A New Development of Ephelis.

ΒY

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AND

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With Plate IV.

"HE genus *Ephelis* of Fries has throughout been involved in mystery. In 1849 a short diagnosis appeared in the 'Summa Vegetabilium Scandinaviae,' where it was included under Discomycetes, near Rhytisma, but the description did not determine its affinity:--- 'Perithecium (stroma) crustaceoeffusum, hinc inde tuberculosum, tuberculis in excipula cupularia dehiscentibus;' the presence of asci seems not to have been determined. In 1869 Berkeley included the genus in his Cuban Fungi as an ally of Sphaeropsis, with Fries's original species, there called *Ephelis mexicana*; and in 1875 another species was added from Ceylon as Ephelis brevis, B. & Br. In the Berkeley Herbarium is a specimen from Fries, inscribed by his own hand 'Ephelis typhina, Fries,' from Mexico, and with it the Cuban specimens, there called *Ephelis typhina*, but described by Berkeley under the name of Ephelis mexicana. Undoubtedly all are the same species, and as we do not find any diagnosis of Ephelis typhina, the later name of Ephelis mexicana will stand. These specimens are stylosporous, and correspond with the description in Saccardo's Sylloge, vol. iii. No. 3645, having spores about 25 μ long. Subsequent to the publication of the last-named work, Mr. Phillips 1 has appropriated the genus Ephelis as an ascomycete, although there is no evidence that Fries intended, or suspected, anything of the

¹ Manual of British Discomycetes, p. 358.

[Annals of Botany, Vol. III. No. IX. February 1889.]

kind, notwithstanding his placing it under Discomycetes, any more than he suspected *Leptostroma*. This is another unfortunate illustration of the mistake of appropriating old genera, retaining the name, but amending the diagnosis. *Ephelis Rhinanthi*, of Phillips, therefore is not congeneric with the *Ephelis mexicana* (or *typhina*), Fries, which has its place correctly assigned in Excipulaceae, a family of Sphaeropsideae.

Recently Mr. J. H. Hart of Trinidad sent to the Kew Herbarium some specimens of *Panicum palmifolium*, strangely metamorphosed by a parasitic fungus, which, upon examination, was found to agree entirely with the genus *Ephelis* of Fries, and indeed very nearly with the type species *Ephelis mexicana*. As in other cases of proven dimorphism, the stylosporous form and the ascigerous form have still been retained separately under their respective genera; so in this case, although not autonomous, as will hereafter be seen, the *Ephelis*-form deserves a place beside the other species in that genus, under the name of—

Ephelis trinitensis, Cooke & Massee.

Stroma solido, nigro, effuso, circumambiente, typhoideo; receptaculis pezizoideis, erumpentibus, ellipticis, margine lacerato, hymenio griseo, sporulis filiformibus continuis, rectis vel leniter curvulis, hyalinis ($25-30 \times 1.5 \mu$) basidiis brevibus suffultis. Downloaded from http://aob.oxfordjournals.org/ at New York University on June 27, 2015

On inflorescence of Panicum palmifolium.

Had no further specimens been collected, it would have been assumed that the above was the complete development of this curious fungus, but, fortunately, other specimens were secured afterwards on the same host, and upon the same estate, which carried the history forward much further. Instead of the discoid, cup-like receptacles, exhibited by *Ephelis*, each of them was transformed, or was in the course of a transformation into a depressedly globose capitulum of I to $I\frac{1}{2}$ mm. diameter, raised upon a peduncle two or three times that length; the transformation being brought about by the replacing of the concave surface of the cups by a convex one and the subsequent elevation of this surface on a stalk. This was practically the production of a secondary capitate stroma from the effete discs of the old effused stroma, each one having somewhat the appearance of enlarged specimens of *Claviceps purpurea*, nearly black in colour all over, the stem being squamulose, and the capitulum enclosing immersed membranaceous perithecia, containing asci with long filiform ascospores. No doubt could be entertained that this new form had its affinities in the Hypocreaceae, and was a sort of gregarious *Claviceps* seated upon a continuous effused stroma.

There is very little doubt the fungus in question must be referred to a new genus called Balansia, of which one species only, and that from South America, has been described under the name of Balansia Claviceps, Speg. This genus differs from Claviceps in the capitate stroma, being developed from the effete discs of the *Ephelis*, which were themselves developed from a circumambient stroma of quite a different character from the sclerotioid base of Claviceps. It differs also from Epichloe in the perithecia not being immersed in the ambient stroma, but in secondary capitate stromata which spring from determinate points in the effused stroma. Altogether the structure and history is a complex one, and must be studied from the figures and details hereafter given, when it will be manifest that the species could not have been included either in Claviceps, Epichlöe, or Hypocriella, the nearest allies.

