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Cochlearia officinalis sensu lato (Brassicaceae) around northern Irish Sea coasts

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Abstract
For over 100 years botanists have found it difficult to identify *Cochlearia* (Scurvygrasses) growing on salt marshes and muddy shores of the northern Irish Sea coasts. They have been variously identified as *C. anglica* L., *C. officinalis* L. and more recently *C. atlantica* Pobed. This study describes the history of recording *Cochlearia* plants on these shores and their varied morphology, and through cytological analysis demonstrates that they are derived from the hybrid between *C. anglica* (2n = 48) and *C. officinalis* (2n = 24) with 2n = 36.

Keywords: salt marshes; cytological analysis; chromosome; hybridisation

Introduction

Greenwood (2012) pointed out in his *Flora of North Lancashire* that he found it difficult to name salt marsh and other coastal *Cochlearia* plants (Scurvygrasses). Halliday (1997) had similarly found difficulty in naming coastal populations of *Cochlearia* in Cumbria but in discussions with Tim Rich suggested that they may be of hybrid origin or an unnamed member of the *C. officinalis* L. complex. This, it was suggested (Greenwood, 2012), could be *C. atlantica* Pobed. named from material from the Hebrides in western Scotland (Pobedimova, 1968; Fig. 1).

However, the difficulty in naming coastal *Cochlearia* was recognised much earlier. Boswell (1875) named northern plants in Britain and Ireland *C. anglica* L. var. *hortii* Syme (holotype from Bidston Marsh, Cheshire but the specimen collected by Robert Brown was not located; a specimen labelled as the type for *C anglica* var. *hortii* at the Natural History Museum, London was collected by J. Harbold Lewis in 1874. Fig. 2). A southern form, *C. anglica* var. *gemina* Hort (holotype from Chepstow, Fig. 3) was recognised as being a different taxon. Boswell (1875) also thought *C. anglica* var. *hortii* occurred on the continent and cited a specimen from Holland collected in 1866 and contained in F.P. Wirtgens's 'Herbarium Plantarum Criticorum' (Herbarium Haussknecht, Jena). Henrard (1914/16) described plants from Holland (image accessed on-line 5 July 2022 available at http://plants.jstor.org/stable/10.5555/al.ap.specimen.l0011819) as the hybrid *C. anglica* x *C. officinalis*, which he named *C. x hollandica* Henrard).

