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# TYPIFICATION OF *JUNGERMANNIA PINGUIS* L. (MARCHANTIOPHYTA, ANEURACEAE)

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*Aneura pinguis* is a complex species shown to include several genetic lineages and partly cryptic species in Europe. The oldest name of the complex, *Jungermannia pinguis* L. (*Aneura pinguis* (L.) Dumort.) was never typified. To stabilise its use for the future, a lectotype and epitype are here selected with an illustration seen by Linnaeus and a DNA-sequenced specimen from near the probable type locality.

*Keywords*. *Aneura*, *Aneura pinguis*, epitypification, *Jungermannia pinguis*, lectotypification.
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## Introduction

DNA barcoding, although not without some technical difficulties when used for plants (Hollingsworth *et al.*, 2009), has become an important tool for characterising plant biodiversity and at the species level has now been applied to a range of genera of liverworts, such as *Anastrophyllum* (Spruce) Steph. and *Herbertus* Gray (Long *et al.*, 2007; Bell *et al.*, 2012). At the Royal Botanic Garden Edinburgh (RBGE), a long-term barcoding study on British and Irish liverworts was initiated in 2007 (Long *et al.*, 2007), which prompted a continuing field programme to assemble a collection of silica-dried and vouchered specimens across the taxonomic, morphological and geographical spectra of these species within Britain and Ireland. This programme is not yet complete, but large numbers of samples are now in storage, of which a significant proportion have been sequenced for a range of plant DNA-barcoding loci.

A taxon that was targeted for sampling from the outset was the simple thalloid genus *Aneura* Dumort., because other workers, such as Bączkiewicz & Buczkowska (2005), had shown, using isozyme markers and later molecular markers, considerable genotypic diversity in samples of *Aneura pinguis* from Poland and elsewhere (Bączkiewicz & Buczkowska, 2016; Bączkiewicz *et al.*, 2017; Myszczyński *et al.*, 2017). These workers did not formally describe any new species but identified a range of cryptic species ‘temporarily’ named A to L, of which at least nine occur in Europe. A further European species, *Aneura*

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*mirabilis* (Malmb.) Wickett & Goffinet, formerly treated under its synonym *Cryptothallus mirabilis* Malmb., is well characterised morphologically because it completely lacks chlorophyll (Wickett & Goffinet, 2008) and is included in the barcoding study.

Apart from collections of *Aneura mirabilis*, most other European specimens of *Aneura* continue to be identified as *Aneura pinguis s.l.* (e.g. Paton, 1999), but in an increasing number of publications two additional named species of *Aneura* have been reported from Europe. The first of these is *Aneura maxima* (Schiffn.) Steph. (a species originally described from Java), which has been reported from several European countries (Andriessen *et al*., 1995; Sotiaux & Sotiaux, 1996; Frahm, 1997; Thingsgaard, 2002; Werner, 2003; Buczkowska & Bączkiewicz, 2006; Sérgio & Garcia, 2009). The second is *Aneura pseudopinguis* (Herzog) Pócs (described from Brazil), which was reported from Portugal by Sérgio & Garcia (2009); its name was synonymised by Gradstein (2013) under *Aneura latissima* Spruce, described from Brazil and Peru. However, the tropical *Aneura maxima* has now been excluded from Europe on the basis of the results of DNA barcoding carried out at RBGE (Forrest, 2015; Paton, 2022).

*Aneura pinguis* (L.) Dumort. is based on the Linnaean basionym *Jungermannia pinguis* L. (see below). Although first described from England, its global distribution has been given as Europe, Africa, Asia, North, Central and South America, Australia, and New Zealand, and is described as 'cosmopolitan' (Damsholt, 2002). However, because no lectotype has yet been designated for *Jungermannia pinguis* L., it is essential to clarify and stabilise the application of this name before formally describing any new species, so that one of the semicryptic molecular species can be accurately linked to the name *Aneura pinguis*. This requires (i) selection of a lectotype informed by the protologue, and (ii) selection of an epitype for which DNA barcoding has been carried out, to place it in one of the known (semi-)cryptic species. In making these selections, we have been guided by the definition of an epitype in ICN Article 9.9 made by Turland *et al.* (2018) and discussed by Lendemer (2020).

