Notes on *Laboulbenia stenolophi* and *Laboulbenia anoplogenii* (Ascomycetes, Laboulbeniales)

Katsuyuki Terada

Omiya 1-2-20-203, Nishi-ku, Hiroshima 733-0007, Japan

Accepted for publication 6 October 2000

Laboulbenia stenolophi is reported for the first time from Japan. Stenolophus iridicolor and S. propinquus are added as new hosts. The crowded antheridia and the protruding (bulging) cell IV are characteristic of this fungus, although thalli with an almost normal cell IV sometimes occur. Laboulbenia anoplogenii on Anoplogenius is easily distinguished from what has been called L. anoplogenii on Stenolophus, Astigis, Abacetus and Chlaeminus by the following characters: 1) no crowded antheridia can be observed throughout thallus development, but many sterile long branches can be observed instead; 2) cell IV starts to undergo cell division early in thallus development; 3) cell V extends downward to the level of cell VII, rather than extending only as far as the perithecial basal cells; and 4) cell VI is usually longer and extends farther distally than cell III. Anoplogenius is the host genus of L. anoplogenii and the records from other hosts represent misapplied names.

Key Words——Anoplogenius; Carabidae; Laboulbenia; Laboulbenia polyphaga; Stenolophus.

Laboulbenia stenolophi Spegazzini (Ascomycetes, Laboulbeniales) was described from an Italian carabid, Stenolophus teutonus (Schrank) (Coleoptera, Carabidae, Harpalini). Later, L. stenolophi was also reported on the same host species from Tunisia (Maire, 1916), Hungary (Banhegyi, 1944), and Germany (Scheloske, 1969). Terada (1976) reported this fungus from Taiwan on Stenolophus quinquepustulatus (Wiedemann). His illustrations (Fig. 2: 4, 5 in Terada, 1976) of L. stenolophi showed a strongly protruding cell IV. On the other hand, various authors have misapplied the name Laboulbenia anoplogenii Thaxter to specimens on Stenolophus (Thaxter, 1908; Baumgartner, 1923; Sugiyama, 1971; Balazuc, 1974, 1982; Rossi, 1982; Sugiyama and Phanichapol, 1984; Santamaria, 1985, 1989, 1998; Majewski, 1999).

Laboulbenia anoplogenii Thaxter was described from a Chinese carabid, Anoplogenius cyanescens (Hope) [=A. circumcinctus (Motschulsky), Harpalini, Carabidae] (Thaxter, 1899). In his monograph, Thaxter (1908, Pl. LV, Figs. 4, 5) illustrated a specimen taken from a North American carabid, Stenolophus fuliginosus Dejean and the type from China as well. Numerous conspicuous antheridia are present on the North American specimen whereas on the type they are not visible. This difference is an important diagnostic character of L. anoplogenii.

Laboulbenia stenolophi Spegazzini, Redia 10: 65. 1914. Type: On Stenolophus (s. str.) teutonus (Schrank), Italy. Figs. 1-11

Records under misapplied names:

Laboulbenia polyphaga Thaxter

on Stenolophus (s. str.) mixtus (Herbst) (Stadelman

and Poelt, 1962).

Laboulbenia anoplogenii Thaxter

on Stenolophus (s. str.) fuliginosus Dejean (Thaxter, 1908; as L. anaplogenii); on Stenolophus (s. str.) mixtus (Herbst) (Baumgartner, 1923; as L. anaplogenii); on Stenolophus sp. (Sugiyama, 1971; as L. anaplogenii); on Stenolophus (s. str.) mixtus (Herbst) (Balazuc, 1974); on Stenolophus (Egadroma) smaragdulus (Fabricius) (Balazuc, 1982); on Stenolophus (Egadroma) relucens (Erichson) (Rossi, 1982); on Stenolophus (Egadroma) quinquepustulatus (Wiedemann) (Sugiyama and Phanichapol, 1984); on Stenolophus (s. str.) teutonus (Schrank) (Santamaria, 1989; Majewski, 1999); on Stenolophus (s. str.) discophorus (Fischer von Waldheim) (Santamaria, 1989); on Stenolophus (s. str.) skrimshiranus Stephens (Santamaria, 1998).

