STUDIES IN THE BRITISH *EPIPACTIS*
V. *EPIPACTIS LEPTOCHILA*; WITH SOME NOTES ON *E. DUNENSIS* AND *E. MUELLERI*

By DONALD P. YOUNG

ABSTRACT

Records for *Epipactis leptochila* (*Godf.*) Godf., *sensu stricto*, are enumerated. In England it is confined to calcareous areas in the south, where it is frequent on the Chilterns and Cotswolds. It also occurs in France, Germany, Denmark and Switzerland. The plant is strongly calcicolous, and its usual habitat is in beech-woods with an open ground-flora and in heavy shade. Some variation in floral morphology occurs in this species. Godfery's type, in particular, has the column and lip much more elongated than in the bulk of specimens. A freak plant from Germany had a column like that of *E. muelleri*, implying that such a column-form can arise by mutation. An achlorophyllose plant has also been seen. The equation of *E media sensu* Bab. non Fr. with *E. leptochila* was based on false premises.

E. cleistogama C. Thomas may be a form or state of the last species.

E. dunensis (T. & T. A. Steph.) Godf. is only known from five British vice-counties; Continental records cannot be substantiated.

E. muelleri Godf. is known from France, Switzerland, the Benelux countries and Germany. It is a plant of lightly shaded habitats, and is closely related to *E. dunensis*.

As originally conceived (Godfery 1921b; Stephenson & Stephenson 1921b), *Epipactis leptochila* (Godf.) Godf. included all the then known self-fertilised forms except *E. muelleri* Godf., which was distinguished by a different fertilisation mechanism. The separation from it of *E. dunensis* (Godfery 1926) and later of *E. vectensis* (Brooke & Rose 1940; now called *E. phyllanthes* G.E.Sm.) has left the residual *E. leptochila* as a much better-defined entity. Now that the somewhat confused records for these species have been sorted out, it is possible to reappraise the distribution, ecology, and morphological variation of *E. leptochila, sensu stricto*.

DISTRIBUTION

In Britain, *E. leptochila* is frequent on the escarpments of the Chilterns and Cotswolds. Elsewhere it is uncommon, in scattered localities along the chalk range from Wiltshire to Kent; on the Carboniferous Limestone of the Wye Valley and Cheddar; and in one or two localities in Devon. On the Continent, it is in rather widely separated localities from Denmark to the Swiss Jura; its distribution is very incompletely known, and its eastern limit is uncertain (Fig. 1). I have seen the colonies marked ! *in situ*.

British Records

V.c. 3. S. DEVON : Dunsford and Cornwood (Martin & Fraser 1939) (**TOR**; the specimen from the first locality is now too worm-eaten to confirm, but the second is correct).

6. N. SOMERSET : ash-whitebeam scrub, Cheddar Gorge, 1957, *J. T. H. Knight* (**K**).

8. S. WILTS.: beech-wood on chalk, Winterslow, 1957, *A. Roseweir*! (**K**).

11. S. HANTS.: beech-woods on chalk, Hursley, 1954 (**K**, herb. Young), and W. Tytherley, 1956, *A. Roseweir*! (**K**). These are the first two authentic records for Hants; all previous ones are referable to *E. phyllanthes*.