*Jungermannia pinguis* L. was described by Linnaeus (1753) in his *Species Plantarum* with a very brief description taken from his earlier *Flora Suecica* (Linnaeus, 1745): 'Jungermannia acaulis, fronde oblonga sinuata pinguis.' He also cited three polynomial synonyms from the pre-Linnaean works of Micheli, Dillenius and Plukenet. Of these, the most important is that of Dillenius (1742). As explained by Isoviita (1970), Dillenius's *Historia Muscorum* was used by Linnaeus as the "foremost source of the hepatic species of 'Species Plantarum'". There appears to be no evidence that Linnaeus critically studied any specimens in the Dillenian herbarium when he visited Oxford in 1736, and therefore Linnaeus's binomials are considered to be entirely based on Dillenius's published descriptions and illustrations, not on the latter's specimens. Therefore, it must be argued that the Dillenian specimens are not eligible as lectotypes but his cited figures are, although specimens may serve as an epitype for morphological understanding when figures are insufficiently detailed. This is at odds with Isoviita's recommendation that "Dillenius's herbarium of the '*Historia Muscorum*' usually forms the best basis for the typification of the names given to them by Linnaeus". In the case of *Jungermannia pinguis*, it is especially useful to use a figure as lectotype, allowing us to fix application of the name to a modern genetically characterised epitype, as is proposed below.

Linnaeus's (1753) relevant Dillenian reference is 'Lichenastrum capitulis oblongis juxta foliorum divisuras enascentibus. *Dill. musc.* 509. t. 74. f. 42'. One of Dillenius's (1742) illustrations under f. 42 (f. 42N) is selected below as lectotype, because it shows a fertile plant with sporophytes and accords well with material of what we consider to be the widespread form of *Aneura pinguis* in lowland Britain, the taxon for which we are selecting an epitype. Dillenius's f. 42 shows a plant with a darker band along the median part of the thallus, which could be interpreted as a midrib. However, this band is not sharply defined and grades from the thicker middle part gradually into the thinner and more translucent wings of the thallus, as can be observed in living plants, as shown in **Figure 1**B. Dillenius cited his material as 'Nascitur locis palustribus, tam circa Londinum, quam hic Oxonii & alibi copiose. Aprili floret'. Although *Jungermannia pinguis* L. has never been lectotypified previously, Grolle (1976) cited as 'syntypes', specimens in the Dillenian herbarium (OXF, H-SOL) named as *Lichenastrum capitulis oblongis*, *juxta foliorum divisuras enascentibus*, 'The jagged Lichenastrum, with long Sheaths and Heads', but Grolle's citation of specimens does not constitute lectotypification (J. McNeill, RBGE, personal communication). Grolle, the foremost authority on European liverworts at the time, was in no doubt that the supporting specimen for f. 42 fitted his concept of *Aneura pinguis*.

Our understanding of the *Aneura pinguis* complex is in its infancy, and there exist only a few datasets, partly non-overlapping and mostly with restricted geographical samplings. From our molecular work (Forrest *et al.*, in preparation), we recognise nine genetic species that at this stage we can only partly characterise morphologically. To stabilise the use of the oldest name in the complex, *Jungermannia pinguis* L., we here lecototypify and epitypify the name.

## Taxonomic treatment

*Jungermannia pinguis* L., Sp. Pl. 1136 (1753) ≡ *Aneura pinguis* (L.) Dumort., [Comment. Bot. 115. Tournay. (1822); *nom. nud.*] Sylloge Jung. Europ. Indig. 86. Tournay. (1831). – Type citation: "Habitat in Europae paludibus"; type: Dillenius, Hist. Musc. t. 74, f. 42N (1742 ["1741"]) (OXF, lectotype, designated here). England, Cambridgeshire (v.-c. 29), west side of long pit, Stow cum Quy Fen, Grid. ref. TL5135 6271, on chalky soil at trampled edge of flooded pit (old coprolite pit), 5 m alt., 14 iv 2021, *J.J. Graham & C.D. Preston s.n.* (E01021874, epitype, designated here). **Figure 1**.