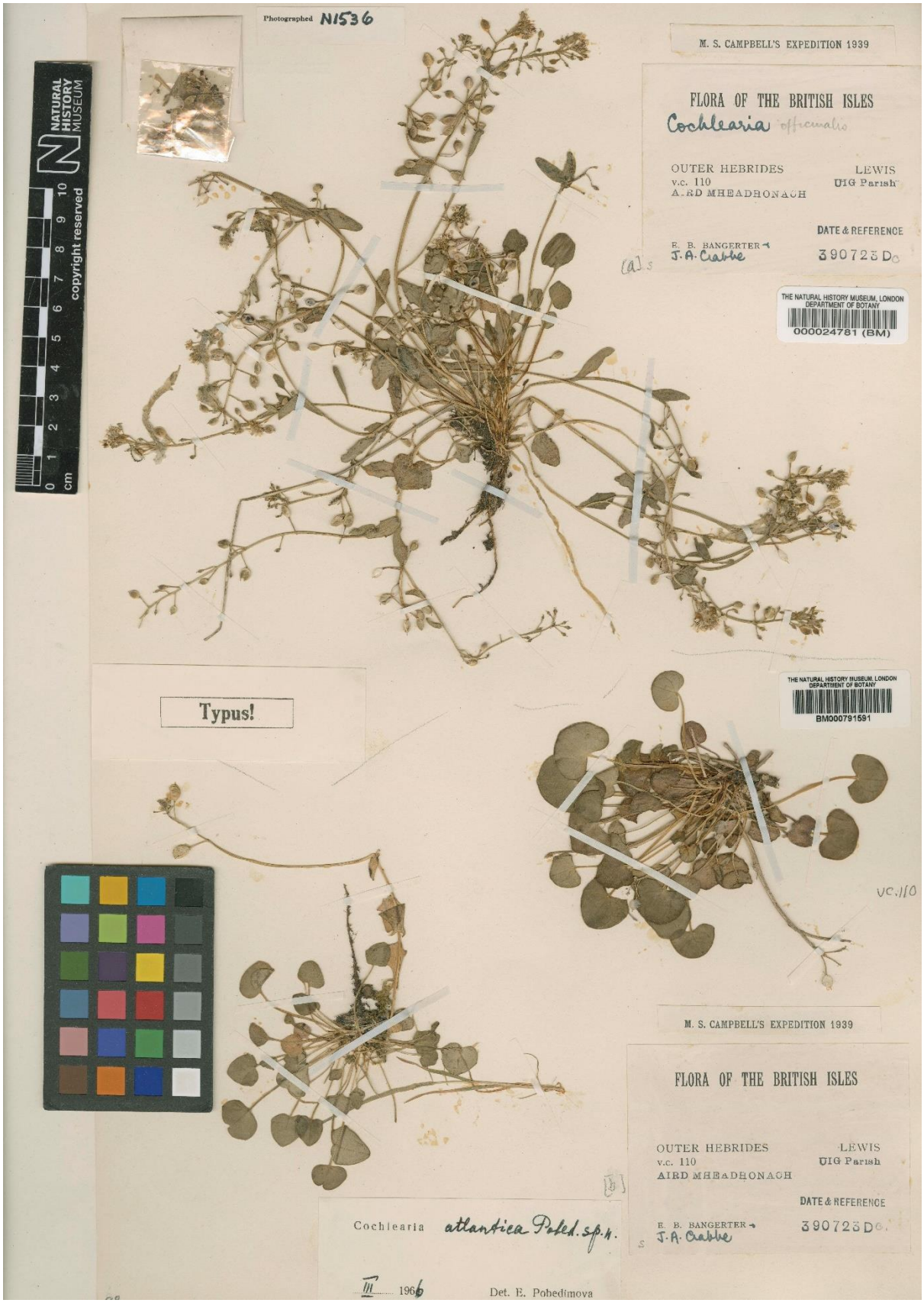

Figure 1. Type specimen of *Cochlearia atlantica* from the Outer Hebrides. Image copyright Natural History Museum, London

Figure 2. *Cochlearia anglica* var *hortii* (lower left) collected from Bidston Marsh, the type locality, in 1871. *Cochlearia anglica* from Kent (lower right). Image copyright South London Botanical Institute (www.slbi.org.uk) accessed online through herbaria@home (herbariaunited.org/atHome)

Figure 3. Type specimen of *Cochlearia anglica* var. *gemini* from Chepstow. Image copyright Natural History Museum, London

Crane and Gairdner (1923) carried out crossing experiments and showed that their hybrid *C. anglica* x *C. officinalis* was similar to that described by Henrard (1914/16). Their experiments were illustrated with a series of photographs of young

plants. This showed that the progeny of the crosses *C. anglica* x *C. officinalis* and *C. officinalis* x *C. anglica* were different. Whilst both showed basal leaves with truncate lamina bases, one showed some with slightly cordate bases but the other with some more or less cuneate. Young plants of *C. anglica* had much narrower laminas at least twice as long as broad with strongly cuneate lamina bases. On the other hand, *C. officinalis* had more or less orbicular laminas with strongly cordate bases. The identity of these taxa was confirmed by chromosome counts (see below). In England further confusion was caused when Druce (1916) described plants from near Plymouth, southern England as *C. briggsii* Druce but later (1923) agreed they were *C. x hollandica*.

Praeger (1932) repeated Crane and Gairdner's (1923) crossing experiments and thought that *C. x hollandica* was widespread on Irish Sea coasts of Ireland particularly in estuarine habitats, a view maintained by other Irish botanists (Hackney, 1992).

In the second half of the 20th century further confusion arose with differing descriptions for various taxa and especially for *C. x hollandica*. Thus, Clapham *et al*., (1957) described *C. x hollandica*, which they equated to *C. anglica* var. *hortii*, as a large plant (no measurements given but possibly *c*.30 cm.). This does not agree with specimens for either taxon. Also, Pegtel (2008) noted that *C. x hollandica* showed hybrid vigour and seemed to be replacing *C. anglica* in Holland. There was also confusion over the identity of *C. atlantica* and *C. scotica* in northern Scotland (Rich, 1991; Scott and Palmer, 1987 and see below). Table 1 provides a chronological summary of selected *Cochlearia* publications.