Laboulbenia anoplogenii Thaxter subsp. anoplogenii on Stenolophus (s. str.) teutonus (Schrank) (Santamaria, 1985).

Specimens examined: [France] On *Stenolophus* (s. str.) *teutonus* (Schrank), KT-1479, Vico Corse, 3-VIII-1968, G. Ledoux leg. On *Stenolophus* (s. str.) *mixtus* (Herbst), KT-1480, Batz sur Mer, Loire Atlantique, 12-VIII-1964, G. Ledoux leg. [Japan] On *Stenolophus* (s. str.) *iridicolor* Redtenbacher, KT-462, Horomui, Iwamizawa, Hokkaido; KT-848, Ichiba, Tokushima Pref. On *Stenolophus* (s. str.) *propinquus* Morawitz, KT-314, Kawazu, Muikaichi, Shimane Pref.; KT-1475, Hurukawa, Hiroshima, Hiroshima Pref. On *Stenolophus* (Egadroma) quinquepustulatus (Wiedemann), KT-1471, Otomi, Iriomote-



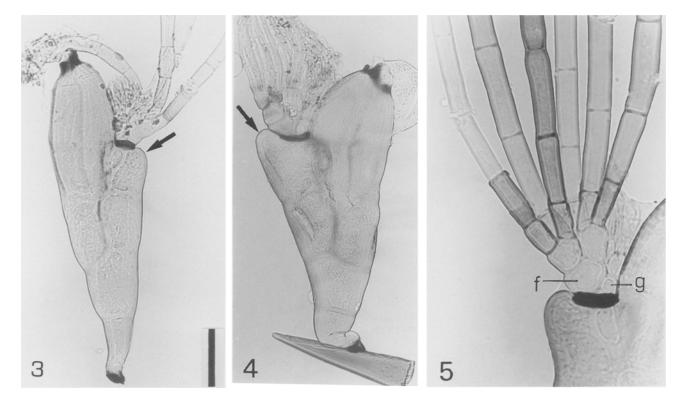
Figs. 1–2. Laboulbenia stenolophi. 1. Thallus with mature perithecium and almost hyaline outer appendage. KT-1479, from S. teutonus.
 2. Thallus with mature perithecium and brown outer appendage. KT-1475, from S. propinguus. Bar=50 μm.

jima, Okinawa Pref.

Measurements: Total length to tip of perithecium 280–390 μ m; perithecia 125–160×55–78 μ m; cell V 23–25×13–15 μ m; appendages up to 400 μ m; ascospores 40–45×4 μ m.

Several specimens on *S. teutonus* (Figs. 1, 3) and *S. mixtus* from France were examined. There were no noticeable differences between those from the two hosts. The color of the thalli is subhyaline at first, becoming brownish yellow to yellowish brown, with a more or less grayish tinge, or sometimes amber-colored. The appendages are almost hyaline or yellowish. The foot, the insertion cell, and the perithecial apex under the hya-

line ostiole are almost black, although a more or less brownish tinge in the black coloration might be noticeable. Cell IV is usually protruding (bulging) at the outer corner, although the degree of protrusion is variable.Cell division in cell IV was not observed. Cell V is wedgeshaped, smaller and shorter than cell IV, and distant from cell VII. Cell VI is variably shorter than cell III. The perithecium is more or less inflated laterally (the most inflated portion is usually at the middle) and forms a well differentiated neck at the apex. The insertion cell is situated far above the base of the perithecium. The outer appendage consists of several long filamentous branches, whereas the inner appendage consists of a



Figs. 3–5. Laboulbenia stenolophi. 3. Thallus with cell IV weakly bulging at outer corner (arrow). KT-1479, from S. teutonus. 4. Stout thallus on spine of host leg. Cell IV is strongly protruding (arrow). KT-1434, from S. propinguus. 5. Brown branches of outer appendage grouped in threes; basal cell (f) is stout and larger than basal cell (g) of inner appendage. KT-1475, from S. propinguus. Bar=25 μm (Fig. 5), 50 μm (Figs. 3, 4).

short branchlet with crowded antheridia on either side. These are similar to those in the original photographs of *L. stenolophi* (Spegazzini, 1914).

