

Phaeoceros sex forms in the BBS herbarium

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Introduction

Taxonomic treatment of the Anthocerotales (hornworts) has a history of instability and revision. The group as a whole exhibits rather limited morphological variation on which to base taxonomic division, and this presents a particular challenge in defining valid species and infraspecific taxa. Schuster (1992) reviews the nomenclatural background in detail.

Within the yellow-spored genus *Phaeoceros*, two taxa are known from Britain and Ireland. They are currently treated as separate species following Paton (1999) and Grolle & Long (2000). Most records are of the dioicous *P. laevis*, which has a world distribution almost restricted to the Mediterranean-Atlantic zone of Europe with only isolated reports from elsewhere (Hasegawa, 1991). It was only relatively recently that Paton (1973) drew attention to the occurrence in southern Britain of the monoicous taxon *P. carolinianus* (see Figure 1), which has a more or less cosmopolitan range. As Paton (1973, 1999) has pointed out, it seems probable that *P. carolinianus* has a wider British distribution than 20th century records suggest. It is also worth noting that Macvicar (1926) described *Anthoceros* (*Phaeoceros*) *laevis* as monoicous, but he did not provide any critical observations on sex forms.

Although *P. laevis* and *P. carolinianus* are now recognised as separate species in the British Isles, they were previously treated as subspecies.

Proskauer (1958) adopted the latter position following a wide-ranging comparative assessment of monoicous and dioicous forms.

Distinction between *Phaeoceros laevis* and *P. carolinianus*



Figure 1. *Phaeoceros carolinianus* at South Tipp, Monmouthshire. Male and female plants are growing over each other, with dense antheridial pits on the male plant and an unpitted surface to the female plant. Photo: Sam Bosanquet.

Sex distribution provides the only practical separation of the two *Phaeoceros* species for the field bryologist. Antheridia occur in small groups within cavities and, when reaching maturity, are clearly visible on the dorsal surface of the thallus; following a phase of antheridial maturation perforate zones may develop on thalli with abundant empty cavities. Archegonia

also form small groups sunken within the thallus but are comparatively difficult to observe from above when immature or unfertilised. Following successful fertilisation, sporophyte development takes place, and is associated with a protective involucre of gametophyte tissue.

Potential difficulties in sexing thalli may arise for various reasons. Firstly, due to protandry, where developing monoicous thalli may have an initial stage with only antheridia evident. Secondly, immature archegonia may be easily overlooked. Thirdly, empty antheridial pits may not be recognised. Fourthly, and perhaps most deceptively, it has often been observed that the abundance of sex organs, especially antheridia, can be highly variable; in some cases bisexual thalli have frequent sporophytes but very few antheridial cavities, which can be readily overlooked.

Hässel de Menéndez (1987) found subtle but distinctive differences between *P. laevis* and *P. carolinianus* in spore ornamentation revealed by scanning electron microscopy. Further observations are required to determine if such features remain constant over the geographical range of the taxa. Paton (1999) found that pseudo-elaters tend to be shorter in *P. carolinianus* than in *P. laevis*, but more extensive data for this character are necessary to assess its taxonomic value.

Recent observations in the field by the second author of this paper suggest that there may be differences between the taxa in the size of thalli and the distribution of gametangia. Colonies of *P. laevis* in tillage fields in eastern Ireland were found to be composed of small male thalli, which were almost completely covered with antheridial pits on their dorsal surface, and much larger female thalli, often with abundant archegonia. In contrast, plants of *P. carolinianus* in Monmouthshire had a few antheridial pits and a few archegonia scattered and intermixed across medium-sized or large thalli. Further investigation is needed to ascertain whether

these differences between the taxa are consistent.

We have not seen any specimens that have dense antheridial pits in the centre of the thallus, surrounded by archegonia, and it is probably safe to refer abundantly male plants to *P. laevis*. Non-fertile plants, small thalli with scattered antheridia (which may be protandrous *P. carolinianus*), and small plants with a few archegonia are probably best left unidentified.

Ecology

Both taxa are usually recorded from moist soil in a limited range of open and often disturbed habitats. Paton (1999) noted that in Britain and Ireland *P. laevis* behaves as an annual in temporary habitats but may be longer lived in more permanent sites, whereas *P. carolinianus* appears to be more restricted to arable fields and other temporary habitats. She also observed that sporophytes may be present in *P. laevis* at any time of year, while they develop between September and December in *P. carolinianus*, which functions as a summer annual. In some cases, perennation in *P. laevis* may be facilitated through the formation of tubers on the margins and ventral surface of the thalli.