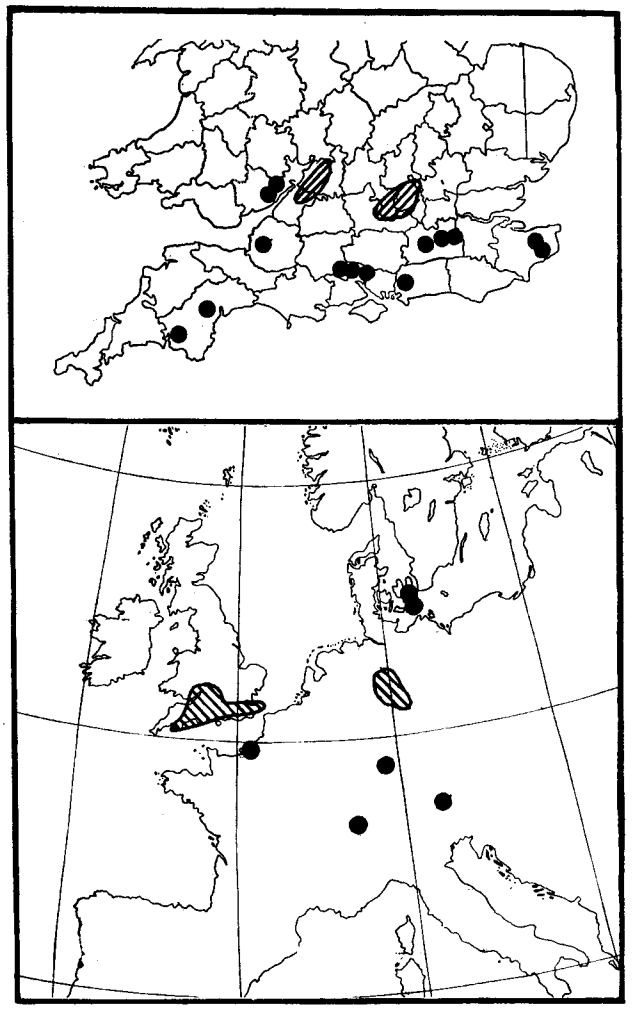

Fig. 1. Known distribution of *Epipactis leptochila.*

13. W. SUSSEX: wood on chalk, Treyford, 1960 *Miss D. W. Fawdry*, conf. *V. S. Summerhayes* who had found a doubtful specimen at the same spot 12 years previously. Earlier records refer to *E. phyllanthes.*
15. E. KENT : ash-hazel coppices on chalk, Kingston! (Brooke & Rose 1940) and Womenswold, 1955, *B. J. Brooke, R. Gorer & F. Rose.*
17. SURREY : beech-woods, W. Horsley (type locality), and E. Horsley, *F. Rose*; beech-yew wood, Woldingham, long known and still extant; Kingswood Valley, 1924 (Salmon 1931), not seen recently. All are on chalk.
20. HERTS.: beech-wood on chalk, Tring, 1943, *H. W. Pugsley* (**BM**), 1953! (**K**, herb. Young).
22. BERKS.: frequent on chalk between Streatley and Pangbourne. Bisham, 1925, *C. B. Tahourdin* (**SLBI**).
23. OXFORD : frequent on the chalk.
24. BUCKS.: frequent on chalk above the Thames between Hambleden and Marlow, and for about 5 miles northwards; thence in scattered localities as far as Chequers.
33. E. GLOS.: frequent on the Cotswold escarpment and valleys from Stroud to Cheltenham, thence apparently less frequent as far as the Worcs. border, and eastwards as far as Guiting (cf. Riddelsdell, Hedley, & Price 1948).

34. W. GLOS.: frequent on the Cotswolds from Stroud to Wotton-under-Edge. Madgett (Wye Valley), 1933, *J. E. Lousley* (herb. Lousley).
35. MONMOUTH : between Tintern and Wyndcliff, 1920, *C. E. Salmon* (BM).

Records for the following vice-counties are either erroneous or based on insufficient evidence, or else refer to segregates now made separate species:

V.C. 9. Three records are given in the *Dorset Flora* (Good 1948). Of these, one (Badbury) is not supported by specimens, and the other two prove to be of *E. helleborine* (specimens in herb. Good).

V.C. 10, 12 : Published records all refer to *E. phyllanthes.*

V.C. 14 : Wolley-Dod's tentative record from Saxonbury Hill (cf. Wolley-Dod 1937) has never been confirmed, and it appears that *E. purpurata* was mistaken for it. The locality is an oak-wood on sandstone, and seems now to be an unlikely habitat for *E. leptochila.*

V.C. 30 : An erroneous record has been withdrawn (Dony 1953).