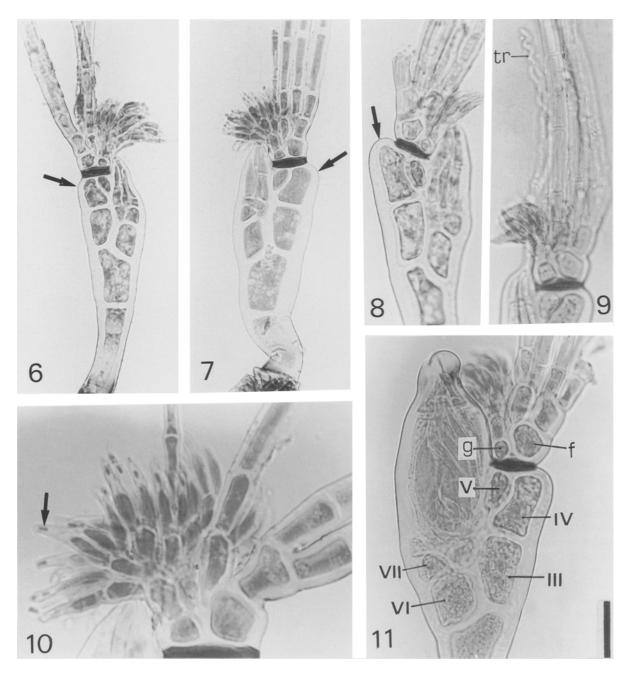
Japanese specimens have also been examined and are similar in character. The color of the perithecium and the receptacle is usually brownish yellow or yellowish brown, sometimes with a gravish tinge, but not with an amber coloration. Some thalli found on S. propinguus had a brown outer appendage (Figs. 2, 5). Cell IV varies from almost normal to protruding (Figs. 4-8). The crowded antheridia arise early in thallus development (Figs. 6, 7, 10) and persist long afterwards (Fig. 2). A long, branched, spirally twisted trichogyne arises from a young perithecium (Fig. 9). The basal cell (f) of the outer appendage is short and thick, larger than the basal cell (g) of the inner appendage, and has two suprabasal cells placed side by side, from which long branches arise (Figs. 5, 11).

Spegazzini (1914) accompanied his description of *L.* stenolophi with three photographs. The host was *S.* teutonus from Italy. These photographs show the following features: 1) in the young thallus (63 a), the inner appendage consists of crowded antheridia and the outer appendage consists of several long filamentous branches, the basal cell of the outer appendage is larger than the basal cell of the inner appendage, cell IV is normal, and cell VI is shorter than cell III; 2) in one mature thallus (63 b, left), cell IV seems to be protruding and the inner appendage has no long branches; 3) another mature thallus (63 b, right) has broken appendages and a bulging cell IV. Spegazzini (1914) described the color of *L. stenolophi* as "melleo-subhyalina", which probably means subhyaline to honey- colored.

Thalli on *S. teutonus* were more clearly illustrated by Santamaria (1985, Fig. 5; 1989, Pl. XV, Figs. c, d) and Majewski (1999, Fig. 3, a-c). They show the inner appendage with numerous antheridia and a protruding cell IV. Thalli with similar characters are also known on *S. mixtus* (Balazuc, 1974, Fig. 13, as *L. anoplogenii*; Stadelmann and Poelt, 1962, Fig. 18, as *L. polyphaga*). Although not illustrated, it is probable that the thalli on Asian *S. smaragdulus* (Balazuc, 1982) and on African *S. relucens* (Rossi, 1982) probably have similar forms.

A North American form on *S. fuliginosus* illustrated by Thaxter (1908, Pl. LV, Fig. 5) and a Rumanian form on *S. discophorus* photographed by Santamaria (1989, Pl. XV, Figs. f, g) clearly showed division of cell IV. Probably because of this, these specimens were considered to be *L. anoplogenii*. However, because of other characters, such as the inner appendage with numerous antheridia, they are referable to *L. stenolophi* instead. Division of cell IV in their reports may only be occasional, and a study of more material including young thalli from these hosts is very much needed.

