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List Br. Vasc. Pl. (1958) no. **441**, 1–4

Pinguicula L.

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The genus *Pinguicula* L. (Lentibulariaceae, Butterworts) consists of some 50 species (Casper 1966) which are present on all continents except Australia and all but the extreme north-west of Africa. In Europe, 12 species were described by Casper (1972). Nine species (including two newly described by Blanca *et al*. 1999) occur on the Iberian peninsula, of which five are endemics. In the British Isles today there are just three species (i) *P. vulgaris*, (ii) *P. grandiflora* and (iii) *P. lusitanica*, and a fourth, *P. alpina* (iv), existed in Scotland at a very limited number of sites in the nineteenth century, and finally became extinct around 1900‡. In common with those in Spain, the representatives of the genus in the British Isles belong to the three subgenera into which it has been subdivided (Casper 1966), subgenus **Pinguicula** Casper for (i) and (ii), subgenus **Isoloba** Barnhart for (iii) and **Micranthus** Casper for (iv). The species are herbaceous, relatively short-lived perennials (although occasionally behaving as annuals) and of rosette habit whilst in active growth, some overwintering as hibernacula. Many reproduce vegetatively by means of bulbils and/or epiphyllous buds which later take root. Unlike members of the other two genera (*Genlisea* and *Utricularia*) in the family, all species of *Pinguicula* bear true roots, which are either fibrous, tufted, and often ephemeral, or, as in *P. alpina*, swollen and perennial. The leaves, which in most species lie appressed to the ground, are occasionally heterophyllous and the later formed ones may be larger and semi-erect (whereby the plant can tolerate more shaded conditions). The leaves are adapted for insectivory and bear glands of two types (stalked and sessile) on the upper surfaces. The stalked glands carry permanent mucilaginous droplets giving the characteristic greasy feel, and the generic name is derived from the Latin *pinguis*- fatty or greasy to the touch. The gland secretions can trap and digest prey, and the glands then absorb the products of digestion (Heslop-Harrison & Knox 1971; Heslop-Harrison 1978; Heslop-Harrison & Heslop-Harrison 1980, 1981), as first reported by Darwin (1875). Most species are confined to wet, relatively open sites and do not withstand much competition from other plants.

Cladistic analyses have shown the ordinal classification of the family Lentibulariaceae to be placed accurately in the Lamiales (APG 1998), and the phylogenetic relationships of the genera *Pinguicula*, and *Genlisea*, inferred from rps16 and trnL-F sequence data, have been made in relation to molecular systematic studies (Jobson *et al*. 2003). Sequence analyses in most of the European species of *Pinguicula* have been made using the internal-transcribed (ITS) R DNA region by A. Schmidt (1998), and from these results he has proposed a phylogenetic tree for the species. The only DNA *C*-value recorded for the genus is for the American *P. primuliflora*, which was estimated to have a 1C DNA amount of 0.68 pg (= 669 Mbp) (Hanson *et al*. 2001).

List Br. Vasc. Pl. (1958) no. **441**, 3

Pinguicula vulgaris L.

Common Butterwort. Subgenus Pinguicula, Section Pinguicula. An insectivorous perennial consisting in summer of a rosette of 4–7(–11) leaves lying close to the ground, shallowly anchored by a tuft of fine, fibrous roots. Overwintering as a hibernaculum. Leaves sessile, bright, yellowish-green ('pod green', 61/1 of British Colour Chart 1941), occasionally pink-tinged on lower surface, somewhat fleshy in texture, the upper surface bearing stalked glands holding secretion droplets giving the characteristic greasy feel. Laminae (1.0–) 2.5–5.0(–9.0) cm long (0.07–)1.0–2.0(–2.7) cm wide, ovate-oblong, increasing in size towards the end of the growing season; margins entire and capable of inrolling after stimulation of the upper surface by an insect or other nitrogenous material. Scapes ebracteate, 1–8 per plant, produced in succession in early summer; one, rarely two, per leaf axil, yellowish-green or tinged with purple, glandular (5–)6–15(–27) cm long, increasing in length as the fruit develops. Flowers solitary, bisexual and zygomorphic. Normally the flower assumes a

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†Abbreviated references are used for standard works: see *Journal of Ecology* (1975), **63**: 335–344. Nomenclature of vascular plants follows Stace (1997).

‡Pertinent comparisons with, and references to, *Pinguicula* species in this account are not always repeated, so each species should be read in conjunction with the others.

horizontal posture at anthesis, but is occasionally held more or less erect. Calyx greenish-purple, glandular externally, bilabiate, the upper lip 3-lobed, with the lobes dissected to the middle or less; lower lip 2-lobed, the lobes ovate or oblong, acute or subacute and split to 2/3 of the calyx length. Corolla lilac or blue-violet (735/1 or 39/1 of British Colour Chart), with darker markings of violet (36/1), 14–20 mm in total length (tip of lower lip to end of spur), with the anterior portion bilabiate and expanding into 5 oblong, flat lobes, 2 above and 3 below; lower corolla lip 0.7–1.2 cm wide, without a palate, the almost rectangular lobes not overlapping and without the wavy margins characteristic of *P. grandiflora*. Honey guide in the form of an indistinct white or paler area on the lower lobe, bearing numerous uniseriate, multicellular hairs guarding the entrance to the corolla tube, the hairs also extending beyond the paler area for *c.* 1/2–1/3 the length of the lower lip. Corolla tube whitish internally, with indistinct brown-purple lines running into the spur. Posterior portion of the corolla tube extending backwards from between the sinus of the lower calyx lip, contracted into a straight or slightly downwardly curved, conical spur, 2–5(–10) mm long, the tip rarely bifid. The 2 stamens inserted opposite the 2 anterior sepals, the white or pale purple filaments curving round the ovary until the 2 patelliform anthers lie side by side, just below the stigmatic flap. Pollen grains spherical, stephanocolporate with 6–8 pores and a finely reticulate sexine, 33–36 µm in diameter. Stigma sessile, reduced to 2 flaps, the upper usually tiny, the lower larger and pendulous, with fringed margins, wet surfaced at maturity, and normally hanging in front of the anthers. Carpels 2, forming a unilocular ovary giving rise to an ovoid or spindle-shaped capsule, 0.5–1.0 cm long and 0.3–0.5 cm wide. Developing fruit at first horizontal, becoming erect at maturity and dehiscing along the placental margins. Ovules anatropous with a single integument, the seeds developing on a free-central, kidney-shaped placenta. Seeds small and powdery, ellipsoidal, 0.5–0.9 mm long, 0.16–0.32 mm wide with a reticulate, brown testa, the alveolar reticulations rather elongated; non-endospermous. Mean seed mass (air-dried) 23.8 µg (from sample from subarctic Sweden, ex Karlsson 1986). Embryo straight. Seedlings with a single cotyledon.

Rather uniform in Britain in the wild, but possibly more variable in size, form and colour elsewhere in Europe, Asia and North America. The var. *bicolor* Nordstr. ex Fries has been recorded from Lough Derg, Ireland (Bot. Irl. 1934, p. 354) and Scandinavia (Casper 1962). *Pinguicula bicolor* Wol. (Zurzycki 1954) has the calyx members more deeply incised, white corolla lobes and purple spur; plants with these features have also been found in some British populations, but the form is best regarded as a variant of *P. vulgaris*, not a distinct species (Casper 1962). A variety with white flowers was found in Morven, Caithness (Dickie 1860), possibly the equivalent of the continental f. *albida* (Behm.) Neumann. Another form with the lobes of the lower lip of the corolla contiguous was recorded in Britain (Newbould ex Sowerby *Engl. Botany* 1863, p. 123) and also in Sweden (Casper 1962; quoting Melander 1883, and Neumann 1901). A form with deformed spurs has been reported in east Ross-shire (Duncan 1980). Many morphological variants have been observed during the cultivation of large numbers of plants of this species; these involved the absence, fusion or bifurcation of one or more of the calyx or corolla lobes, and occasional petaloidy of the calyx or stamens (Y. Heslop-Harrison, unpublished); the extent of white colouration at the entrance to the corolla tube also appeared to vary considerably.

Native. This insectivorous perennial occurs mainly in seepage channels in the less acid parts of bogs, mires, calcareous fens and flushes, wet heaths and on wet rocks.

I. Geographical and altitudinal distribution

Pinguicula vulgaris is a northern, disjunctly circumpolar species, and belongs to the Circumpolar Boreal-montane element (Preston & Hill 1997). It is common in the northern and upland parts of the British Isles, but becomes much more local in south Ireland; in lowland and southern parts of England it is absent from large areas (Fig. 1). In East Anglia there is a marked reduction in the Norfolk sites since 1962; its scarcity has been probably accentuated recently by the drainage of suitable habitats for agricultural and other purposes. The species is widespread in Europe, extending into Corsica, Italy and Macedonia and across Siberia into north Asia (Casper 1970) but it thins out eastwards to western Ukraine (Fig. 2). Its most northerly limit is on the east coast of Greenland (73°11′ N) and it occurs in Iceland, throughout Scandinavia (Hultén 1950), and southwards into central Spain and north Portugal. Its occurrence in north Morocco is reported by Blanca *et al.* (1999), but some earlier reports were said to be based on misidentifications (Romo *et al.* 1996). In North America it extends from Alaska in the north, throughout Canada from Newfoundland to British Columbia, and as far south in the USA as northern New York State (Fernald in Gray's *Manual*, edn 8, 1950; Hitchcock *et al.* 1959), the southern limit being roughly equivalent to that in Europe. In China, Japan and the western coastline of North America it seems to be replaced by *P. macroceras* Link, distinguishable from *P. vulgaris* by the larger calyx, with the lobes of the lower lip separated for half of their length, the larger corolla with deeply rounded lobes to the corolla lip, and the longer spur (Casper 1962). The northern and eastern limits of *P. macroceras* in the USA, however, are incompletely known (Fig. 2), and Hultén (1948) was unsure that this species could always be regarded as distinct from *P. vulgaris*.

Of the representatives of the genus in the British Isles, *P. vulgaris* has the greatest altitudinal range for it grows luxuriantly close to sea level on the west coast of

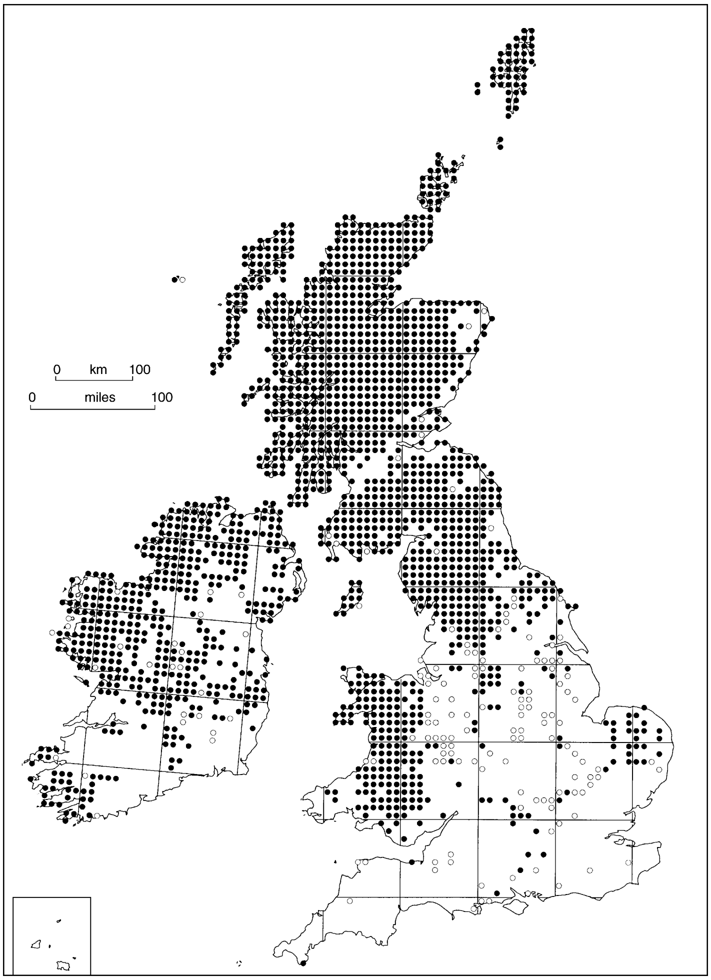

Fig. 1 The distribution of *Pinguicula vulgaris* in the British Isles. (○) Pre-1950; (●) 1950 onwards. Each symbol represents at least one record in a 10-km square of the National Grid. Mapped by Henry Arnold, Biological Records Centre, Centre for Ecology and Hydrology, using the DMAP programme. Records mainly collected by members of the Botanical Society of the British Isles.

Scotland and in Ireland; in Wales and northern England it is quite common above 300 m (even 'abundant', Bevis & Jeffery 1911) and in Scotland it occurs up to *c.* 1040 m (Fl. Br. Isl.); in west Mayo it occurs over 600 m (Praeger 1909, 1930, 1950). Elsewhere in Europe it grows most commonly in subalpine stations from 600 m to 850 m but ascends to *c.* 2600 m in the Pyrenees (Blanca *et al.* 1999), *c.* 2200 m in the Alps and up to 910 m in Norway (Casper 1962). Geographical and altitudinal tolerance of the species is correlated with the seasonal variations in temperature that it can withstand, and the duration of the growing season; altitude does not appear to limit its distribution in the British Isles (see also II).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

A high humidity requirement during the growing season limits the number of suitable habitats available (by means of a high water table, a constant water supply, snow melt and rainfall, etc.) for the species, and it can survive only some degree of desiccation as a hibernaculum. In Britain its distribution seems limited by the number of suitable wet areas available, whether sloping or flat; also presumably wherever the precipitation/evaporation (P/E) ratio (effectively humidity) is high enough for it to grow. Thus it can be found colonizing slopes of as much as 30° on hillsides facing the sea with a sandy substratum in the west of Scotland. It also grows occasionally in very slowly moving shallow water that neither immerses the leaves nor dislodges the shallow root system. On hills in Sutherland it was found predominantly on north-facing slopes (Gimingham & Cormack 1964), perhaps because the south-facing areas became too dry during periods of summer sunshine. This northerly preference confirms an early record of its occurrence only on the north-west side of the Malvern hills (Worcestershire), but not on the south or south-eastern slopes (Ballard, ex Withering 1818). Although primarily distributed in the north-west of Scotland, Wales, Ireland and the western parts of England where the average rainfall may be *c.* 800–1200 mm per annum, it also occurs in a runnel flora in the fens in East Anglia, where it is part of the *Schoenus nigricans–Juncus subnodulosus* mire community (Rodwell 1991b).

