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FULL PAPER

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Morphological variation in *Laboulbenia polymorpha* (Laboulbeniales)

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Abstract Specimens of the type collection of *Laboulbenia polymorpha* Sugiyama (1978) were reexamined. The holotype, M. Ishikawa 673, is composed of three slides and includes three morphologically different forms of thalli, of which two forms were illustrated (Sugiyama 1978, fig. 1-D, 1-E). On the other hand, one of the paratypes, M. Ishikawa 674, has now been lost but photographs were made earlier from this slide, in which one mature individual illustrated as fig. 1-C (Sugiyama 1978) is included. This individual was not correctly shown in Sugiyama's illustration, but actually has a strong resemblance to a form in slide 673-b that was not illustrated by Sugiyama (1978). Thus, three different forms have been recognized as variations of *L. polymorpha*. In the present article, each variation was termed C-form, D-form, and E-form because Sugiyama (1978) used the same notation in his figures. A mature specimen of C-form in slide 673-b has been selected as a lectotype. Slide 673-d includes only young thalli, one of which was illustrated as fig. 1-G (Sugiyama 1978). This young thallus undoubtedly belongs to another species; mature thalli of the same species were also found in slide 673-b. Another paratype, K. Sugiyama 2101, includes C- and D-forms of *L. polymorpha*. Infection sites of the C- and D-forms have been determined: the C-form grows mainly on the lateral margins of the elytra of the host, and the D-form occurs mainly on the basal part of the elytra and the mesothorax.

Key words Carabidae · Laboulbeniales · Morphological variation · Taxonomy · Type specimens

Introduction

In 1978, Sugiyama described a new laboulbenialean fungus, *Laboulbenia polymorpha*, from Taiwan and Japan. The name of this fungus is suggestive of polymorphism; Sugiyama (1978) presented this species as a complex of three distinct forms: "shorter form with coarse perithecial apex," "shorter form with slender perithecial apex," and "longer form with perithecial projection." Each form presumably has its own position on the host body, but this was not reported by Sugiyama (1978). The host was listed as *Ophionea indica* (Thunberg) [Coleoptera, Carabidae, Odacanthini]. M. Ishikawa 673 was designated as the holotype. However, this slide actually consists of three slides (673-b, 673-c, and 673-d) and includes several forms of thalli.

The purpose of this study is to reexamine the specimens of the type collection of *L. polymorpha*, to describe variation of the species, and to determine the infection sites of each form of the variation.

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Materials and methods

Type specimens of *Laboulbenia polymorpha* described by Sugiyama (1978) were reexamined microscopically. Fungus-bearing hosts collected by myself and by other collectors were also examined. All the specimens used in the present article are deposited in TNS (Department of Botany, National Science Museum, Tokyo).

In the following paragraphs, the thallus length was measured from the foot to the perithecial tip and the length of the perithecium was from the base of the basal cells to the perithecial tip excluding apical outgrowths; the stalk and secondary stalk cells (VI and VII) were excluded from the height of the perithecium. Morphological terms and abbreviations are basically the same as those used by Tavares (1985).

Type specimens

Sugiyama (1978) designated M. Ishikawa 673 (Taiwan) as the holotype of *L. polymorpha*; M. Ishikawa 674 (Taiwan)

and K. Sugiyama 2101 (Japan) are paratypes. The host insects appear to have been lost, except for K. Sugiyama 2101.

At least four slides formerly existed under M. Ishikawa 673, of which I have examined three slides (673-b, 673-c, and 673-d). Slide 673-b contains morphologically different individuals that can be grouped into three distinct forms. One individual is characterized by a perithecium with abruptly narrowed apex bearing peculiar posterior lip cells (see Fig. 13; all parts of the appendages are broken off in this individual as illustrated). Sugiyama (1978) described this individual as "shorter form with slender perithecial apex" and illustrated it as fig. 1-D in his illustrations. Therefore, it is called here the D-form (see Fig. 13). One of the two others is characterized by an ovoid perithecium tapering to a similar peculiar blunt apex and by the darkedged appendage base lying across the perithecium (see Fig. 2). This form was not illustrated by Sugiyama (1978), but actually has a strong resemblance to fig. 1-C of his illustrations. Therefore, it is called here the C-form (see Fig. 2). The third form was also not illustrated by Sugiyama (1978) and was considered as another distinct species from *L. polymorpha*. It has a perithecium with normal (not specially modified) apex. Slide 673-c contains several individuals whose perithecia are considerably elongated and have a short outgrowth on each apex. This form was described as "longer form with perithecial projection" by Sugiyama (1978); with respect to this form, only the apical portion of the perithecium and the appendages were separately illustrated by Sugiyama (1978, fig. 1-E, 1-F). It is called here E-form (see Figs. 26, 27). Slide 673-d includes only young thalli, one of which was illustrated as fig. 1-G (Sugiyama 1978). M. Ishikawa 673-a seems to have been lost.

Unfortunately, all the M. Ishikawa 674 slides are missing now. However, photographs were made earlier from slide 674-a, in which one mature individual illustrated as fig. 1-C (Sugiyama 1978) was included. Sugiyama (1978) described it as "shorter form with coarse perithecial apex," although the posterior lip cells of this individual were not correctly shown in Sugiyama's fig. 1-C. Apparently, this form should be considered as a mere variant of the C-form (Fig. 1). Thus, three different forms have been recognized as variation of *L. polymorpha.* In the present article, each variation was termed C-form, D-form, and E-form because Sugiyama (1978) gave these designations to his figures. A mature specimen of C-form in slide 673-b is now selected as a lectotype (Fig. 2). K. Sugiyama 2101 consists of two slides, of which slide 2101-a includes D-form and slide 2101-b includes C-form.