Irish Sea *Cochlearia*

Table 2 summarises the treatment of *Cochlearia* taxa in local floras around northern Irish Sea coasts. Most recognise the difficulty of naming plants but recorded *C. anglica, C. officinalis* and *C. danica*. Only rarely was *C. x hollandica* mentioned or *C. atlantica* suggested as a possibility but Chater (2010) thought *C. atlantica* might be a stabilised hybrid. However, a small plant agreeing with the description of *C. atlantica* (Rich, 1991) was recorded from a number of marshes, often in a short sward of *Festuca rubra* L. or in open habitats with low growing vegetation.

Early cytological studies

Crane and Gairdner (1923) supported their crossing experiments with cytological studies. These were early days for this technology but demonstrated that the hybrid between *C. anglica* and *C. officinalis* had between 39 and 40 chromosomes with *C. anglica c*.48 and *C. officinalis c*.24.

Saunte (1955) made further chromosome counts on coastal Cochlearia and observed that plants with 2n = 36 bred true in Britain. Chromosome counts were also made by Gill (1971a), Gill *et al*., (1978) and Nordal & Laane (1996) leading the latter authors to conclude that coastal species consisted of a single species, *C. officinalis* with subsp. *norvegica* Nordal & Stabbetorp from northern Norway and subsp. *officinalis* more generally distributed but both with 2n = 24; subsp. *astuaria* (Loyd) Nordal & Laane from northern Spain and France, 2n = 12 and subsp. *anglica* more generally distributed, 2n = 48, with artificial hybrids between *C. anglica* and *C. officinalis*, 2n = 36.

Table 1. Selected publications on coastal *Cochlearia*

Publication	**Comment**
Boswell (1875)	Describes *C. anglica* var *gemina* and var. *hortii*
Hooker (1884)	Recognises *C. anglica* var. *gemina* and var. *hortii*
Henrard (1914/16)	Describes *C. x hollandica*
Druce (1916)	Describes x *C. briggsii*
Druce (1923)	Considers x *C. briggsii* is *C. x hollandica*
Crane & Gairdner (1923)	Experiments in crossing *Cochlearia* taxa (*C. anglica* x *C. officinalis*)
Druce (1929)	Re-names British & Irish *C. groenlandica* as *C. scotica*
Praeger (1932)	Confirms *C. x hollandica* in Ireland and describes crosses and back crosses
Saunte (1955)	Chromosome counts, *C. groenlandica* 2n = 14; *C. danica* 2n = 42; *C. officinalis* 2n = 24; *C. anglica* 2n = 48; C '*anglica*' 2n = 36; artificial *C. anglica* x *C. officinalis* hybrid 2n = 36
Clapham *et al*. (1957)	Suggests *C. anglica* x *C. officinalis* is *C. anglica* var. *hortii* but describes a large plant.
Pobedimova (1968)	Describes *C. atlantica*
Gill (1971)	Chromosome count for *C. scotica* 2n = 24, therefore a form of *C. officinalis*
Gill (1975)	Provides details of the hybrid *C. anglica* x *C. officinalis*
Jermy & Crabbe (1978)	Describes seed characters for *C. atlantica*
Clapham *et al*. (1987)	Includes *C. scotica* as occurring in Isle of Man
Scott and Palmer (1987)	Considers *C. scotica* a form of *C. officinalis*
Rich (1991)	Includes *C. atlantica*, doubts *C. scotica* and refers to *C. x hollandica*
Nordal and Laane (1996)	Revision of *Cochlearia*: *C. astuaria* 2n = 12; *C. anglica* 2n = 48; *C. norvegica* 2n = 24, all part of *C. officinalis* s.l.
Gill (2007)	No genetic differences in different taxa of *C. officinalis* s.l.
Pegtel (2008)	Notes hybrid vigour of *C. x hollandica* in Holland. Replacing *C. anglica*?
Godfrey (2010)	Chromosome count *C. atlantica* 2n = 24 or 12. Error?
Stace (2010)	Includes *C. atlantica* within *C. officinalis*
Sell & Murrell (2014)	Does not recognise hybrids, includes all taxa as species. Treats *C. briggsii* as a species, not a hybrid as described by Druce (1916)
Brandrud (2014)	Recognises genetic distinctions in *C. officinalis* s.l. in northern Norway.
Stace *et al*. (2015)	Reviews *Cochlearia* hybrids
Brandrud *et al*. (2017)	Confirms correlation of genetic variation with morphology and ecology
Stace (2019)	Considers *C. atlantica* might be a species

Table 2. Treatment of coastal *Cochlearia* by local Flora writers around the northern Irish Sea

