dealing with groups that have experienced totally different histories in the Tertiary. *Astyanax ruberrimus* from central and eastern Panama and Colombia, although of the *A. fasciatus* type, has a New Southern distribution pattern. Thus, I hypothesize that the Mexican and northern Central American *Astyanax* are descendants of an Old Southern *fasciatus* stock, whereas *A. rub-*

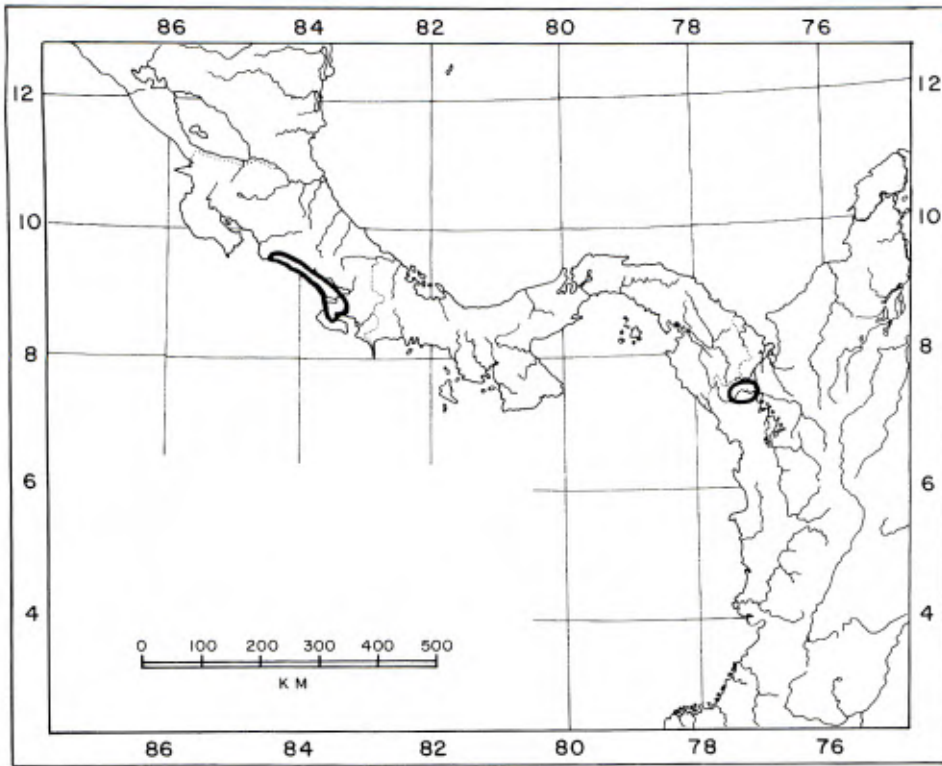


Figure 8. Distribution of the two species of the New Southern characid genus *Pterobrycon* in Central and South America.

errimus, also of a *fasciatus* stock and *A. orthodus* of a distinct lineage, represent New Southern species.

Similarly, *Roeboides* can be divided into an Old Southern *guatemalensis* extending from the Isthmus of Tehuantepec on the Pacific side and eastern Honduras on the Atlantic slope to eastern Panama, a possibly New Southern *occidentalis* in central and eastern Panama, and an allied undescribed species from southeastern Costa Rica.

The phylogenetic relationships of the species of *Brycon*, *Bryconamericus* and *Hyphessobrycon* are not as easily assessed, although each has at least one species representing the Old Southern Element, one or more species in Panama that could correspond to the New Southern Element, and similar or identical species in the Río Atrato and San Juan basins of Colombia. All are also represented by disjunct populations in southeastern Costa Rica, a pattern that is common to both Old and New Southern Elements. Thus, the number of the species of these genera assigned to either historical element in Table I is only tentative. Likewise, it is possible that Panamanian species of *Rivulus* could turn out to belong to the New Southern Element.

3.4. Northern Element

This assemblage consists of four families containing four genera and seven species (Table I). The average number of species per genus is 1.8. The general distribution pattern shared by the four genera extends between the southeastern United States along the Gulf