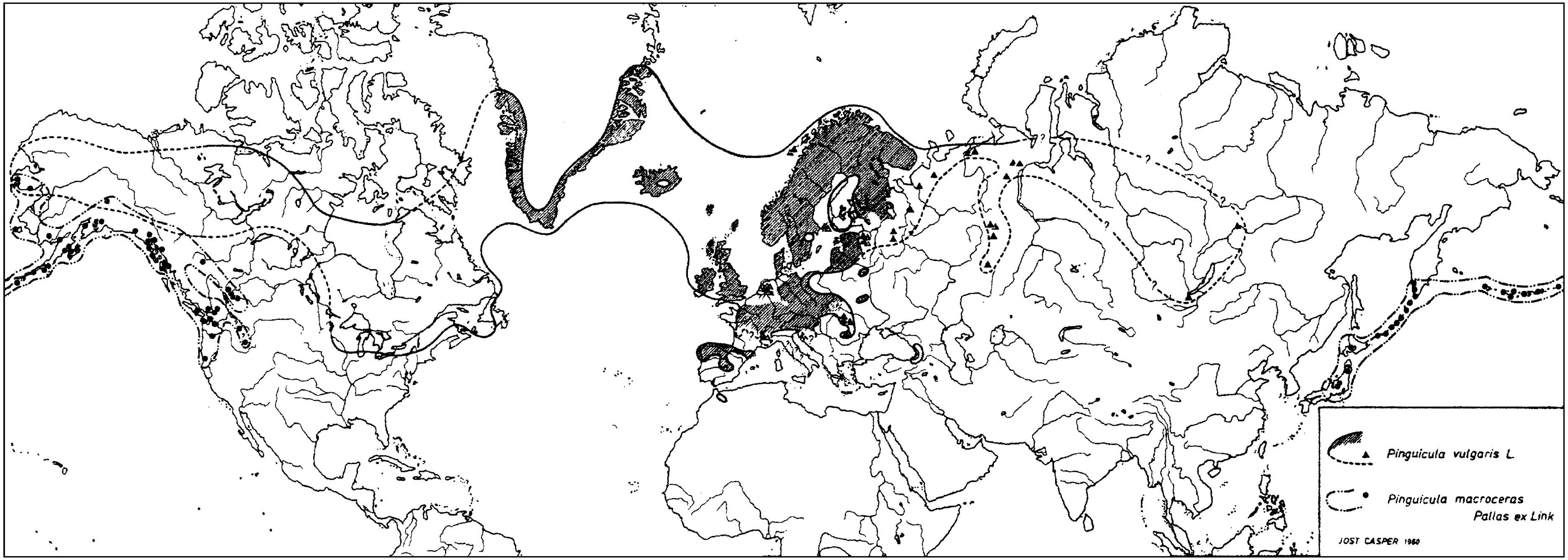

Fig. 2 The distribution of *Pinguicula vulgaris* world-wide; its main area of distribution lies within the shaded areas within the continuous line, and the triangles show its scarcer presence within the dotted lines. The distribution of the related *P. macroceras* in Asia and North America is also shown (see text); its presence is shown as circles within dot/dashed areas. Adapted by Glyn Woods, from Casper (1962) and Hultén (1950, 1958).

Pinguicula vulgaris can withstand freezing as a hibernaculum, but not during the growing season, and the duration of this will control its altitudinal limits throughout its range. The hibernaculum can withstand several centimetres of snow cover for some months. In subarctic Sweden it is most commonly found in stabilized frost polygons, whereas *P. alpina* occurs in more active polygons (Karlsson 1986; Svensson *et al*. 1993; Eckstein & Karlsson 2001), but the two species may occasionally grow together in 'wet holes' amongst polygons (Mendez & Karlsson 1999).

(B) SUBSTRATUM

The occurrence of *P. vulgaris* in any particular locality seems to be governed mainly by the availability of water rather than by the type of substratum. Although shallow rooting, it can colonize wet rock faces as well as peaty or sandy ground kept permanently moist by seepage.

The minimum and maximum soil pH ranges of the communities in which *P. vulgaris* occurs are in the *Calluna vulgaris–Eriophorum vaginatum* blanket mire (M19) at 3.1–6.2 and the *Carex dioica–Pinguicula vulgaris* mire (M10) at 5.8–7.2 (Rodwell 1991b). In western Scotland, where *P. vulgaris* occurred on calcareous peat or marl in a *Schoenus nigricans* mire, a pH of 8.0 was recorded (Veg. Scot., p. 439). In the *Schoenus nigricans–Juncus subnodulosus* mires (M13) of East Anglia and Anglesey (Rodwell 1991b) the flushing waters had a pH of between 6.5 and 8.0, with dissolved calcium levels of 60–200 mg L^{-1} (Wheeler 1975, 1984). In Ireland, apart from its more typical habitat, it occurs along the shores of the calcareous lakes of Lough Derg, Co. Donegal, and Loughs Corrib and Carra, Co. Galway (Bot. Irl.). Praeger describes the waters of the latter as a 'wonderful pale pellucid green … (being derived mainly from springs) … partly due to a curious soft, whitish calcareous deposit which envelops the whole bottom of the lough and reflects the light'. Values of soil and water pH for *P. vulgaris* in British fens are given in Table 1, and at three sites in northern Sweden, together with soil water and ash content.

Within the United Kingdom it 'seems to show pronounced regional variation in the range of base-richness it regularly accommodates' (B.D. Wheeler, personal communication), and its occurrence does not always relate to the type of habitat available in any area. Thus 'in East Anglia, to the best of my knowledge, it is invariably associated with highly calcareous mires, though lower pH mires, whilst rather scarce in the area, do occur'. Wheeler also notes that 'in the New Forest area *P. vulgaris* is absent from base-rich sites which are well within its normal range elsewhere in lowland England, as well as being absent from the base-poor mires that are also within its range elsewhere in the UK (but not in southern or eastern England)'. He also wonders 'why does *P. vulgaris* not grow in many of the base-poor sites favoured by *P. lusitanica*, as these are undoubtedly within its ecological range' (this is discussed further in the account of the latter species).

Table 1 pH values for soil and water for some English fen (FenBASE communities) and northern Swedish habitats of *Pinguicula vulgaris*

pH	Extreme minimum	Typical minimum	Typical maximum	Extreme maximum
Location				
(a) UK*				
Soil pH	3.94	5.64	7.28	7.56
Water pH	4.14	5.64	7.08	8.22
(b) Sweden†		Means ± SD		
pH (KCl)$^+$	Site A	3.9 ± 0.16		
	Site B	5.0 ± 0.27		
	Site C	4.2 ± 0.20		
Water content	Site A	16.4 ± 0.03		
Ash content	Site A	97.0 ± 1.2		

*Data from B. D. Wheeler & S. C. Shaw 1992 (personal communication).

†Data from Karlsson (1986), from top 5 cm of soil on sites. Ash and water content expressed as percentage dry weight. Sites A and B at *c.* 68°21′ N, 18°49′ E, and site C at *c.* 68°25′ N, 18°10′ E, north Sweden, all with different edaphic conditions. *n* = 5.

$^+$KCl analyses give pH values appreciably lower than measurement in water.

In 1911, in east Leicestershire, *P. vulgaris* grew 'in a limestone swamp' and was 'rediscovered' there in 1933 on leached-out detritus and peat on limestone (Horwood & Gainsborough 1933).

Elsewhere in Europe *P. vulgaris* is 'indifferent to soil type' (Blanca *et al*. 1999). As in the British Isles it has a wide pH tolerance from *Scirpus cespitosus* associations, pH 4.9 (Böcher 1954), to pH 5.7–7.2 in others in the west Pyrenees (Turmel ex Casper 1962). In Swedish Lapland, in a subalpine tundra at Abisko (68°21′ N, 18°49′ E), the soil pH surrounding plants of *P. vulgaris* was 5.6 ± 0.2, but at Katterjakk, 24 km west of Abisko, it was 4.1 ± 0.1 (Aldenius *et al*. 1983). In the Norwegian arctic it occurs occasionally in areas inundated by the sea (Norman 1894–1901). According to Molau (1993), who studied the species in west Greenland, and at sites in the Abisko mountains and at Latnjajaure Field Station, Sweden, it was found in base-rich habitats. Braun-Blanquet (quoted by Bauquis & Mirimanoff 1970) believed that *P. vulgaris* was usually asssociated only with areas rich in calcium and that, if the species occurred on gneiss, it was because there was a supplementary source of calcium. Favarger (1962) proposed the testing of this theory by analysing the calcium content of water running off gneiss in Val d'Emaney, Haute Savoie, France. However, Bauquis & Mirimanoff (1970) analysed the seepage water from this, as well as from other localities where the substratum was of calcareous origin (and where the species was abundant) and concluded that calcium was not a factor governing the distribution of *P. vulgaris*; the amounts of calcium in ground water varied from 7.15 to 164.0 mg L^{-1}.

That *P. vulgaris* is absent from certain areas of Scandinavia and Germany, as well as parts of North America well within its range, suggests that some of its requirements, or tolerances, are not, as yet, understood. Ratcliffe (1964a Veg. Scot., p. 433) draws attention to the fact that some species have different nutrient tolerances in different parts of their geographical range 'with the general tendency to become more exacting and calcicolous towards their limits'. In the eastern United States the species is chiefly limited to calcareous soils (Fernald 1950, p. 1308).

III. Communities

In the British Isles *Pinguicula vulgaris* is most characteristic of marshes, mires and wet, peaty heaths and fens. In these habitats it is restricted to areas where the associated plants are relatively low growing for, being a rosette plant appressed to the ground, it cannot tolerate much shade from taller vegetation. Wherever sites have been subjected to drainage in the past it is usually lost to the community. Its comparative rarity in the East Anglian Fens has been explained by the excessive height of this community of plants, as well as drainage of the area (Gilmour & Walters 1954); whilst in Dorset its disappearance was explained by possible climatic amelioration in recent times (Good 1953, p. 257). It never grows directly amongst *Sphagnum*, perhaps because it cannot compete here with the upward growth of this plant, so it tends to be associated rather with the wetter seepage channels. In Scotland, it is often found in open stony flushes with a very sparse plant cover (often of less than 50%), which, nevertheless, consists of a very distinct assemblage of plants, the most abundant species, apart from *P. vulgaris*, being *Carex demissa* (*C. viridula* ssp. *oedocarpa*), *C. panicea*, *Festuca ovina* agg., *Juncus triglumis*, *Saxifraga aizoides*, *Thalictrum alpinum* and *Blindia acuta* – such assemblages being found in open places between birch-juniper woods (Veg. Scot.). In the west of Scotland it is also found as a member of wet areas of the machair community, but this habitat is rather atypical for it. On the Isle of Skye it was recorded in a rich upland fen as a constant in the *Eriophorum latifolium–Carex hostiana* association along with *Carex viridula* ssp. *oedocarpa*, *C. panicea*, *Drosera anglica*. *Eleocharis quinqueflora*, *Eriophorum latifolium*, *Schoenus nigricans*, *Campylium stellatum* and *Scorpidium scorpioides* (Birks 1973).

The British National Vegetation Classification (NVC) (Rodwell 1991b, 1992) records *P. vulgaris* in a range of mire, blanket mire, springs, flushes, wet heath and heath, and calcicolous and calcifugous grassland communities as well as on wet rock ledges, exposed rocks and cliffs.

Pinguicula vulgaris is a constant, with a frequency of 81–100% occurrence in the samples examined in the *Carex dioica-Pinguicula vulgaris* mire (M10) as a whole and in several of its subcommunities and variants (Table 2). These are of widespread, but local, occurrence in northern England and Scotland, on soligenous mineral soils and shallow surface peats kept wet by base-rich, calcareous and oligotrophic waters. It is also constant in the *Cratoneuron commutatum–Eleocharis quinqueflora* subcommunity of the *Carex viridula* ssp. *oedocarpa–Saxifraga aizoides* mire (M11) which occurs in the Scottish Highlands, Southern Uplands, the Lake District, the northern Pennines and in north Wales.

Other mire communities in which *P. vulgaris* occurs with a frequency of 61–80% in the samples studied are: the *Carex hostiana–Ctenidium molluscum* variant of the subcommunity (M10a), which is confined mainly to northern England and Scotland; and the *Briza media–Primula farinosa* subcommunity (M10b) and its flush vegetation variant *Molinia caerulea–Eriophorum latifolium*. In the latter variant, from Tarn Moor in Cumbria, and Upper Teesdale, the hummocks produced by the trampling of grazing animals provide excellent habitats for *P. vulgaris* rosettes. In the third subcommunity of M10, *Gymnostomum recurvirostrum* (which is confined to Upper Teesdale) hummocks are produced by the breakdown of this moss by wind erosion and age. The sheltered lee sides of the hummocks, amongst the gravel flushes, then provide sites for *P. vulgaris* and other rosette-forming dicotyledons.

Pinguicula vulgaris is also a constant, but with the lower frequency, in the *Carex viridula* ssp. *oedocarpa–Saxifraga aizoides* (M11) community of open, stony flushes irrigated by relatively moderate base-rich waters on slopes in the montane to submontane parts of Britain; it is also present in the *Thalictrum alpinum–Juncus triglumis* subcommunity, which is confined to higher altitudes. It occurs likewise in the *Polygonum viviparum* variant (limited to the Clova-Caenlochan area) of this subcommunity and in the *Juncus bulbosus/kochii–Saxifraga stellaris* variant. Other communities in which it has the same constancy are the *Briza media–Pinguicula vulgaris* subcommunity of the *Schoenus nigricans–Juncus subnodulosus* mire (M13), which is restricted to Anglesey and East Anglia, and the *Carex panicea* subcommunity of the *Scirpus cespitosus* (*Trichophorum cespitosum*)–*Erica tetralix* wet heath (M15). This latter occurs mainly as small stands in soakways or water tracks in the wetter western and northern parts of Britain. *Pinguicula vulgaris* occurs with the same frequency in the *Saxifraga aizoides–Alchemilla glabra* banks community (U15), which is restricted to calcareous cliff faces in the Scottish Highlands and, occasionally, the Lake District.

