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AN UNUSUAL MEMBER OF THE CAGE FUNGUS FAMILY

D.N. PEGLER¹ & L.D. GOMEZ²

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¹The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE

²Organización para Estudios Tropicales, Jardín Botánico, San Vito de Java, Coto Brus, Costa Rica

The Cage Fungus Family (*Clathraceae* E. Fischer) is closely allied to the Stinkhorn Family (*Phallaceae* Corda), which together constitute the order *Phallales* G. H. Cunn. The distinction between the two families may be found in the key which accompanies this paper. Although rare, the Cage Fungi are quite familiar to European collectors, especially the Red Cage Fungus (*Clathrus ruber* Mich. ex Pers.), which forms a gasterocarp of net- or lattice-like construction, emerging as a result of expansion from a round, gelatinous egg-like structure ('mycoegg'). There are, however, many additional genera in the *Clathraceae*, many of which were monographed by Dring (1980).

Most genera are tropical-subtropical and even those reported from temperate regions are generally introduced. The clathroid basidiocarps are extremely variable and probably come nearest within the Fungi to the flowers of the Plant Kingdom, fulfilling the similar role of attracting insects for spore/pollen dispersal. Their stellate or latticed forms, together with bright colours, including pink, red, orange, yellow and white, make them particularly conspicuous in the forests.

There is a basic pattern covering the overall structure of the gasterocarp, the soft mycoegg develops in a hypogeous to subepigeous position and comprises an outer peridial layer enclosing the developing fruitbody which is embedded in a gelatinous matrix. The fruitbody consists of the gleba, which is the fertile tissue within which the basidia and spores are formed and this is supported by the receptacle, a structure unique to the Phallales, which at maturity rapidly expands, forcing its way out of the ruptured mycoegg and elevating the gleba above ground level. Broadly, clathroid gasterocarps may be arranged into two groupings on the basis of their overall appearance, either a receptacle is formed with two to

several arms (columns) which may be either apically joined e.g. *Blumenavia* A. Möller, *Linderiella* G. H. Cunn. (= *Linderia* G.H. Cunn.), *Pseudocolus* Lloyd, or the columns may radiate in a stellate fashion e.g. *Anthurus* Kalchbr. & MacOwan, *Aseroë* Labidillardière, *Lysurus* Fr. Alternatively, the receptacle forks and anastomoses to produce a lattice e.g. *Clathrus* Mich. ex Pers., *Ileodictyon* Tul., *Simblum* Klotzsch. Further complexities can result in a combination of radiating arms and a lattice e.g. *Colus* Cavalier & Sechier, *Kalchbrennera* Berk., *Neolyosurus* Miller, Ovrebo & Burk. There can also be much variation within individual genera, and much discussion has been devoted in the past over generic delimitations. Dring (1980) took the conservative approach of including *Anthurus* within *Clathrus*, and *Kalchbrennera* and *Simblum* within *Lysurus*, regarding the receptacle configuration to be of secondary importance.

An overview of the all the genera leads to two main conclusions concerning the development of the family. First, there is a tendency from a simple configuration of unbranched arms towards a lattice formation, providing increased surface area for the exposure of the gleba. Secondly, three developmental series can be recognized (Fig. 1):

(i) Clathroid Series: receptacle is sessile or fused below into a short, inconspicuous stem ('pseudostipe'); gleba dispersed over the inner surface of the receptacle, sometimes as scattered, discrete glebifers - *Anthurus*, *Blumenavia*, *Clathrus*, *Ileodictyon*.

(ii) Lysuroid Series: lower receptacle forms a short to long, tubular pseudostipe and remains sterile; gleba restricted to upper receptacle, and may be dispersed over the inner, side or even upper surfaces - *Aseroë*, *Colus*, *Lysurus*, *Kalchbrennera*, *Neolyosurus*, *Pseudocolus*, *Simblum*.

(iii) Laternoid Series: receptacle sessile, not

forming a pseudostipe, but lower receptacle remaining sterile; gleba limited to the underside of arch forming the upper receptacle - *Laternea*, *Linderiella*.

Recently collections of a remarkable member of the Clathraceae has been gathered in the rain forests of Costa Rica, which cannot be accommodated in any of the genera described above. It does, however, strongly resemble the fungus described by Saenz (1980), under the name *Ligiella rodrigueziana*.