Plants (**Figure 1**A, B, C) thallose, prostrate in mats or irregular medium-sized rosettes, 1–5 cm in diameter, firmly attached to substrate. Thalli dull above, with a somewhat greasy appearance, opaque, bright to dark green in colour. *Thallus* sparingly branched, branches ± obovate or elliptical from narrow base, to 20 mm long (1.5–)2.5–6 mm broad,

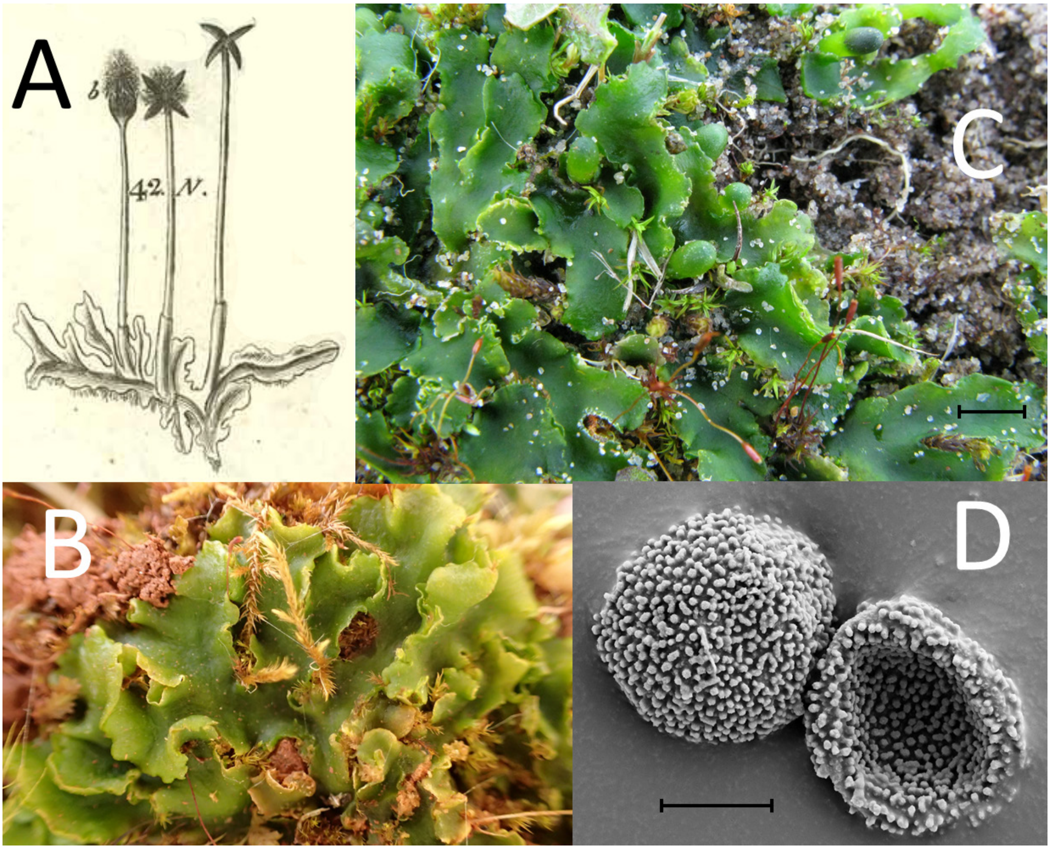


**Figure 1.** A, Lectotype of *Jungermannia pinguis* L., from Dillenius, Historia Muscorum t. 74, f. 42N (1742). B, *Aneura pinguis s.s.* at Greenlaw Dean, Berwickshire, UK (*Long* 47077) (scale bar as for Figure 1C). C, *Aneura pinguis s.s.* with young sporophytes enclosed by calyptrae, from Holy Island, Northumberland, UK (*Long* 38186) (scale bar, 4 mm). D, Spores of *Aneura pinguis s.s.* under scanning electron microscope; epitype, from Stow cum Quy Fen, Cambridgeshire, UK (*Graham & Preston s.n.*) (scale bar, 10 μm). Photographs and micrograph: B and C, David Long, D, Frieda Christie.