Pinguicula vulgaris is also frequent (III, 41–60%) in the following communities (Rodwell 1991b, 1992): the *Briza media–Primula farinosa* subcommuniy of the *Carex dioica–Pinguicula vulgaris* community (M10), *Thymus polytrichus–Racomitrium uliginosum* variant, centred in Upper Teesdale, with *Plantago maritima* and *Thalictrum alpinum* occasional; the *Carex saxatilis* mire (M12) which occupies high-montane flushes irrigated with base-rich and calcareous waters in Scotland;

Table 2 Floristic tables for some *Pinguicula vulgaris* communities, subcommunities and variants. Roman numerals I to V denote the frequencies and give the percentage of stands in which the species has been recorded (I = 1–20%, II = 21–40%, III = 41–60%, IV = 61–80% and V = 81–100%). All tables listed had 81–100% (V) of stands in which *P. vulgaris* was present. The numbers in brackets refer to the range of Domin values reported. Species having a frequency no greater than I are omitted unless present in three or more of the stands. *n* = the number of stands recorded. Data from Rodwell (1991b)

NVC subcommunity/variant	M10				M11	
		a	**ai**	**aiii**	**bi**	**b**
	n = 217	*n* = 143	*n* = 51	*n* = 36	*n* = 9	*n* = 26
Agrostis stolonifera	–	–	–	–	–	II(1–3)
Anthoxanthum odoratum	II(1–7)	II(1–7)	II(1–7)		III(1–3)	–
Briza media	I(1–6)	II(1–4)	I(1–6)	–	–	–
Carex capillaris	I(1–3)	I(1–4)	I(1–3)	–	–	–
Carex dioica	III(1–6)	IV(1–6)	III(1–6)	III(1–5)	III(1–4)	II(1)
Carex echinata	II(1–7)	II(1–7)	II(1–5)	III(1–5)	II(1–3)	I(1)
Carex flacca	II(1–5)	I(1–6)	I(1–5)	II(1–5)	IV(1–4)	III(1–5)
Carex hostiana	IV(1–7)	IV(1–7)	II(1–6)	IV(1–5)	V(1–6)	II(1–3)
Carex nigra	III(1–7)	III(1–7)	III(1–7)	II(1–5)	IV(1–3)	I(1–5)
Carex panicea	V(1–5)	V(1–5)	V(1–9)	V(1–3)	V(1–4)	IV(1–5)
Carex pulicaris	IV(1–6)	III(1–6)	III(1–5)	II(1–3)	IV(1–3)	III(1–5)
Carex rostrata	–	–	–	–	–	II(1–7)
Carex viridula ssp. *brachyrrhyncha*	IV(1–6)	II(1–6)	II(1–6)	I(1–5)	IV(1–6)	–
Carex viridula ssp. *oedocarpa*	III(1–9)	III(1–9)	III(1–7)	III(1–5)	–	IV(1–5)
Eleocharis quinqueflora	III(1–7)	III(1–7)	IV(1–7)	III(1–7)	III(1–4)	IV(1–10)
Eriophorum angustifolium	IV(1–7)	III(1–7)	V(1–7)	IV(1–5)	III(1–3)	III(1–3)
Eriophorum latifolium	II(1–8)	II(1–8)	I(2)	III(1–8)	II(1–4)	–
Festuca ovina	II(1–5)	II(1–7)	I(1–5)	I(1–5)	I(1)	II(1–3)
Festuca rubra	I(1–5)	–	I(1–3)	–	II(1–3)	I(1–3)
Festuca vivipara	–	–	–	–	–	II(1–5)
Holcus lanatus	I(1–3)	–	–	–	III(1–3)	–
Juncus acutiflorus	I(1–4)	–	–	–	III(1–3)	–
Juncus articulatus	IV(1–5)	III(1–5)	III(1–3)	II(1–5)	IV(1–4)	IV(1–5)
Juncus bulbosus/kochii	II(1–6)	III(1–6)	III(1–6)	III(1–5)	–	I(1)
Juncus squarrosus	I(1–5)	II(1–5)	I(1–3)	I(1)	–	I(1)
Juncus triglumis	I(1–3)	I(1–2)	I(1–3)	–	–	II(1–3)
Kobresia simpliciuscula	II(1–8)	–	–	–	–	–
Luzula multiflora	I(1–3)	–	–	–	III(1–3)	–
Molinia caerulea	III(1–7)	III(1–7)	II(1–5)	IV(1–5)	V(1–6)	II(1–5)
Nardus stricta	I(1–7)	I(1–7)	I(1–5)	–	II(1–3)	–
Schoenus ferrugineus	I(1–10)	I(1–10)	–	I(1–10)	–	–
Schoenus nigricans	I(1–5)	II(1–5)	–	V(2–5)	I(1)	II(5–10)
Trichophorum cespitosum	I(1–5)	I(1–5)	I(1–5)	II(1–5)	–	I(1)
Angelica sylvestris	I(1–3)	–	–	–	IV(1–3)	–
Caltha palustris	I(1–4)	–	–	–	III(1–4)	–
Cardamine pratensis	I(1–3)	I(1)	–	–	V(1–3)	I(1–3)
Cirsium palustre	I(1–3)	I(1–3)	–	–	V(1–3)	–
Dactylorhiza fuchsii	I(1–3)	–	–	–	III(1–3)	–
Drosera anglica	I(1–5)	I(1–5)	–	IV(1–5)	–	–
Drosera rotundifolia	I(1–5)	II(1–5)	I(1–5)	II(1–3)	I(1)	–
Erica tetralix	II(1–7)	III(1–7)	II(1–5)	IV(1–5)	II(1–3)	I(1)
Euphrasia officinalis agg.	II(1–5)	II(1–5)	II(1–4)	I(1–3)	III(1–3)	II(1–3)
Filipendula ulmaria	I(1–5)	I(5)	–	I(1–5)	–	–
Galium palustre	I(1–3)	–	–	–	III(1–3)	–
Galium uliginosum	I(1–3)	–	–	–	IV(1–3)	–
Leontodon autumnalis	I(1–5)	I(1–5)	I(1–3)	–	III(1–3)	II(1–3)
Leontodon saxatilis	I(1–4)	–	II(1–3)	–	–	–
Linum catharticum	II(1–4)	II(1–3)	I(1–3)	I(1)	III(1–3)	II(1–3)
Minuartia verna	II(2–4)	–	–	–	–	–
Myrica gale	I(1–5)	I(1–5)	–	II(1–5)	–	–
Narthecium ossifragum	I(1–5)	II(1–5)	II(1–4)	III(1–5)	–	I(1)
Parnassia palustris	II(1–5)	I(1–3)	I(1)	–	IV(1–3)	–
Pedicularis palustris	I(1–4)	I(1–3)	–	I(1–3)	–	–
Pedicularis sylvatica	I(1–3)	I(1–3)	I(1–3)	I(1–3)	–	–
Pinguicula vulgaris	**V(1–5)**	**V(1–5)**	**V(1–4)**	**V(1–5)**	**V(1–3)**	**V(1–5)**
Pinguicula lusitanica	**I(1–5)**	**I(1–5)**	**–**	**II(1–5)**	**–**	**–**
Plantago maritima	II(1–5)	I(1–5)	I(1–2)	I(1)	–	I(1–5)
Polygonum viviparum	I(1–4)	I(1–4)	I(1–3)	–	–	–
Potentilla erecta	III(1–6)	III(1–5)	III(1–5)	II(1–3)	III(1–3)	I(1)
Primula farinosa	II(1–4)	I(1–5)	–	–	II(1–3)	–

Table 2 *continued*

NVC subcommunity/variant	M10				M11	
		a	**ai**	**aiii**	**bi**	**b**
	n = 217	*n* = 143	*n* = 51	*n* = 36	*n* = 9	*n* = 26
Prunella vulgaris	II(1–6)	I(1–6)	I(1–4)	I(1)	III(1–3)	I(1–3)
Ranunculus acris	I(1–4)	I(1–4)	I(1–3)	–	I(1–3)	–
Ranunculus flammula	I(1–4)	I(1–4)	II(1–4)	I(1–3)	II(1–3)	I(1)
Saxifraga aizoides	I(1–5)	II(1–5)	I(1–3)	II(1–5)	–	IV(1–8)
Succisa pratensis	III(1–6)	III(1–6)	II(1–3)	III(1–3)	V(1–3)	I(1–3)
Taraxacum officinale agg.	I(1–3)	I(1–3)	I(1–3)	–	I(1–3)	–
Thalictrum alpinum	I(1–5)	I(1–5)	I(1–5)	I(1)	–	II(1–3)
Tofieldia pusilla	I(1–4)	I(1–3)	I(1–3)	I(1)	–	II(1–3)
Triglochin palustre	III(1–4)	II(1–4)	II(1–3)	II(1–3)	V(1–3)	II(1–3)
Valeriana dioica	I(1–3)	–	–	–	IV(1–5)	–
Equisetum palustre	II(1–5)	II(1–5)	III(1–5)	I(5)	IV(1–3)	I(1–5)
Selaginella selaginoides	III(1–5)	III(1–5)	III(1–3)	III(1–5)	II(1–3)	III(1–3)
Aneura pinguis	IV(1–5)	III(1–5)	III(1–5)	II(1–3)	IV(1–3)	III(1–3)
Blindia acuta	I(1–3)	I(1–3)	–	III(1–3)	–	IV(1–5)
Breutelia chrysocoma	I(1–3)	I(1–3)	–	I(1–3)	–	–
Bryum pseudotriquetrum	IV(1–5)	II(1–5)	II(1–5)	I(1–3)	V(1–3)	III(1–3)
Calliergon cuspidatum	I(1–8)	I(1–8)	I(1–4)	I(1)	V(1–4)	I(1–3)
Campylium stellatum	III(1–5)	V(1–7)	V(1–7)	V(1–7)	IV(1–4)	IV(1–5)
Cratoneuron commutatum	II(1–60	I(1–5)	I(1–5)	I(1–3)	IV(1–6)	V(1–8)
Ctenidium molluscum	IV(1–8)	III(1–9)	I(1–5)	II(1–5)	IV(1–3)	II(1–3)
Drepanocladus revolvens	IV(1–9)	III(1–9)	III(1–9)	III(1–5)	III(1–4)	IV(1–5)
Fissidens adianthoides	II(1–5)	II(1–5)	I(1–5)	I(1–3)	III(1–3)	III(1–3)
Hylocomium splendens	I(1–3)	I(1–3)	I(1–3)	–	I(1)	–
Pellia endiviifolia	I(1–5)	I(1–5)	I(5)	I(1)	II(1–3)	I(1–3)
Racomitrium lanuginosum	II(1–9)	I(1–4)	–	I(1–4)	–	–
Scorpidium scorpioides	II(1–8)	III(1–8)	III(1–8)	V(1–7)	I(1)	III(1–7)
Sphagnum subnitens	I(1–3)	I(1–3)	I(1–3)	–	I(1)	–

the mainly upland *Saxifraga aizoides–Ditrichum flexicaule* subcommunity of the *Festuca ovina–Agrostis capillaris–Thymus polytrichus* grassland community (CG10c); and in the *Dryas octopetala–Silene acaulis* ledge community (CG14) on ungrazed ledges and crags of calcareous bedrock at 300–900 m, mainly in the central and southern Highlands of Scotland.

At frequency II (21–40%), *P. vulgaris* occurs in various other open fen and flush communities (Rodwell 1991b, 1992): the *Carex rostrata–Calliergon cuspidatum/giganteum* mire (M9) in north-west Britain and (frequency I) Anglesey; the *Schoenus nigricans–Juncus subnodulosus* mire (M13), widespread but local in England and Wales; the montane *Anthelia julacea–Sphagnum auriculatum* spring community (M31) where the ground in north-west Britain is kept wet by the trickling oligotrophic water (pH 4.5–5.0); the *Calluna vulgaris–Arctostaphylos alpinus* heath community (H17a) in the north-west Highlands of Scotland; the *Sesleria albicans–Galium sterneri* grassland community (CG9c) on calcareous soils in the northern Pennines; the *Festuca ovina–Agrostis capillaris–Alchemilla alpina* grass heath community (CG11b) in Scotland and Cumbria; the *Dryas octopetala–Carex flacca* heath (CG13a) in calcareous flushes in north-west Scotland; and the *Luzula sylvatica–Geum rivale* tall-herb community (U17a) on ungrazed calcareous mountain ledges in north-west Britain.

In many NVC communities (Rodwell 1991b, 1992), *P. vulgaris* is scarce (I) including: the *Carex rostrata–Sphagnum warnstorfii* mire (M8), on raw peat with calcareous drainage, in the central Highlands of Scotland; base-rich seepages within the *Trichophorum cespitosum–Erica tetralix* wet heath (M15) in the wetter western and northern parts of Britain; *Philonotis fontana–Saxifraga stellaris* spring (M32) in the Scottish Highlands, Lake District, Pennines and Northern Wales; *Carex viridula* ssp. *oedocarpa–Koenigia islandica* flush (M34) on Skye only, with seepage water from springs of pH *c.* 6.0; *Cratoneuron commutatum–Festuca rubra* spring (M37), with seepage from lime-rich bedrock, in the north-western uplands of Britain and *Calluna vulgaris–Arctostaphylos alpinus* heath (H17) in Scotland and Orkney. Other notable communities supporting *P. vulgaris* in Britain are given in Table 3.

The Ecological Flora of the British Isles (Fitter & Peat 1994) lists the following Corine habitats (Corine codes in brackets) for *P. vulgaris*: Atlantic cliff communities (C18.21), northern wet heaths (C31.11), Boreo-alpine Scottish heaths (C31.45), mountain avens mats (C31.49), British roseroot community (C31.64), sub-Atlantic semi-dry calcareous grasslands (C34.32), *Agrostis–Festuca* grasslands (C35.12), lowland blanket bogs (C52.1), upland blanket bogs (C52.2), soft-water springs (54.11), hard-water springs (C54.12), black bog-rush fens (C54.21), brown bog-rush fens (C54.22),

Table 3 Some community types for UK lowland mires in which *P. vulgaris* occurs (from FenBASE 60 database, held by B. D. Wheeler, University of Sheffield), not recorded by Rodwell (1991a,b, 1992). The NVC community numbers and numbers of records made for each community type are shown

Sub-community *Festuca rubra–Juncus acutiflorus* of the *Schoenus nigricans–Juncus subnodulosus* mire (M13, 5).
Schoenus nigricans–Narthecium ossifragum mire (M14, 6), and its typical subcommunity (1).
Typical subcommunity (1), and *Briza media–Trifolium* spp. subcommunity (8) of the *Juncus subnodulosus–Cirsium palustre* fen meadow (M22).
The *Molinia caerulea–Cirsium dissectum* fen meadow (M24, 1), its typical subcommunity (1), and *Eupatorium cannabinum* subcommunity (2).
The subcommunities *Sanguisorba officinalis* (1) and *Festuca rubra* (2) of the *Molinia caerulea–Crepis paludosa* mire (M26).

dioecious-flea-yellow sedge fens (C54.25), arcto-alpine riverine swards (C54.3), acidic fens (C54.4), transition mires (C54.5) and inland cliffs and exposed rocks (C62).

In the typical mire (M10) of Rodwell (1991b), and its *Schoenus nigricans* variant, *P. vulgaris* occurs with a frequency of 81–100%, *P. lusitanica* is also present, but with smaller frequency (Table 2). However, *P. vulgaris* often occurs independently of this species. Similarly, *P. lusitanica* may grow in communities independent of *P. vulgaris*, indicating their ecological differences. For the association of *P. vulgaris* with *P. alpina* see Section II(A); and for its association with *P. grandiflora* see the account of that species.