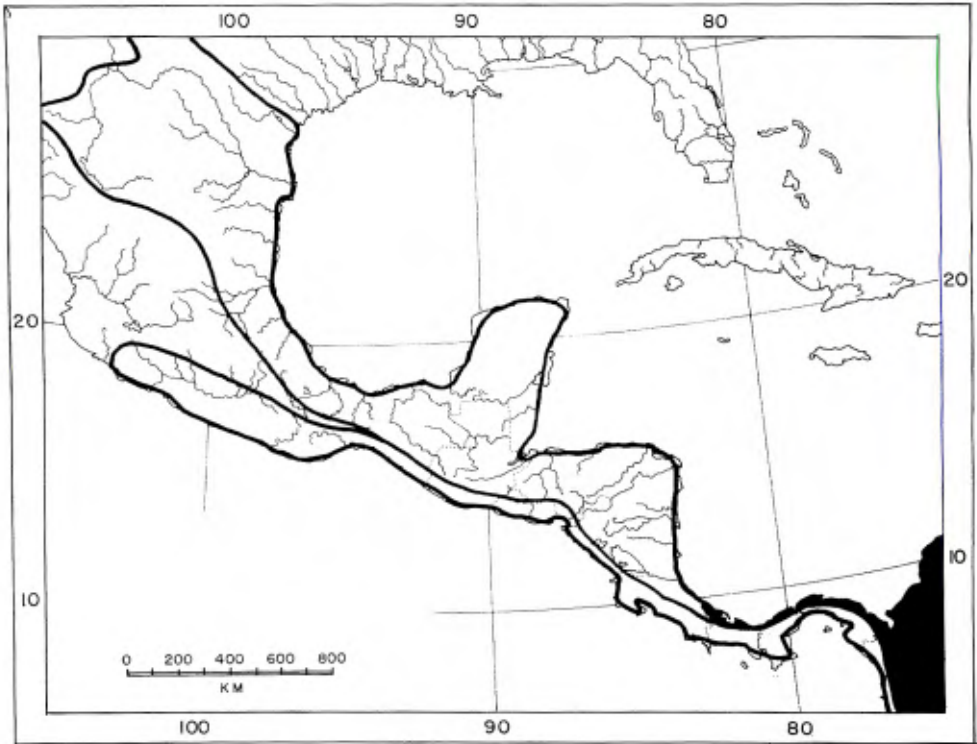


Figure 9. Distribution of the species of the characid genus *Astyanax* in North and Middle America. Northern populations are considered of Old Southern origin, whereas *A. orthodus* (in black) represents a New Southern lineage.

coast to northern Guatemala, embraces both versants, and, not surprisingly, shares similar patterns of subdivision with members of the Old Southern Element (Fig. 1). All four genera reach as far south as the Usumacinta fish province. The gar, *Atractosteus tropicus* (Bussing, 1976), and gizzard shad, *Dorosoma* (Fig. 10), also occur in the Great Lakes of Nicaragua of the Río San Juan system and on the Pacific versant (*Atractosteus* in the Chiapas-Nicaragua Province and *Dorosoma* in northwestern Mexico). The appearance of *Atractosteus* in North America predates the formation of the Central American region (Wiley, 1976), thus the gars (and perhaps the other northern species) probably shared a similar history with numerous genera of the Old Southern Element throughout the Cenozoic.

4. Temporal Factors

Now that basic distributional information has been presented, a number of questions arise regarding temporal aspects of the history of Central American fishes. Do we have an adequate fossil record or other means of estimating the rate of evolution in various groups of the Central American ichthyofauna? What has been the direction and rate of dispersal of fresh-water fishes during the relatively unstable history of the region?

A fossil, cichlid, *Cichlasoma woodringi* from the Miocene of the Greater Antillean island of Hispaniola is very similar to a species, *C. haitiensis*, now inhabiting the island

Table I. Component Genera of Historical Assemblages of the Middle American Fresh-Water Ichthyofauna^a