in section plano-convex or concavo-convex, 12–16 cells (450–550 μm) high. Dorsal surface plane in middle, towards margins undulate and weakly to strongly ascending, sometimes canaliculate. Margins weakly to sinuate to shallowly lobed, in transverse section margins 2- to 3-stratose or in places narrowly 1-stratose for a width of only one cell. *Epidermal cells* mostly 40–75 × 30–45 μm, thin-walled; outer walls of marginal cells weakly convex. *Oil bodies* present in all cells, 6–12 per cell, ± regularly globose, 3–5 μm in diameter, surface faintly granular, not persistent. *Fungal hyphae* absent or abundant in lower 3–6 layers of rhizoid-bearing part of thallus, when present forming dense cluster of hyphae almost filling cells. *Rhizoids* numerous, borne on 30–50% of width of ventral surface. *Gemmae* lacking.

Dioicous, often fertile. Male plants often narrower than female plants, 2–3 mm wide; androecial branches often numerous, lateral along thallus margins, unbranched or bifid, concave or canaliculate, 0.3–4 × 0.4–2 mm; antheridial chambers in 1–3 rows. *Gynoecial branches* short, swollen, ciliate, borne in sinus of thallus margin; archegonia hidden amongst cilia. *Calyptra* clavate, green when young (Figure 1C), becoming whitish, massive, 3–7 × 1.1–1.4 mm, smooth when young, sometimes becoming warted and sparsely hairy when old. *Seta* 9–34 mm long, 14–16 cells across diameter; capsule oblong-ellipsoid, dark brownish black, 1.6–1.75 × 0.9–1.1 mm, valves when dehisced 1.2–2 × 0.5–0.9 mm. *Spores* 18–22 μm diameter, finely papillose (Figure 1D); elaters 135–410 × 7.5–10 μm, unispiral.

*Distribution*. Great Britain (England, Scotland, Wales), Ireland, Albania, Poland, Russia (Mari El, Vladimir), USA (Connecticut, Michigan) (Figure 2).

*Habitat and ecology*. Damp calcareous meadows, dune slacks, floor of limestone quarries.

*Notes*. From the nine European genetic species we can recognise, one is predominantly a lowland species in Britain that can be partly characterised morphologically and best fits the concept of Linnaeus's *Jungermannia pinguis*. This name is therefore lectotypified here by a published illustration supported by a genetically characterised epitype from the south of England. From Great Britain, we have now sequenced 13 samples of this widespread taxon with further samples from Ireland, Albania and Russia (Table 1 and Barcode of Life