Taxonomy

Laboulbenia polymorpha K. Sugiyama, J. Jpn. Bot. 53: 284, 1978

Lectotype (here designated): M. Ishikawa 673-b (TNS), specimen shown in Figs. 2–4 in the present article. On *Ophionea indica* (Thunberg), Taiwan.

Specimens examined: On *Ophionea indica* (Thunberg) [Carabidae, Odacanthini], Taiwan: M. Ishikawa 673 and 674 (now missing), exact localities unknown; K. Terada 1535 (Aug. 16, 2001, K. Terada and M.H. Hsu leg.), 1556 (Oct. 8, 2001, K. Terada and M.H. Hsu leg.), 1617 (Nov. 8, 2001, K. Terada and M.H. Hsu leg.), Yangmei, Taoyuan County; K. Terada 1536 (Apr. 6, 2002, M.H. Hsu leg.), 1561 (Apr. 13, 2002, M.H. Hsu leg.), Kengtzu, Taoyuan County. Japan: K. Sugiyama 2101 (May 28, 1977, J. Okuma leg.), Sonai, Iriomote-jima, Okinawa Pref.; K. Terada 884 and 929 (June 8, 1978, K. Terada leg.), Ohara, Iriomote-jima, Okinawa Pref.

Note: An individual of C-form on M. Ishikawa 673-b has been selected as the lectotype. The individual (D-form) on slide 673-b, illustrated by Sugiyama (1978, fig. 1-D), lacks intact appendages; intact thalli of E-form on 673-c slide are present, but the position of E-form thalli on the host has not been determined in fresh material. These are the reasons why I preferred to designate as lectotype an individual of C-form rather than one of D-form or E-form.