| Old Southern | New Southern | Northern |
|--|---------------------------|-------------------------|
| Characidae | Characidae | Lepisosteidae |
| <i>Astyanax</i> (5) | <i>Astyanax</i> (2) | <i>Atractosteus</i> (1) |
| <i>Bramocharax</i> (3) | <i>Brycon</i> (3) | Clupeidae |
| <i>Brycon</i> (4) | <i>Bryconamericus</i> (3) | <i>Dorosoma</i> (3) |
| <i>Bryconamericus</i> (2) | <i>Characidium</i> (1) | Catostomidae |
| <i>Carlana</i> (1) | <i>Cheirodon</i> (5) | <i>Ictiobus</i> (2) |
| <i>Hyphessobrycon</i> (4) | <i>Creagrutus</i> (2) | Ictaluridae |
| <i>Roeboides</i> (1) | <i>Eretmobrycon</i> (1) | <i>Ictalurus</i> (1) |
| Gymnotidae | <i>Gephyrocharax</i> (3) | |
| <i>Gymnotus</i> (3) | <i>Hemibrycon</i> (1) | |
| Pimelodidae | <i>Hyphessobrycon</i> (1) | |
| <i>Rhamdia</i> (14) | <i>Phanagoniates</i> (1) | |
| Cyprinodontidae | <i>Pterobrycon</i> (1) | |
| <i>Cyprinodon</i> (2) | <i>Roeboides</i> (2) | |
| <i>Floridichthys</i> (1) | Curimatidae | |
| <i>Fundulus</i> (2) | <i>Curimata</i> (1) | |
| <i>Garmanella</i> (1) | Paradontidae | |
| <i>Oxyzygonectes</i> (1) | <i>Apareiodon</i> (2) | |
| <i>Profundulus</i> (5) | Lebiasinidae | |
| <i>Rivulus</i> (11) | <i>Piabucina</i> (3) | |
| Anablepidae | Gasteropelecidae | |
| <i>Anableps</i> (1) | <i>Gasteropelecus</i> (1) | |
| Poeciliidae | Ctenoluciidae | |
| <i>Alfaro</i> (2) | <i>Ctenolucius</i> (1) | |
| <i>Belonesox</i> (1) | Erythrinidae | |
| <i>Brachyrhaphis</i> (8) | <i>Hoplias</i> (2) | |
| <i>Carlhubbisia</i> (2) | Apterodontidae | |
| <i>Gambusia</i> (5) | <i>Apteronotus</i> (1) | |
| <i>Heterandria</i> (9) | Sternopygidae | |
| <i>Neoheterandria</i> (3) | <i>Eigenmannia</i> (1) | |
| <i>Phallichthys</i> (4) | <i>Hypopomus</i> (1) | |
| <i>Poecilia</i> (<i>Poecilia</i>) (10) | <i>Sternopygus</i> (1) | |
| <i>Poeciliopsis</i> (8) | Auchenipteridae | |
| <i>Priapella</i> (3) | <i>Trachycorystes</i> (1) | |
| <i>Priapichthys</i> (3) | Ageneiosidae | |
| <i>Scolichthys</i> (2) | <i>Ageneiosus</i> (1) | |
| <i>Xenodexia</i> (1) | Pimelodidae | |
| <i>Xiphophorus</i> (17) | <i>Imparales</i> (1) | |
| Atherinidae | <i>Nannorhamdia</i> (1) | |
| <i>Melaniris</i> (11) | <i>Pimelodella</i> (1) | |
| Cichlidae | <i>Pimelodus</i> (1) | |
| <i>Cichlasoma</i> (75) | Trichomycteridae | |
| <i>Herotilapia</i> (1) | <i>Pygidium</i> (2) | |
| <i>Neetroplus</i> (1) | Callichthyidae | |
| <i>Petenia</i> (1) | <i>Hoplosternum</i> (1) | |

(continued)

Table I. (continued)

| Old Southern | New Southern | Northern |
|------------------------|----------------------------|----------|
| Synbranchidae | Loricariidae | |
| <i>Ophisternon</i> (2) | <i>Ancistrus</i> (2) | |
| <i>Synbranchus</i> (1) | <i>Astroblepus</i> (1) | |
| | <i>Chaetostoma</i> (1) | |
| | <i>Crossoloricaria</i> (1) | |
| | <i>Dasylicaria</i> (3) | |
| | <i>Hypostomus</i> (1) | |
| | <i>Lasiancistrus</i> (1) | |
| | <i>Leptoancistrus</i> (1) | |
| | <i>Rineloricaria</i> (2) | |
| | <i>Sturiosoma</i> (2) | |
| | Cichlidae | |
| | <i>Aequidens</i> (1) | |
| | <i>Geophagus</i> (2) | |

^a Number of species in parentheses.

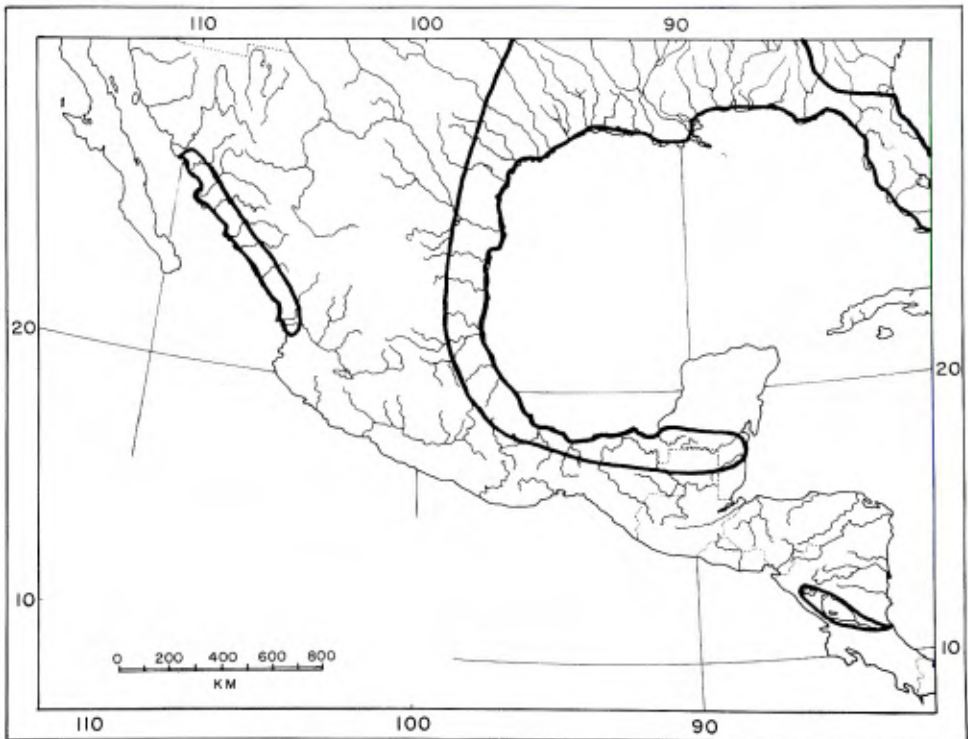


Figure 10. Distribution of the species of the clupeid genus *Dorosoma* in North (part) and Middle America. An example of a Northern Element.