As to the species itself, it differs in such important particulars from *Balansia Claviceps*, Speg., that we do not think it could be maintained as a mere variety of that species. The following is a technical description :---

Balansia trinitensis, Cooke & Massee.

Stromatibus globulosis, subtus impressis $(1-1\frac{1}{2} \text{ mm. diam.})$, duris, atris, extus papillatis. Stipite erecto, squamuloso $(2-4 \text{ mm. long, } \frac{1}{2} \text{ mm. crass.})$, atris. Peritheciis in stromatum capitulis periphericis, constipatis, obovatis, ostiolo exiguo perforato, Ascis cylindraceis, basi attenuatis $(120-130 \times 9-10 \mu)$, octosporis, sporidiis filiformibus, continuis, flexuosis, hyalinis (90–100 x $1\frac{1}{2}\mu$). Stroma conidiifera = Ephelis trinitensis, Cooke & Massee.

On inflorescence of *Panicum palmifolium*, from Trinidad. Com. J. H. Hart.

The above will be seen to differ from *Balansia Claviceps*, Speg., as described by Saccardo¹, in the following points :--

1. In its development from the effete discs of a species of *Ephelis*, of which it appears to be the ultimate and ascigerous condition.

2. In the stems of the capitate stromata being distinctly squamulose; and

3. In the smaller size of the asci and ascospores.

Externally there is very little difference in the appearance of the two species, and in the manner in which the spikes of the grass are deformed; but the association of the ascigerous fungus in such an intimate manner with an *Ephelis*, seems to warrant either the description of a new species, or the modification of the diagnosis of the previous one to an extent which could certainly not be justified without the consent of the author. M. C. COOKE.

MORPHOLOGY.

The inflorescence of *Panicum palmifolium* is a loose panicle from 14-18 cm. long, and when attacked by the fungus is converted into a rigid, black, simple spike, about 4 mm. thick (Fig. 1); sometimes one or two of the lower branches remain free, although attacked by the fungus (Fig. 1 a, a). Owing to the material arriving in a dried condition, and for the most part fully developed, but little can be ascertained respecting the earliest stages of development. The stroma of the fungus is formed while the inflorescence is yet surrounded by the leaf-sheath, with its branches closely appressed to the main axis, and in all probability the young flowers are first attacked, from which the hyphae extend in all directions, and form a continuous felt-like sheath enclosing the branches and main axis of the inflorescence, a transverse section presenting the appearance of a stem with scattered vascular

¹ Sylloge Additamenta, p. 220.

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bundles (Fig. 3). The stroma consists of a compact, colourless, uniform, pseudo-parenchymatous tissue, surrounded by a blackish rind or cortex. The hyphae of the central portion are frequently branched, aseptate, or with only an occasional septum, thick-walled, and with small lumina, and as they pass to the outside to form the cortex become thin-walled, dark-coloured, and furnished with numerous septa. The greater part of the surface of the cortex is smooth, but here and there some of the dark cortical cells continue to elongate beyond the general surface, and form velvety patches (Fig. 3, c). It is remarkable how comparatively few hyphae are to be met with in the tissues of the main axis or branches of the host, there being no displacement of cells or general disintegration of the cell-walls; even the hairs on the surface remaining intact (Figs. 4, d and 5, d). The hyphae pierce the walls of the cells, and sometimes give off short, inflated branches, which probably act as organs of absorption (Fig. 4, c). The earliest external evidence of the *Ephelis* or gonidial stage of reproduction is indicated by the presence of numerous minute elevations scattered somewhat uniformly at short distances over the hitherto even surface of the stroma. A vertical section through one of the pustules at this stage shows the hyphae of the colourless portion of the stroma immediately below the cortex to be arranged more or less parallel and vertical to the surface for a depth of $20-30 \mu$. This mass of differentiated hyphae, which is biconvex in vertical section, continues to increase in size on the side next the cortex until the latter is eventually ruptured, forming an elliptical or irregularly circular opening from 1-2 mm. across. The margin of the ruptured cortex is raised in the form of a border surrounding the central exposed portion, and presents under a low power a fringed appearance, due to the component hyphae of the cortex becoming separated by the pressure from below, and standing erect round the torn margin (Figs. 5 and 8). The parallel hyphae forming the disc of the cavity consist at first of aseptate branched filaments, the apices of which are eventually abscised as continuous, filiform, colourless gonidia, measuring from 25-30 \times 1.5 μ (Fig. 6). These gonidia under a magnifying power of 400 diameters present an appearance which might be mistaken for septation, but when more highly magnified is seen to be due to the presence of a single row of vacuoles There appears to be a considerable interval of (Fig. 7). time between the full development of the gonidia and the ascigerous condition which follows. The specimens collected by Balansa¹, from which the genus was established by Spegazzini², illustrate the ascigerous condition; hence the generic character is imperfect, inasmuch as the *Ephelis* stage is not mentioned. In the specimens sent from Trinidad by Mr. Hart, the two conditions are present. The secondary ascigerous stroma not unfrequently originates immediately below an old empty gonidial cavity, through which it bursts, and remains until the spores are mature as a sessile, sphericodepressed swelling, surrounded by the raised margin of the Ephelis (Fig. 9). When the ascigerous structure does not occupy an old gonidial cavity the earliest external indication of its existence is a swelling of the primary stroma, the cortex being eventually ruptured by the growth of the ascigerous stroma, round which it forms a raised pilose border exactly as in the gonidial condition. In some spikes nearly every ascigerous stroma occupies a gonidial cavity, whereas in others there is no evidence of the *Ephelis* stage having existed, the ascigerous condition bursting directly through the cortex of the primary stroma; in others, again, both modes of origin of the ascigerous stage are present.