Publication	Locality	Comment
De Tabley (1899)	Cheshire (v.c.58)	Notes presence of *C. anglica* and *C. danica* but confirms *C. officinalis* not found.
Wheldon & Wilson (1907)	West Lancashire (v.c.60)	Records *C. officinalis, C. danica, C. anglica*
Savidge *et al*. (1963)	South Lancashire (v.c.59)	Records *C. anglica* var. *gemina* and var. *hortii*
Newton (1971)	Cheshire (v.c.58)	Records *C. anglica* and *C. danica*
Allen (1984)	Isle of Man (v.c.71)	Doubts presence of *C. scotica* and problems with identity of *C. anglica*
Hackney (1992)	N.E. Ireland	Records *C. x hollandica*
Wynne (1993)	Flintshire (v.c.51)	Records *C. anglica, C. officinalis* and *C. danica*
Halliday (1997)	Cumbria (v.c.69, 70)	Records *C. officinalis* and *C. danica* but doubtful about *C. anglica*
Chater (2010)	Cardiganshire (v.c.46)	Records *C. atlantica* as a stabilised hybrid
Greenwood (2012)	North Lancashire (v.c.60 & part of 64)	Many salt marsh plants may be *C. atlantica*
Hannah (2019)	Isle of Bute part of v.c.100)	Records *C. officinalis, C. atlantica* (probably) and *C. danica*

In addition, plants on exposed shores of northern Scotland were described as morphologically distinct by 19th century botanists but were superficially similar to plants elsewhere in western Scotland and from the shores of the northern Irish Sea. Druce (1929) named them as *C. scotica* (holotype at **K**) but it was originally named *C. groenlandica* by Marshall in 1892. However, the status of *C. scotica* in Scotland was questioned by Scott and Palmer (1987) and Rich (1991) who considered it a variant of *C. officinalis*. Earlier chromosome counts of 2n = 24 by Gill (1971) suggested this was the case.

There have been no confirmed counts for *C. atlantica* although Godfrey (2010) published a count of 2n = 24 or 12 for plants gathered in Sutherland, northern Scotland but this was thought to be suspect (Rich, pers. comm.). As *C. atlantica* and *C. scotica* can be confused it is possible the counts were for *C. scotica*.

Recent Studies

In order to ascertain the identity of salt marsh *Cochlearia*, plants were gathered in April/May when basal leaves were still present from the Isle of Man, Lancashire, Merseyside, Cheshire and Flintshire. Many of the plants were growing in the short turf of *Festuca rubra* dominated marshes or in open habitats on stabilised shingle. These plants (Fig. 4) were similar to *C. atlantica* as described by Rich (1991). It was also apparent that larger plants occurred in various salt marsh habitats with the largest plants (*c*.35 cm) found in tall mid-marsh communities on the Dee estuary (Fig. 5). These plants were initially identified as *C. anglica*. Nevertheless, it soon became apparent there was a continuum in morphologies between small plants growing in low growing vegetation and those growing in the tall vegetation of mid-marsh communities. None of the plants quite fitted the published descriptions for recognised species. Nevertheless, they all had at least some rosette/basal leaves where the lamina base was truncate and all were at least partially fertile. Many of the larger plants on the Dee estuary also had leaf laminas with cuneate bases and were about twice as long as broad. Isle of Man plants from Ramsey had more or less orbicular basal leaves with slightly cordate lamina bases. Fruit shapes and sizes varied with small rounded fruits in *Festuca rubra* marshes in the Isle of Man to large capsules with indented septa for some plants from mid-marsh communities on the Dee estuary. It was also observed that on the Dee estuary some plants produced axillary shoots late in the season confirming the observation of T.R.A. Briggs (MS note, *c*.1875, found with *Cochlearia* specimens at **BM**) that vegetative reproduction was possible. Some of the variation noted is summarised in Table 3.