and also remarkably like other members of the *Parapetenia* species complex inhabiting Central America. Pleistocene diatomite deposits in the Río Sisimico Valley in El Salvador are rich in fish fossils (Schmidt-Thomé, 1975) as are similar sediments in the Río Tárcoles drainage of Costa Rica. These Pleistocene fossils are referable to recent species of the families Poeciliidae, Cichlidae and Characidae. Two of the Costa Rican fossils (*Cichlasoma longimanus?* and *Roeboides* sp.) are of principal importance in suggesting a wetter climate here in the past (*C. longimanus* no longer is present in the drainage) and in revealing that a characid, *Roeboides*, was living in the Chiapas-Nicaraguan Province perhaps as long as a million years ago. This latter fact strengthens my contention that some characids did form part of the Old Southern Element.

Certainly the groups common to South America and Africa, the Characidae, Cichlidae, Cyprinodontidae, and the siluriforms, were in existence during the Cretaceous (about 90 million years b.p.) when the two continents began drifting apart. In the introduction to his treatise on Central American fishes, Regan (1906–1908) noted that “not one of the genera [of Cichlidae] is common to Africa and America, but the South American *Acara* [= *Aquidens*] is scarcely generically distinct from the African *Paratilapia*, and there can be no doubt that these are the most generalized of living Cichlidae and very near to the ancestral type of the family.” This and other evidence shows that in some cases (fluvial environments?) cichlids may show remarkably little change over periods of millions of years, although extremely rapid speciation rates in the order of hundreds of thousands of years or less, have been shown for cichlids in the rift lakes of Africa. If the hypothesis is correct that not only cichlids, but poeciliids, cyprinodonts, pimelodids, and some characids, belong to the Old Southern Element, it is clear that these forms too have changed little during the Tertiary.

5. Dispersal

Terrestrial interchange between North and South America has been of primary importance in the history of the region. The separation of present day distribution patterns into two basic types composed of markedly distinct ichthyofaunas suggests that two widely spaced dispersal events took place. I believe that fresh-water fishes (primary and secondary fishes of Myers; 1938, 1966) as here defined are capable of resisting only brief periods in full-strength sea water. With few exceptions these fishes probably do not “island hop,” but expand their ranges through fresh or at most, brackish water connections (Bussing, 1976). Thus, fresh-water fish disperse much more slowly than other continental organisms, consequently, they tend to reveal older distribution patterns more closely and, by their absence or low diversity, point out regions of past extinctions. By a study of overall distribution patterns perhaps the following questions can be clarified. Was there a true fusion of faunas as sometimes stated or was net dispersal of fishes mainly unidirectional? What were the precursors like of the Old Southern and New Southern ichthyofauna, and why were these assemblages so different from each other?

5.1. Early Dispersal

Any discussion of the spatial factors involved in the biogeography of Central America necessarily begins with the history of the source of more than 95% of our ichthyofauna—South America. It would be extremely valuable to know which fish groups inhabited north-western South America in Cretaceous–Paleocene times when a land connection between Nuclear Central America and South America was established and the Old Southern dis-

persal northward began. One can hypothesize that this fresh-water ichthyofauna included the precursors of the major lineages now present in Central America: six species of *Cichlasoma*, five poeciliids, two *Rivulus*, two or three other cyprinodonts, two or three *Rhamdia*, one or two *Melaniris*, and a species each of *Astyanax*, *Brycon*, *Bryconamericus*, *Roebooides*, *Hypessobrycon*, *Gymnotus*, *Synbranchus*, and *Ophisternon*. Probably several of the members of this generalized South American assemblage already occupied the region when the isthmian land bridge first united North and South America. These northwestern basins have been well isolated since the rise of the Andes which began before the Tertiary. The Andes in northwestern Colombia expand into a fanlike structure (Cordilleras Occidental, Central, and Oriental), which provides a succession of formidable barriers isolating the Atrato, Cauca, and Magdalena basins from the rest of the continent.

Apparently only euryhaline fishes and perhaps some northern fresh-water groups inhabited Nuclear Middle America in late Cretaceous times when the Isthmian Link was first established. Thus, net migration of the Old South American fresh-water fishes must have been in a northward direction along the isthmian corridor. There is no evidence that any northern fresh-water groups reached South America at this time, nor do they extend south of the Río San Juan drainage of Costa Rica even at the present time.