V.C. 40 : The record by Godfery (1919) from Bomere Pool was based on a single admittedly poor specimen, said to be of 'the only *Epipactis* in sight' there. This specimen is not now extant, nor has the record ever been confirmed. Independent searches of the woods around Bomere Pool by Miss E. P. A. Jones and myself brought to light only *E. helleborine*, in a somewhat small-leaved form that might simulate *E. leptochila* if in poor condition. A specimen of *E. helleborine* collected there by Leighton in 1835 is in herb. **BM.** These woods are on sandstone, and vary from very dry to marshy, but seem unlikely to support *E. leptochila.*

V.C. 51 : The record refers to *E. phyllanthes.*

V.C. 52, 59, and 60 : The records refer to *E. dunensis.*

V.C. 66 in the *Comital Flora* was a misprint for 60, but has been repeated by copyists.

European Records

FRANCE

Seine-Mme.: beech-forests on chalk in two places, Forêt d'Eu, 1959, *B.S.B.I. field meeting*! (herb. Young).

GERMANY

Lr. Saxony : on calcareous soils in the neighbourhood of Stadtoldendorf and Hildesheim (Krösche 1929); beech-forests on Jurassic Limestone, S.E. of Hildesheim and Osterwald W. of Elze! on chalk, Sieben Berge E. of Alfeld! on Muschelkalk, Holzberg S. of Stadtoldendorf! (herb. Young).

Württemberg : beech-forests on Jurassic Limestone around Urach, 1953, F. Rose! (Herb. Young).

Sachsen-Anhalt : " in sylvis mont. calc. umbrosis," Alte Stolberg, 1885, Vocke (**UPS**).

DENMARK

On chalk, Møns Klint and near Hesnæs (Falster) (Young 1953).

SWITZERLAND

Berne : fir-beech forests on Jurassic Limestone near Tavannes (Young & Renz 1958) (herb. Young, herb. Renz)

AUSTRIA

Ost-Tirol : mixed woods on limestone, Matrei, 1961, *C. D. Sayers* (K).

The record from Bomere Pool raises a point of synonymy. Bomere Pool is the *locus classicus* for *Epipactis media, sensu* Babington, and on this basis Godfery (1919; 1933, p. 75) regarded *E. media* Bab. non Fr. as a synonym of *E. leptochila*, at least in part. Since *E. leptochila* does not in fact grow there, and *E. helleborine* certainly does, this synonymy cannot be upheld. The question of what Babington intended by *E. media* has been discussed by Stephenson and Stephenson (1921a), and there is little to add to their remarks, except to note Babington's revealing statement (1852), ' The true *E. latifolia* is a much less frequent plant in this country than my *E. media*, which is often mistaken for it by British botanists.'

ECOLOGY

The most striking feature that emerges is that the plant is strongly calcicolous – much more strictly so than any other European *Epipactis.* Every station for which geological

data is available is on calcareous rock, and this comprises the great bulk of records. It is also noticeable that it occurs particularly on steep slopes where the calcareous rock is free from overlying drift. Conversely, no station has been recorded as on neutral or acid soils (the Devonshire records ought to be reinvestigated with this in mind).

Tree cover is usually beech, occasionally admixed with yew or fir. At Cheddar it is under heavily-shading scrub, and in Kent it is in ash-hazel coppices. The species usually affects heavy shade, and soon disappears if the trees are cleared. It is normally associated with a low and very open ground-flora. In a typical locality on the Cotswolds, the principal associated species were *Fragaria vesca*, *Sanicula*, *Viola riviniana*, *Bromus ramosus*, *Hedera*, *Hieracium* sp., *Epipactis helleborine*, *Cephalanthera damasonium*, *Neottia nidus-avis*, and *Pyrola minor*.