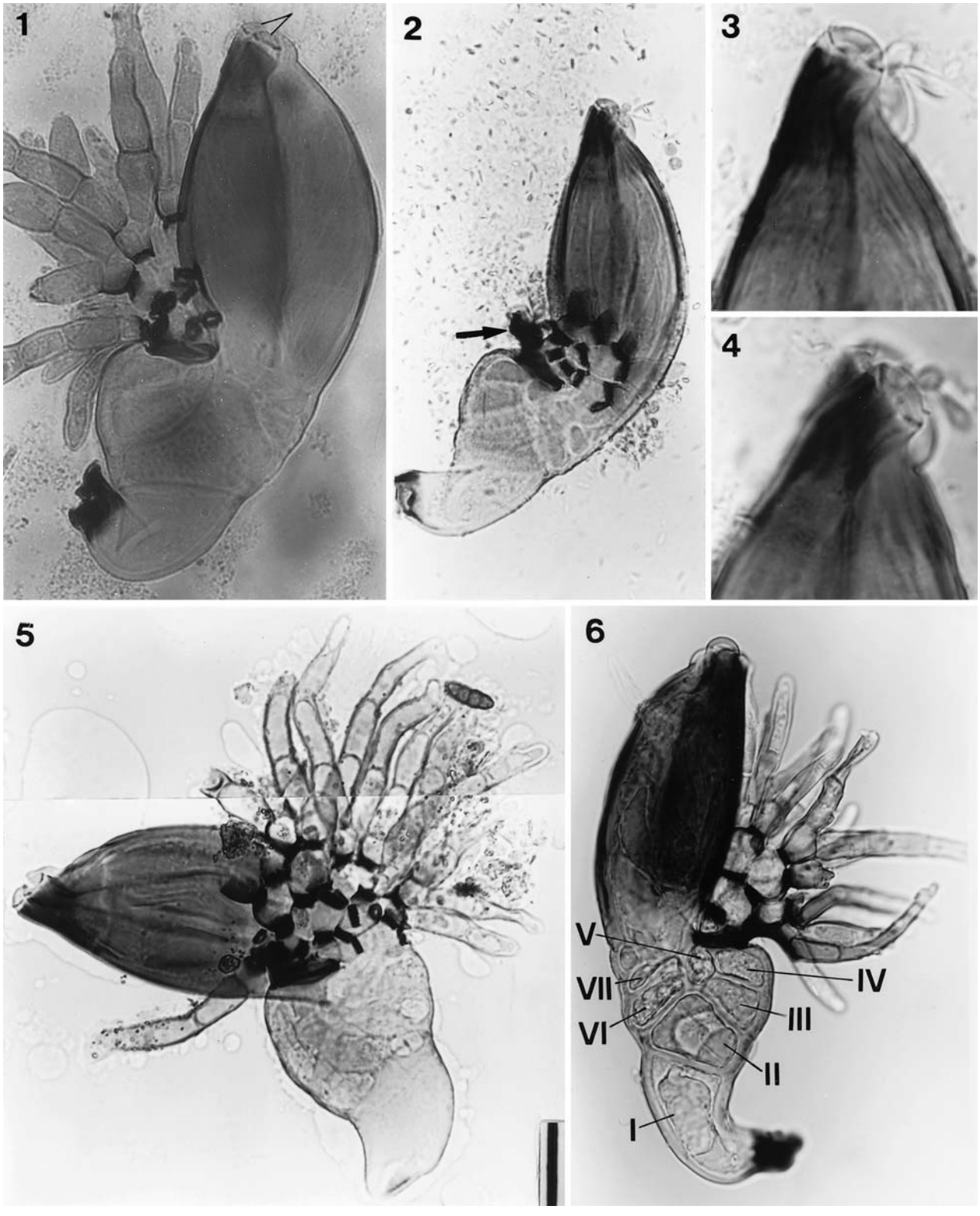
C-form

Figs. 1–11

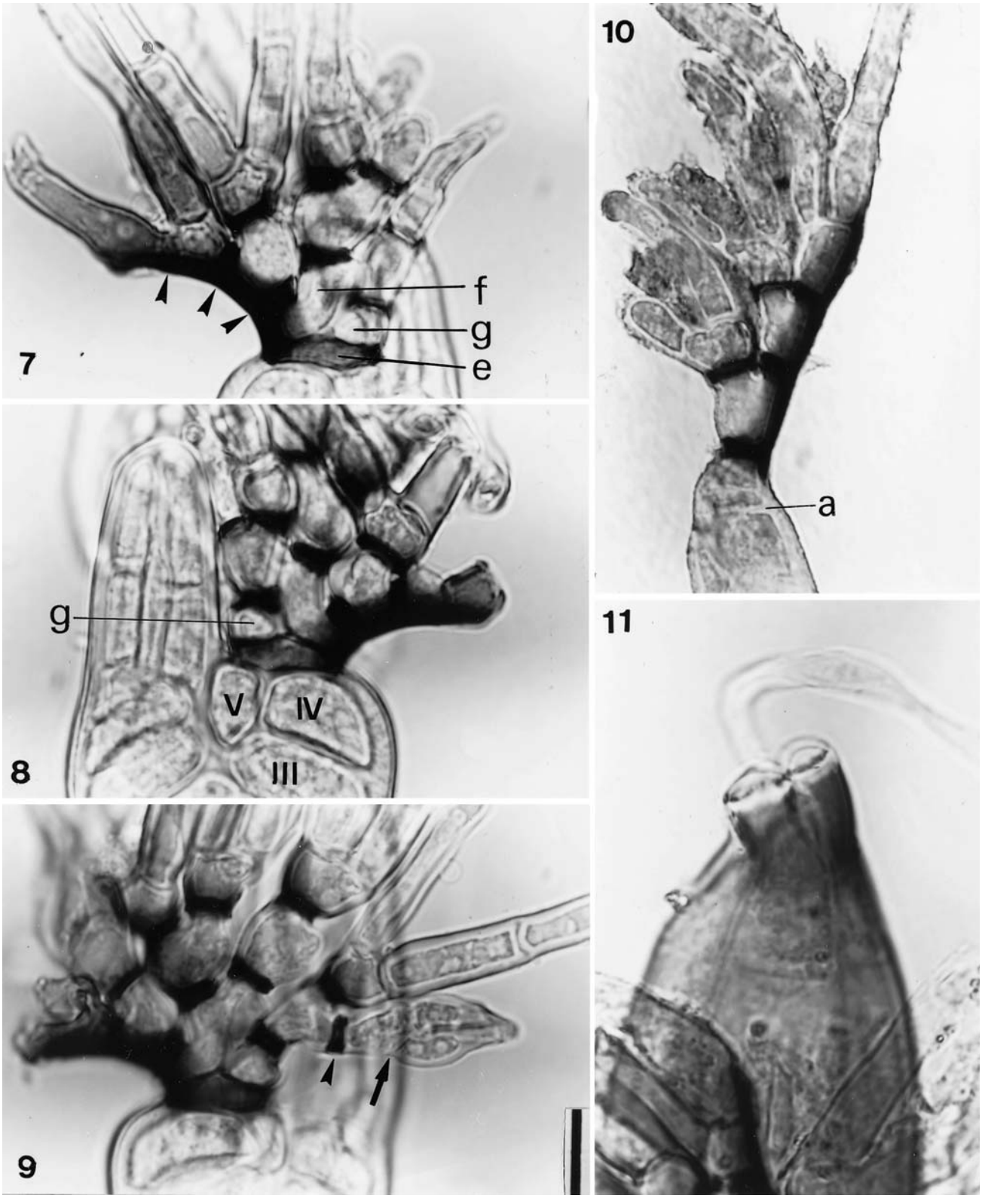
Perithecium blackish-brown, but yellowish-brown near the base, stout, pear-shaped or egg-shaped. Anterior lip cells hyaline and tapered, not exceeding the height of the posterior lip cells. Each of the posterior lip cells black except for the hyaline, broad, truncate, disklike apical part, bending toward the anterior side (Figs. 3, 4, 11). Cells VI and VII flattened and oblique. Perithecial basal cells quadrate or rounded in optical section.