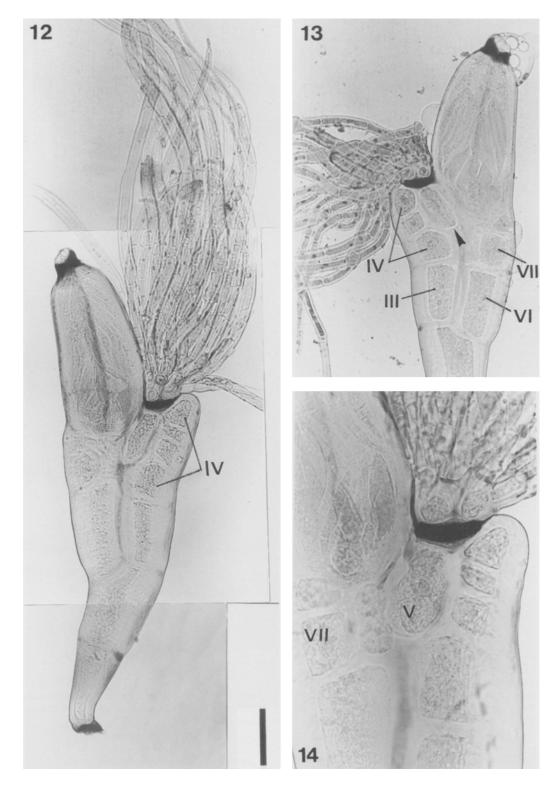
Bánhegyi (1940, Pl. IX, Fig. D) reported a thallus having a normal cell IV as *L. polyphaga* on a Hungarian *S.*



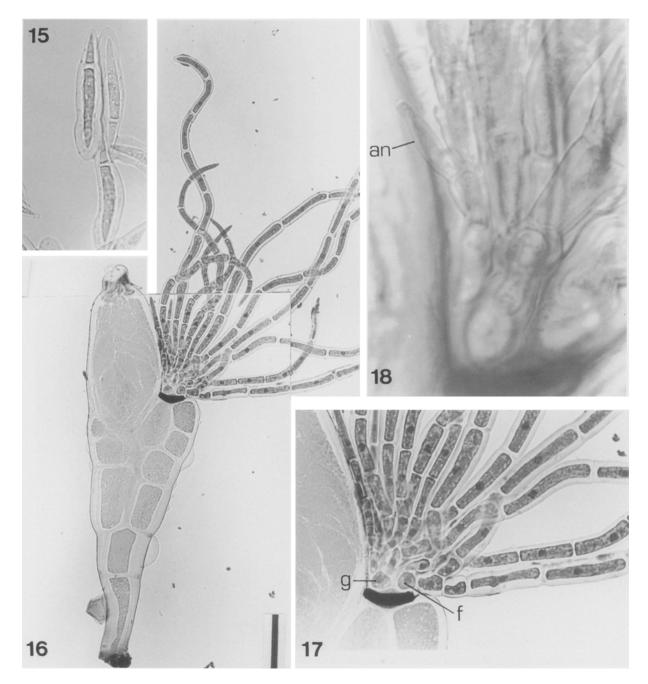
Figs. 6–11. Laboulbenia stenolophi. 6, 7, 10: KT-1471, from S. quinquepustulatus, and 8, 9, 11: KT-1435, from S. propinquus.
6. Young thallus with normal cell IV (arrow). 7. Young thallus with slightly bulging cell IV (arrow). 8. Young thallus with conspicuous protrusion of cell IV (arrow). 9. Young thallus with long, spirally twisted trichogyne (tr). 10. Basal portion of appendages, showing numerous antheridia. Arrow indicates spermatium in antheridial neck. 11. Thallus with almost mature perithecium and weakly bulging cell IV. Basal cell (f) of outer appendage is stout and larger than basal cell (g) of inner appendage. Cell V is small and far from cell VII. Cell VI is shorter than cell III. Black insertion cell is situated at the middle of the perithecium. Bar=10 μm (Fig. 10) and 25 μm (remaining figures). Stained with acetocarmine.