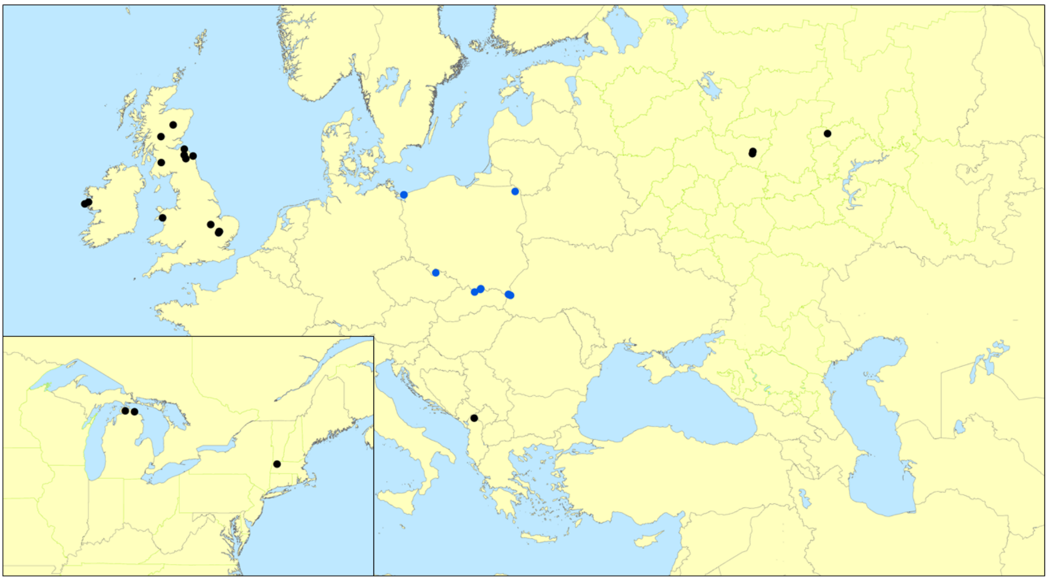

**Figure 2.** Distribution map (Europe with Eastern North America inset) of *Aneura pinguis* (L.) Dumort. *s.s.*, based on DNA-sequenced specimens. Black dots, *Aneura pinguis* specimens; blue dots, specimens of 'cryptic sp. F' from *Bączkiewicz* et al. (2017), which corresponds genetically to our selected type lineage.

**Table 1.** *Aneura pinguis* samples sequenced in the present study (further details at dx.doi.org/10.5883/DS-ANEPINGU)

| EDNA/DNA sample no. | Country | Vice-county or region | Locality | Coordinates | Habitat | Altitude (m) | Date | Collector and number | Voucher no. |
|---|---|---|---|---|---|---|---|---|---|
| 21-0060814 | Great Britain | England, Cambridgeshire (29) | Stow cum Quy Fen | 52.24177°, 0.21525° | Edge of flooded pit | 5 | 14 iv 2021 | *Graham & Preston s.n.* | E01021874 |
| 08-00497 | Great Britain | England, Cambridgeshire (29) | Anglesey Abbey | 52.23855°, 0.23780° | Under young trees | 5 | 24 iii 2008 | *Jordan & Preston s.n.* | E00768197 |
| 11-0023174 | Great Britain | England, Cambridgeshire (29) | Cherry Hinton | 52.17780°, 0.16892° | Chalky soil on cliff | 30 | 8 xii 2008 | *Graham & Preston s.n.* | E00758184 |
| 07-01663 | Great Britain | England, Northamptonshire (32) | Nassington Woods | 52.56950°, −0.43745° | Disused quarry | 50 | 14 iv 2007 | *Flagmeier s.n.* | E00255494 |
| 07-01734 | Great Britain | England, North Northumberland (68) | Holy Island | 55.68248°, −1.80197° | Sandy field | 6 | 23 iv 2006 | *Long* et al. 35642 | E00758211 |
| 09-01189 | Great Britain | England, North Northumberland (68) | Holy Island | 55.68382°, −1.79735° | Fixed dunes | 7 | 17 iv 2009 | *Long* 38355a | E00758271 |
| 10-03217 | Great Britain | England, North Northumberland (68) | Holy Island | 55.68382°, −1.79735° | Ditch on dunes | 15 | 24 iii 2010 | *Long* 38917 | E00758210 |
| 09-01171 | Great Britain | Scotland, Ayrshire (75) | Dalricket Mill | 55.39388°, −4.25617° | Open cast mine | 210 | 4 iv 2009 | *Preston s.n.* | E00774651 |
| 08-01300 | Great Britain | Scotland, Roxburghshire (80) | Blakelaw | 55.56514°, −2.35498° | Ditch | 175 | 14 vi 2008 | *Long & Corner* 37858 | E00774649 |
| 21-0060812 | Great Britain | Scotland, Berwickshire (81) | Greenlaw Dean | 55.72290°, −2.49094° | Mossy slope | 190 | 28 iv 2021 | *Long & Lusby* 47077 | E01021872 |
| 14-003638 | Great Britain | Scotland, East Lothian (82) | White Sands | 55.98281°, −2.47499° | Former quarry | 20 | 8 vi 2014 | *Long* 42937 | E00774564 |