Appendages yellowish-brown, sometimes becoming dark in color, consisting of lower stout cells with black septa and upper elongate cells with colorless septa, very closely branched in the lower part (Figs. 7, 10); upper portion of branches longer, but tapering only slightly to a broad rounded tip (Figs. 5, 6). Outer appendage having black outer edge that extends down to the insertion cell, bending outward and producing a series of lateral branches on one side (Figs. 7–10). Cell f at first cubical, then showing a curious upward elongation anteriorly and, as a result, an erect branch is formed from cell f (Fig. 7). The unilateral branching of the outer appendage has been observed on a very young thallus (Fig. 10), in which three superposed cells of this appendage are bordered by a black outer edge; each of those cells bears two septa (terminal one separating the superposed cells of the outer appendage and subterminal one underlying the lateral branches); the terminal septa are almost indistinguishable from the dark color of the black outer edge (see also arrowheads in Fig. 7). Inner appendage extending into a branch on either side. Cell g cubical, but shorter than cell f (Figs. 7, 8). Antheridia clustered, each bearing a colorless basal septum (Fig. 9, arrow), arising on a stalk cell with a lower black septum (Fig. 9, arrowhead).

Receptacle yellowish-brown, nearly colorless in cell I; cell I longer than broad, narrowed toward the base, usually with a slightly oblique upper septum; cell II subpentagonal



Figs. 1–6. *Laboulbenia polymorpha*, C-forms. **1** One of the specimens illustrated by Sugiyama (1978, Fig. 1-C). Each of the posterior lip cells has a broad circular termination or disk (*v-line*). Black edge of the outer appendage is presumably hidden by the massive branches or broken off. M. Ishikawa 674-a. **2** Lectotype. Similar form to **1**, but the appendages extend over the perithecial base. Black edge of the outer appendage is broken off, and only the basal part remains (*arrow*). M. Ishikawa 673-b. **3** Same specimen showing one of apical disks of the perithecium. **4** Same specimen, at another level of focus, showing apical disks of perithecium. **5** Paratype, in which appendages and perithecium cross over one another. Perithecial wall cell rows are slightly twisted. K. Sugiyama 2101-b. **6** Mature thallus with normal (erect) disposition of both appendages and perithecium. Black edge of the outer appendage curves toward the outer side. Receptacle cells and perithecial stalk cells are shown as *I* to *VII*. K. Terada 1535. *Bar* **1** 23.5 μm; **2, 5, 6** 25 μm; **3, 4** 10 μm



Figs. 7–11. *L. polymorpha*, C-forms. **7** Young thallus showing appendages. Black edge of the outer appendage reaches insertion cell *e*. Cell *f* shows curious elongation upward in the anterior direction, extending beyond cell *g*. Septa along the outer edge of the outer appendage are hidden by the blackening of the edge (*arrowheads*). K. Terada 1617. **8** Young thallus showing immature perithecium, appendages, and upper portion of receptacle. Cell *g* has a thick upper black septum. Upper cells of receptacle are shown as *III*, *IV*, and *V*. K. Terada 1617. **9** Young thallus showing appendages. The inner appendage bears clustered (or paired) antheridia near the base; each antheridium bears a colorless septum at the base (*arrow*); antheridial stalk cell bears a basal black septum (*arrowhead*). K. Terada 1617. **10** Very young thallus showing unilateral branching in the outer appendage (inner appendage is not formed yet). Original spore septum is indicated by *small letter a.* K. Sugiyama 2101-c. **11** Mature thallus showing perithecium with apical disks. K. Sugiyama 2101-d. *Bar* **7–11** 10 μm

in optical section, slightly flattened, shorter than cell I; cells III and IV flattened, similar in height; outer corner of cell IV rounded or protruding laterally below insertion cell; cell V small, rounded, separated from cell IV by a subvertical septum, touching cell III at the lower end (Fig. 8). Insertion cell blackened, discoid, and constricted. (Cell arrangement mentioned above is shown well in Fig. 6.)

Measurements: Total length from foot to tip of perithecium 130–150 μm; perithecia 75–100 × 35–50 μm; appendages about 100 μm; ascospores about 40 × 3 μm.

Note: The C-form was found on the elytral margins including elytral-epipleural parts, metasternum, and abdominal sternites of the host. In many individuals of C-form, the appendages and the perithecum lie across one another (Fig. 5). This habit appears to be related to the more strongly bent perithecium and more oblique position of the insertion cell. The lectotype of *L. polymorpha* designated in the present article has such characters (Fig. 2). However, some individuals had a normal (erect) disposition of both appendages and perithecium as shown in fig. 6. Sugiyama's illustration (fig. 1-C) presumably corresponds to this variant of the C-form (see also Fig. 1 in the present article).

The unique structure of the posterior lip cells of *L. polymorpha* is reminiscent of that of *Laboulbenia bidentata* Thaxter, described from Australia (Figs. 3, 4, 11; see Thaxter 1908, p. 344, plate LIII, figs. 18–20). However, in *L. bidentata*, there appears to be only one black septum on the appendage and the upper receptacle cells are not flattened. Its host is *Homethes* (not *Homothis*) sp. (the taxonomic position of *Homethes* was discussed by Liebherr 1990, who placed it in the tribe Odacanthini).

D-form

Figs. 12–25

Perithecium blackish-brown on the middle wall, yellowish-brown on the lower wall, subhyaline on the upper wall, subconical (but bending back at the apex). Anterior lip cells hyaline and tapered, not exceeding the height of the posterior lip cells. Each of the posterior lip cells black except for the hyaline, broad, disklike apical part, bending backward (Figs. 15, 16). Cell VI is flattened and cell VII is quadrate in optical section or flattened, slightly oblique. Perithecial basal cells quadrate or rounded in optical section.