mixtus. His illustration showed an outer appendage with a tall basal cell (about two times longer than wide) from which two long branches arose. Thaxter (1896) showed a long, narrow basal cell of the outer appendage in *L. polyphaga*, rather than a short, broad cell as in *L. stenolophi*. No type was designated by Thaxter for *L. polyphaga* (Thaxter, 1893), although Farlow Herbarium

slide 8460 is labelled as type, the host being *Olisthopus parmatus* (Say), [Carabidae, Platynini], from York, Maine; the color was umber (yellowish brown, not orange-brown), with perithecium and upper receptacle darkest and cell V almost colorless (personal communication from I. Tavares). In the original description of *L. polyphaga*, Thaxter listed four different carabid genera as its



Figs. 12–14. Laboulbenia anoplogenii. KT-1470, from A. cyanescens. 12. Fully mature thallus with cell IV divided into four superposed cells. 13. Mature thallus showing cell IV divided into three superposed cells; bottom level of cell V (arrowhead) is close to upper end of cell VII; cell VI is slightly longer than cell III. 14. Middle part of thallus showing insertion cell situated near perithecial base; base of cell V extends downward almost to bottom level of cell VII. Bar=25 μm (Fig. 14) and 50 μm (Figs. 12, 13).



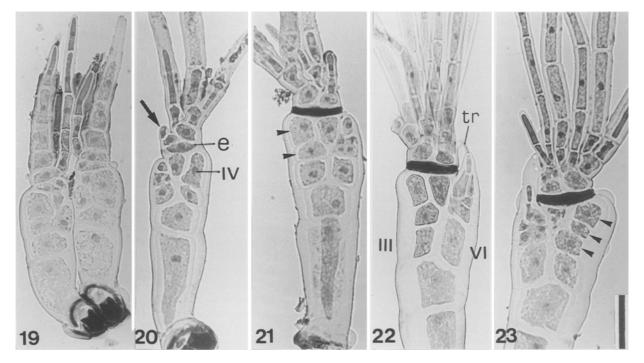
 Figs. 15–18. Laboulbenia anoplogenii. KT-1470, from A. cyanescens. 15. Ascospores. 16. Thallus with almost mature perithecium and filamentous appendages. 17. Enlargement of Fig. 16, in which two stout basal cells (f, g) of appendages are similar in size. (18) Basal portion of appendages showing a single solitary antheridium (an) which arises laterally on a branch. Bar=10 μm (Fig. 18), 25 μm (Figs. 15, 17), and 50 μm (Fig. 16) Stained with acetocarmine.

hosts, including *Stenolophus*. He (Thaxter, 1896) later reported North American *S. fuliginosus* as a host of *L. polyphaga*. Picard (1913) reported *L. polyphaga* on *S. teutonus* from France. A lectotype should be designated for *L. polyphaga* and the characteristics of specimens on different host genera carefully compared.

Laboulbenia anoplogenii Thaxter, Proc. Amer. Acad. Arts Sci. 35: 156. 1899. Type: No. 665, on Anoplogenius cyanescens (Hope) [syn. A. circumcinctus (Motsch.)], China. Figs. 12-23

Specimens examined: On *Anoplogenius cyanescens* (Hope), KT-845, 853, Ichinoki, Yamato, Hukushima Pref.; KT-357, Ishiyama, Otsu, Shiga Pref.; KT-1063, Hesaka, Hiroshima, Hiroshima Pref.; KT-1117, Yoshida, Hiroshima Pref.; KT-1470, Seto, Imari, Saga Pref. 12-VI-1999, M. Nishida leg.; KT-846, Hentona, Okinawa Pref.

Measurements: Total length to tip of perithecium



Figs. 19–23. Developmental stages of young thalli in Laboulbenia anoplogenii. KT-1470, from A. cyanescens. 19. Very young thalli. 20. Young thallus with insertion cell (e) not blackened yet and cell IV still undivided. Basal cell of inner appendages begins to divide (arrow). 21. Young thallus at a more advanced stage of thallus development in which cell IV has divided into two superposed cells (arrow-heads) and insertion cell is blackened. 22. Young thallus with a short, simple trichogyne (tr); several long filamentous branches form outer and inner appendages; cell VI becomes longer than cell III. 23. Young thallus, in which further division occurs in cell IV area, forming three superposed cells (arrowheads). Bar=25 μm. Stained with acetocarmine.