In this country, *E. leptochila* can be found in good quantity in most stations, and hundreds of plants may occur in a square km. of woodland. The reverse seems to be the case in Germany, where it is very unusual to find more than half-a-dozen plants together. This seems to be the consequence of the rather different nature of central European beech forests, where beech regenerates freely. They are subjected to regular attention of foresters engaged in trimming, thinning, and felling. This leads to a cycle of disturbance of the shade cover, alternating with the growth of a shrub layer of beech (and ash) seedlings, *Rubus idaeus*, etc. The places most productive of *Epipactis* spp. are forests of young trees which have not reached the reproductive stage, and which shelter a ground flora which is quite open or almost absent. In suitable places in the Schwäbische Alb around Urach, *E. leptochila* is associated with *E. helleborine*, *E. atrorubens*, *Cardamine bulbifera*, *Lathyrus vernus*, *Cephalanthera damasonium*, *C. rubra*, and *Epipogium aphyllum*. At the other end of its range, at Møns Klint in Denmark, *E. leptochila* is again associated with *E. atrorubens*, but in Britain their ecological requirements have diverged and the two are confined to quite different areas. *Cephalanthera rubra* is, in all its known stations in this country, in areas where *E. leptochila* is frequent. *Epipogium* is also associated with *E. leptochila* in the Chilterns, and *Cardamine bulbifera* is frequent in the same area, but the association is not invariable because neither of these is strictly calcicole.

E. leptochila is one of the earliest species in the genus to flower. In a normal English summer it starts in mid-July and continues for 3-4 weeks, thus being about 3 weeks ahead of *E. helleborine*. On the Continent it is later, commencing in early August, still ahead of *E. helleborine* but later than *E. atrorubens*.

VARIATION

Like other species of the genus, *E. leptochila* shows considerable and sometimes puzzling variability. Variation in size and number of flowers is dependent on the age and state of nourishment of the plant, and has no other significance. There is a moderate range of leaf-size, from 6·0 × 2·5 to 10·0 × 4·5 cm. for the largest leaf of mature plants; the length/breadth ratio is fairly constant, but narrower leaves (to 8·5 × 1·5 cm.) do occur

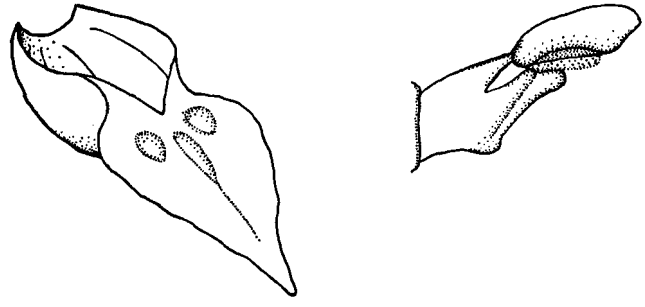

Fig. 2. Labellum and column of *Epipactis leptochila* (v.c. 33 : Cranham Woods). × 5.

occasionally. The floral architecture shows some variability, mainly in the breadth of the labellum and the shape of the column. Perhaps the only definable characters of the species (apart from absence of rostellum) are that the epichile is acute and at least as long as broad, and that the column has a well-marked clinandrium. Characteristic, but not invariable, features are that the epichile is usually very noticeably longer than broad, acuminate, and prolonged at the base into broad wings decurrent on the hypochile, giving the epichile a sagittate shape; and that the prominence on the column that bears the anther is prolonged forward, sometimes so much so as to form a short broad filament (Fig. 2). It is unfortunate that Godfery's type, represented by a population at West Horsley, is an unusual and extreme variant having a long narrow epichile and a longly stipitate anther, well shown in his illustrations (Godfery 1920, pl. 553 fig. 1, and 1933, pl. K fig. 1). *E. leptochila* var. *cordata* Brooke (1950), which perhaps represents the other extreme, is described as having a cordate and broadly acuminate epichile. Unfortunately the colony on which this was based has disappeared, and no specimens or illustrations survive. An elaborate catalogue of variations has been given by Krösche (1930, 1932, 1936). The value of this compilation is more than doubtful, since it includes, uncritically, both normal and teratological variants, and is overshadowed by attempts to force them into a taxonomic framework. The West Horsley population is the only one known to me where the distinct characters of the population are obvious, but genotypic differentiation between populations is to be expected and could probably be demonstrated biometrically.