In Central Europe, Ellenberg (1988) lists *P. vulgaris* as a character species of the Order Tofieldietalia (calcareous small sedge fens) and characterizes it as a light-loving plant of moderately wet, weakly acid to weakly basic, nitrogen-poor soils; Oberdorfer (Pfl. Exk.) noted its occurrence in mostly base-rich spring communities. In the Netherlands, Schaminee *et al*. (1995) have it in the *Parvocaricetea*, small sedge-fens, notably the *Campylio–Caricetum dioicae*, and also in species-rich examples of wet heath. Further north, in the Rondane, in south Norway, Dahl (1956) recorded it on hard acid rocks in only two communities, the *Drepanocladeetum revolventis* (constancy II) at 1100–1170 m. In central Sweden, in the mire complex at Skatiosberg Stormosse, Sjörs (1948) reported *P. vulgaris* with high constancy only in the *Schoenus ferrugineus–Tomenthypnum–Campylium stellatum–intermedius* association in a limited area which had a high calcium level (18 mg L^{-1}; pH 7.1); he also noted it, but rarely, in the spring community, the *Geum rivale–Philonotus fontana–Drepanocladus purpurascens* association. In northern Sweden, the dominant species, where *P. vulgaris* occurs, are *Arctostaphylos alpina*, *Betula nana*, *Empetrum nigrum* ssp. *hermaphroditum*, *Loiseleuria procumbens* and *Cladonia* spp. (Karlsson *et al*. 1987); other associated species in this area are *Eriophorum vaginatum*, *Rhododendron lapponicum*, *Tofieldia pusilla*, *Vaccinium* spp. and carpets of *Sphagnum* spp. (Karlsson 1986, 1988). In west-central Iceland, species listed most constantly associated with *P. vulgaris* in damp, dwarf-shrub heath included *Empetrum hermaphroditum* and *Betula nana*. In nearby areas, *P. vulgaris* was in heath associated with *Vaccinium uliginosum*, *Empetrum hermaphroditum*, *Salix herbacea*, *S. lanata*, *Bistorta vivipara*, *Thalictrum alpinum*, *Bartsia alpina* and *Carex bigelowii* (Proctor 1972). In Greenland *P. vulgaris* grows in gravelly tracts associated with *Betula nana* and *Loiseleuria procumbens* (Heide 1912).

IV. Response to biotic factors

Pinguicula vulgaris is shallow rooting and the rosette leaves are both delicate and brittle, and as such it does not survive either direct trampling or grazing by large herbivores such as sheep, cattle, ponies and various species of deer, during the growing season. However, the areas where it grows are usually unenclosed, and the trampling effect of such stock may contribute towards keeping the communities rich and open, and the more vigorous and taller species in check. Poaching may even be beneficial in the long term, by providing regenerative niches in which recruitment from seed may occur (B. D. Wheeler, personal communication). Furthermore, the slightly raised hummocks produced by trampling provide favourable habitats for the plant. More intensive trampling can disrupt the sward and expose and break up the underlying bedrock; augmented by weathering and flushing, this distributes fresh supplies of minerals, many of nutritional value (Rodwell 1991b). The collection of its leaves for use in the production of ‘ropy milk’, and for therapeutic purposes by early herbalists, e.g. as an antispasmodic, may also have reduced its numbers in certain areas (see also Section X). Drainage and peat cutting are responsible for the loss of many of its previously reported habitats, both by the lowering of the water table and the loss of associated insect prey, many with aquatic larval phases.

During the early summer, June to July, insect and other prey are trapped on the mucopolysaccharide slime held on the stalked glands of the freshly opening, fully functional, rosette leaves; if the prey is plentiful the effect of leaf inrolling reduces the photosynthetic surface available, but new leaves overlay the older ones in succession to provide new surfaces for further prey capture and/or photosynthesis. Large prey can overstimulate gland secretion and this, coupled with the presence of the rotting carcase on the leaf surface, can kill the affected leaf – a case of the plant suffering from 'indigestion' (Heslop-Harrison 1978). Prey is also trapped to a much smaller degree wherever stalked secretory glands occur, e.g. on the flowering scapes and the outer surfaces of the sepals. In the British Isles the prey consists mainly of small Diptera, such as midges and gnats (Nematocera), and Thysanoptera (thrips). In the Swedish subarctic small Nematocera were the dominant prey caught, by weight; mites (Acarina) were caught in large numbers, but, being tiny, contributed little to the total captured biomass. The trapping efficiency of *P. vulgaris* was high compared with both *P. alpina* and *P. villosa*, amounting to 21–37 μg prey trapped cm^{-2} day^{-1} for the first species, compared with 14–18 μg cm^{-2} day^{-1} for the latter two (Karlsson *et al.* 1987). A list of the prey caught according to taxonomic group, mainly Collembola and Nematocera for *P. vulgaris* and Collembola alone for *P. alpina*, growing on subalpine heaths at a range of localities near Abisko, Sweden, is given by Karlsson *et al.* (1994). The total amount of prey caught varied from season to season and from one plant to another in different, and even in adjacent, microhabitats (see also Karlsson *et al.* 1996). Reproductive (i.e. plants in flower) plants always trapped more prey than purely vegetative ones. Of the total seasonal catch, 50–75% was caught during June, but this fell off markedly in July, with less than 5% caught during August. The benefits of carnivory are discussed in Sections V(B) and VI(E)ii.

V. Response to environment

(A) GREGARIOUSNESS

Pinguicula vulgaris grows typically in rather open situations where the total plant cover may be less than 50% (Veg. Scot.). In favourable habitats, free from competition, it forms small, often scattered, groups of some 10–20 plants, but never in the British Isles does it compete in quantity with the extensive swards of *P. grandiflora* 'which deck the moors and rocks over thousands of acres in Kerry' (Praeger 1939). Flood water, from rain or snow melt, trampling by stock, and peat cutting all contribute to keeping the ground open, although potentially destroying many plants. In some habitats where it occurs alternate freezing and thawing of the substratum also contributes to the openness of the ground cover.

(B) PERFORMANCE IN VARIOUS HABITATS

In favourable habitats in the British Isles a well-grown rosette may measure up to 12 cm in diameter, and the fruiting scapes may reach up to *c.* 20 cm in length. A vigorous plant may produce up to eight flowers in a single season, in succession, all finally setting seed. In poorly grown plants, where climatic, nutritional or other factors restrict growth, the rosettes may reach a diameter of only 5 cm and only one flower, or none, may be produced during the season (Y. H.-H., unpublished). This compares with (1–)2–3(–6) per plant at certain sites in northern Sweden, with rosettes 4–8 cm in diameter, the higher numbers being confined to the richer habitats (Karlsson 1986). Over a six-year period of study of high altitude populations of *P. vulgaris* in the subarctic, reproduction by seed failed in plants which were fed artificially with *Drosophila* as well as in unfed controls, suggesting that seed output may be more dependent on abiotic factors; on the whole, however, at both higher and lower altitudes, rosettes were larger, more flowers were produced and the weight of the overwintering hibernacula was greater in fed plants (Thoren & Karlsson 1998). Captured prey could contribute up to 85% of the mean seasonal turnover of nutrients (N and P) in *P. vulgaris* in native habitats, but there was great variation amongst individual plants (Karlsson *et al.* 1994). Studies on *P. vulgaris* (as well as *P. alpina*, *P. villosa* and *Drosera rotundifolia*) grown either at high or low soil nutrient levels, in a subarctic environment, showed that they tended to respond to fed prey to a greater degree in soil with low nutrient levels, in terms of several characteristics including plant weight, N and P content, and amount of seed set – but not consistently so; and the species were not entirely limited to wet, sunny, nutrient-poor habitats; they could also occur in richer habitats provided competition was low (Karlsson *et al.* 1991). Numbers of flowers per plant and dry matter allocated to reproduction in flowering individuals of *P. vulgaris* in various sites are given in Table 4 (data from Karlsson 1986). In subarctic Sweden, seed is not necessarily set every year, and depends on the season and the size of the plant. In Greenland and Disko, *P. vulgaris* plants may also flower well, but late in the summer, and only in favourable habitats and seasons do ripe fruits develop successfully (Porsild 1920). In the British Isles, plants usually flower and set seed every year in favourable habitats.

The weights of hibernacula, as recorded in early September, from a rich habitat, were four times heavier

Table 4 Numbers of flowers per plant, reproductive biomass per seed and weights of hibernacula in flowering and non-flowering plants of *Pinguicula vulgaris* at different sites in north Sweden. ND, not determined

	Site A	Site B	Site C
Number of flowers	1.0 ± 0.0	1.1 ± 0.3	2.7 ± 1.1
Flower stalk and capsule weight (mg)	5.8 ± 2.4	7.0 ± 2.2	15.2 ± 3.7
Reproductive biomass per seed* (μg seed^{-1})	47.3	ND	ND
Hibernaculum weight (in early September) (mg)			
(a) Flowering	7.0 ± 3.0	5.7 ± 4.2	37.1 ± 18.6
(b) Non-flowering	8.5 ± 2.2	10.0 ± 5.2	ND

*The reproductive biomass included flower stalk, seed capsule and seeds, taken in mid-August. Data from Karlsson (1986). Site locations as in Table 1.

than from a poorer one (Table 4). Although the rosette is intolerant of shade, seeds may germinate in partial shade and seedlings are then capable of some internodal extension before developing into rosettes (see VIII(E)).

Performance in various habitats is regulated by a range of, often conflicting, factors, and may be difficult to judge, except under experimental conditions and observation over more than one year, since flower primordia are produced and storage products are accumulated in the hibernaculum developed in the previous season in *P. vulgaris*, and most other European species. The optimum combination of factors (as noted by Zamora *et al*. 1998 in careful experimental work on the Pyrenean endemic *P. vallisneriifolia*) were found to be (i) degree of irradiance (regulating photosynthesis according to degree of shading) and (ii) and (iii) availability of prey and water. These conditions may be conflicting, because prey are most prolific in the shade, whilst photosynthesis is at an optimum in bright sunlight, but sunny places are normally dry. This partly explains Gimingham & Cormack's observation (1964) that *P. vulgaris* in Scotland is normally confined to north-facing slopes (see II(A) above). However, Zamora *et al*. (1998) also found that deep shade led to low stalked-gland mucilage secretion and viscosity, and therefore a lower retention of insect prey. In southern Europe they concluded that a compromise was reached in partly shaded conditions that were not fully optimal for overall growth and reproduction, yet excluded fully exposed habitats. This would also explain the tendency for *P. vulgaris* to be found in rather sheltered depressions, rather than in fully exposed sites in the British Isles. Enhanced UV-B radiation, under field conditions, was found not to affect growth in *P. vulgaris*, but reduced the risk of photo-inhibition and increased the levels of anthocyanin (Mendez *et al*. 1999).

(C) EFFECTS OF FROST, DROUGHT, ETC.

Unlike the summer rosette, the hibernaculum can resist frost, snow cover, drought or immersion in water for some weeks at least. It is always partially sunken, *c.* 1 cm, below ground level, and is thus slightly protected from being swept away in water currents. In parts of Minnesota, USA, and in Scandinavia northwards, as well as in montane areas further south, it may survive under snow for some 4 months or more. In other areas, such as the west of Scotland and milder parts of southern Europe, the hibernacula survive under relatively, or wholly, frost-free conditions. The rosette is very vulnerable and cannot survive any degree of drought as the leaves are very thin (see also Section VI(A)). There is some evidence, from cultivation of rosettes under glasshouse conditions, that drought may accelerate, or stimulate, the onset of dormancy, a condition normally regulated by short days and cooler nights (see VI(E)). Rosette leaves were observed on *P. vulgaris* plants long after the flowering period in its more temperate areas of distribution, and after hibernacula had formed in plants from the north, where surrounding rosette leaves no longer persisted (Heide 1912). This was taken as evidence that foliage leaves continue to be produced after flowering in the former case and not in the latter; this report was from observations in the wild, however, and not based on experimental evidence; the presence of rosette leaves in the former could have been a case of survival of old leaves in conditions of slow growth, rather than the initiation of new ones.

VI. Structure and physiology

(A) MORPHOLOGY

The seedling at first bears a taproot, but this is quickly replaced by a tuft of adventitious roots. The hibernaculum, formed in the autumn, consists of an abbreviated stem bearing 4–5 outer scales swollen with starch, surrounding some 9–15 leaf primordia, the younger ones with axillary flower primordia. In shape it is somewhat ovoid, whereas that of *P. grandiflora* is more spherical (Y. H.-H., unpublished). Of a sample of hibernacula from Arisaig, Scotland, the mean length was 6.75 mm (range 4–10 mm; $n = 62$), and the mean maximum width was 4.1 mm (range 2–7 mm; $n = 62$). In early spring the bud scales open into a star shape, extending somewhat in length, and they provide a photosynthetic surface before the leaf primordia finally emerge in succession. In *P. grandiflora*, on the other hand, the bud scales loosen only slightly and never expand, the young, true leaves emerging from the narrow apical gap between the scales.

Young rosettes of *P. vulgaris* and *P. grandiflora* remain distinguishable in cultivation, those of the former appearing more markedly stellate. Later in the season specific vegetative differences tend to disappear, although the leaves of *P. grandiflora* are nearly always larger and differ slightly in shape, tending to be broader.

When the plant is dislodged the leaves become revolute. One to three adventitious roots are produced per leaf axil, rarely exceeding 3–5 cm in length and *c.* 1 mm in diameter; they are spreading, and do not penetrate far below the surface, and anchorage of the rosette remains shallow and hence rather hazardous; they die as the new hibernaculum is formed. Total root lengths of samples from flowering and non-flowering plants during July and August never exceeded 10 cm in the Swedish subarctic (Karlsson 1986). Whilst the old leaves come to lie horizontally on the ground, the new ones are at first erect and involute, in cultivation reaching a height of 3–4 cm before opening fully and flattening to overlie the older ones. In cultivation in the Midlands and in Belfast the plastochron index is about 5 days, and the leaf phyllotaxis 2/5. A rosette towards the end of the growing season therefore consists of *c.* 4–7 active leaves at succeeding stages of maturity, overlying about the same number of older ones in various stages of decay – a factor of importance in connection with the plant's specialization for insectivory.

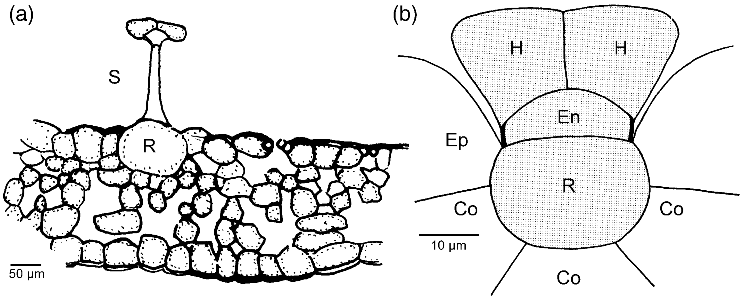

Fig. 3 (a) Transverse section of part of the lamina of a leaf of *Pinguicula vulgaris* showing mesophyll cells (aerenchyma) between the upper and lower epidermi, and absence of a palisade layer. A stalked gland and two stomata are shown on the upper surface. S, stalk cell of stalked gland; R, basal or reservoir cell. (b) Diagram of a median longitudinal section of a sessile, digestive, gland from the upper leaf surface showing its principal features (after Heslop-Harrison & Heslop-Harrison 1981). En, endodermal cell, with Casparian strip-like outer wall; H, head or secretory cell, with 'spongy' radial walls for enzyme storage; R, reservoir cell. Each sessile gland is partially sunk into the upper epidermis (Ep), and the reservoir cell is surrounded by collecting cells radiating from it (Co).