Ligiella rodrigueziana

Saenz in *Mycologia* 72:
349 (1980).

Gasterocarp multipileate, clathroid. *Immature gasterocarp* forming a mycoegg, 1.5–3 cm, diam, globose, obovoid or pyriform, dull sooty grey when fresh, ageing to a violaceous brown over the upper surface, cream colour below, smooth then cracking and tessellate, eventually rupturing apically, sometimes by a single fissure, often by irregular radial splitting to release the expanding receptacle; peridial remnants retained as a persistent volva; with a few, dull white, basal rhizomorphs (~1.5 mm diam). *Peridium* comprising three layers; *exoperidium* thin, ca 0.5 mm thick, firm, membranous, consisting of repent, loosely woven hyphae, 7–15 µm diam, slightly inflated, with a thickened wall (0.8 µm) and a brown vacuolar pigment; *mesoperidium* up to 1.5 mm thick, white, consisting of hyaline, thin-walled hyphae, 3–14 µm diam; *endoperidium* a thick gelatinous matrix, especially in the mycoegg, containing, hyaline, thin-walled, narrow hyphae, 2.5–3.5 µm diam. *Clamp-*

connexions absent on all hyphae. *Receptacle* comprising 4–6, white, stout, chambered columns, each initially attached by a peridial suture prior to rupture of the peridium, finally elongating to 5–6.5 cm high and united at the apex, at times anastomosing to form a simple lattice; at first joined at their base to the peridium but never

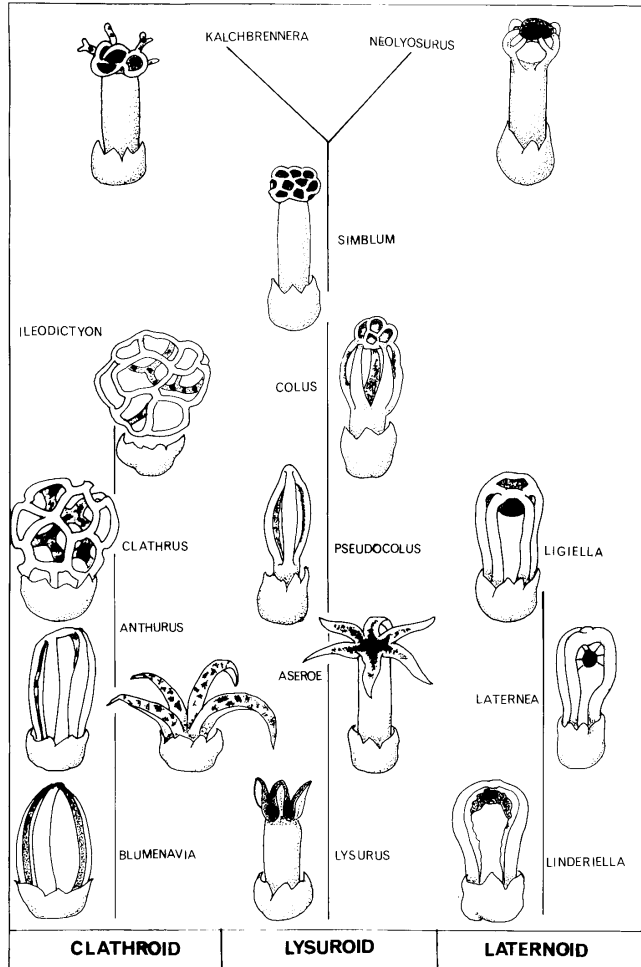


Fig 1 Clathraceae, with genera arranged into a clathroid series with the gleba disseminated over the receptacle surface, often extending to the sides and upper surfaces; a lysuroid series, with a lower, sterile pseudostipe; and a laternoid series, sessile, with the gleba restricted to and supported by an upper receptacle arch. All three series tend towards a clathrate condition.