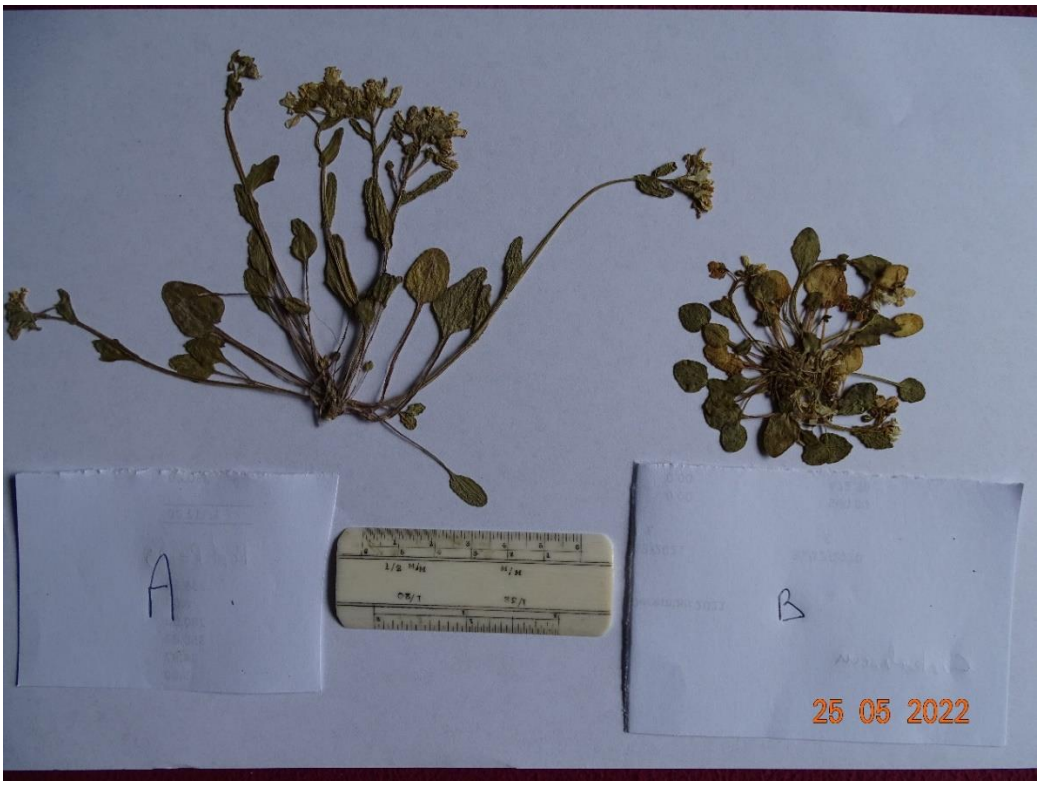

Figure 4. Small plants similar to *Cochlearia atlantica*. A. upper salt marsh, Red Rocks, Hoylake, Merseyside. B. Stabilised muddy shingle, Cockerham, Lancashire

Figure 5. Large *Cochlearia* plants in mid-marsh salt marsh communities, Heswall, Dee estuary, Merseyside

Table 3. Characteristics of *Cochlearia* plants from northern Irish Sea localities

Locality	Leaf base	Flower diameter (mm)	Seed morphology	Seed (mm)	Plant height (cm)
Port Cornaa, Isle of Man (v.c.71)	Truncate/ cuneate	8	Orbicular Tuberculate	1.4	20
Ramsey, Isle of Man, Sulby River *Festuca rubra* marsh (v.c.71)	Truncate/ cordate	11	Orbicular Tuberculate		20
Ramsey, Isle of Man, inner harbour (v.c.71)	Weakly cordate	11	Orbicular		20
Pot grown, ex West Kirby (v.c.58)	Truncate/ cuneate	16	Orbicular? Tuberculate esp. on keel	2.0	25
Flint Castle (v.c.51)	Truncate/ cuneate	16	Bilobed/orbicular, Serrate	1.2	20
Lancashire marshes (v.c.60)	Truncate	10	Orbicular Tuberculate		20
West Kirby 1 (v.c.58)	Cuneate	9	Orbicular Minutely tuberculate	1.1	40
West Kirby 2 (v.c.58)	Cuneate	15	Oblong compressed, constricted Minutely tuberculate esp. on keel	1.3, 1.5	40

Seeds were taken from a range of plants and these germinated readily in the autumn. The young plants grew rapidly during the winter and irrespective of the parents they all grew into large vigorous plants. But, seedlings from large parents on the Dee estuary when grown in stressed (pot bound) conditions, produced small plants with orbicular laminas with truncate to slightly cordate lamina leaf bases (Fig. 6). These cultivation experiments suggested that gross morphologies were influenced by environmental factors. Furthermore, both in the wild and in plants grown from seed the morphological features involved characters found in both *C. anglica* and *C. officinalis.*

Figure 6. Small basal leaves of plant illustrated in Figure 7 but grown in stressed (pot bound) conditions showing slightly cordate lamina bases

Rich (1991) suggested seed characters could separate *C. anglica* from *C. officinalis* and that those for *C. atlantica* were intermediate. Table 4 shows that for a range of plants the seed sizes were intermediate between the two supposed parents and similar to *C. atlantica*. The seed sculpturing was also different with two rows of prominent tubercles on the keel of seeds of *C. anglica* but more or less evenly covered with small tubercles in *C. officinalis*. Jermy & Crabbe (1978) reported that seeds of *C. atlantica* from the Island of Mull in western Scotland had tubercles that were slightly more pronounced on the keel.