Anatomically the leaf is very simple, being without a true palisade layer (Fenner 1904, and Fig. 3a); according to Mendez & Karlsson (1999) this may have physiological implications resulting in 'lower mesophyll conductance and thus lower photosynthetic rates'. The main lamina consists of only 3–4 layers of isodiametric mesophyll cells in the form of aerenchyma – which taper to a single layer at the leaf margins, held between the upper and lower epidermal layers, each with a very thin cuticle; this explains fully why the plant requires a constantly humid environment, for even towards the midrib the mesophyll is only 8–10 cells thick, but here without air spaces.

The leaf margins inroll laterally upon stimulation by insect prey, and the radial walls of the epidermal cells can be thrown into zigzag folds, so the cells can accommodate to the bending movements without damage. The cuticle on the outer wall of the epidermis is very thin and can also accommodate to the bending. In addition, the stomata on both surfaces (*c.* 40 mm^{-2}) are supported on raised arches of epidermal cells, a further adaptation to curling, without tearing.

The topography of the upper leaf surface is best interpreted with the aid of scanning electron microscopy which shows the distinctions between the two types of glands, sessile and stalked, distributed more or less evenly over most of the lamina (Heslop-Harrison 1970; Heslop-Harrison & Knox 1971) and which are modified trichomes of epidermal origin (Klein 1883; Goebel 1891; Fenner 1904; Haberlandt 1914). Contrary to the earlier reports by Fenner, the lateral leaf margin cells are never secretory. Gland development is described by Komiya (1975) and Heslop-Harrison & Heslop-Harrison (1981). Whilst each stalked gland is raised on a basal cell platform, each sessile gland is sunken in a pit formed from the surrounding epidermal cells (Fig. 3a,b); this conformation is of some significance in relation to the secretion and absorption of the fluids after insect stimulation (Heslop-Harrison 1970; Heslop-Harrison & Heslop-Harrison 1981). Varying numbers of uniseriate 3–5-celled trichomes also occur, sometimes with rather simple gland heads, being most plentiful towards the leaf base, and thinning out towards the petiole; they may hold any excess secretions after stimulation which would otherwise be lost as 'run-off'. The stalked glands, always less numerous than the sessile, are specialized for insect capture, and bear glistening secretion droplets with adhesive properties. Each gland head consists of up to 16 secretory cells radiating from and supported on a single 'endodermal' cell, notable for its thickened lateral walls, analogous to a Casparian strip (Heslop-Harrison & Knox 1971); this surmounts the single, elongated stalk cell with a marked entasis, and which is borne on a swollen basal (reservoir) cell which replaces an epidermal cell (Fig. 3a). The secretory cells of the gland head have lateral walls of transfer-cell type (see below). The sessile glands are more numerous than the stalked glands, and again are dispersed relatively evenly over the entire upper leaf surface, *c.* 112 mm^{-2}. Each sessile gland consists of a gland head (Fig. 3b, 46.6 ± 0.72 µm in diameter; Heslop-Harrison & Heslop-Harrison 1981) of usually 8 cells which do not secrete unless stimulated. These secretory cells also have radial walls again of transfer-cell type, and are the principal storage sites of a range of hydrolytic enzymes (see below). The secretory cells abut a single endodermal cell which stands on a 'reservoir cell', partially sunk into the surrounding epidermal cells; each reservoir cell is surrounded by a series of 'collecting cells' radiating from it (Heslop-Harrison & Heslop-Harrison 1981) and is also intimately associated with the termination of a tracheid (Heslop-Harrison & Knox 1971), of importance in connection with the rapidity of the processes of gland secretion and absorption in relation to carnivory. The ultrastructure of the digestive glands of *P. vulgaris* have also been described by Vassilyev & Muravnik (1988a,b) both during maturation and after stimulation. Their fine-structural interpretation of the gland head cells and the secretory process differs somewhat from that of Heslop-Harrison & Knox (1971), Heslop-Harrison (1975, 1976a,b), and Heslop-Harrison & Heslop-Harrison (1981). The staining properties of the differing components of the walls of the digestive glands are listed by Heslop-Harrison & Heslop-Harrison (1981).

The natural prey are small flying Diptera and other insects (perhaps attracted by the glistening appearance of the leaf) and, as the prey struggles to release itself from the capturing mucilage on the stalked glands, many are damaged beyond recovery (Heslop-Harrison 1970; Heslop-Harrison & Knox 1971) and not renewable. The lower epidermis is without glands, but bears hydathodes and stomata.

Stalked and sessile glands, rather similar in form to those on the leaf surface, are also present on the flowering scapes, the exterior of the sepals, the back of the corolla tube and spur, and on the ovary wall. However, a test of the amount of N absorbed from prey caught on the flower scapes showed that little (*c.* 2.5% or less) of that available was absorbed (Hanslin & Karlsson 1996).

Three types of trichome occur on the inner surface of the corolla: (i) those having a head of 5–11 cells, without pigment, on a 3–4-celled, purplish-tinged stalk and limited to the inner 1/3–1/2 of the lower corolla lobes; (ii) those intermediate between (i) and (iii), and (iii) those of the corolla throat where it constricts into the spur; these consist of 6–8 uniseriate cells, unpigmented, which taper to the apex (illustrated by Casper 1962).

The embryo sac has three large antipodal cells of which two degenerate. The remaining one then enlarges to occupy almost the whole of the upper half of the embryo sac. The embryogeny is of the Onagraceous type (Davis 1966).

(B) MYCORRHIZA

Absent (Harley & Harley 1986).

(C) PERENNATION: REPRODUCTION

Pinguicula vulgaris is a rosette-hemicryptophyte. Perennation is by means of hibernacula – see also Section VI(A). In Scotland (Arisaig) these are produced towards the end of July, whereas in cultivation in the Midlands (Birmingham) they are formed during August and September. Under the same conditions stocks of Irish *P. grandiflora* developed hibernacula rather later in September. Plants from Kraknotind (67° N, 16° E) at an altitude of 763 m, also cultivated in the Midlands, started to produce hibernacula by mid-June, only some 5 weeks after the first flowers had appeared, suggesting that the variation was in part genetically determined. Individual plants have been kept in cultivation for 10 years, but their longevity is not known beyond this time (Y. H.-H., unpublished). The population half-life of *P. vulgaris*, as well as of *P. alpina*, in the Swedish subarctic was 7.5 years (Svensson *et al.* 1993).

Pinguicula vulgaris reproduces vegetatively by means of brood buds (bulbils or gemmae), formed in the axils of the last foliage leaves of the season. Of 70 hibernacula from 3-year-old plants grown from seed from English, Scottish and Irish sources, the mean number of bulbils was 1.9 (range 0–10), far fewer than the number formed in *P. grandiflora* (see that account, herein). According to Soyrinki (1938) arctic plants of *P. vulgaris* failed to form bulbils and they are rather rare according to Karlsson (1986) at subarctic Swedish sites; however, they are regularly produced in mid-Europe.

A typical bulbil consists of 1–2 bud scales, containing starch reserves, enclosing 1–2 leaf primordia. They are readily detached from the parent plant (hibernaculum) after the foliage leaves die back in the autumn, and could be dispersed by water flow during autumn and spring flooding. As with the hibernacula, bulbils survive freezing. Plants produce flowers, after being grown from seed or bulbils, usually in their third year, i.e. after their second season of vegetative growth, and initiation of flower buds at that time. Flowering and subsequent seed set are usually then of annual occurrence, if conditions are favourable. Opening bulbils, if in slight shade, may show some slight internodal extension as in germinating seedlings (see below).

Occasionally the species will reproduce vegetatively from small plants arising from damaged hibernaculum scales or rosette leaves when in cultivation (Y. H.-H., unpublished). This feature arises rather more commonly in the fleshy-leaved species such as *Pinguicula caudata* Schlecht.

(D) CHROMOSOMES

Pinguicula vulgaris has the somatic chromosome number of $2n = 64$, as determined from plants in Greenland (Jorgensen *et al.* 1958), Abisko (Sweden) and Iceland (Löve & Löve 1944, 1948, 1956), Norway (Laane 1967, 1969), Denmark (Larsen, in Löve & Solbrig 1965); and from France, Austria and Switzerland (Doulat 1947; Casper 1963), Poland (Zurzycki 1953 ex Skalinska *et al.* 1959; Casper 1962), Slovakia (Murin 1976a,b), the Iberian peninsula (Löve & Kjellqvist 1974; Zamora *et al.* 1996) and from Scottish (Arisaig) and Irish sources (Y. H.-H., unpublished). The same number was reported from the United States of America (Wood & Godfrey 1957). Casper (1962) also noted the numbers $2n = 32$, as well as $2n = 64$, and that $2n = 50$ had been recorded by Rosenberg (1909, ex Casper 1962) and Tischler (1950). The var. *macroceras*, sometimes regarded as conspecific (see Section I), the source being from Japan, had $2n = 64$ (Ochiyama 1990). Illustrations of the chromosomes at metaphase I (from Romania and Switzerland) are given by Casper (1962).

See also under Hybrids, VIII(B).

(E) PHYSIOLOGICAL DATA

(i) Developmental physiology

Flower primordia are produced in the axils of leaf primordia during the previous late summer (Y. H.-H., unpublished), the latter being enclosed by bud scales as the overwintering hibernaculum develops. As with *P. grandiflora*, dormancy of the rosette is induced in the autumn by a combination of cooler nights and shortening daylength (Heslop-Harrison 1962). Vernalization of the hibernaculum of *P. vulgaris* is not required, but after vernalization the opening rosettes of the following season will flower more or less synchronously in *c.* 40 days after transference into long days and a night temperature of 10 °C. Bulbils also have no vernalization requirement, but again develop more rapidly and relatively synchronously after vernalization. As with the bulbils of *P. grandiflora*, it is possible that inhibitors released from the decaying rosette leaves in the autumn reinforce their initial dormancy in a mild autumn (Y. H.-H., unpublished), and thereby delay their development until the increasing daylength and rising temperatures of spring allow renewed growth. Experiments on the developmental physiology of *P. grandiflora* (Heslop-Harrison 1962; see also the account of *P. grandiflora*, below) indicate that *P. vulgaris* differs in its response to daylength and night temperature from that species. During the summer the mode of growth of the rosette, whereby a new leaf expands (*c.* every 5 days under optimum conditions) means that fresh leaf surfaces are continuously being presented for the efficient capture, digestion and absorption of insect prey (see below).

(ii) Leaf gland physiology, in relation to insectivory

Darwin (1875) was the first to show that nitrogenous material from a range of substances caused leaf stimulation and the discharge of acid secretions from the leaf glands of *Pinguicula*. The carnivorous habit was studied further by Morren (1875), Batalin (1877), Tischutkin (1889), Mirimanoff (1938), Olivet & Mirimanoff (1940) and Lloyd (1942). Extracts from expressed leaves were found to contain digestive enzymes by Dernby (1927).

The significance of carnivory for *P. vulgaris* was studied experimentally by comparing sets of untreated controls (one from a relatively nutrient-poor habitat, Abisko, Sweden, the other relatively rich, at Katterjakk, 24 km west of Abisko), with plants fed with insects to the leaves, and/or supplied with a complete nutrient solution to the substrate (Aldenius *et al*. 1983). In most cases those plants fed with insects alone, or in combination with fertilizer, had higher values for dry weight, number and length of leaves, and concentrations of N and P. However, the total plant N increased by a larger amount than the insects contained in the Abisko plants, implying that perhaps other substances, possibly Mo or Fe ions, derived from the insects, actually stimulated an increase in the uptake of N from the soil. Neither did the results support specific benefits from insect feeding to plants grown in nutrient-poor habitats. In a later paper, Karlsson & Carlsson (1984) showed that, whilst the principal benefit of carnivory is usually thought to be a supplementary supply of N, P was perhaps the more important; micronutrients also seemed to play a regulatory, interactive nutrient role when combined with N and P. According to Karlsson *et al*. (1996), a few individual plants of *P. vulgaris* gained their whole annual nutrient requirement through trapped prey. The nitrogen uptake from N^{15}-enriched *Drosophila* flies fed to *P. vulgaris* plants in a subarctic environment was found to be variable, from 29% to 41% of the prey N, but higher in glasshouse-grown plants (40–50%); the discrepancy was explained by the absence of rain and higher temperatures in the latter plants; the prey-derived N^{15} was later traced to the reproductive organs and the developing winter buds. As with the work reported above (Aldenius *et al*. 1983), uptake of nitrogen from the roots appeared to be stimulated by prey capture.

Since the leaves and flower primordia of the following year are initiated and present in the overwintering hibernaculum (see VI(Ei)), it was found that in *P. vulgaris* from Alberta, Canada, the feeding of leaves with *Drosophila melanogaster* enhanced neither within-season size of vegetative rosettes, nor incidence of flowering nor fruiting; however, larger plants produced more leaf and flower primordia and bulbils for the following year (Worley & Harder 1996, 1999). The benefits of feeding *Pinguicula* plants in a Mediterranean environment are discussed by Zamora *et al*. (1997). The phenotypic costs of reproduction in *P. vulgaris*, as compared with *P. alpina* growing in subarctic Sweden, were quantified (by comparing dry weight, N and P) in reproductive and non-reproductive plants by Thoren *et al*. (1996). It was found that, unless these species could enhance nutrient acquisition, the cost of production of flowers could affect future vegetative growth and even survival (Eckstein & Karlsson 2001).

The resorption pathway of the products of digestion was traced in *Pinguicula* leaves by introducing small amounts of colloidal lanthanum nitrate into the secretion pool just developing on a freshly insect-fed leaf surface, and then fixing it for ultramicroscopic examination some time later whilst the absorption process was at its most active (Heslop-Harrison 1975). Results showed that, whilst the surrounding epidermal cells offered a complete barrier to the tracer, it was able to pass through the cuticular discontinuities of the gland head cells, penetrating first into the underlying pectocellulosic wall and then entering the spongy inner wall; it was traced as far as the endodermal cell. Digestion on the leaf surface and resorption was also followed autoradiographically after feeding ^{14}C-labelled protein to *Pinguicula* leaves and examining them afterwards periodically (Heslop-Harrison & Knox 1971). It was shown that digestion products move into the leaf within 2 hours, reaching the vascular system and, within 12 hours, they leave the leaf itself, via the midrib; microautoradiographs also showed a concentration of the product around the sessile gland heads – indicating an active inward flow – and within the cells of the gland head itself. The onset of secretion, after stimulation, is due mainly to the rapid movement of Cl^- ions from the reservoir cell of each secretory cell, through the endodermal cell and thence into the glandular head cells; this movement of Cl^- ions induces a rapid flux of water through the system, flushing the enzymes held in the head cells on to the leaf surface (Heslop-Harrison & Heslop-Harrison 1980). The counter ions were not determined, but are likely to be H^+ or K^+ (Lüttge 1983; Juniper *et al*. 1989). A more limited, but contributory, cause of active secretion may also be the release of sugars from the dissolution of the spongy walls of the head cells, thereby lowering the water potential of the head cells (Heslop-Harrison 1975).