Two abnormal plants seen in recent years deserve mention. The first was from a scattered population in the Sieben Berge (Germany) showing rather considerable variation in floral architecture. In one plant the column, in every flower, had no clinandrium, so that the pollinia overhung the stigma exactly as in *E. muelleri*. This variant does not appear anywhere in Krösche's papers, but on his arrangement it would fall within *E. muelleri* – where, from the shape of the labellum, tepal size, and other characters, it certainly did not belong. Assuming that the absence of clinandrium was genotypic – and there is no reason for supposing otherwise – then the occurrence of this form amongst an otherwise normal population implies that it had arisen by mutation. Hence the similar column-shape of *E. muelleri* could conceivably have arisen from a single mutation, rather than by gradual evolution.

The other noteworthy freak was a single achlorophyllose plant found in Hampshire (v.c. 11) by Mr. A. Roseweir in 1954, amongst a large and otherwise normal population. This plant reappeared yearly up to 1957. Despite its deficiency in chlorophyll, and also despite being picked (by persons unknown) on two occasions before reaching anthesis, it kept all the vigour of a normal plant. Its cells were probably not completely without chlorophyll, since the stems and flowers were lemon-yellow and the leaves a pale greenish-yellow. [Coloured photographs of this were taken by Mr. D. E. Kimmins, and a copy has been deposited in the British Museum (Natural History)]. Achlorophyllose plants have been reported in other species of *Epipactis* and in *Cephalanthera*. The phenomenon has recently been discussed by Burgeff (1959), who regards it as demonstrating that the plants can live entirely saprophytically with the aid of the symbiotic fungus. No other explanation appears possible, although objections have been raised in the past to this idea; not the least of these is that the roots are often well below the humus layer which supplies saprophytic nourishment. Burgeff suggests that nourishment can be transmitted for some distance through the fungal hyphae; it would be desirable to have more direct evidence on this.

The hypochile of *E. leptochila* usually contains nectar, which is sweetish to the taste but does not seem to attract insects. In other autogamous species the hypochile is always quite dry inside.

E. CLEISTOGAMA C. THOMAS

This taxon has been distinguished from *E. leptochila* by the different fertilisation mechanism : instead of the pollinia falling bodily on to the stigma in the opened flower,

in *E. cleistogama* the flowers do not open, and friable pollen is scattered in the bud stage (Thomas 1948). On gross morphology there seems to be no significant difference between the two; the distinctive features ascribed to *E. cleistogama*, such as robust habit, are within the range of *E. leptochila*. The plant has, moreover, apparently vanished from its former stations (where *E. leptochila* still occurs). If it reappears, it would be desirable to watch marked plants for several seasons to see whether they are constantly cleistogamous. For the present, it seems best to regard it as a form or state of *E. leptochila*. According to Krösche (1929, 1932, 1936), all German forms of *E. leptochila* shed friable pollen in the bud, but complete cleistogamy has not been noted in German examples.

E. DUNENSIS (T. & T. A. STEPH.) GODF.

The known distribution of *E. dunensis* in Britain is as follows :

V.C. 52. ANGLESEY : Newborough Warren, well-known.
59. S. LANCS.: Hall Rd. to Southport, well-known.
60. W. LANCS.: Lytham, 1873, *E. F. Linton* (CGE)—probably other records exist, but plant not seen recently.
68. CHEVIOTLAND : Holy I., 1958, *A. J. Smith*! (E).
69b. N. LANCS.: Roanhead-Sandscale dunes, 1952, *G. Wilson* (K).

The following records for *E. dunensis* on the Continent have been published, but in no case do any specimens exist :

FRANCE : Coutainville (Manche) (Meslin 1928).
BELGIUM : Nieuport-Bains and (?) le Coq-sur-Mer (Godfery 1933, p. 78).
GERMANY : coast opposite Usedom (Pomerania) (Godfery 1933, p. 78).