Appendages nearly colorless, consisting of lower stout cells with black septa and upper elongate cells with colorless septa, very closely branched in the lower part; upper portion of branches long and tapered to a narrow tip (Fig. 12). Outer appendage without black outer edge (Figs. 20, 23, 24, 25). Cell f cubical at first, later elongating anteriorly to form several branches successively, bearing distinct black basal septa by which each branch is separated from cell f (Figs. 19, 21). Inner appendage extending into a branch on either side (Fig. 18). Cell g at first cubical, then elongating anteriorly to form several branches on cell g (Figs. 12, 22). Antheridia clustered, each bearing a colorless basal septum (Fig. 22, arrowheads), arising on a stalk cell with a lower black septum (Fig. 17, arrow).

Receptacle yellowish-brown, but nearly colorless in cell I; cell I long, narrowed toward the base, usually with a slightly oblique upper septum; cell II subpentagonal in optical section, slightly flattened, much shorter than cell I; cells III and IV flattened, similar in height; cell IV nearly straight on the outer side; cell V small, nearly rounded, separated from cell IV by an oblique septum, touching cell III at the lower end (Fig. 21). Insertion cell blackened and discoid.

Measurements: Total length from foot to tip of perithecium 180–250 μm; perithecia 100–125 × 40–60 μm; appendages 100–180 μm; ascospores about 40 × 3 μm.

Note: The D-form was found on the basal part of the elytra, mesothorax (mesopleura), and mesocoxae. Structure of the posterior lip cells is the same as in the C-form, but its direction of bending is different (cf. Fig. 11 and Figs. 15, 16). Spore size is also the same as in the C-form, although in size of the thallus, D-form is larger than C-form. The D-form differs from the C-form chiefly by the appendage structure. The outer appendage of the D-form lacks a black outer edge on the outermost branch, whereas in the C-form it is always present (cf. Fig. 20 and Figs. 7–10). Cell f bears several branches; each branch bears a black septum on cell f (a newly formed septum is located higher in position than an earlier formed one; see Fig. 21).