**Table 1** (*continued*).

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 07-01697 | Great Britain | Scotland, Mid Perthshire (88) | Lochan na Lairige | 56.52114°, −4.27674° | Gravel track | 490 | 11 v 2007 | *Long & Mackinnon* 36690 | E00774601 |
| 09-01157 | Great Britain | Scotland, South Aberdeenshire (92) | Craig Leek | 57.01971°, −3.33720° | Limestone slope | 422 | 18 iii 2009 | *Long* 38262 | E0078336 |
| 07-01865 | Ireland | West Galway (H16) | Glassillaun Bay | 53.61615°, −9.87557° | Sandy hollow | 5 | 3 vii 2007 | *Long* 36771 | E00774619 |
| 09-01693 | Ireland | West Galway (H16) | Omey Island | 53.53033°, −10.16347° | Damp sandy lake shore; in turf | 5 | 12 vii 2009 | *Long* 38555 | E00758323 |
| 14-0036564 | Albania | Albanian Alps | Valbona | 42.45919°, 19.92213° | Limestone outcrop | 740 | 6 vii 2014 | *Long* 43063 | E00774677 |
| 365A-AS | Russia | Mariy El Republic | Bol'shaya Kokshaga State Nature Reserve; valley of Volga River, floodplain of Bol'shaya Kokshaga River, the right tributuary of Volga River | 56.64944°, 47.22611° | On fine earth and small stones on edge of old railroad embankment | 95 | 14 ix 2009 | *Konstantinova* | KPABG108033 |
| 371A-AS | Russia | Vladimir District | Gus'Khrustalnyi Region; 1.5 km to the north-west from Dobryatino Village | 55.88111°, 41.45777° | Old lime-pit, on pile of limestone | 140 | 12 vi 2008 | *Kokoshnikova* | KPABG113205 |
| 379A-AS | Russia | Vladimir District | Selivanovskiy Region; 0.5 km to the south from Kostenets Village | 55.78333°, 41.41666° | Ditch on pine forest edge, on soil-covered limestone | 117 | 8 iv 2007 | *Kokoshnikova* | KPABG113182 |

EDNA, extracted DNA.