Phaeoceros spores are known to remain viable for over ten years (Proskauer, 1958), and their presence in the diaspore bank may be crucial for long-term persistence in cultivated habitats (Bisang, 1995).

Phaeoceros taxa in the BBS herbarium (BBSUK)

The current interest in cropland bryophytes promoted by the BBS Survey of the Bryophytes of Arable Land has already revealed the presence of *P. carolinianus* well beyond its previously recorded distribution in Britain. During 2002, populations were recorded in the Scottish Border counties of Roxburghshire (v.-c. 80) and Berwickshire (v.-c. 81) (Long, 2003), and also in

Shropshire (v.-c. 40) by J. Ricketts and M. Lawley (Blackstock, 2003). In 2003, it was discovered at a locality in East Perthshire (v.-c. 89) during the BBS summer meeting (Lawley, 2004). Four new populations were also found by Sam Bosanquet in Monmouthshire (v.-c. 35), from where there had been a single previous record (Bosanquet, 2003). It thus seemed timely to ascertain whether further material of this taxon resides in BBSUK within packets attributed to *P. laevis*.

During the spring of 2004, we examined plants from all packets of both *P. laevis* and *P. carolinianus* held in BBSUK. In each case, the sex forms were determined as far as possible. In cases where clearly monoicous thalli were observed the material was (re)determined as *P. carolinianus*, even if accompanied by unisexual thallus segments. In samples where only single-sex thalli (male and/or female) were present the vouchers were accepted as *P. laevis*, unless only very limited fertile material was available. In the latter situation, it is recommended that new vouchers should be sought; the same applies when only non-fertile thalli (lacking sex organs) were present.

In all, we found bisexual thalli in nine packets (from eight vice-counties) out of a total of 61 specimens labelled *P. laevis*, and these are listed under *P. carolinianus* in Annex 1. Together with specimens already recognised as *P. carolinianus*, there is now material held in BBSUK of this species from 13 vice-counties. Additional records of *P. carolinianus* from North Cornwall (v.-c. 2), West Sussex (v.-c. 13), Surrey (v.-c. 17) and South Essex (v.-c. 18) are given in Paton (1973). Details of specimens in BBSUK containing only unisexual thalli are compiled under *P. laevis* in Annex 1. We have been reluctant to reject fertile vouchers of *P. laevis* at this stage, but it is possible that some of these should also be referred to *P. carolinianus* although no definite evidence of bisexuality was observed. The few specimens comprising indeterminate

non-fertile or very sparse material are listed separately.

Tuberous thalli were only observed in two *P. laevis* collections from Radnorshire (v.-c. 43) and Pembrokeshire (v.-c. 45).

This revision of *Phaeoceros* in BBSUK has confirmed that *P. carolinianus* has a wide geographical range in Britain, extending from southern England to East Perthshire (v.-c. 89) and Mull (v.-c. 103) in northern Scotland. Almost all the British records are from arable habitats. No specimens of *P. carolinianus* from Ireland were detected. Our findings also indicate that *P. laevis* is the most frequent species in both Britain and Ireland.

It seems highly probable that other populations of *P. carolinianus* await discovery. We strongly recommend that recorders seek the most well-grown and fertile material available in the field, as this greatly enhances ease of identification. The possibility that mixed populations of *P. laevis* and *P. carolinianus* occur needs further investigation.

Acknowledgements

We thank David Long and Mark Lawley for drawing our attention to recent new finds of *P. carolinianus* in Britain. We are also very grateful to Sally Whyman at the National Museum & Gallery in Cardiff for arranging the loan of material in BBSUK.