As noted above, the struggles of insect prey trapped by cables of mucilage often damage or destroy some of the surrounding glands, and the leaf surface also becomes overlain by carcase remains, the larger ones rotting. However, new leaf surfaces are constantly being presented for further insect capture and photosynthesis at the height of the growing season; in temperate regions at least, a new leaf expands every 5 days (Heslop-Harrison 1976a,b). In consequence, the older leaves are overlain by the younger ones with glands in pristine condition. The trapping efficiency of the younger leaves as compared with older ones has also been noted by Karlsson *et al*. (1994). That the secretory and the absorptive processes are designed to function only once for each gland, if it is stimulated therefore scarcely matters (Heslop-Harrison 1976a,b, 1978). Prey may be actively lured to the leaf surfaces of *Pinguicula* plants by the glistening appearance of the droplets held on the stalked glands, by UV patterns (Joel *et al*. 1985) or, possibly, by a fungus-like odour (Lloyd 1942).

(iii) Response to shade, and other conditions

As noted in Section V(B), optimum growth conditions are a compromise in *P. vulgaris* because, whilst full sun produces optimum photosynthetic rates, shade is often an optimum for insect visitation and humidity; furthermore, insect trapping reduces the availability of photosynthetic surface. Many of these conditions, including soil nutrient status, have been studied; see papers by Eckstein & Karlsson (2001) and Karlsson *et al*. (1991, 1994, 1996) for species of *Pinguicula* in the Swedish subarctic, and by Zamora *et al*. (1998) in Spain. Photosynthetic rates, either leaf area based (Pa) or mass based (Pw), were the same in *P. vulgaris* from two sites (from a 'wet hole' amongst frost polygons, and from a poor fen); in comparison with *P. alpina*, both Pa and Pw rates were lower. Photosynthetic performance in *P. vulgaris* showed no significant relationship with leaf nitrogen content, whereas both Pa and Pw increased with leaf nitrogen content in *P. alpina* (Mendez & Karlsson 1999).

At the onset of dormancy, the result of shortening days and lower night temperatures, the rosette leaves of the current season senesce, and a re-allocation of nutrients occurs. Starch is stored in the outer scales of the hibernaculum as it develops, and contributes to the swollen character of the scales and the form of the hibernaculum itself (Y. H.-H., unpublished); to a lesser degree, but in parallel, there is also some re-allocation of nutrients to the bulbils.

(F) BIOCHEMICAL DATA

Propionic, butyric and valerianic acids were found in *Pinguicula* sp. leaves by Richter (1930, ex Fournier 1948); and Bate-Smith (1962) found evidence of the presence of *p*-coumaric, caffeic, ferulic and sinapic acids. Fresh leaves, and those dried below 45 °C, of *P. vulgaris* (as well as *P. alpina*) were also found to contain *trans*-cinnamic acid, and as heterosides; total cinnamic acid was estimated as 0.08% in fresh leaves, corresponding to 1.6% in dried material (Bauquis & Mirimanoff 1970); this confirmed the findings of Christen & Gordonoff (1961) and Christen (1961). On desiccation above 45 °C the *trans*-cinnamic acid was found to be degraded to benzoic acid (Bauquis & Mirimanoff 1970), the acid having been detected previously in the leaves of *P. vulgaris* (Loew & Aso 1907 ex Juniper *et al*. 1989). Bauquis & Mirimanoff (1970) found benzoic acid, both free and esterified, together with small amounts of cinnamaldehyde. Early, supposedly effective, uses by herbalists, perhaps attributable to these and other substances, are given in Section X. Iridoid glucosides were reported in *P. vulgaris* by Damtoft *et al*. (1985, 1994) and Marco (1985), who both detected globularin. The former authors also isolated 10-(Z)-cinnamoyl catalpol, while the latter author isolated globularicin, scutellarioside-II and 1-O-*p*-cumaroyl-B-D-glucopyranoside. Wieffering, in 1966 (ex Juniper *et al*. 1989), reported the presence of catalpol. No alkaloids have so far been detected in any species of *Pinguicula* (Juniper *et al*. 1989). Of the flavonoids (including flavones, flavonones, flavonols) the following have been detected in the leaves of *P. vulgaris* (Jay & Gonnet 1974, 1975 ex Juniper *et al*. 1989): apigenin, 6-hydroxyluteolin, hypolaetin (8-hydroxyluteolin), isoscutellarin (8-hydroxyapigenin), luteolin and scutellarin (6-hydroxyapigenin). Histamines, in the concentration range 2–13 $\mu g\ g^{-1}$ fresh weight, were also found in the leaf tissues of *Pinguicula* sp. (Werle 1955, ex Juniper *et al*. 1989).

The presence of the enzymes acid phosphatase, esterase, ribonuclease and amylase was determined using high resolution cytochemical techniques on fresh leaves in several *Pinguicula* species, including *P. vulgaris* (Heslop-Harrison & Knox 1971; Heslop-Harrison 1976b); a variety of optical microscope techniques detected the presence of the enzyme in fresh frozen leaf sections and cleared whole mounts after the appropriate treatment. The use of substrate films, with fresh portions of upper leaf surfaces applied, was also used to detect the presence of amylolytic and proteolytic enzymic digestion on the appropriate substrates. The enzymes were found to be localized in the head cells of the digestive glands on the leaf surfaces, being most concentrated in the sessile glands, with less in the stalked glands. Stimulated glands contained no, or smaller amounts, of enzyme, than unstimulated ones because the enzymes are released into the secretion pool being built up surrounding the prey within 10 minutes of stimulation (Heslop-Harrison & Heslop-Harrison 1981). Unstimulated stalked glands each carry a secretion droplet rich in muco-polysaccharides and with detergent properties, responsible for wetting the prey and capturing it; the fluid virtually drowns small insect prey by penetrating them through the spiracles. Amylase activity was confined to the stalked gland head cells, and the sessile glands were richer in proteolytic activity. No evidence of the presence of either lipase or chitinase was detected in any of the species of *Pinguicula* examined; chitin from an insect's wing and chitin prepared as a substrate film showed no signs of digestion after the application of a partly stimulated leaf surface (Heslop-Harrison 1976a,b, 1978 and Y. H.-H., unpublished).

The secretion of all of the cells of a sessile gland head is not always synchronous; and each cell can obviously operate independently of the others, as seen in partially stimulated leaf surface preparations (e.g., figures 14, 15 and 16 of Heslop-Harrison 1976a; which show variable amounts of the acid phosphatase reaction product in the head cells depending on whether they were stimulated or not, and degree of stimulation). The enzymes are mostly stored in the radial walls of the head cells, which are of transfer-cell type, and to a lesser extent in the outer pectocellosic walls; they are not released on to the leaf surface until the glands are stimulated, first by contact with prey, and then by the nitrogenous and other products contributing to the secretion pool, the size of which depends on the degree of stimulation.

VII. Phenology

In a bog garden in the Midlands (at Birmingham University Botanic Garden), root growth was initiated from the overwintering hibernaculum as soon as conditions became favourable, usually from the middle to the end of April. In the Swedish subarctic the roots emerge in early June, and die back during August and early September; the roots account for 5–10% of the non-reproductive biomass (Karlsson 1986). The first obvious sign of activation (in the Midlands) is the loosening of the bud scales (see VI(A)). The new rosette leaves then emerge and expand, followed by the extension of flowering scapes from mid-May and throughout June. If several of the succeeding leaves contain axillary flower primordia (preformed in the hibernaculum the previous season), flowering continues successively over 3 weeks to 1 month, the timing depending on weather conditions, particularly temperature. Flowering was observed in *P. vulgaris* from May to June in Denmark, and from June to July in north Greenland (Heide 1912).

In northern Sweden Svensson *et al*. (1993) and Karlsson *et al*. (1996) found that there was great variation in the proportion of plants that flowered in any one season – from 8% to over 50%; plants with the largest rosettes were most likely to flower, and those at some sites produced up to six flowers (Karlsson 1986). Whilst all 'mature' plants (of a rosette diameter greater than *c.* 6 cm) in the British Isles seem to produce at least one flower, and then set seed, in subarctic Sweden only 14.4% of mature rosettes in the population finally set seed (Karlsson 1988). A possible explanation for this is that it takes several years before resource levels become high enough for successful seed production if the growing season is short (as little as 60–90 days in the subarctic). All plants of *P. vulgaris* from a high altitude site at *c.* 400 m a.s.l. failed to produce seeds in three years out of six, perhaps owing to lower temperatures at the end of the growing season (Thoren & Karlsson 1998). In the English Midlands, when grown out of doors, the seeds matured and were shed from July to August; here active vegetative growth ceased from mid-July into August, in terms of current rosette leaf emergence and expansion, but a new hibernaculum started to develop, containing the following year's leaf and flower primordia in the centre of the rosette.

Depending on weather conditions, the mature rosette leaves persist for varying periods into September; this may be of some importance because these surviving leaves, if continuing actively in a photosynthetic capacity, could transfer storage products into the developing hibernaculum and surrounding bulbils – forming important starch reserves for early renewed growth the following season (Y. H.-H., unpublished); the re-allocation of nutrients from senescing leaves in another species of *Pinguicula*, *P. vallisneriifolia* in its Spanish habitat, is discussed by Zamora *et al.* (1997). That the size of hibernacula, developed after a period of flowering in the Swedish subarctic, may be smaller and contain less N than after a season of purely vegetative growth is explained in terms of the relative somatic cost of reproduction by Thoren *et al*. (1996) and Eckstein & Karlsson (2001). In cultivation in the English Midlands the hibernacula and associated bulbils are produced as a result of the shortening day-length and lower night temperatures of autumn (see VI(C) above), as in *P. grandiflora* (see that account and Heslop-Harrison 1962). According to Heide (1912, p. 456) the arctic form of *P. vulgaris* produces hibernacula almost immediately after flowering, whereas those forms from more temperate regions continue vegetative growth for a period; possibly, however, this involves survival of the old rosette leaves under relatively mild conditions, rather than the initiation of new ones. Both hibernacula and bulbils remain dormant until spring; inhibitors from the decaying leaves may maintain the dormancy of the bulbils during the autumn, as in *P. grandiflora* (Y. H.-H., unpublished).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

The flower is adapted for pollination by bees, which are attracted by its colour, honey guide and scent (Kerner 1894). Nectar is secreted at the base of the thin, downwardly curving spur (Dickson 1869). The flowers are slightly protandrous. The sessile stigmatic lobe forms a hinged flap, 1–2 mm across, at the entrance to the corolla throat and this hides the two anthers, which lie behind and beneath it. A bee visiting the flower first touches the papillate slightly wet stigmatic flap (Heslop-Harrison & Shivanna 1977), dusting it with pollen from a flower previously visited. Penetrating further into the flower, the bee's head and back are next dusted with fresh pollen. As the bee retreats the stigmatic lobe is folded upwards, thus preventing self pollination. However, if cross pollination does not occur, the pendant stigmatic border curves backwards and comes into contact with the anthers and self pollination can then take place – thus seed is almost always set if weather conditions are favourable. The flowers are self-compatible and reproduction is amphimictic. Cleistogamy, vivipary and apomixis have not been recorded for any species of *Pinguicula*. The flowers are mainly bee pollinated, but no specific pollinators have been named except that the bee, *Osmia caementaria* Gerst., was observed visiting *P. vulgaris* flowers in the Alps (Muller 1881, 1886) as well as an unnamed Lepidopterid and two beetles. In the Pyrenees, the beetle *Anthobium atrum* Heer was observed in the spur of the flower, but it may not have been active in pollinating (MacLeod- ex Knuth Poll. **3**). Pollinator–prey conflict in another species of *Pinguicula*, which has more erect leaves at the time of flowering, is discussed by Zamora (1999); in *P. vallisneriifolia* the semi-erect insect-trapping leaves and flowers are closely associated, whereas in *P. vulgaris* the flat, rosette leaves are not normally in the flight path of the pollinating insects.

(B) HYBRIDS

In the British Isles, natural hybrids between *P. vulgaris* and *P. grandiflora* (× *P. scullyi* Druce) are rather rare because *P. vulgaris* is not common in the area of Ireland where *P. grandiflora* is most plentiful. This hybrid has a flower intermediate in size between the two parent species, the corolla being about 2 cm across; the lower corolla lobes are less divergent than those in *P. vulgaris*, but not as broad as in *P. grandiflora*, nor are the margins undulate. The white patch at the corolla throat is rather intermediate in shape between the short, broad patch of *P. vulgaris* and the long, curved cuneate patch of *P. grandiflora* (Bot. Irl., Fig. 13). Praeger also noted that forms more resembling one or other of the two parents may be backcrosses; × *P. scullyi* is said to be largely, though not entirely, sterile (Stace 1997). This hybrid has also been recorded by Casper (1962) from the Pyrenees. Since the chromosome numbers of *P. vulgaris* and *P. grandiflora* are $2n = 64$ (rarely $2n = 32$, see VI(D)) and $2n = 32$, respectively, one would suspect that the hybrid would be triploid, $2n = 48$; however, the possibility of amphidiploid hybrids containing either a full set of *P. grandiflora*, or a full set of *P. vulgaris* chromosomes, is not excluded. Such potential amphidiploidy would go some way to explaining Praeger's observations (Bot. Irl.) of a range of types existing, apart from backcrosses. The two species can be hybridized artificially, but the chromosome numbers of the wild or artificial hybrids have not been established. A new species, *P. submediterranea* Zamora, Jamilena, Ruiz-Rejon & Blanca, recorded recently for southern Spain, may also have arisen originally as a cross between *P. grandiflora* and *P. vulgaris* (Zamora *et al.* 1996).

That *P. alpina* at one time existed in some areas of Scotland alongside *P. vulgaris* suggests that another hybrid, *P.* × *hybrida* Wettst., may also have occurred here, but it has not been recorded. It does occur, however, in Austria (Wettstein 1919 ex Casper 1962), Finland and Czechoslovakia (Bergroth & Lindroth ex Casper 1962). This hybrid is sterile, and its chromosome number has not been established.

Molau (1993) studied large populations of three species of *Pinguicula* (*vulgaris*, *alpina* and *villosa*) growing sympatrically in a subarctic-subalpine site at Abisko, north Sweden, within a 50 × 50 m area; whereas the two former species were confined to base-rich habitats, the latter was confined to nutrient-poor *Sphagnum* bogs. He concluded that illegitimate pollen flow would probably not be prevented by such habitat separation. However, Molau noted that the differences between pollination biology, flowering phenology and breeding systems were sufficient to account for a highly efficient reproductive isolation of the species, this being coupled with differing ploidy levels. Furthermore, *P. vulgaris* was an 'opportunistic' late-flowering inbreeder, *P. alpina* an early flowering outbreeder whilst *P. villosa* was an intermediate between these two extremes. He did not report the existence of any hybrids in the area which he studied. J. F. Steiger (personal communication, 1988) noted that *P. vulgaris* and *P. alpina*, although common and growing together (at 1500 m at Trogenmoos, above Interlaken, Switzerland) 'never hybridized', *P. vulgaris* usually flowering some three to five weeks later than *P. alpina*.