390–580 μ m; perithecium 155–200 (225)×60–85 (105) μ m; cell V 40–55×25–35 μ m; appendages up to 500 μ m long; ascospores 50–53×5 μ m.

In Japanese specimens on A. cyanescens that I have studied, the color of the thalli is brownish vellow to vellowish brown, sometimes with a gravish tinge. The color is very similar to that of L. stenolophi of Japan. On the other hand, Thaxter (1899) described the Chinese type material as "pale yellowish or nearly hyaline, becoming tinged with pale amber brown." In the Japanese material, the appendages are almost hyaline or pale yellowish. The foot, the insertion cell, and the perithecial apex under the hyaline ostiole are almost black. The earliest stages of thallus development in this fungus are shown in Figs. 19 and 20, in which cell IV is not yet divided and the insertion cell (e) is not yet blackened. Two superposed cells are formed by the division of cell IV by the time the insertion cell is blackened (Fig. 21). A short, simple trichogyne (tr) is then formed (Fig. 22). The upper cell of the two daughter cells of cell IV divides and the cell IV area is consequently occupied by three superposed cells (Fig. 23, arrowheads). At a fully mature stage, thalli have four superposed cells in the cell IV area, of which the uppermost cell protrudes upward and outward (Fig. 12). Cell V is close to the level of cell VII (Fig. 14). Cell VI is taller than cell III (Figs. 12, 13, 16). The perithecium is relatively long, sometimes inflated laterally (the most inflated portion is usually below the middle),

and forms a well-distinguished neck at the apex. The level of the insertion cell is slightly above the perithecial base (Figs. 12, 13). More than three branches arise from each basal cell of the outer and inner appendages (Figs. 17, 23). The basal cell of the outer appendage is similar in size to the basal cell of the inner appendage (Fig. 17, f, g). Thaxter (1899) also described those cells as "nearly equal", but his illustration of the type of this fungus shows the basal cell of the outer appendage as larger than the basal cell of the inner appendage (see Thaxter, 1908, Pl. LX, fig. 4). No crowded antheridia arise at any stage of thallus development (Figs. 17, 19-23). I have observed only one solitary antheridium near the base of an appendage branch (Fig. 18, an). The ascospores (Fig. 15) are slightly larger than those of L. stenolophi.

Laboulbenia anoplogenii was described from a Chinese carabid, A. cyanescens (Thaxter, 1899). Thaxter (1908) later included two or three additional hosts, Stenolophus (Thaxter listed Agonoderus pallipes Fabr., which is now placed in Stenolophus), Abacetus, and probably Astigis [Thaxter listed Abacetus rubripes Dejean from France with some doubt, however, the species is known as a synonym of Astigis salzmanni (Germar)] and supplemented the description of this fungus as follows: 1) there are many specimens having a normal, undivided cell IV; 2) the antheridia often grow in clusters; and 3) there are specimens having red-brown to claret-colored insertion cells. However none of these additional characters apply to the specimens on *Anoplogenius*.

Specimens on Astigis salzmanni (as Abacetus salzmanni) from Spain were described as L. anoplogenii subsp. abaceti by Santamaria (1985, Fig. 4), in which the thallus color was reported as "pallide viridis", and reddish insertion cells were not mentioned; crowded antheridia were formed; cell VI was slightly shorter than cell III; and the basal cell of the outer appendage was taller than the basal cell of the inner appendage (see also Santamaria, 1989, Pl. XV, Fig. e, where the host was referred to as Astigis; 1998, Fig. 1, e). Santamaria (1989, 1998) placed L. anoplogenii subsp. abaceti in synonymy with L. anoplogenii subsp. anoplogenii, but its characteristics show it to be not related to L. anoplogenii at all. The taxonomic status of L. anoplogenii subsp. abaceti is uncertain at the present time. Further study is needed to determine whether there are significant differences between thalli on Stenolophus and those on Astigis, as well as the other hosts listed by Santamaria (1989) and Thaxter (1908).