The ascophore originates at some distance below the primary cortex as a spherical weft of intricately interlaced hyphae (Fig. 15), that appear to become directly differentiated on the side towards the cortex into the spherico-depressed head of the ascophore, which is umbilicate below, and furnished with a very short stem-like base, sunk in the umbilicus. The

¹ B. Balansa, Pl. du Paraguay, n. 253.

² Speg., Fung. Guaranit., Pug. I, n. 253; also in Sacc., Syll. Fung. Additamenta to Vols. I-IV, n. 7249.

hyphae forming the stem run mostly parallel in the direction of its length, are thick-walled, sparsely septate, and on entering the head diverge in a radiating manner towards the circumference, where they increase in thickness, are furnished with numerous septa, and form the cortex, which eventually becomes black (Fig. 16). The structure of the ascophore is at first uniform, and smooth externally; but before it bursts through the primary cortex a number of minute differentiated spherical coils of hyphae or primordia are formed at a short distance below the cortex. These primordia, the minute structure of which could not be determined from dried material, are the starting-points of perithecia, which, when mature are flask-shaped, with an elongated neck, opening by a definitely formed ostiolum through the blackened cortex, which is raised as a papilla; hence the surface of the mature ascophore is warted (Fig. 10). When mature the perithecia consist of a thin wall composed of very slender interwoven hyphae, sharply differentiated from the stroma in which they are imbedded, and filled with cylindrico-clavate asci measuring 120–130 x 10–12 μ (Fig. 12), each containing eight filiform, colourless, continuous sporidia $90-100 \times 1.5 \mu$ (Fig. 13). The stem of the ascophore remains rudimentary until the perithecia are completely formed, when it elongates until it reaches a length varying in different individuals from 3-4 mm. During the increase in length the axial portion grows at a greater rate than the peripheral, in consequence the cortical hyphae are ruptured, the free tips spreading and giving the stem a minutely scaly appearance (Fig. 10). The general structure of the ascigerous stroma agrees closely with that of *Claviceps purpurea*, as described and figured by Tulasne¹; but in the latter the gonidial mode of reproduction differs considerably from what occurs in the plant under consideration.

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¹ Mémoire sur l'Ergot des Glumacées, in Ann. Sci. Nat., sér. 3, vol. xx. p. 5, Pl. 1-4. Figures reproduced by De Bary in Biol. of Fungi, Mycetozoa and Bacteria (Engl. ed.), Fig. 108.

EXPLANATION OF FIGURES IN PLATE IV.

Illustrating Dr. Cooke's and Mr. Massee's paper on a new development of Ephelis.

Fig. 1. An inflorescence of *Panicum palmifolium* infested with *Balansia trinitensis.* a, basal branches of the inflorescence infested with the fungus, but not adpressed to the main axis; the greater part of the fungus is in the early ascigerous condition; at b, the stem of the ascophore is becoming elongated. Nat. size.

Fig. 2. Portion of a spike with the ascosporous condition of the fungus fully developed. Nat. size.

Fig. 3. Transverse section of a diseased inflorescence. a, rachis of inflorescence. b, a branch of the inflorescence. c, stroma of fungus. d, cortex or rind of stroma. \times 80.

Fig. 4. Transverse section through part of a diseased inflorescence. a, portion of branch. b, stroma of fungus. c, c, hyphae with lateral swollen branches. d, a hair on the branch. \times 400.

Fig. 5. Vertical section through a gonidial disc (*Ephelis trinitensis*). a, gonidia. b, coloured hyphae forming fringed margin bordering the *Ephelis*. c, portion of a branch of the inflorescence. d, hair from epidermis of branch. \times 400.