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- Annex 1. Specimens of *Phaeoceros* in BBSUK examined in 2004.**
- Phaeoceros laevis*. C:** sandy ground by cliff stream, Saint's Valley, Guernsey, 1909, P.G.M. Rhodes. **1:** fallow field, near Gue Graze, 1946, T.G. Tutin; stream bank, Nanjizal Bay, near Land's End, 1964, J.A. Paton. **3:** base of roadside bank, near Totnes, 1950, J.H.G. Peterken. **5:** Quantock Hills, 1935, W. W(atson); on more or less vertical face of wet sandstone, Cushuish, near Taunton, 1939, W. Watson. **8:** ditch, near Redlynch, 1952, J. Appleyard. **9:** Eype Mouth, 1952, J. Appleyard. **18:** gravel pits, off Southend Road, near Grays, 1959, E. Saunders. **36:** Bodenham, 1916, G. Armitage. **43:** Brilley Mountain, 1916, G. Armitage. **45:** on a very wet patch of woodland, just W of Tenby, 1999, J. Hambly & R. Holmes. **47:** bank of River Llyfnant, Pont Llyfnant, SN7097, 1974, P.M. Benoit. **64:** Bramham Park, NE of Leeds, 1963, G.A. Shaw. **70:** earth bank by the shore, Ravenglass, SD09, 1973, J. Appleyard. **73:** meadow near East Hill, W of Dumfries, NX9174, 1961, J.A. Paton. **88:** meadow, beside mill dam, Birnam, NO0538, 1964, J.A. Paton & J. Appleyard. **90:** Ethie meadow, Parkhill, Arbroath, NO6545, 1963, J.A. Paton. **98:** on muddy bank of road by sea, Bagh Dun Mhuilig, Craignish, NM778016, 1965, M.F.V. Corley. **100:** field, near Port Bannatyne, Isle of Bute, 1957, A.C. Crundwell. **102:** on edges of cut turf by track, ca 50 m alt., broad-leaved policy woodland, Dunlossit House, Port Askaig, Islay, NR430689, 1998, D.G. Long. **104:** soil on side of a ditch, near Flodigaray, Skye, 1975, W.D. Foster. **107:** edge of barley field, Little Creinch, near Bonar Bridge, 1968, A.C. Crundwell *et al.* **H5:** wet track, Castle Cook, Kilworth, 1966, J.G. Duckett *et al.* **H6:** field near Clogheen, N of Ballymacarbry, 1966, G. Argent, E.R.B. Little & J.A. Paton. **H8:** on soil in grass field, Glenbrohane, Ballylanders, 1966, M.F.V. Corley & J.S. Parker. **H13:** on near vertical soil at base of bank beside track, ca 65 m alt., just W of Bunclody, S95, 2002, D.T. Holyoak. **H14:** damp ground amongst grass on farm track, near Abbeyleix, 1966, G. Argent. **H16:** roadside bank, Tullywee Bridge, Kylemore, 1957, A.C. Crundwell. **H19:** stubble field, 70 m alt., 'Furry Field', NE of Coursetown House, Courttown East townland, Athy, S69, 2002, H.F. Fox & C.D. Preston. **H20:** gravel path, Devil's Glen, Ashford, T2399, 1975, J.A. Paton. **H21:** stubble field, 60 m alt., SE of Hazelhatch Station, N93, 2002, C.D. Preston. **H22:** side of ditch, Petersville Crossroads, N of Moynalty, 1978, D. Synnott. **H23:** spring barley stubbles by R156 road, Balrowan, W of Killucan, N55, 2003, S.D.S. Bosanquet & C.D. Preston. **H24:** side of ditch, roadside by L Gowna, N of Inchmore, 1980, D. Synnott. **H27:** earthy bank by track, W of Bundorragha, N of Killary Harbour, 1970, J.A. Paton. **H29:** Glencar, 1928, F.E. M(ilsom). **H31:** stubble field, S of Dromiskin, 1966, D. Synnott. **H32:** moist bank in field, Castlehane, near Monaghan, 1961, F.W. Fitzgerald. **H34:** stubble field, Newtown Cunningham, 1962, J. Appleyard *et al.* **H35:** stubble field, Ards Peninsula, 1962, J. Appleyard *et al.* **H36:** on wet mica schist detritus by stream, Glen Curry Bridge, near Omagh, 1956, M.P.H. Kertland & J.W. Fitzgerald. **H37:** stubble field, between Moy and Portadown, 1962, J. Appleyard, A.C. Crundwell & E.C. Wallace. **H38:** on soil in arable field, ca 14 m alt., W of B1, NW of Ballyhosset, SE of Downpatrick, J54, 2002, D.T. Holyoak. **H40:** stubble field, Coleraine, 1952, E.W. Jones.
- Phaeoceros carolinianus*. 24:** in field, beside Rassler Wood, near Medmenham, 1967, J.G. Duckett & E.R.B. Little. **35:** stubble field, NW of Llanayo, N of Usk, SO3603, 1980, J.A. Paton & A.R. Perry. **40:** arable field, Tinkers Hill, SO57, 2002, J. Ricketts & M. Lawley. **44:** stubble field, near Llandinio, SN22, 1981, J. Appleyard. **46:** cornfield, near Llanfarian, 1920, C.V.B. Marquand (two packets). **72:** on soil in field of grass and stubble, near Georgetown, 1943, A.D. Banwell. **80:** on soil, stubble field margin, ca 116 m alt., Leader Valley, below Cowdenknowes,