(C) SEED PRODUCTION AND DISPERSAL

The seeds are fine, light and powdery and released as the fruits ripen successively over about a month. In the subarctic, 110–140 seeds are produced per capsule (Karlsson 1986). The developing fruits, horizontal at first, become erect, so the seeds are not released unless the capsule is shaken; they are held above ground level on the lengthening scapes. The capsule, 0.5–1 cm in length, is ripe 2–3 weeks after the flowers have been pollinated and dehisces apically along the placental margins by two slits. In dry weather the two valves open to release the seeds, which are minute and easily wind dispersed; in wet weather the valves close.

(D) VIABILITY AND GERMINATION

Seeds do not normally germinate in the British Isles until the following spring and their germination capacity is *c.* 100% when overwintered at normal outdoor temperatures. Seeds stored either fully imbibed at *c.* 1–2 °C, or stored dry for 6 months, and then sown in 18 h days (LD) and a minimum day and night temperature above 10 °C (WN) gave 100% germination within 2 weeks. Seed germination and germination capacity were also the same in seeds (i) stored dry, then chilled at *c.* 1–5 °C, fully imbibed, for 6 weeks, and then introduced into LD/WN conditions in February as compared to (ii) untreated controls; thus vernalization did not accelerate germination (Y. H.-H., unpublished).

Early season precipitation was correlated with seedling production in *P. vulgaris* in the Swedish subarctic, and seedling establishment was much higher for this species than for *P. alpina* and *P. villosa* growing in the same area. Seedling survival was, in general, very low (Karlsson *et al.* 1996) for these three species, *P. alpina* being the most variable in this respect, perhaps owing to the larger and more erratic frost movements in the *P. alpina* quadrats (Svensson *et al.* 1993).

Seedling establishment in the wild is precarious because the tiny seed size provides negligible food reserves, and suitable wet sites free from competition by other species are rare; seedlings have not been observed in the British Isles. Although not tested, it is unlikely that seeds survive beyond a single season. Seeds, however, do represent 'the lottery in colonizing' the rare, suitable sites available by wind dispersal some distance from the parent plant (Zamora *et al.* 1998) compared to bulbil establishment on an already occupied, adjacent microsite. But bulbils can also be dispersed further afield by autumn and spring rains (see VI(C) and VIII(F)).

(E) SEEDLING MORPHOLOGY

A cap at one end of the testa opens and the radicle emerges first and bears a tuft of root hairs which serve for initial anchorage; the radicle never grows much longer than *c.* 0.5 cm and then decays. The single cotyledon, which is strongly infolded (and could be interpreted as two according to Goebel, 1891) bears both sessile and stalked glands (Fig. 4). Succeeding adventitious roots emerge as new leaves are differentiated, about one to two per leaf node. In slightly shaded areas, on a mossy substratum, the first one to two internodes may extend somewhat and the rosette will then develop a little higher up the seedling 'stem' (Fig. 4j); see also VI(C). Internodal extension is severely limited by the very small food reserves in the seed, so is only a slight survival mechanism. Where there is sufficient light, the young rosette remains virtually stemless.

(F) EFFECTIVE REPRODUCTION

Although small in number in temperate regions, the bulbils (gemmae) probably provide an effective method of reproduction because opening bulbils can draw on relatively large starch reserves stored in the bud scales (Y. H.-H., unpublished). Establishment is usually around the parent plant, but water currents may also carry detached bulbils over some distance after autumn rains, snow melt or spring flooding. Dispersal over a wider area is possible, however, because seeds are light enough to be carried by the wind. Both dispersal methods are hazardous because suitable environments are very limited. In the Swedish subarctic, vegetative reproduction by means of bulbils is not mentioned as a way of population survival, or population increase, in recent papers (Svensson *et al.* 1993; Thoren *et al.* 1996); so here, if occurring at all, vegetative reproduction must be very rare. See also VI(C).

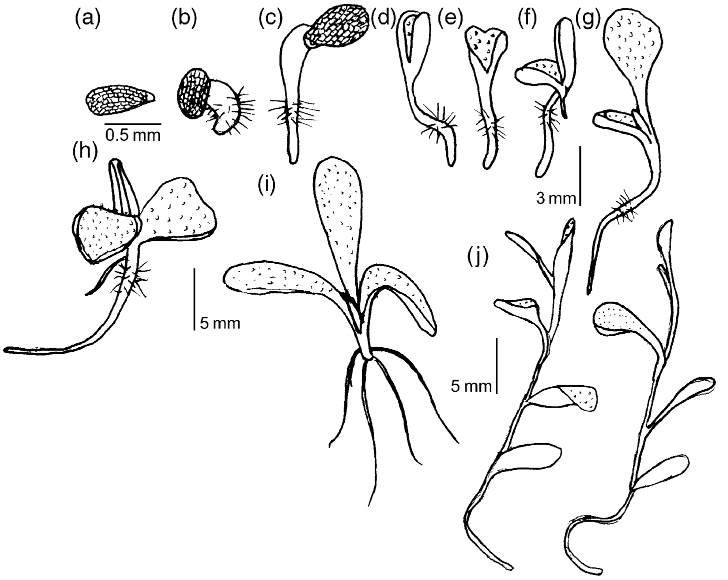

Fig. 4 Stages in the development of *Pinguicula vulgaris* during germination: (a) germinating seed, (b)–(e) 1–4 days after emergence, showing development of single cotyledon bearing glands on upper surface, (f)–(h) 8–10 days after germination, and (i) after 12–14 days, when a true rosette is usually formed. (j) Also after 12–14 days, if the seedling is growing amongst moss, then some internodal extension occurs before a rosette is established at the last formed node.

IX. Herbivory and disease

(A) ANIMAL FEEDERS AND PARASITES

No published references to these for *P. vulgaris* in Britain have been found. However, some relevant observations on a *Pinguicula* species endemic to southern Spain have been made by Zamora (1995) and Zamora & Gomez (1996). Here the secondary eating (by slugs, arachnids and reptiles) of prey trapped first by the leaf glands could represent a significant nutritional loss to the plant, as well as causing indirect damage.

(i) Mollusca

Slugs, as herbivores, may eat the leaves of *Pinguicula* species in cultivation in Britain, but this damage has not been observed in the field (Y. H.-H., unpublished). However, the slug *Deroceras hilbrandi* Altena (Agriolimacidae) is sometimes a significant kleptoparasite on the leaves of *P. vallisneriifolia* (Zamora & Gomez 1996). Whilst the slug incidence was low, those found had a robbing rate of up to nine captured flies per plant per 12 h, a significant loss of mineral salts to the plant in a nutrient-poor environment. The slugs were able to glide over the leaves without harm. If eating large, newly trapped prey (e.g., Tipulidae) a slug could spend up to 90 min eating one corpse, whilst smaller prey (e.g., small Nematocera) did not slow down its progression across a leaf. In Spain, slugs, as herbivores, may eat hibernacula, but have not been observed to attack the summer rosette leaves (Zamora & Gomez 1996).

(ii) Lepidoptera

Larvae of *Orthosia gothica* L. (the Hebrew character moth) have been observed eating the leaves of *P. vulgaris*, in cultivation in the English Midlands (Y. H.-H., unpublished).

(iii) Tipulidae

Tipulid larvae have been observed feeding on the basal leaves of *P. vallisneriifolia* occasionally (Zamora & Gomez 1996). Tipulid herbivory was distinguishable from slug herbivory because of the absence of mucus trails.

(B AND C) PLANT PARASITES AND DISEASES

The anthers of *P. vulgaris* are attacked by *Ustilago pinguiculae* Rostrup in Europe (Casper 1962); a brownish discoloration of the anthers has sometimes been observed in British plants, perhaps also owing to this infection. No diseases have been recorded.

X. History

As a member of the northern circumpolar element *P. vulgaris* perhaps reached its maximum abundance in Boreal times. Its Quaternary postglacial history could be traced in peat deposits by means of pollen and seeds, but so far no such records exist either in the Palaeontology Department of the Natural History Museum, nor the Palynology Unit of the Royal Botanic Gardens, Kew (personal letters from Paul Kenrick and Madeline Harley). There are no records of *Pinguicula* pollen given by Muller (1981), Collinson *et al*. (1993) nor West (2000). The generic characters of its pollen are described as being hexazonocolporate with a finely reticulate exine; the grains are suboblate and *c*. 40 × 30 µm (Moore *et al*. 1991), and so would be fully recognizable in peat deposits.

In the British Isles its occurrence has diminished within the last century mainly from drainage and exploitation of its previous habitats for arable cultivation (Fig. 1). Another significant factor might be the decline of rough grazing and increased use of fertilizers, with the consequence that former habitats have become overgrown by tall, dense fen vegetation.

Leaf extracts of butterwort were found by early herbalists to be effective in giving spasmodic relief (antipertussis) in cases of whooping cough, asthma, tuberculosis and spasms of intestinal pain (Fournier 1948; Christen 1961; Hegnauer 1966) the effectiveness is possibly attributed to the presence of certain acids in the extracts (see VI(F)). *Pinguicula* leaves, when rubbed on to the affected parts, were believed to have a therapeutic effect in treating chapped, or infected cows' udders in Scandinavia and Switzerland (Gerard 1633). Apart from the name 'common butterwort', *P. vulgaris* was called 'Yorkshire Sanicle' in some early English *Floras* (Withering 1818; Smith 1828) indicating its continued use in England for this purpose where 'the viscid exudation of the leaves is reputed to be good for the sore dugs of cows'. The name *Sanicula*, according to Prior (1879) was given by Bauhin, 1591, because of its healing properties, and the name '*Yorkshire* sanicle' derives according to Parkinson (1840, ex Prior 1879) 'because of its growing so plentifully in Yorkshire'. When mixed with linseed oil, the leaves were also used medicinally for the treatment of warts (Hornemann 1821 ex Lloyd 1942). According to McNeill (1910) the plant was believed to act as a charm against witchcraft in the Hebrides, and cows that ate it were said to be safe from supernatural ailments.

The association of *P. vulgaris* with wet pastures, and 'liver sickness' in sheep, meant that the species itself was sometimes blamed for disease in sheep at a time before infection by the liver fluke had been established (Lloyd 1942); and Praeger (1909) gives the name 'rot water' as the equivalent of the gaelic name, leithe uisge, in connection with *P. vulgaris*, in his *Tourist's Flora of the West of Ireland*. In north-east Ireland it was known as 'steep grass' (Stewart & Corry 1888). In the Hebrides the gaelic name was 'modalan', and the general gaelic name, though not that used locally, was 'badan maesgan' (McNeill 1910). In Orkney it was known as ecclegrass (Spence 1914).

By scouring the container with fresh *P. vulgaris* leaves before the addition of warm (cows' or reindeers') milk, a ropy or curdled milk, a form of junket, was obtained in some parts of Europe, including Swedish Lapland, the Italian Alps, Switzerland, Wales and the English Lake District (Linnaeus 1792; Francis Darwin 1875; ex Lloyd 1942). Vernacular names of *P. vulgaris* associating the plant with the making of the yogurt-type milk were used in both Norway and the Faeroes, where it was given the name equivalent to 'curdle grass' (Lloyd 1942). Although hydrolytic enzymes from the leaves are usually said to be responsible for the action, thus resembling rennet, an association of microorganisms with the leaf-gland mucilage may be the real cause (Juniper *et al.* 1989).

The sticky slime from the stalked glands on the leaf surface was also used by Dutch peasants in the nineteenth century and earlier as a hair pomade (Poiret ex Fournier 1948).

Pinguicula vulgaris was first recorded in the British Isles in 1597, in Gerard's *Herbal*, on Ingleborough Fells, Yorkshire (Druce 1922; *Comit. Fl.* 1932). It was originally named by Linnaeus in 1753. Some 50 years later, William Stackhouse provided William How (the author of *Phytologia Britannicum*, 1650) with a record of *Primula farinosa* 'most plentifully mixt with Pinguicula on a very low and squalid meadow near Knaresborough': How's book is now known to be little more than a revised version of Johnson's *Mercuris* of 1639; and William Stackhouse was also a colleague of Thomas Johnson, the editor and emendator of Gerard's *Herbal* (Raven & Walters 1956).

List Br.Vasc. Pl. (1958) no. **441**, 4

Pinguicula grandiflora Lam.

Large-flowered or great butterwort (in Ireland, bog violet). Plant with the same general habit as *P. vulgaris*, but more robust and tending to be larger in its vegetative parts, and with foliar shape differences noticeable particularly in the young rosette, and with distinctive floral characteristics. There are two subspecies, ssp. *grandiflora* Lam., distributed throughout its range, and ssp. *rosea* (Mutel) Casper, confined to south-east France; it is a highly variable species with a number of taxa of low taxonomic value (Blanca *et al.* 1999). The form of *P. grandiflora* from Ireland has been said to be an extreme of that found on the continent, but in cultivation there appear to be no real morphological differences between it and samples from the Pyrenees (Y. H.-H., unpublished); however, the two samples did differ in their developmental responses (see below under VI(E)ii).

Subgenus Pinguicula, Section Pinguicula. An insectivorous perennial consisting in summer of a rosette of 5–9 active leaves lying close to the ground, shallowly anchored by fibrous roots. Overwintering as a hibernaculum. Leaves involute, somewhat broader than in *P. vulgaris* with a blunter apex – clearly apparent particularly in the opening rosette, and of a brighter, yellow green ('sap green', 62/1–62/2 of British Colour Chart); 2.5–8.8 cm long by 1.0–3.0 cm wide. Leaves can inroll along the margins upon stimulation by insect prey, and bear digestive glands on the upper surface. Flowering scapes glandular, often a little taller than those of *P. vulgaris*, one per leaf axil, 1–7 produced in succession from early summer. Calyx lobes rather more deeply divided than in *P. vulgaris*, apically obtuse (acute in *P. vulgaris*), glandular externally. Corolla deep violet (Victorian violet 738/3–738/2, or spectrum violet 214 of British Colour Chart 1941), the lobes, particularly of the lower lip, distinctly rounded, broader than long, with overlapping, undulate margins. Lower corolla lip can be up to nearly 3.0 cm across with a distinctive cuneate, white patch traversed by 9–13 deep purple (736 738 of British Colour Chart) veins leading into the entrance of the corolla tube; the central vein of each lobe extends outwards towards the corolla margin, then bifurcates and curves round to meet the two lateral veins. In the central lobe particularly, the areas between the diverging pair of main veins may be slightly raised up to form two roughish tongues on the corolla floor. The hairs on the inner surface of the corolla lip differ slightly in form and distribution from those of *P. vulgaris* (see Section VI(A)). Corolla spur noticeably longer than in *P. vulgaris* (up to 1.6 cm compared with up to 1.0 cm), and sometimes bifid. Anthers, pollen, and stigmas as in *P. vulgaris*. Capsule 0.5–0.8 cm long, more spherical than in *P. vulgaris*. Seeds ellipsoidal (0.6–) 0.85(–1.1) mm long by (0.2–)0.3(–0.4) mm wide, with a reticulate testa, the reticulations often isodiametric.