I have visited the alleged localities in France and Belgium, and have found no *E. dunensis* nor ground apparently suitable for it. At Coutainville and also a few miles north of it, there is a little of a dwarf dunal form of *E. helleborine*. Meslin's description and figure could well refer to this. The plant he depicts has internodes shorter than the leaves, and a very flexuous stem, which point to *E. helleborine* rather than to *E. dunensis*. He speaks of the rostellum being evanescent in the freshly-opened flower; in exposed situations this does in fact occur with *E. helleborine*. In *E. dunensis* the rostellum disappears in the early bud stage. (A further diagnostic difference is the usual dull purple suffusion of the flowers of *E. helleborine*, whereas *E. dunensis* has pale green tepals and the lip marked with

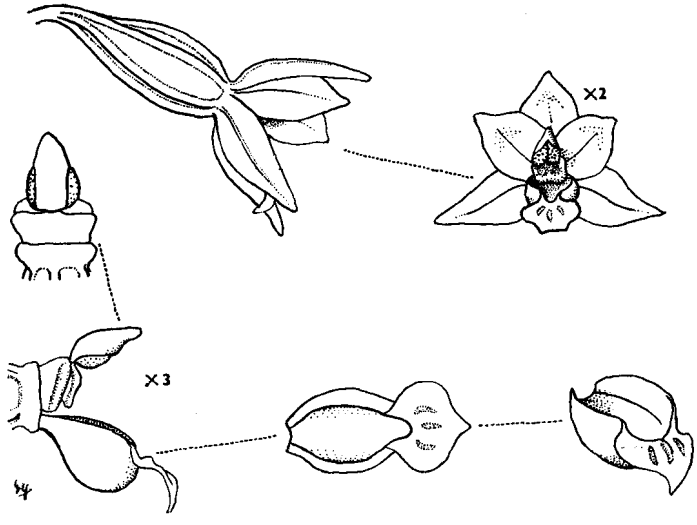

Fig. 3. Dissections of flower of *Epipactis muelleri* (France : Thorenc). The items are from different flowers, and show minor differences of shape and size.

rose-pink). Several specimens from coastal localities in Belgium in the herbarium of the Brussels botanic garden (**BR**), labelled *E. dunensis*, are either *E. helleborine* or *E. palustris*. The Belgian coastal dunes have suffered much in recent years from building and desiccation. Nannfeldt (1946, p. 5 footnote) similarly doubts the Pomeranian record, after examination of much herbarium material from that area.

The evidence for the occurrence of *E. dunensis* on the Continent is thus unsatisfactory, and we may claim it as a British endemic. However, suitable habitats for it do exist on the French and Dutch coasts, and it would be worth searching for there. It is curious that the common dunal species of the Channel and North Sea coasts of the Continent is *E. helleborine*, whereas in Britain this is extremely rare in dunes – Kenfig is the only such station certainly known to me.

E. MUELLERI GODF.

This species is not British, but it is appropriate to summarise present knowledge of it in relation to our own species. Detailed descriptions have been given by Godfery (1921a), Zimmermann (1922, as *Parapactis epipactoides*), and Krösche (1934), and recently an excellent one, illustrated, by Reichling (1955). Some diagrams of the dissected flower are given here (Fig. 3). Throughout its range it varies but little. Characteristic recognition features are the slender habit and narrow undulate leaves. The column is constantly as described by Godfery and other authors, with virtually no clinandrium, i.e. the anther is attached almost directly above the stigma and the pollinia overhang the latter. The anther has, usually, a hooked empty tip which may be clearly visible in soaked-out herbarium specimens. The labellum only varies to the extent that it may be cordate or rhomboid, but it is always short, broader than long, and obtuse. The flowers are smaller than those of *E. leptochila*.