forming a pseudostipe. *Individual columns* 3–6 mm diam, more or less triangular in section, lacunate; all surfaces transversely wrinkled but becoming smoother with elongation. *Gleba* compound, formed by discrete units, with one pair of

units to each receptacular column; individual units ellipsoid, each united to inner side of the apex of the column, tearing free below as the column elongates at maturity; dark olive-green, with numerous minute, labyrinthoid chambers;

odour aromatic, recalling cinnamon. *Hymenium* continuous, of crowded basidia, lacking cystidia. *Basidiospores* statismosporic, $3.2\text{--}5.2 \times 1.5\text{--}2.8$ ($4 \pm 0.3 \times 1.8 \pm 0.2$) μm , $Q = 2.2$, elongate ellipsoid with a truncated base, thin-walled or a slightly thickened wall, subhyaline to pale greenish. *Basidia* 8-spored, $15\text{--}24 \times 4\text{--}5$ μm (base), $\times 1.5\text{--}3$ μm (apex), lageniform, with a slightly inflated base and a long tapering neck. *Chemical reactions* on mature peridium: 50% nitric acid discolours the purplish brown to yellow; conc. nitric acid to chestnut red; 10% sodium hydroxide to oxblood red; potassium hydroxide to bright sepia; 2% phenol negative; columns and glebifers negative to all. (Figs. 2–3).

Specimens examined: Costa Rica, Puntarenas Prov., Coto Brus, under bamboos, 1200 m, Gomez 25446 (Herb. Tulane); Las Cruces, under *Phyllostachys aurea* var. *sulcata*, 1100 m, Gomez 25645 (F); Coto Brus, Fila Zapote, in mixed forest under *Quercus*, 1400 m, Gomez 25658; Coto Brus, Las Cruces, 1100 m. Gomez 25688a-f (K-M22361; F, Cr, USJ); Cartoago, El Enpalme, 2000 m, Saenz 3233 (USJ, paratype).

The species was originally described from material collected in a low montane

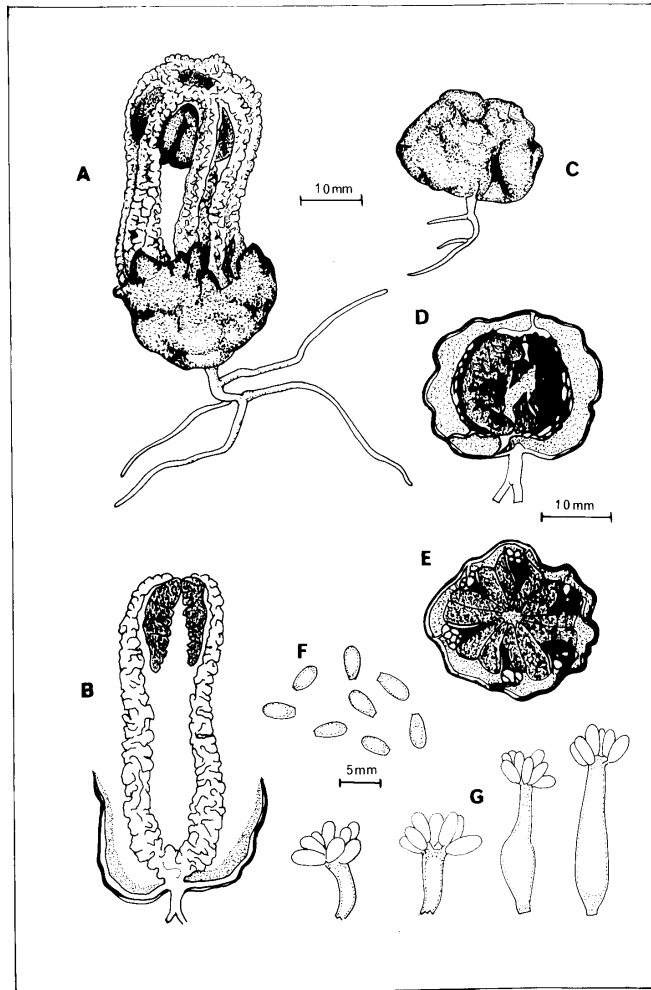


Fig 2 *Ligiella rodrigueziana*. (A) Open gasterocarp, with expanded receptacle, $\times 1$; (B) vertical section through open gasterocarp, $\times 1$; (C) mycoegg, $\times 1$; (D) vertical section through mycoegg, showing outer peridium enclosing receptacle columns and compound gleba, embedded in a gelatinous endoperidium, $\times 1.2$; (E) transverse section through mycoegg, showing six receptacle columns, each attached by a peridial suture, and each associated with a pair of glebal units, $\times 1.2$; (F) basidiospores, $\times 1700$; (G) basidia, $\times 1700$.

forest growing amongst woody humus. A second collection was found attached to a rotting log. The fungus apparently requires high relative humidity. The type collections differs in smaller overall dimensions, the lack of any violaceous hue on the exoperidium, and more abundant rhizomorphs, but otherwise structurally similar.