Plants from the Dee estuary had a range of seed sculpturing from pronounced tubercles on the keel to ones almost evenly covered with tubercles. Seeds from Lancashire and Isle of Man showed less variation and were more evenly covered in tubercles. Although seed of *C. officinalis* from Peel Castle had tubercles all over the seed they were more pronounced on the keel. Leaf morphologies for some of the plants are illustrated in Figs. 7–11.

Table 4. *Cochlearia* seed dimensions from northern Irish Sea plants. (Seed sizes ex Rich, 1991: *C. officinalis* s.s. 1.1–1.5 mm; *C. anglica* 1.5–2.3 mm; *C. atlantica* 1.4–1.8 mm)

Site	Date collected	Dimensions (mm)	Average	Putative identity
Peel Castle (Fig. 10)	July 2021 May 2022	1.5 x 1.25 1.7 x 1.4	1.6 x 1.3	*C. officinalis*
Strand line Sulby River, Isle of Man (Fig. 11)	July 2021 May 2022	1.6 x 1.4 1.5 x 1.2 1.7 x 1.3	1.6 x 1.3	*C. officinalis*
Heswall ex axillary shoot (Fig. 7)	July 2021 May 2022	2.5 x 2.0 2.0 x 1.5	2.2 x 1.0	Hybrid origin?
Red Rocks, Hoylake (a) (Fig. 8)	July 2021 July 2021 May 2022	2.2 1.9 2.2 x 1.7 2.1 x 1.4 1.9 x 1.5	2.1 x 1.6	Hybrid origin?
Heswall ex root cutting	July 2021 May 2022	1.25 x 1.1 1.8 x 1.6	1.5 x 1.3	Hybrid origin
Red Rocks, Hoylake (b)	July 2021	1.6 x 1.5 2.1 x 1.8 1.6 x 1.5	1.8 x 1.6	Hybrid origin
Stannah, Lancashire (Fig. 9)	May 2021	2.0 x 1.5	2.0 x 1.5	Hybrid origin

Figure 7. Basal leaves of plant grown from an axillary shoot. Parent from Heswall, Merseyside mid-marsh salt marsh community