5.2. Late Dispersal

During the ensuing period the Old Southern Element became more speciose in Central America, while the rich Amazonian fauna gradually supplemented the semi-isolated northwestern drainages of South America. At the outset of the New Southern migration northward sometime in Pliocene, the ichthyofauna of northwestern South America must have been much as it is now and considerably more diverse than in early Tertiary times. The contemporary fish fauna of Nuclear Middle America also must closely resemble that of Pliocene times. It is generally accepted that lower Central America was partially or totally submerged (or displaced) during most of the Tertiary. At the time the Talamancan emergence and other middle Tertiary islands were fusing to form the Isthmian Link, a relatively depauperate ichthyofauna must have been slowly extending southward into the region. Similarly, a strikingly different fish fauna was establishing itself on the edge of the Bolivar Trough at the extreme northwestern corner of South America. This latter assemblage was especially rich in characoid and catfish species, whereas the Central American ichthyofauna consisted mostly of cichlids and poeciliids with only a few characids and catfishes (Table I).

After the intercontinental land bridge was reestablished by the closure of the Bolivar seaway in eastern Panama, an interchange of these two distinctive faunas took place. It was evident to Eigenmann (1920b) that the present-day fishes of the Río Tuira, Panama, were derived from the Río Atrato on the opposite side of the continental divide. He noted the marked similarity of the Tuira and Atrato faunas and, on the basis of his knowledge of fish distributions in Colombia and Panama, concluded that dispersal was overwhelmingly in a westward direction through an Atrato–Tuira connection. Eigenmann also compared the Río Chagres and Río Grande faunas on the opposite sides of Panama before completion of the Canal. About 43% of the Chagres species were shared with the Bayano (Chepo), 27% with the Tuira, and 18% with the Atrato. He concluded that most southern immigrants reached the Chagres basin via the route Atrato, Tuira, Bayano, Chagres. That is, by crossing the continental divide from the Atrato to the Tuira, from there to the Bayano, and recrossing the divide to reach the Chagres, rather than directly from the Atrato to the Chagres along the Atlantic coastline. He mentioned *Hypessobrycon panamensis* and eleotrids as possible exceptions; *Astyanax orthodus* appears to have had a similar history and likewise does not appear on the Pacific versant.

Some species (*Geophagus crassilabris*, *Chaetostoma fischeri*, *Pimelodus clarias*, and *Pygidium striatum*) are present on both slopes of eastern Panama and thus may have reached central Panama along either or both versants. Other species inhabiting the Pacific versant of western Panama (*Rineloricaria uracantha*) or eastern Panama (*Creagrutus affinis*) have disjunct populations on the Atlantic slope in central Panama, which suggests that extinctions have taken place which can obscure the past dispersal routes of some species. Eigenmann (1920b) also noted that while many species of fresh-water fishes crossed the Panama divide, the lowland euryhaline gobies and eleotrids, with few exceptions, had become specifically distinct on the two sides and thus the strictly fresh-water species had dispersed more recently. The fresh-water gobioids are much more numerous near the coast, and most species avoid high-gradient streams, so this might explain why they have not crossed the low continental divide in Panama.

Current knowledge of fish distributions does nothing to alter what was evident to Eigenmann. I also see no reason to diverge from Eigenmann's (1920b) generalization that the ". . . tide of migration has all flowed westwards." Nevertheless, distribution patterns suggest that some Old Southern fishes have extended into Colombia and possibly even Ecuador. The poeciliids *Gambusia lemaitrei*, *Poecilia caucana*, *Neoheterandria elegans*, *Poeciliopsis turrubarensis*, the atherinid *Melaniris pachylepis*, and the cichlid *Cichlasoma atromaculatum* reveal such distributions and most of these forms are euryhaline, which would facilitate a coastwise migration. The genus *Priapichthys* was included in the Old Southern genera because *P. annectens* occurs on both versants of northern Costa Rica and *P. panamensis* in southern Nicaragua; six other nominal species are found in Panama, Colombia, or Ecuador. It is possible that this genus is comprised of Old and New Southern Elements. How would these Old Southern fishes disperse southeastwards and into a region of a much more diverse and species-rich ichthyofauna? I believe these euryhaline fishes of the poeciliid and cichlid-rich Central American fauna are expanding into Panama and Colombia because few of these fishes exist immediately to the south. Conversely, the characoid and catfish-rich Colombian fauna is now successfully invading the Central American region, which is poor in these groups.