Possibly the most unique feature lies in the structure of the gleba. In many ways it might be compared to *Laternea*, also from tropical America, in which the brightly coloured glebifer is suspended below the receptacular apical arch. This glebifer, however, is a simple structure whilst in *Ligiella* the glebifer is of compound construction

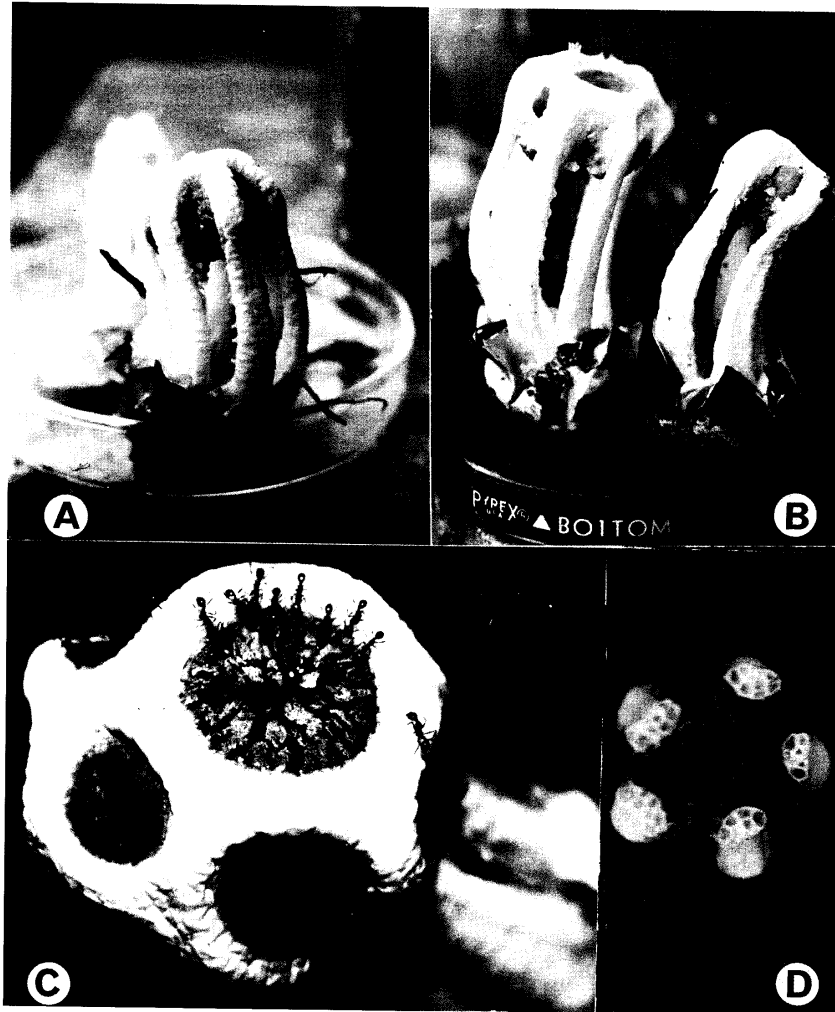


Fig 3 *Ligiella rodrigueziana*. (A) Gasterocarp with expanding receptacle; (B) fully expanded receptacle; (C) fertile, upper receptacle, with ants and stingless bees attracted to the gleba, aiding spore dispersal; (D) underside of receptacle head, showing sections through five, lacunate columns, each supporting a pair of glebal units.



formed of pairs of units associated with each receptacular column (Figs 2E, 3D). In *Linderiella*, the gleba is dispersed over the inner surface of the upper receptacle and does not form distinct glebiferous units. Comparison might also be made with *Colus*, *Simblum* and *Neolysurus*, which have an apical gleba, but all three genera have a well developed, tubular pseudostipe and gleba of different construction.

A further surprising feature in *Ligiella* is the octosporic basidia, instead of the more usual tetrasporic basidia. The spores are radially symmetrical, typically statismosporic and incapable of active release. The basidia produce only very reduced sterigmata.