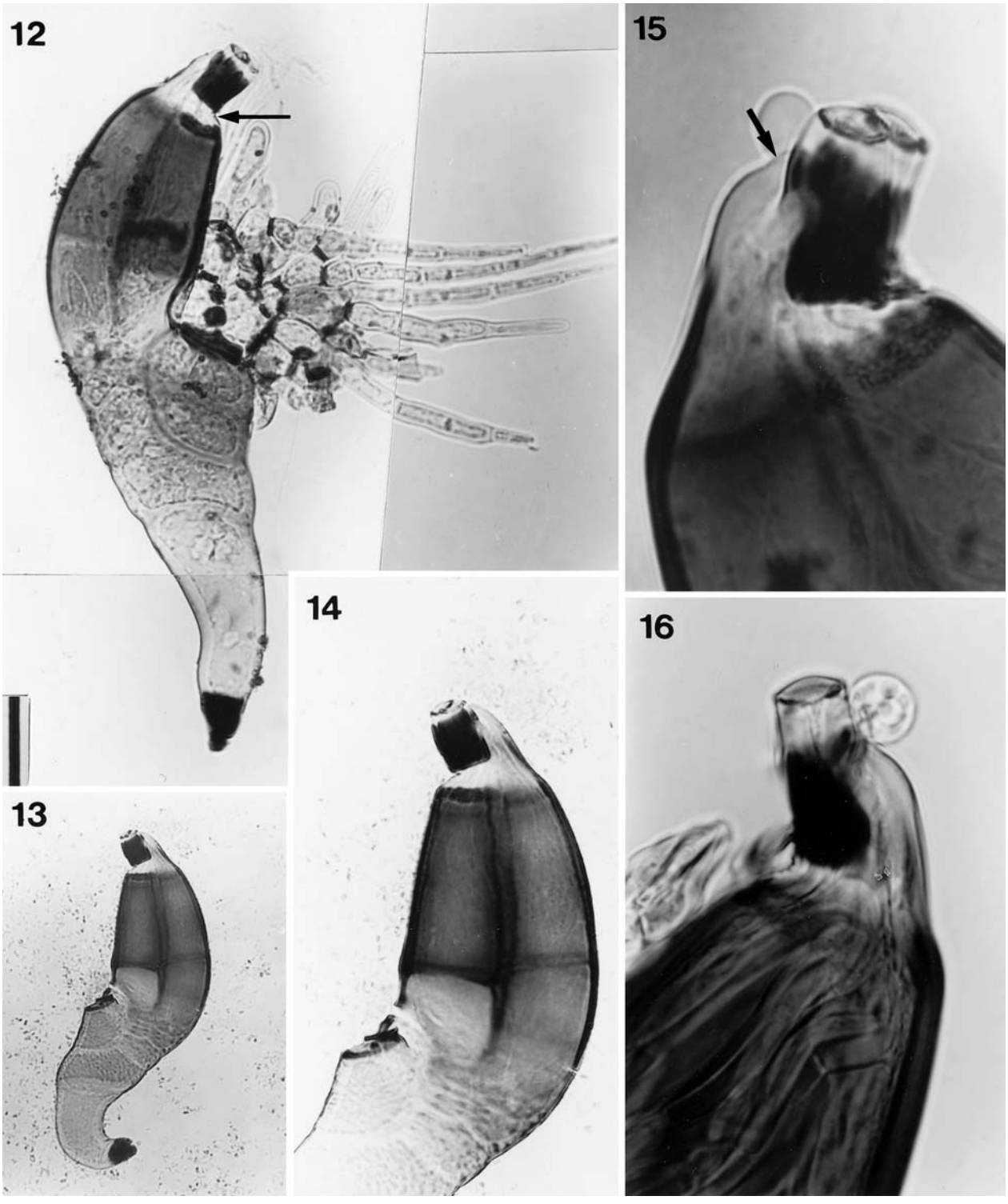
E-form

Figs. 26–30

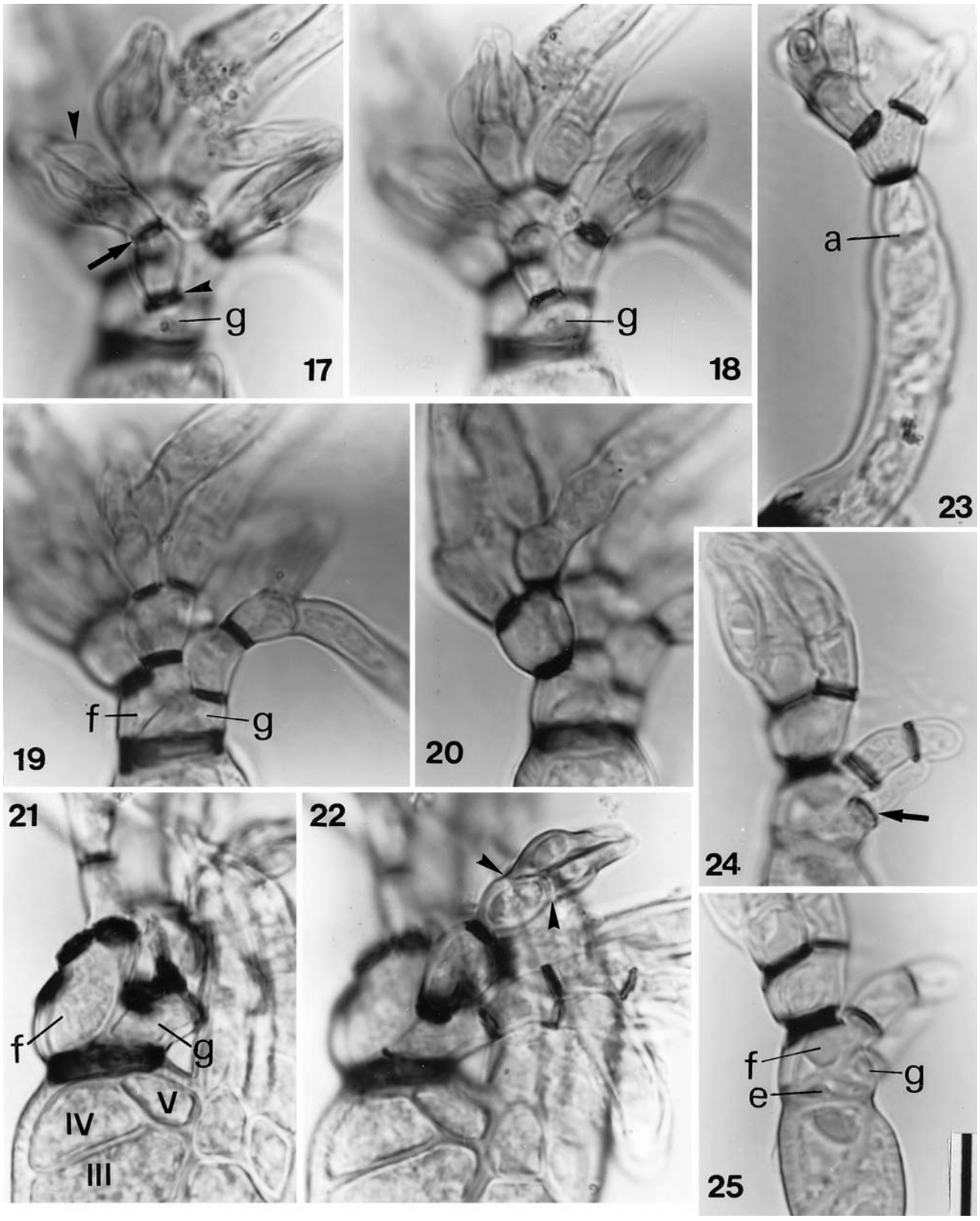
Perithecium blackish-brown, but somewhat pale at the base, long, slender, and subconical. Anterior lip cells projecting (one of the two cells elongates more) and extending far above the posterior lip cells (Fig. 26, arrowhead). Each of the posterior lip cells black except for the hyaline, conical upper portion with a very small, circular, truncate apex (Fig. 30, arrow). Cell VI and perithecial basal cells more or less elongated, but cell VII almost quadrate in optical section.

Appendages brownish, consisting of lower short cells with black septa and upper elongate cells with colorless septa, very closely branched in their lower part; upper portion of branches more or less long and tapering only slightly to a broad rounded tip (Fig. 27). Outer appendage having a black outer edge that does not extend down to the insertion cell (Fig. 28), and bending outward and producing a series of lateral branches on one side. Cell f elongating anteriorly to form several branches successively, bearing distinct black septa by which each branch is separated from cell f (Fig. 28). Inner appendage probably at first extending into a branch on either side. Cell g elongating anteriorly to form several branches, presumably in the same way. Antheridia not observed.