The much greater success of the South American fauna in migrating northward over the Central American fishes in extending southward suggests that the former is a more mature assemblage, that is, more highly adapted in this case to a fluvial biotope. Cichlids and poeciliids, on the other hand, represent "peripheral" species that have radiated considerably in a riverine environment with few of the more fluvial characoids and catfishes. In mature fish communities, cichlids are often restricted to lacustrine habitats and poeciliids are usually confined to coastal streams or thermal or hypersaline biotopes. Myers (1966) felt that the relatively rapid evolution of cichlids and poeciliids in Central America is due to their arrival prior to the Characidae and that the latter recent arrivals, in a geological sense, raced northward in Pliocene or Pleistocene times. I feel that fresh-water fishes dispersed much more slowly in Central America and that the Old Southern characids for some reason did not find the conditions appropriate to a rapid rate of evolution in Central America. They did speciate in lower Central America, but their northern limits (except *Astyanax*) roughly coincide with the southern distribution of other cypriniform fishes, the Cyprinidae and Catostomidae. This competition with an established cypriniform assemblage in northern Central America and Mexico may have been an important factor in halting dispersal and reducing radiation.

6. Vicariance

An examination of the total extension of patterns of distribution has confirmed that an early and later dispersal into Central America from the south has apparently taken place. A closer look at the component species of each genus (or subgeneric lineage) has shown

that in many cases these species have largely allopatric, but contiguous distributions. It is believed that this fundamental pattern is the result of the fragmentation *in situ* of an ancestral species into descendent species as a consequence of past events. Where sympatry occurs between the species of these monophyletic groups, it is supposed that dispersal has taken place subsequent to the disappearance of former isolation mechanisms (Croizat *et al.*, 1974).

In dealing with the San Juan ichthyofauna of Central America, I assigned the genera occurring in that province to their respective historical assemblages on the basis of their extension northwards and especially on the pattern of discontinuities of the respective species (Bussing, 1976). For example, I cited *Hyphessobrycon* as an Old Southern lineage because, to have become subdivided as it is now, it must have been present in Central America well in the past when certain geological events isolated populations of the widespread ancestral species. I considered the genus *Brycon* a member of the New Southern Element because of its great differentiation in the Isthmian region, whereas it is represented by only one species north of Costa Rica. In that study I gave great emphasis to the degree that each genus has differentiated into species, but I now feel this is not of prime importance, especially in regards to the poorly studied groups mentioned. Thus, I now consider the above-mentioned genera and several others (Table I) to be composed of both Old and New Southern species. Future studies may reveal that groups such as *Brycon*, *Astyanax*, and *Roeboides* have indeed differentiated in northern Central America, as has *Hyphessobrycon*, into species populations not yet recognized.

The coincidence of several generic distributions to form consistent patterns of speciation suggests that the separate components have shared similar histories, and the causes of these major coincident disjunctions may thus be identified. Ultimately, geographic cladograms, representing a sequence of major geologic or climatic events, may be compared with biological cladograms, representing allopatric speciation events (Rosen, 1978). Cladistic comparisons await considerably more critical phylogenetic studies of Central American fishes and much more geological information.

6.1. Vicariance of the Old Southern Element

Bussing (1976) pointed out some outstanding geological events that coincide with major disruptions in the distributions of Old Southern fishes:

1. Subsequent to an ancient land connection between Nuclear Central America and South America, the isolation of the two continents by a marine seaway through lower Central America during most of Cenozoic.
2. The Nicaraguan Trough persisting as an embayment until Pliocene, thus creating an important barrier on the Atlantic versant.
3. The presence of the Amatique embayment as a filter barrier between Atlantic slope Guatemala and Honduras from early Miocene until Pliocene.
4. The presence of the Mosquitia embayment over much of the Honduran–Nicaraguan Atlantic lowland between the Eocene and Pliocene.

The significance of these barriers can be seen in the generalized patterns of Old Southern fishes (Fig. 1). The effect of the Amatique and Mosquitia embayments is evident in the depauperate ichthyofauna on the Atlantic slope of Honduras where numerous species terminate their distributions near each border. After disappearance of the embayments, dispersal has perhaps been limited by steep cordilleras extending to the sea between the major drainage basins of Honduras. On the other hand, the area formerly occupied by the Nicaraguan Trough now encompasses two large lakes and the immense San Juan drainage

basin. Numerous closely related species share the region and there is evidence of only incipient speciation taking place in the lakes. Hence, the conclusion that the marine portal first provided the vicariant event necessary for ancestral species to evolve into distinct forms and later come together as cognate pairs in the relatively diverse drainage basin. This is not evident on a distribution map, but from the high diversity and nature of the San Juan ichthyofauna.

Rosen (1978, 1979) in a new revision of the poeciliid general *Xiphophorus* and *Heterandria*, showed that cladograms of relationship possess a number of cladistic similarities in relation to geography. He determined three principal regions of endemism for these genera: (1) eastern North America to the Río Grande, (2) the Río Pánuco, and (3) the rivers of southeastern Mexico and Central America to the Great Lakes of Nicaragua. Other poeciliids (*Gambusia* and *Poecilia*), cyprinodonts (*Cyprinodon*, *Fundulus-Profundulus* and *Floridichthys*), the *Herichthys* group of *Cichlasoma* and perhaps the characid *Astyanax* of the Old Southern Element, and *Dorosoma*, *Atractosteus*, *Ictalurus*, and *Ictiobus* of the Northern Element appear to share, at least in part, these same patterns of disjunction and partly for that reason I believe they form part of the generalized Old Southern and Northern distribution patterns respectively (Fig. 1).