Fig. 6. Isolated gonidiophores. a, supporting gonidia. b, belonging to gonidial or *Ephelis*-stage of reproduction. \times 400.

Fig. 7. Gonidia. x 1000.

Fig. 8. Gonidial or *Ephelis*-stage of reproduction. × 75.

Fig. 9. Young and yet sessile ascophore seen from above. \times 75.

Fig. 10. Group of mature ascophores springing from gonidial cavities, a, a. \times 75.

Fig. 11. Vertical section through an ascophore. a, capitate stroma with perithecia. b, persistent gonidiophores of the gonidial disc. c, remains of the primordium. \times 400.

Fig. 12. Asci. x 400.

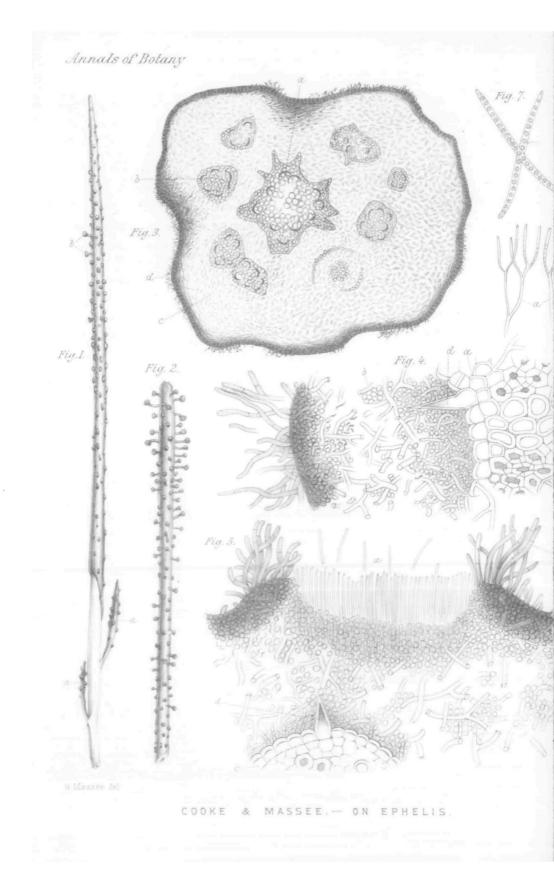
Fig. 13. Ascospores. × 400.

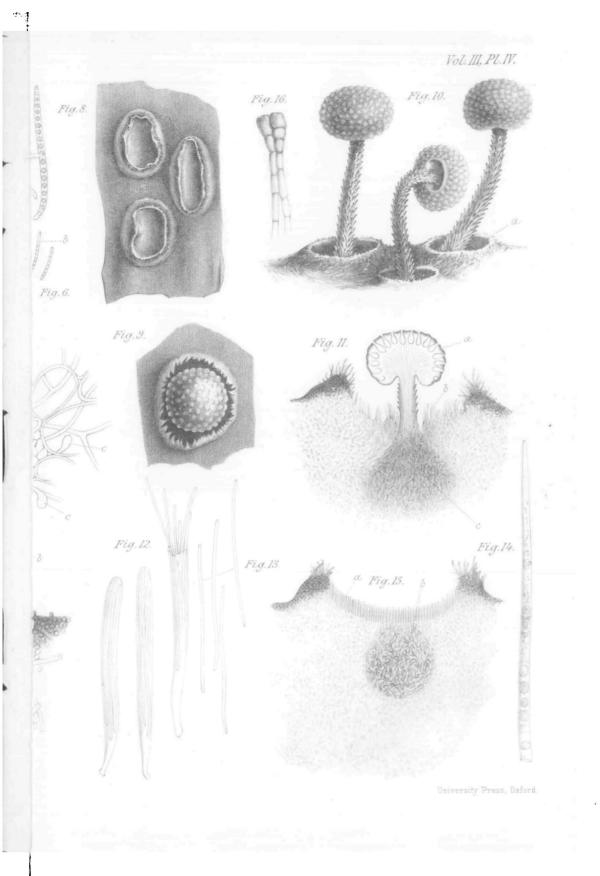
Fig. 14. Portion of an ascospore, showing the protoplasm broken up into separate pieces, which produces the appearance of septation under a power of 400 diam. \times 1000.

Fig. 15. Vertical section through the primary stroma passing through an old gonidial disc with the permanent gonidiophore, a. b, young primordium of an ascophore. \times 400.

Fig. 16. Hyphae from the capitate stroma of an ascophore which become thickened, closely septate, and brown towards the exterior. \times 400.

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