Several specimens on Asian Abacetus were examined (K. Sugiyama slide 4200, Malaysia; Y. Nakamura slide unnumbered, India; and K. Terada slide 1488, Japan). The general color of the thalli is pale amber yellow at first, then becoming amber brown. The outer appendage is pale yellowish, sometimes becoming amber colored later; one specimen (K. Terada-1488) has a dichotomously branched outer appendage wine-red in color. The insertion cell is dark brown (the color might be what Thaxter called "red-brown") or blackish brown; the foot is almost black. Cell IV is divided into two or three superposed cells or undivided (all of the Japanese specimens have an undivided cell IV). Cell VI is shorter than cell III, and cell V is distant from cell VII (in two fully mature thalli on Indian Abacetus sp., cell VI is slightly taller than cell III, and cell V is somewhat close to cell VII). The inner appendage consists of a short branchlet with crowded antheridia on either side. The outer appendage has a tall basal cell (about two times longer than wide in the Japanese specimens).

I have also examined a slide bearing one immature thallus from Malaysian *Chlaeminus* sp. (K. Sugiyama slide 4198; see Sugiyama and Majewski, 1985, who mentioned this as a host of *L. anoplogenii*). The color of the thallus is pale yellow except for the blackish brown insertion cell and foot; cell IV is divided into two superposed cells; cell III and cell VI are nearly equal in height; and the crowded antheridia arise on either side of the basal cell of the inner appendage. The basal cell of the outer appendage is larger than the basal cell of the inner appendage.

A fully mature thallus with several characteristics in common with that on Japanese *Abacetus* was illustrated by Batra (1963, Figs. 1, 2), who described it as a new species, *Laboulbenia olitskyi*, from Indian *Chlaeminus biguttatus* Motschulsky. This fungus is characterized by the long, dichotomously branched outer appendage, the clusters of antheridia, the undivided cell IV, cell VI as equal in height as cell III, the pale yellow-brown perithecium, and the hyaline receptacle with smoky patches in the septa and at the lower end of the basal cell. *Astigis*, *Abacetus* and *Chlaeminus* are placed in the tribe Pterostichini (Coleoptera, Carabidae) (see Andrewes, 1928, p. 14; Jeannel, 1948, p. 425).

As mentioned above, in the present study, thalli on *Stenolophus, Astigis, Abacetus* and *Chlaeminus* were found to have different characters from those of *L. anoplogenii* on *Anoplogenius. Anoplogenius* is here regarded as the only host genus for *L. anoplogenii* and the known localities are China (type locality), Taiwan (Sugiyama and Shazawa, 1977, with *A. philippinus* Jedlička recorded as a host), and Japan (Sugiyama, 1973; with *A. cyanescens* recorded as a host).

Acknowledgements——I wish to thank Dr. Isabelle I. Tavares, University of California, Berkeley, for correcting the English manuscript and valuable comments. I also thank Dr. Keiichi Sugiyama, and Mr. Yositaka Nakamura for the loan of the slides, and Dr. Kazuyoshi Kurosa, Mr. Mitsuyasu Nishida and Mr. Georges Ledoux for sending material. Mr. Seiji Morita is thanked for copies of some entomological papers.