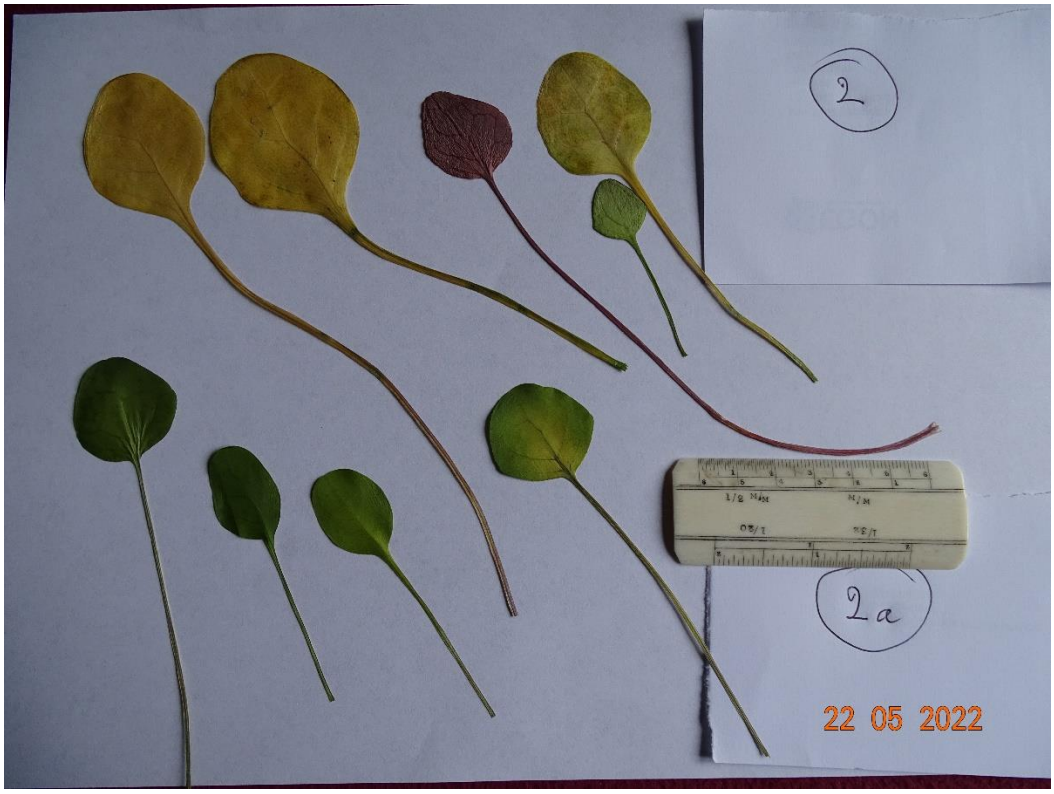

Figure 8. Basal leaves of plant grown from a large plant at Red Rocks, Hoylake, Merseyside

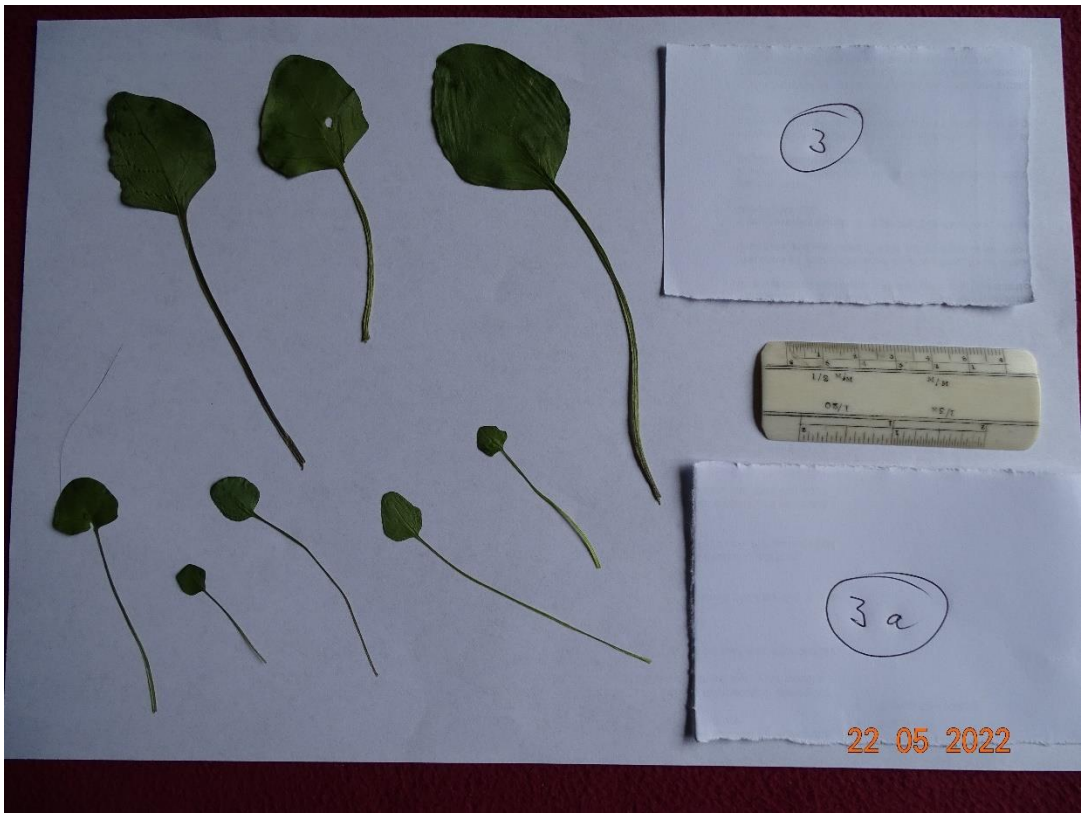

Figure 9. Basal leaves of plant grown from a plant at Stannah, Wyre estuary, Lancashire

Figure 10. Basal leaves of plant grown from a plant at Peel Castle, Isle of Man with cordate lamina bases. *Cochlearia officinalis*

Figure 11. Basal leaves of plant grown from a plant on the strand-line by the Sulby River, Ramsey, Isle of Man with slightly cordate lamina bases. *Cochlearia officinalis*

With a wide range of morphological variation in coastal *Cochlearia* plants from the coasts of the northern Irish Sea but with characters from both *C. anglica* and *C. officinalis* it was suggesting that they were derived from the hybrid *C. anglica* x *C. officinalis*. Such a conclusion should be confirmed by cytology.