**Table 2.** Additional *Aneura pinguis* samples from previous publications

| DNA sample no. | Cited in[a] | Country | Region | Locality | Habitat | Coordinates | Collector/no. |
|---|---|---|---|---|---|---|---|
| F 1 | 1 | Poland | NW Poland | Wolin Island, Gosań Mt | On a cliff | 53.95000°, 14.48333° | *POZW* 42889 |
| F 2 | 1 | Poland | NW Poland | Wolin Island, Świdna Kępa Mt | On a cliff | 53.95000°, 14.50000° | *POZW* 42890 |
| F 3 | 1 | Poland | NW Poland | Wolin Island, Gosań Mt | On a cliff | 53.95000°, 14.50000° | *POZW* 16086 |
| F 4 | 1 | Poland | NE Poland | Suwałki Lake District, Lake Pierty | | 54.10000°, 23.08333° | *POZW* 40182 |
| F 5 | 1 | Poland | SE Poland | Bieszczady Mts, near Brzegi Górne | Old quarry | 49.15000°, 22.56666° | *POZW* 42901 |
| F 6 | 1 | Poland | SE Poland | Bieszczady Mts, near Brzegi Górne | Old quarry | 49.15000°, 22.56666° | *POZW* 42771 |
| F 7 | 1 | Poland | SE Poland | Bieszczady Mts,, valley of Terebowiec stream | | 49.10000°, 22.73333° | *POZW* 42797 |
| F 8 | 1 | Poland | SE Poland | Bieszczady Mts, tributary of Wołosaty stream | | 49.11666°, 22.66666° | *POZW* 42891 |
| F 9 | 1 | Poland | SE Poland | Bieszczady Mts, tributary of Wołosaty stream | | 49.11666°, 22.66666° | *POZW* 42892 |
| F 10 | 1 | Poland | SE Poland | Bieszczady Mts, tributary of Wołosaty stream | | 49.11666°, 22.66666° | *POZW* 42893 |
| F 11 | 1 | Poland | S Poland | Beskidy Mts, valley of Kozłecki stream | | 49.43333°, 20.43333° | *POZW* 42495 |
| F 12 | 1 | Poland | S Poland | Beskidy Mts, valley of Kozłecki stream | | 49.43333°, 20.43333° | *POZW* 42818 |
| F 13 | 1 | Poland | S Poland | Beskidy Mts | | 49.43333°, 20.43333° | *POZW* 42894 |
| F 14 | 1 | Poland | S Poland | Pieniny Mts, Kotłowy Potok stream | | 49.40000°, 20.40000° | *POZW* 42910 |
| F 15 | 1 | Poland | S Poland | Tatry Mts, valley of Biały Potok stream | | 49.26666°, 19.95000° | *POZW* 42895 |
| F 16 | 1 | Poland | SW Poland | Góry Bialskie Mts | | 50.23333°, 16.95000° | *POZW* 16062 |
| F 17 | 1 | US | Michigan | Cheboygan Co., Carp Creek, N of Horgsback Road | Rotting log | 45.5427°, −84.6815° | *Buck s.n.*, *NYBG* 263899 |
| F 18 | 1 | US | Michigan | Presque Isle Co., Lake Huron, Evergreen Beach, N of Evergreen Highway | | 45.4942°, −83.9678° | *Buck* 42054, *NYBG* 576889 |
| F a, b (DQ986142, EF547815) | 1, 2, 3 | US | Connecticut | Northwest Connecticut | Limestone | | *Wickett* 338 (CONN) |
| F b (EF547822); EDNA06-06228 | 1, 3 | Wales | Merioneth (48) | Morfa Harlech | Dune slack | 52.88385°, −4.15636° | *Duckett s.n.* |

[a] 1, Bączkiewicz et al. (2017); 2, Wickett & Goffinet (2008); and 3, Wickett et al. (2008).

Database [BOLD] dataset DS-ANEPINGU). Genetic data also show that the same taxon occurs additionally in Poland and the USA as 'Cryptic sp. F' from Poland, as *Aneura pinguis* from Michigan *Buck s.n.* and *Buck* 42054 (NY) and *Wickett* 338 (CONN) from Connecticut (Myszczyński *et al.*, 2017; Wickett & Goffinet, 2008) (**Table 2**).

The description of *Aneura pinguis* (L.) Dumort. *s.s.* is based largely on *Graham & Preston s.n.* (the epitype), *Long* et al. 35642 and *Long & Lusby* 47077, all DNA-sequenced populations listed in **Table 1**.

## Discussion

*Aneura pinguis s.s.* at the moment can be accurately identified only by DNA sequencing. It is quite distinctive morphologically from some of the other genetic species we have identified in Europe, but at least one of these cannot yet be distinguished from it morphologically. It has characteristic ecology but can grow on occasion close to at least one other of the segregate species. It is quite distinctive in several morphological characters, particularly its relatively flat thalli with weakly upturned margins, dull and opaque green in colour, closely appressed to the substrate and firmly attached by numerous rhizoids. Oil bodies are relatively few and small, 6–12 per cell, globose, 3–5 μm in diameter, very faintly roughened. Fungal hyphae may be absent or abundant in a band along the ventral epidermis, immediately above the zone of rhizoidal attachment. However, until the other segregate species at present placed with *Aneura pinguis s.l.* are described fully, it is not possible to tabulate the differences between them.

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