E. muelleri is very closely related to *E. dunensis*, which it resembles in vegetative parts and in flower size, structure (except the column), and colour. The roots are thicker ($2{\cdot}24 \pm 0{\cdot}54$ mm., against $1{\cdot}48 \pm 0{\cdot}28$), but this could be the result of different habit

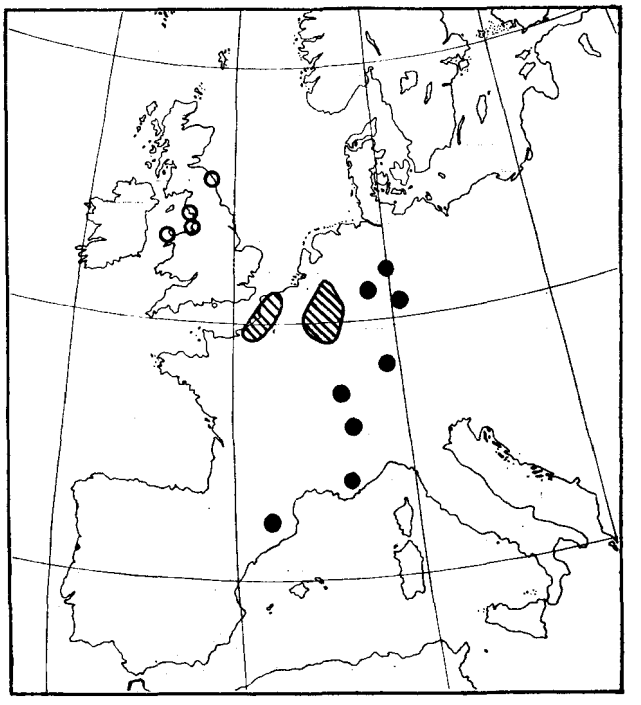

Fig. 4. Known distribution of *Epipactis muelleri* (black circles and shading) and of *E. dunensis* (open circles)

(see Part VII, p. 140). The ecological requirements of the two species are somewhat similar, except that *E. dunensis* is entirely maritime and *E. muelleri* entirely inland.

The autecology of *E. muelleri* has been discussed by Reichling (1955). It is a thermophile, affecting open woods and forest borders and clearings, often amongst grass. It is calcicole, but not so strongly so as *E. leptochila*. The ecology of the latter, which favours cool, heavily shaded situations, is in strong contrast.

The authenticated distribution of *E. muelleri* is as follows, although it must be very incompletely known (see also Fig. 4).

FRANCE

Pas-de-Calais : Desvres, 1959, *B.S.B.I. field meeting*!
Somme : Cambron, 1959, *idem*!
Seine-Mme.: near Hodeng, 1959, *idem*! (L, herb. Young); near Bazinval, 1960, *M. de Blangermont & J. Liger* (Herb. Young).
Hte. Saône : N. of Champlitte, 1959, *B. J. Brooke & R. Gorer* (Herb. Young).
Alpes-Mme.: Thorenc! (K, herb. Young; *locus typicus*).
Pyr. Or.: Bourgmadame, 1926, *Sennen* (Pl. d'Esp., 5883) (LD).

SWITZERLAND

Valais : near Vallorbe, 1955, *C. Sipkes* (L, herb. Young).

BELGIUM

District Calcaire Moisan, in several places (Young 1958).

LUXEMBURG

Frequent! (Reichling 1955).

HOLLAND

Limburg : near Maastricht, 1945, *H. W. E. Croockewit* (herb. Vermeulen).

GERMANY

Rheinland : Driburg (Müller 1868, p. 7; the classical description) : Echternachterbrück, 1908, *J. Groves* (BM); near Münstereifel, 1927–8, *H. Höppner* (Orchid. exsicc. VI, 137 & 76) (LD).
Lr. Saxony : Hildesheim region and near Stadtoldenorf (Krösche 1934).
Württemberg : Tuttlingen, Würmlingen (Zimmermann 1922).
Thüringen : near Sondershausen, 1885, *F. Heinmann* (UPS).

Other records are given by Godfery, Zimmermann, Soó, etc., but without seeing specimens or precise descriptions I defer acceptance of them. Further search is needed to determine its distribution more precisely.

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