A prime example of a vicariant event is the recurrent pattern of numerous geminate species pairs occupying opposite sides of the Talamancan Cordillera in lower Central America (Bussing, 1976). As the Talamanca Island emerged and became connected to Nuclear Central America and the Isthmian Link became a continental divide, they permanently subdivided Atlantic and Pacific populations of an ancestral assemblage. I formerly accepted a geological model whereby certain lower Central American land masses remained emergent throughout the Cenozoic. However, Rosen (1976) found biogeographic evidence to support a geophysical drift theory that the Antilles were originally a part of an early lower Central American archipelago that was displaced into the Caribbean, and later replaced by a similar, present-day, lower Central America. If this were the case and one does not accept "island hopping" by fresh-water fishes, it follows that the Talamancas were first united to Nuclear Central America by the disappearance of the Nicaraguan Trough, before they were connected to South America. This is in agreement with the generally accepted belief that the Bolivar seaway in Panama-Colombia was the last marine barrier to close in late Cenozoic time.

Throughout Central America one finds local highland species of the catfish genus *Rhamdia*. These isolated populations are rather similar morphologically and differ in several respects from lowland populations. Highland species of *Rivulus* and *Profundulus* are also known in the region. These examples of headwater isolation may have arisen as a result of the elevation of the Central American cordilleras while carrying with them certain fishes capable of adapting to the changing conditions—a vicariance event subsequent to an earlier dispersal event.

6.2. Vicariance of the New Southern Element

The genera of this element usually have continuous distributions throughout the Central American portion of their range and generally are represented by species in South America. A few genera, however, present disjunct populations in lower Central America and all but *Imparales* have endemic representatives in southeastern Costa Rica: the catfish *Nannorhamdia*, characoids *Pterobrycon* (Fig. 8), *Gephyrocharax*, *Cheirodon* (Fig. 7), and *Piabucina*. The New Southern representatives of the characins (*Roeboides*, *Brycon*, *Bryconamericus*, and *Hyphessobrycon*) also have southern Costa Rican endemics that may have shared similar histories. The ubiquitous genus *Poecilia* is also absent only from a gap between the Río Coto, Costa Rica, and Río Grande drainage in Coclé Province, Panama.

Subsequent to the arrival of these fishes in Costa Rica, conditions in extreme western Panama have clearly become unsuitable to their existence, thus creating a hiatus in the distributions of these genera. The vicariant event involved may have been an increasingly xeric climate coupled with an increase in sea level.

Aside from the southeastern Costa Rican disjunction, other patterns of New Southern endemism are not apparent. Loftin (1965) however, identified several filter barriers on the Pacific versant of Panama that have produced significant shifts in faunal composition: the Río Grande (Pacific terminus of the Canal), Cerro Campana, and the Soná Peninsula. The most striking aspect of these faunal shifts is the abrupt change of species of two common characid genera, *Astyanax* and *Roeboides*: from the Río San Pablo eastward, these are *A. ruberrimus* and *R. occidentalis*; from the Río Tabasará westward, they are *A. albeolus* and *R. guatemalensis*. Loftin suggested that on the poorly known Atlantic slope the Chagres basin is a major center of dispersal, which in turn derived the majority of its fauna from the eastern and central Pacific slope. There is also evidence of exchange of fishes between the Atlantic slope Río Coclé del Norte and Río Indio and Pacific slope streams.

6.3. Extinctions

Massive extinctions of fish species have undoubtedly occurred in Central America. Gaps are common in the distribution of the species of most Central American genera. The characid genus *Bramocharax* with two Guatemalan species and another in the San Juan drainage of Nicaragua and Costa Rica have not been collected in the intervening region. The characid *Carlana eigenmanni* and cichlid *Cichlasoma nicaraguense* of the San Juan drainage have no closely related relatives in Central America, although *Carlana* may be related to members of the genus *Rhoadsia* of northern South America. New Southern genera already mentioned are the characid *Pterobrycon* and pimelodids *Nannorhamdia* and *Imparales*. *Pterobrycon* is known only from two species, one in southeastern Costa Rica, the other in Colombia. *Nannorhamdia lineata* inhabits southeastern Costa Rica and other species occur throughout South America. The genus *Imparales* is represented only in Panama and the Río Meta, Colombia. It is assumed that numerous other lineages have disappeared without leaving living representatives.

7. Historical Perspective

Günther (1861) first noted the great similarity between the fish species of both coasts of Central America; he considered many species to be represented on both coasts. Wagner (1864) made the same observation on freshwater species from both versants. Günther (1868) concluded that “. . . the Isthmus did not form a continuous barrier between the two oceans at a former period. . . .” He also divided the ichthyofauna in six provinces including Lakes Petén, Managua and Nicaragua, Nuclear Central America and the Isthmian region.