Finally, *Ligiella* spores are not dispersed by Dipteran flies, as is the case for most Phallales, but by stingless bees (mainly *Trigona fulviventris*, rarely also *T. corvina*) and one as yet unidentified ant (Hymenoptera, Formicidae), both of which can be seen in Fig. 3C. Occasionally Mycetophagidae beetles are found inside the very mature mycoegg.

Key to Genera of Clathraceae

1. Gasterocarp development unipileate; receptacle simple, forming a hollow column; peridial sutures not formed; gleba borne apically on outer surface of receptacle —*Phallaceae*
 - (not considered further)
1. Gasterocarp development multipileate; receptacle sessile or stipitate, of several columns or latticed; peridial sutures present; gleba borne on inner surface of receptacle, at least initially —*Clathraceae* Fischer, 2
 2. Lower receptacle sterile, forming a conspicuous, elongate, hollow column (resembling Phallaceae), with a strongly differentiated, fertile, apical region, forming either arms or a lattice —3
 2. Receptacle either sessile or fused below into a short, inconspicuous pseudostipe, formed of columns, simple or branched —7
 3. Gleba formed on an apical, pulvinate glebifer with polygonal compartments, borne on branching and anastomosing columns of receptacle; Costa Rica =1. *Neolysurus* Miller, Ovrebo & Burk
3. Gleba distributed on surface of receptacular columns —4
 4. Fertile region comprising either columnar arms or a lattice, with the gleba borne on the sides or even the upper surface —5
 4. Fertile region with the gleba restricted to the inner surface —8
 5. Fertile region formed of unbranched arms which are not apically fused —6
 5. Fertile region clathrate, forming an apical lattice —7
 6. Fertile region formed by diverging columnar arms, arising from the discoid expansion of the stipe apex; gleba on upper surface; pantropical —2. *Aseroe* Labillardière
 6. Fertile region of short, erect paired columns; pantropical, subtemperate —3. *Lysurus* Fr.
 7. Apical lattice simple, lacking branching arms; pantropical —4. *Simblum* Klotzsch
 7. Apical lattice giving rise at the intersections to short, erect, simple or forked appendages; Africa —5. *Kalchbrennera*
 8. Slender, fertile columnar arms of receptable, up to 10, fused at apex to form a lattice; pantropical, subtemperate —6. *Colus* Cavalier & Sechier
 8. Fertile columnar arms, 3–4, at first united at apex but apt to break apart; tropical —7. *Pseudocolus* Lloyd
 9. Columns simple, tubular; receptacle spherical, white, forming a lattice, soon detached from the peridial remnants, lacking any basal differentiation; cosmopolitan but rare —8. *Ileodictyon* Tul.
 9. Columns compound, internally lacunate, with few to numerous tubes —10
 10. Gleba confined to the apex of the receptacle —11
 10. Gleba scattered over the inner surface of receptacle —13
 11. Gleba borne directly on underside of arch formed by the receptacle apex —12
 11. Gleba borne on reddish orange glebifer, suspended beneath the arch formed by 2–4 pinkish arms, united at apex but free at the base; tropical America —9. *Laternea* Turpin ex Turpin

12. Gleba simple, attached to inner, upper surface of 2-5 columnar arms of receptacle, which do not anastomose; Pacific —10. *Linderiella* G.H. Cunn. (= *Linderia* G.H. Cunn.)
12. Gleba compound, formed from glebiferous tissue attached to apex of each of 4-5 arms, which may be united and slightly anastomosing apically and initially joined at base but soon free; Costa Rica —11. **GEN NOV** (*Ligiella* Saenz)
13. Gleba dispersed irregularly over entire inner surface of receptacle, or on small, scattered glebifers —14
13. Gleba confined to regular glebifers on inner surface of receptacle; receptacle formed of 3-6 columns attached at apex, becoming free at the base; pantropical —12. *Blumenavia* A. Möller
14. Receptacle forming a lattice; cosmopolitan —13. *Clathrus* Mich. ex Pers.
14. Receptacle developing radial arms; cosmopolitan —14. *Anthurus* Kalchbr. & MacOwan

References

- Dring, D.M. (1980) Contributions towards a rational arrangement of the Clathraceae. *Kew Bull.* 35: 1-96, figs. 1-27.
- Saenz, J.A. (1980) *Ligiella*, a new genus for the Clathraceae. *Mycologia* 72: 338-349, figs. 1-16.

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