Cytology of northern Irish Sea *Cochlearia*

The technique used was a modification of that developed by Dyer (1963).
Pretreatment - Rapidly growing root tips were put into vials of a saturated aqueous solution of 1-bromo-naphthalein and placed overnight in a refrigerator at 1°C.
Fixation - The following morning these were transferred to freshly mixed 3:1 ethyl alcohol:glacial acetic acid and stored for at least 12 hours in a fridge ice box.
Hydrolysis – The root tips were transferred to vials of 1M HCl at 60°C in a water bath for 5 mins, then to 70% ethanol for storage.
Slide preparation - The densely cytoplasmic region of root tip was cut off and placed in drop of 3:2 lacto-proprionic acid on a slide, a coverslip applied, and the root tip tapped out to a monolayer of cells and then squashed and examined by phase contrast microscopy. Table 5 shows the chromosome counts for nine samples.

Table 5. Chromosome counts for *Cochlearia* from around the shores of the northern Irish Sea

Site	Habitat	Count (2n)
Peel Castle	Maritime cliffs	24
Sulby River, Ramsey	Strand line	24
Sulby River, Ramsey	*Festuca rubra* salt marsh	36
Ramsey Inner Harbour	Stabilised shingle	36
Stannah, Lancashire	Upper salt marsh	36
Heswall, from axillary shoot	Mid marsh	36
Red Rocks, Hoylake (a)	Mid marsh	36
West Kirby	Mid marsh	36
Flint Castle	*Festuca rubra* marsh	36

Plants from Peel Castle and the strand line at Ramsey, both in the Isle of Man had counts of 2n = 24. The rosette leaves had more or less orbicular fleshy laminas with cordate bases (Figs. 10 and 11). These plants were considered typical of *C. officinalis*. All other samples had counts of 2n = 36.

The larger plants from the Dee estuary and elsewhere have often been recorded as *C. anglica* or *C. officinalis* (Taylor & Burrows, 1968; Wynne, 1993) but agree with descriptions of *C. x hollandica* that show hybrid vigour (Clapham *et al*., 1957; Pegtel, 2008) whilst small plants agree with the type description of *C. x hollandica* (Henrard, 1914/16) but also *C. anglica* var. *hortii*, *C. briggsii* and *C. atlantica*.

In this study plants with 2n = 48 have not been seen so that it has not been possible to clarify the morphology for *C. anglica*. Perhaps it is significant that 19th century material labelled as *C. anglica* often showed plants with long narrow basal leaves several times longer than broad, with strongly cuneate lamina bases (Fig. 2, lower right-hand plant).

Discussion

It is our belief that the hybrid derivative *of C. anglica* x *C. officinalis* is widespread and common in coastal salt marshes of N.W. Europe and that *C. anglica* is much less common. On the coasts of the northern Irish Sea *C. anglica* has not been confirmed whilst *C. officinalis* occurs on rocky shores, strand lines and occasionally as a casual elsewhere, e.g. Parkgate, Cheshire (Gill *et al*., 1978), the first confirmed record for the Dee estuary; central reservation north of Queensferry Bridge, Flintshire (Wynne, 1993); Ainsdale 'green beach', Phil Smith, pers. comm.). Throughout much of its range the hybrid derivative is probably found in the absence of either parent. On the Wirral *Equisetum x meridionale* (Milde) Chiov. is similarly found in the absence of one or possibly both parents whilst more widely distributed *Circaea x intermedia* Errh. is well-known for occurring in the absence of its parents (Stace, 2019).

The origin and clearly self-replicating 'species-like' behaviour of *C. anglica* x *C. officinalis* is paralleled by the examples of *Rubus loganobaccus* L.H. Bailey, the Loganberry (Crane, 1940) and the birch, *Betula x utahensis* Britton (Brittain & Grant, 1966); two species of different ploidy levels giving rise, often repeatedly, to what should probably be treated for practical taxonomic purposes as a new species of intermediate ploidy level.

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