Literature cited

- Andrewes, H. E. 1928. On the types of Oriental Carabidae described by V. de Motchulsky. Trans. Ent. Soc. Lond. **76**: 1–24.
- Balazuc, J. 1974. Laboulbeniales de France (suite). Bull. Mens. Soc. Linn. Soc. Bot. Lyon **43**: 12–21, 57–64, 73–79, 253–262, 295–315, 346–368.
- Balazuc, J. 1982. Laboulbeniales (Ascomycetes) de Madagascar, des Comores et des Mascareignes. Bull. Mens. Soc. Linn. Soc. Bot. Lyon 51: 6–27.
- Bánhegyi, J. 1940. Elömunkálatok a magyarországi Laboulbenia-félék monografiájához. Index Horti Bot. Univ. Budapest. 4: 39–59.
- Bánhegyi, J. 1944. A Balaton környékének Laboulbenia-féléi. Bot. Közlem. 41: 49-61.
- Batra, S. W. T. 1963. Some Laboulbeniaceae (Ascomycetes) on insects from India and Indonesia. Amer. J. Bot. 50: 986–992.
- Baumgartner, R. 1923. Contribution à l'étude des Laboulbéniales de la Suisse. Jahrb. Philos. Fak. II. Univ. Bern 3: 257–265.
- Jeannel, R. 1948. Coléoptères Carabiques de la région margache (deuxième partie). Faune de l'Empire Français 10: 373-765.
- Maire, R. 1916. Deuxième contribution à l'étude des Laboulbéniales de l'Afrique du Nord. Bull. Soc. Hist. Nat. Afrique N. 7: 6-39.
- Majewski, T. 1999. New and rare Laboulbeniales (Ascomycetes) from the Bialowieza Forest (NE Poland). Acta Mycologica 34: 7–39.
- Picard, F. 1913. Contribution à l'étude des Laboulbéniacées d'Europe et du nord de l'Afrique. Bull. Soc. Mycol. France 29: 503–571.
- Rossi, W. 1982. Laboulbeniali della Sierra Leone (Ascomycetes). Accad. Naz. dei Lincei, Quaderno N. 255: 9–22.
- Santamaria, S. 1985. Laboulbeniales (Ascomycetes) ibéricos. Descripción de una especie y subespecie nuevas. Anales Jard. Bot. Madrid 42: 25–32.

- Santamaria, S. 1989. El orden Laboulbeniales (Fungi, Ascomycotina) en la Peninsula Ibérica e Islas Baleares. Ed. Espec. Soc. Catalana Micol. 3: 1–396.
- Santamaria, S. 1998. Laboulbeniales, I. Laboulbenia. Fl. Mycol. Iber. 4: 1–186.
- Scheloske, H. -W. 1969. Beiträge zur Biologie, Ökologie und Systematik der Laboulbeniales (Ascomycetes) unter besonderer Berücksichtigung des Parasit-Wirt-Verhältnisses. Parasitol. Schriftenreihe 19: 1–176.
- Spegazzini, C. 1914. Primo contributo alla conoscenza delle Laboulbeniali italiane. Redia 10: 21-75.
- Stadelmann, M. and Poelt, J. 1962. Zur Kenntnis der mitteleuropäischen Laboulbeniales. Ber. Bayer. Bot. Ges. 35: 120–132.
- Sugiyama, K. 1971. On three species of Laboulbeniales collected in Interior-Sabah (Borneo). Trans. Mycol. Soc. Japan 12: 14–17.
- Sugiyama, K. 1973. Species and genera of the Laboubeniales (Ascomycetes) in Japan. Ginkgoana 2: 1–97.
- Sugiyama, K. and Majewski, T. 1985. The Laboulbeniomycetes (Ascomycotina) of Peninsular Malaysia II. Trans.

Mycol. Soc. Japan 26: 449-462.

- Sugiyama, K. and Phanichapol, D. 1984. Laboulbeniomycetes (Ascomycotina) in Thailand, I. Nat. Hist. Bull. Siam Soc. 31: 47–88.
- Sugiyama, K. and Shazawa, E. 1977. Notes on Laboulbeniomycetes of Formosa. Trans. Mycol. Soc. Japan 18: 270–278.
- Terada, K. 1976. Some species of the Laboulbeniales from Taiwan. Trans. Mycol. Soc. Japan 17: 23–34.
- Thaxter, R. 1893. New species of Laboulbeniaceae from various localities. Proc. Amer. Acad. Arts Sci. 28: 156–188.
- Thaxter, R. 1896. Contribution towards a monograph of the Laboulbeniaceae. Mem. Amer. Acad. Arts Sci. 12: 187–429.
- Thaxter, R. 1899. Preliminary diagnoses of new species of Laboulbeniaceae. I. Proc. Amer. Acad. Arts Sci. 35: 151–209.
- Thaxter, R. 1908. Contribution toward a monograph of the Laboulbeniaceae. Part II. Mem. Amer. Acad. Arts Sci. 13: 217–469.