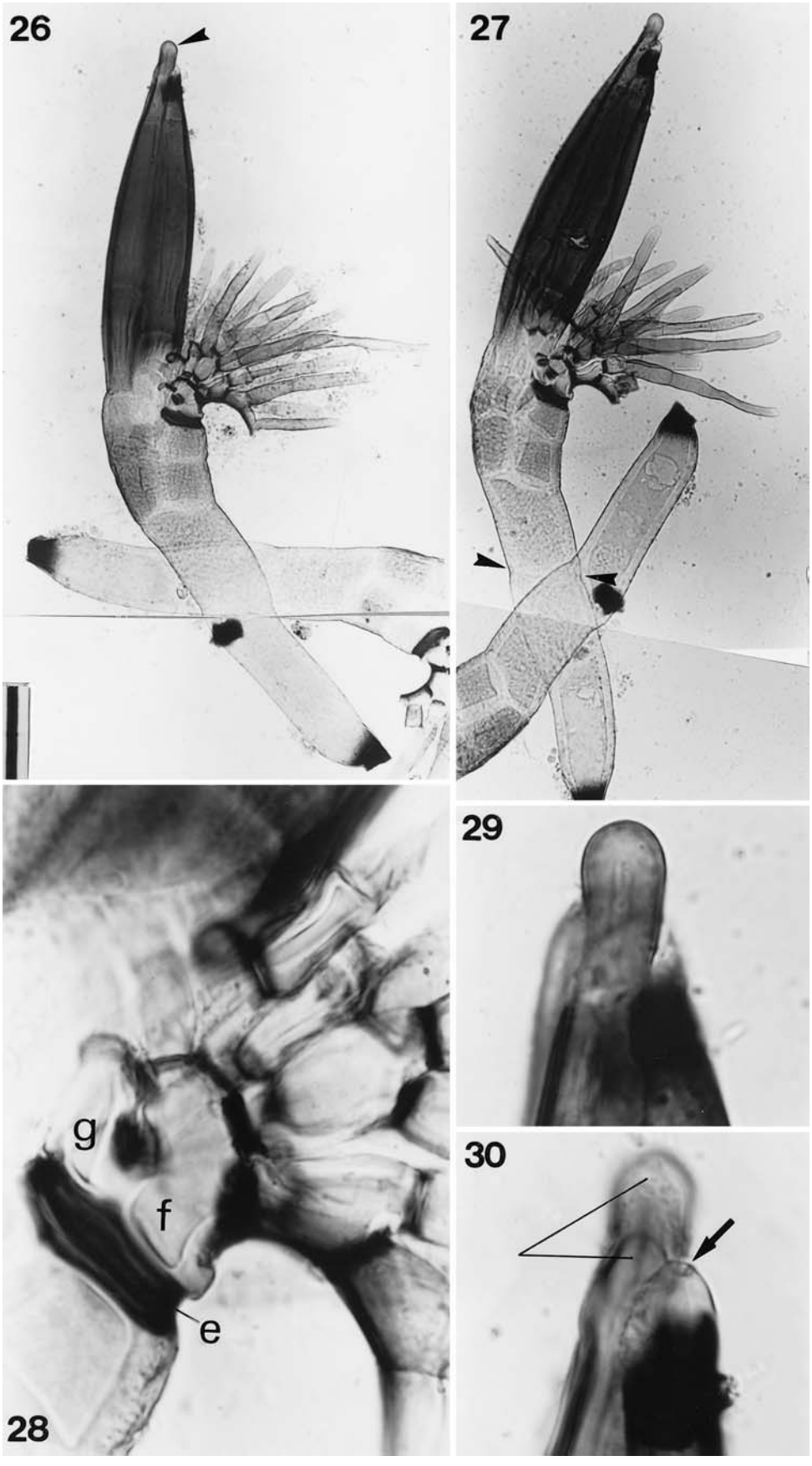
Receptacle yellowish-brown, nearly colorless in cell I; cell I cylindrical, usually with a slightly oblique upper septum (Fig. 27, arrowhead); cell II subcylindrical, much shorter than cell I; cells III and IV almost quadrate in optical section; cell IV a little shorter than cell III in height, nearly straight on the outer side; cell V small,



Figs. 12–16. *L. polymorpha*, D-forms. **12** Mature thallus showing typical D-form. Upper portion of each branch of the appendages is tapering and longer than that of C-form. Perithecial apex slightly bends backward, forming a bulge; colorless area lies just below the black posterior lip cells (*arrow*). K. Terada 884-b. **13** One of the specimens illustrated by Sugiyama (1978, Fig. 1-D). M. Ishikawa 673-b. **14** Same specimen showing perithecium on a larger scale. **15** Mature thallus showing apical disks of the perithecium. Hyaline anterior lip cells are tapered toward the apex (*arrow*). K. Terada 884-b. **16** Mature thallus showing apical disks of the perithecium (one disk is out of focus); colorless apical portion of disks is more elongated than that of **15**. K. Terada 1917-d. *Bar* **12, 14** 25 μm; **13** 50 μm; **15, 16** 10 μm