Regan (1906–1908) recognized the close relationship between African and South American Cichlidae, Characidae, and Cyprinodontidae and rejected the hypothesis that the Cichlidae were originally a northern group, instead proposing an early Eocene land connection between Africa and South America on one hand and with India via Madagascar on the other. He also provisionally divided Central America into three provinces: Guatemalan, San Juan, and Isthmian.

Myers (1938) believed that fresh-water fishes unable to survive in the sea (primary division) are grouped on natural family lines and present more conservative distributions than salt-tolerant (secondary division) fresh-water families. He later (1966) suggested that

the secondary division Cichlidae and Poeciliidae, by means of their salt tolerance, occupied Central America first, followed by the primary division characoids and pimelodids.

Croizat (1976, Fig. 145) envisioned a Central American land encompassing the entire Caribbean Sea and extending in width between the Antilles and the Galapagos Islands. Although this region contained three deep marine basins, the vast extension of land would have greatly facilitated dispersal between sites presently isolated from one another. Croizat considered the Central American ichthyofauna to be very ancient and that the proper way to look at dispersal in the region is to stress the east–west axis more than the north–south axis. That is, considering Central America as an integral part of the now submerged lands of the Caribbean and Eastern Pacific, the biota would have migrated most recently from east and west toward present-day Central America.

A vicariance model of Caribbean biogeography was proposed by Rosen (1976). The geophysical theory most consistent with the distribution patterns he studied suggests that an early lower Central American archipelago drifted into the Caribbean to give rise to the Antilles. Later, the early Central American land was reestablished by a new archipelago, now represented by a continuous isthmus. Rosen's model specifies where dispersal is the most probable explanation of a particular distribution but interprets disjunct segments of distribution patterns as remnants of an ancestral biota that underwent geographical fragmentation followed by allopatric speciation.

Rosen (1978, 1979) has continued to pursue his rigorous methodology of comparing biological cladograms with cladograms of geographic areas in order to determine the most probable geologic, climatic, or geographic events that have acted upon a biota. He has shown in considerable detail how two Middle American fish genera have shared, in part, a common history in the region (Rosen, 1979).

Savage, who has written major papers on the Central American herpetofauna and mammals (1966, 1974), has reviewed his earlier data and conclusions in view of recent controversy between dispersal and vicariance biogeographers (Savage, 1982). Although no new information on fishes is presented, this report presents a critical reexamination of the major points and conclusions pertaining to vertebrate distribution patterns in Central America in light of recent methodologies. The reanalysis of data for angiosperms as well as vertebrates indicates a repetitive general pattern for all groups except placental mammals, which apparently were not present in the Americas when North and South America were first separated in early Paleocene. This pattern involves an early dispersal event between Central and South America, a vicariance event during much of Tertiary and a second and continuing dispersal between the continents.

8. Conclusions

Three assemblages of fresh-water fish distribution are recognized in Central America: (1) Old Southern, extending from lower Central America into the southern United States and fragmenting into five centers of endemism in Middle America; (2) New Southern, essentially an extension of South American taxa into Central America as far north as southeastern Costa Rica; and (3) Northern, a minor penetration of a few temperate fishes as far south as northern Costa Rica. A group of five characid genera contain species representative of both Old and New Southern Elements. The Old Southern Element comprises derivatives of a South American dispersal northwards by way of an ancient land connection. A long period of isolation followed, and the New Southern Element is now migrating over the present intercontinental land bridge. The Northern Element contains descendants of old North American lineages that have, in part, shared a common history with the Old Southern fishes.

Dispersal, mainly from south to north, has produced the Central American ichthyofauna. The rate of dispersal of most of the fresh-water fishes has been exceedingly low judging from the short distance attained in Central America by the South American fishes of the New Southern Element since the closure of the Bolivar seaway, perhaps as long ago as 5 million years. This low dispersal rate is precisely what makes a study of fresh-water fish distributions more valuable than that of more vagile organisms. I conclude likewise that the rate of evolutionary change of fresh-water fishes in Central America has been conservative. The poeciliids show the greatest adaptive radiation, but the Cichlidae, although speciose in the area, has not diversified as much in 50 million years as some African lake cichlids have in 2–6 million years. The pimelodids, cyprinodontids, and, surprisingly, the Old Southern characids have shown little adaptive radiation, preferring to maintain generalized morphotypes and ecologies.

The vicariance biogeographical approach is useful in focusing attention on monophyletic groups and generalized patterns of distribution or "tracks." The geographic pattern of fragmentation of these groups in turn, points out areas where important vicariant events have taken place and invites an explanation. The interspaces between the areas of endemism of the Old Southern element (Fig. 1) mark barriers of considerable importance in the history of this fauna, some of which are discussed herein. Furthermore, by using biological cladograms, it is possible to determine the sequence of vicariant events (Rosen, 1978), and, finally, biological cladograms can be tested against geographic cladograms, when available, to determine their nature.

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