NT53, 2002, D.G. Long. **81:** field by Lintlaw Burn, 1926, J.B. Duncan; on soil, stubble field margin, ca 120 m alt., Leader Valley, below The Park, NT53, 2002, D.G. Long. **86:** stubble field, near Bandowie, 1949, A.C. Crundwell. **87:** arable field, Ledard Burn, Loch Ard, 1964, A.M. Stirling & A.C. Crundwell. **89:** setaside arable field, Delvine, NO13, 2003, M. Lawley. **99:** grass ley, near Milngavie, 1949, A.C. Crundwell. **103:** bare patch of soil in grass field, Kilfinichen, Loch Seridain, Mull, NM4824, 1968, U.K. Duncan & P.W. James.

Phaeoceros indeterminate at species level. **51:** on damp calcareous mud in moat, Ewloe Castle, 1966, J. Dransfield (referred to *Anthoceros laevis* but non-fertile). **58:** in arable field, above the Dungeon, Thurstaston, 1967, J. Dransfield (labelled *Anthoceros*

laevis but a minute gathering with only two (male) thalli segments). **H7:** cornfield, W of Longfordpass Bridge, Urlingford, 03/12, 1966, J.A. Paton & E.R.B. Little (referred to *Anthoceros laevis* but fertile (female) thalli minute). **H9:** ditch by path from Fisherstreet to cliffs of Moher, 1962, J. Lane (referred to *Anthoceros laevis* but non-fertile). **H12:** forestry track, SE of Killinierin, N of Gorey, 31/1665, 1975, J.A. Paton (referred to *Anthoceros laevis* but non-fertile). **H26:** ditch bank, W of Pollagh R, NE of Balla, 1970, J.A. Paton (referred to *Anthoceros laevis* but non-fertile).

Specimen incorrectly determined at generic level. **105:** in deep cleft in sea cliff, Seana Chamas near Melvaig, Gairloch, NG742848, 1984, D.G. Long (specimen is male *Pellia endiviifolia*).

Bygone bryologists

This is the second article in a series about prominent British and Irish field-bryologists of the past. The author would be very pleased to learn of any information that supplements its content.

A more general and at present unfinished *Social and biographical history of British and Irish field-bryologists* is available on-line at <http://ralph.cs.cf.ac.uk/HOB/HOBBintro.htm>.

Robert Kaye Greville (1794-1866)

Mark Lawley

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Summary of bryological career

Robert Kay Greville (see Figure 1) was a notable field-bryologist in the first half of the 19th century. Much of his time in the field was spent in the Scottish Highlands, and his huge collection of plants today forms a core of the herbarium at the Botanic Garden in Edinburgh.

Together with W.J. Hooker and G.A. Walker Arnott, Greville found a number of mosses new to Britain as they jointly explored the Scottish Highlands, including *Blindia caespiticia*,

Campylophyllum halleri, *Cirriphyllum cirrosum* and *Heterocladium dimorphum* on Ben Lawers. He also added to the Scottish bryoflora the liverworts *Anastrophyllum saxicola*, *Cephaloxia lunulifolia*, *Frullania microphylla*, *F. teneriffae*, *Gymnomitrium coralloides*, *Jungermannia gracillima*, *Marchesinia mackaii*, *Mastigophora woodsii*, *Metzgeria conjugata*, *M. leptoneura*, *Plagiochila carringtonii*, *Reboulia hemisphaerica* and *Riccia fluitans*.

Greville's most important contribution to bryological literature was his illustrated *Scottish Cryptogamic Flora* (1822-28).