Figs. 17–25. *L. polymorpha*, D-forms. **17–20** Appendages of a young thallus. K. Terada 884. **17** Cell *g* is out of focus, but one of the antheridial branchlets from cell *g* is visible. Clustered antheridia are indicated by *upper arrowhead*; black septum at the base of antheridial stalk cell is indicated by *arrow*; and black septum on cell *g* is indicated by *lower arrowhead*. **18** Two black septa are shown to be located on cell *g*, each separating a branch of the inner appendage on either side. **19** Cells *f* and *g* are shown to be located side by side. Cell *f* bears two black septa. **20** The outer appendage is shown to lack a black edge along the outer side. **21, 22** Appendages of a young thallus. K. Terada 1617 d. **21** Basal portion of the appendages, in which cells *f* and *g* elongate and form several branches respectively (only black septa are visible). Upper cells of receptacle are shown as *III*, *IV*, and *V*. **22** Inner appendage with antheridial branchlet. Each of the antherida bears a colorless basal septum (*arrowheads*). **23** Very immature thallus. Original spore septum is indicated by *small letter a*. K. Terada 929. **24, 25** An immature thallus. K. Terada 929. **24** Black septum on cell *g* has been formed (*arrow*). **25** Another focus, showing arrangement of cells *e*, *f*, and *g*. *Bar* **17–25** 10 μm



Figs. 26–30. *L. polymorpha*, E-forms, all from M. Ishikawa 673-c. **26** Mature thallus showing typical E-form, forming a projection at the perithecial apex (*arrowhead*). **27** Another typical mature thallus. An oblique septum between cells *I* and *II* is indicated by *arrowheads*. **28** Appendage base at higher magnification; cells *f* and *g* have black septa in rows similar to those of D-form; black edge of the outer appendage does not reach cell *e*. **29** Apical portion of perithecium of mature thallus, showing the prominent apical projection. **30** Similar apex in another focus level, showing a small disk (*arrow*). Anterior lip cells differ in height (*v-line*). *Bar* **26, 27** 50 μm; **28–30** 10 μm

wedge-shaped, separated from cell IV by a subvertical septum, almost touching cell III. Insertion cell blackened and discoid.

Measurements: Total length from foot to tip of perithecium 390–430 μm; perithecia 185–200 × 40–45 μm; apical outgrowths of perithecia 15–17.5 μm; appendages about 150 μm; ascospores not observed.

Note: With respect to characters of the outer appendage, the E-form is intermediate between C-form and D-form. However, the lip cells of the E-form are quite different from those of the latter two forms (Figs. 29, 30).

The E-form recalls *Laboulbenia heimansii* Jeekel described from Sumatra (Fig. 27; see Jeekel 1959, fig. 1) because of the elongated perithecia and the elongated receptacles, in which cell VI and basal cells are elongated to some extent (in *L. heimansii*, the lower part of the perithecium is more elongated and the perithecial projection is absent), and an oblique septum is present between the longer cell I and the shorter cell II. The host was listed as *Casnoidea interstitialis* (Schmidt-Goebel) (*Ophionea* instead of *Casnoidea* is used in the present article; see Habu 1962, p. 113). According to Jeekel (1959), *L. heimansii* was found on the inferior surface of the prothorax of *O. interstitialis*.

Discussion

In *L. polymorpha*, three distinct forms have been recognized. They have the following common characteristics. (1) Cells I and II of the receptacle are separated by a slightly oblique septum (Figs. 6, 27; not clearly shown in photographs of D-form), and cells IV and V are equal in height (Figs. 8, 22, 27). (2) Cell g of the inner appendage always has upper thick black septa (Figs. 8, 18, 28); this blackening of septa occurs from the beginning of the inner appendage formation in thallus development (Fig. 24, arrow). (3) Antheridia are borne on colorless septa (Figs. 9, 22; antheridia not seen in E-form); perithecia have broad terminal disks (Figs. 11, 15; very small and inconspicuous in E-form); and receptacle cell II is subpentagonal in optical section (Figs. 6, 13; short cylindrical in E-form). However, each of these three forms could be separable as a distinct species if the shape of the perithecial apex, extent of darkness along the outer edge of the outer appendage (reaching cell e in C-form, not quite reaching cell e in E-form, and no darkness evident in D-form), and minor characters such as amount of tapering of appendages are given sufficient taxonomic importance.

The perithecia of the genus *Laboulbenia* generally have a minute disklike structure on the apex of at least one lip cell. Thaxter (1896, p. 230, pl. II, fig. 14) suggested that it might act as a valve. However, in *L. polymorpha* and *L. bidentata*, the posterior lip cells seem to lack such small structures and form broad terminal disks instead (in the E-form of *L. polymorpha*, the structure of the posterior lip cells is not as clearly observed, but small disks are visible in Fig. 30). Or, it may be more appropriate to say that the "valve" is considerably widened in *L. polymorpha* (C-form and D-form: Figs. 11, 15, 16) and *L. bidentata* (Thaxter 1908, pl. LIII, fig. 20). Besides *Ophionea* and *Homethes*, the terminal disks occur on *Laboulbenia* species on other hosts in Odacanthini such as *Archicolliuris*, *Eucolliuris*, *Mimocolliuris*, and *Odacantha* (Terada, unpublished data).

Several thalli of unknown form were found together with thalli of *L. polymorpha* on slides 673-b and 673-d. Undoubtedly, these thalli belong to a species different from *L. polymorpha*. They have normal perithecia, whose apices are not specially modified; clustered antheridia, each bearing a black septum at the base; and cell g with colorless upper septa. Sugiyama (1978, fig. 1-G) illustrated a young individual with such characteristics from slide 673-d and included it in *L. polymorpha*. He was obviously wrong about his identification of this specimen illustrated in his figure.

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