Pinguicula grandiflora has sometimes been regarded as a subspecies of *P. vulgaris*, but usually it is given specific rank (for further discussion, see VIII(B)). First recorded for the British Isles (in south-west Ireland, near Macroom, Co. Cork) in 1809 by Drummond (More *et al.* 1898). Plants with white, pale lilac or purplish-pink flowers have been recorded in Ireland by Praeger (Bot. Irl., Sect. 145); some of these may correspond with subspecies and forms described from continental Europe, e.g. ssp. *rosea* (Mutel) Casper which has a pale lilac or rose corolla, and smaller corolla lobes and spur; f. *pallida* (Gaudin) Casper has pale lilac flowers. A white-flowered form was recorded by Nelson (1993) from the Burren, Co. Clare, Ireland.

Occasionally, under extensive cultivation in either glasshouse or bog garden, forms have arisen with flowers in which the corolla is completely split into two distinct upper and lower portions united only by the spur; such flowers resemble those of *P. crenatiloba* DC. of the subgenus Temnoceras of Barnhart (1916). Polypetalous flowers have also occurred, of interest in showing that the lobes of the upper lip seem to play no part in the formation of the corolla tube and spur, both of which are part of the lower lip. Fewer corolla abnormalities have been observed than in *P. vulgaris* (Y. H.-H., unpublished). However, plants may show some aberrations of the calyx such as petaloidy of one or more of its members, or varying degrees of fusion or bifurcation of the sepals. Occasionally there may be three or four stamens instead of the usual two, or they, too, may be petaloid. Up to three well-developed stigmatic lobes may sometimes occur. No colour variations of the corolla were observed, either in the field or in cultivation, of Irish stocks or their propagules or seedlings.

Native only in south-west Ireland. Naturalized (with varying degrees of success, based on observations over some 40 years) on Tremithick Moor, Trangle Moor and Land's End, Cornwall, and also in calcareous seepage on Venn Ottery Common, Devon; in Merioneth in Wales; at Killane, Blackstairs in Co. Wexford, and on peat bogs at Carraghblagh, Lough Swilly, Co. Donegal (Praeger, Bot. Irl.; Stace 1997; M.C.F. Proctor, personal communication). Usually occurring in bogs and wet heaths and damp pastures, but also on wet rock surfaces.

I. Geographical and altitudinal distribution

Restricted to south-west Ireland in parts of Galway, Kerry, Cork and Clare (Bot. Irl.), its extreme northern limit for Europe (Fig. 5). The species is well known for its disjunct distribution, forming part of the so-called Lusitanian element of the flora of the British Isles (Forbes 1846; Heslop-Harrison 1953), or the Hiberno-Lusitanian, Hiberno-Cantabrian, Hiberno-Pyrenean group of species of Webb (1952b, p. 66). Its most eastern native station in Ireland is at Carrignavar, at 8°30′ W (More *et al.* 1898). Elsewhere in Europe (Fig. 6) it occurs in the mountains and subalpine regions of the Jura, the French Alps, the Pyrenees and the mountains of northern Spain (Asturia and Galicia). It reaches south to the Penalara massif, Madrid Province, and the Sierra Nevada, Almeria Province (Blanca *et al.* 1999). In Ireland it ascends from close on sea level in Co. Clare to 853 m in Co. Kerry (Alt. range Br. Pl.); in the latter county it is replaced at higher levels by *P. vulgaris* (More *et al.* 1898; Webb 1952a, p. 29). In the Pyrenees it reaches an altitude of 2300 m and in the subalpine regions there it ascends to 1525 m (Turmel 1955 ex Casper 1962; Blanca *et al.* 1999).

Pinguicula grandiflora is classified as Oceanic, or sub-Oceanic Temperate by Preston & Hill (1997).

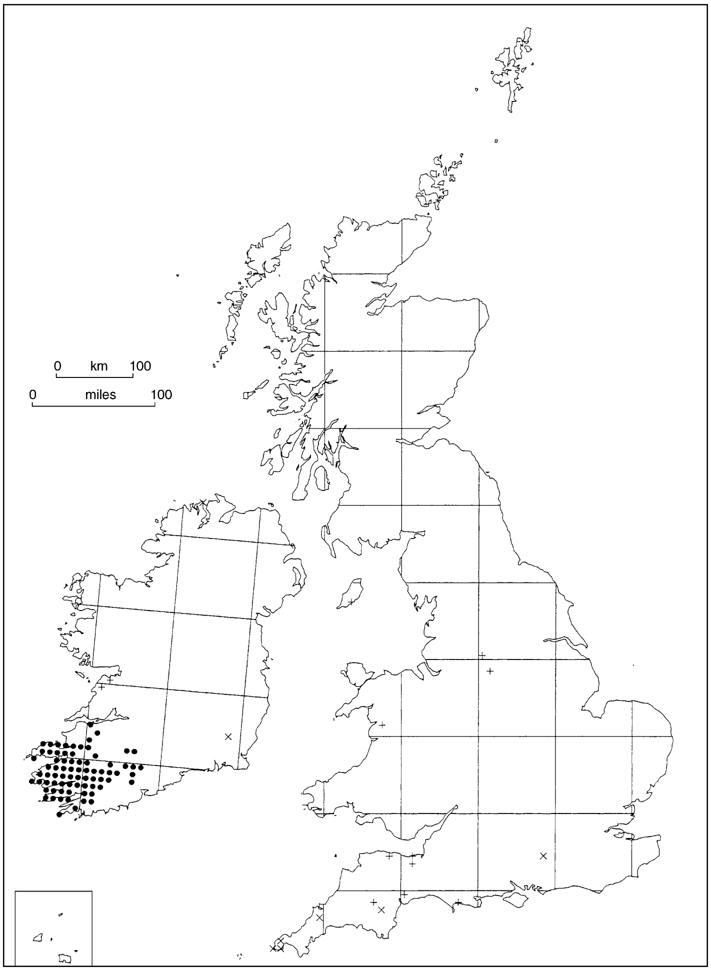

Fig. 5 The distribution of *Pinguicula grandiflora* in the British Isles. Native: (○) Pre-1950 (●) 1950 onwards. Each dot represents at least one record in a 10-km square of the National Grid. Introduced plants: (×) pre 1950 (+) 1950 onwards. Mapped by Henry Arnold, Biological Records Centre, Centre for Ecology and Hydrology, using Dr A. Morton's DMAP programme, mainly from records collected by members of the Botanical Society of the British Isles.

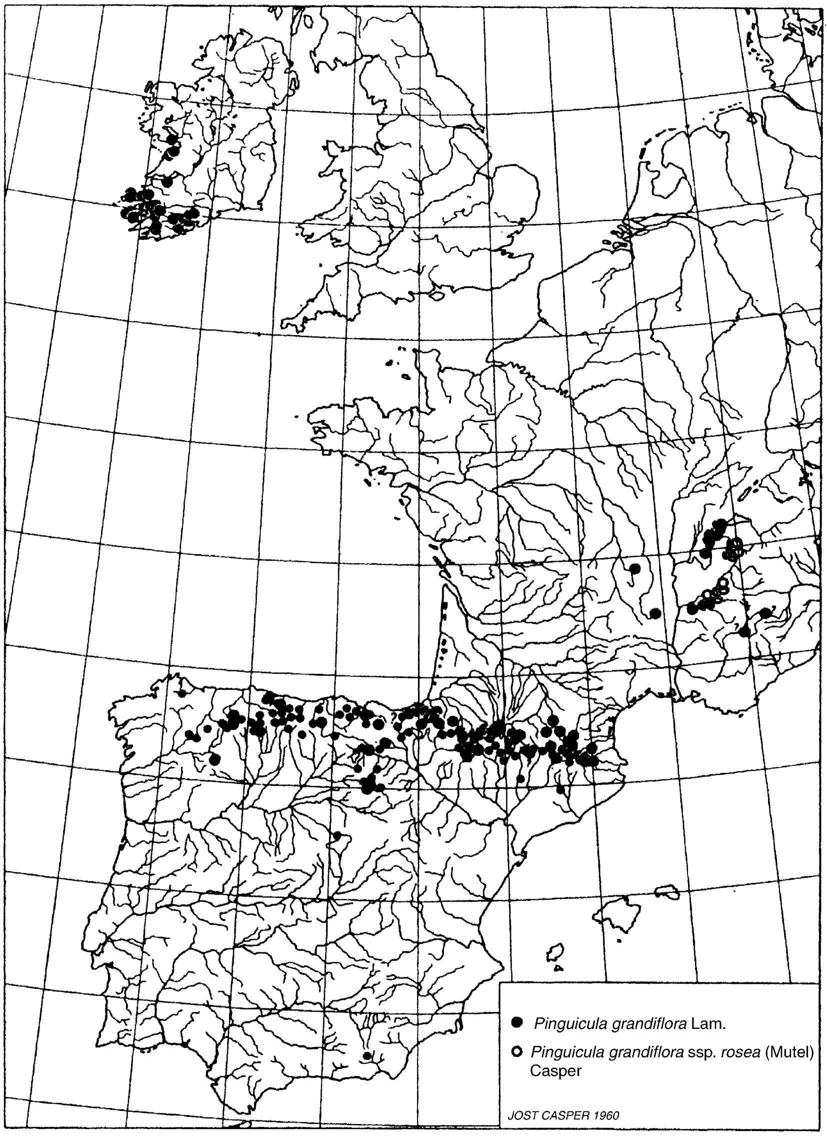

Fig. 6 The European distribution of *Pinguicula grandiflora*, based on Casper (1962) and (for the Iberian peninsula) Blanca *et al*. (1999).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

In the British Isles there seems no obvious climatic reason (and origins apart) why *P. grandiflora* should be restricted to south-west Ireland, except that the P/E ratio is very high there. Whilst it is abundant where it occurs it does not appear to be extending its range, and attempts to establish it elsewhere have not been wholly successful; thus, within 35 years, six plants of *P. grandiflora* introduced to an area near Killanne, Co. Wexford, had increased to nearly one hundred, but then disappeared (Bot. Irl.). Some climatic vicissitude was at least suspect. The mature hibernaculum in Ireland is fully frost resistant and it actually requires a period of vernalization in the neighbourhood of freezing before growth can be resumed (Heslop-Harrison 1962). It is thus unlike another member of the Lusitanian element, *Arbutus unedo*, which is also confined to south-west Ireland, but has differing environmental requirements; Sealy (1949) explained the distribution of this species as being limited to areas with a mean January temperature of *c.* 7.5 °C or higher. If the winter temperature is insufficient for the vernalization of the older hibernacula of *P. grandiflora* in any given season in Ireland, however, the survival of the species is ensured by daughter bulbils or the progeny of seedlings forming 1-year-old hibernacula, neither of which requires vernalizing (see also VI(E)). The date of the first frost of winter (November–December) is not significant because all plants are then fully frost resistant; the most vulnerable period would be a late frost when the older hibernacula and younger plants were emerging from dormancy, when young and mature foliage leaves would be susceptible to frost damage. Emergence from dormancy is usually staggered over some days, even weeks, again protecting the survival of the species from climatic or other vicissitudes.

The actively growing rosettes do not survive any degree of desiccation in cultivation, nor in the wild; however, hibernacula and bulbils can withstand this condition for short periods.

(B) SUBSTRATUM

Pinguicula grandiflora normally grows on boggy surfaces in south-west Ireland but seems to survive wherever conditions are sufficiently wet or humid; it is therefore to be found on wet rocks and even on piles of discarded roadside grit in Co. Kerry; presumably the merit of this type of habitat is the absence of competition, and the species appears to be indifferent to substratum type. Thus in continental Europe it is found on Bunter sandstone, granitic rocks and on calcareous soil (Chouard 1949, *ex* Casper 1962), and Fournier (1977) also notes its calcareous preference. According to Blanca *et al.* (1999), it occurs in Spain in waterlogged pastures, on rocky banks, banks of streams and springs as well as peat bogs. In the Asturias, in northern Spain, it was found on a calcareous, wet cliff (S. M. Walters, personal communication). Losa (1954, *ex* Casper 1962) places it among the rock-loving alpine element.

III. Communities

No precise community lists of species, nor species frequencies, in the areas where *Pinguicula grandiflora* grows in south-west Ireland seem available. However, three sources of information have been used in Table 5 from five localities where *P. grandiflora* occurs. Columns 1–3 give associated species (listed during the 1950s by J. & Y. Heslop-Harrison, unpublished). Column 1 records are from a bog near Cloonee Lake, Co. Kerry, column 2 records from dripping rocks on pass behind Glengariff, west Cork, and column 3 records beside a stream side, Glengariff. Column 4 gives species in the *Carex echinata-Juncus bulbosus* association listed by Tüxen (from Braun-Blanquet & Tüxen, Ir. Pfl., table 36, p. 309), a bog near Glencar, Co. Kerry. Floristically, columns 1–4 are indicative of rather base-rich wet heaths with seepage of base-rich water. Column 5 lists plants from Cloonee, 14 km from Kenmare along the north shore and noted by Praeger (Bot. Irl., Sect. 311–312) where 'many of the characteristic Kerry plants grow in abundance.' Species from the Killarney woods, and their frequencies, were listed by R. W. Scully (pp. 139–140, Tansley 1911), and *P. grandiflora* is included here with a frequency of 'f', along with many tree species, including *Arbutus unedo* – a truly unique assemblage of plants.

The Ecological Flora of the British Isles (Fitter & Peat 1994) lists *P. grandiflora* as occurring in the Corine habitats 'Northern wet heaths' (Corine code No. C31.11) and 'lowland blanket bogs' (Corine code No. C52.1).

In northern Spain (Desfiliado de Ponton nr. Covadonga, Asturias) it was noted on a wet, shaded, calcareous cliff, where it was associated with *Adiantum*, *Globularia*, *Saxifraga hirsuta* and *Sesleria* (S. M. Walters, collected

Table 5 Species lists for some Irish communities in which *Pinguicula grandiflora* occurs; frequencies not recorded. 1–3, localities as noted by J. & Y. Heslop-Harrison, data from 1950s (see text); 4, species noted by Tüxen (Ir. Pfl. 1952); 5, species noted by Praeger (Bot. Irl. 1934) from Co. Kerry

	Locality				
Species	1	2	3	4	5
Anagallis tenella	–	–	+	+	–
Calluna vulgaris	–	+	–	–	–
Carex binervis	+	–	–	–	–
Carex echinata	+	–	–	+	–
Carex hostiana	–	–	+	–	–
Carex nigra	+	–	–	–	–
Carex panicea	+	–	+	+	–
Carex pulicaris	–	+	–	+	–
Carex punctata	–	–	–	–	+
Carex verticillatum	–	–	–	–	+
Carex viridula ssp. *brachyrrhyncha*	+	–	–	–	–
Carex viridula ssp. *viridula*	–	–	+	–	–
Dactylorhiza maculata ssp. *ericetorum*	+	–	–	–	–
Dactylorhiza majalis	+	–	+	–	–
Drosera rotundifolia	+	–	+	–	–
Eleocharis multicaulis	–	–	+	+	–
Epilobium pedunculare	–	+	–	–	–
Erica tetralix	+	+	+	+	–
Euphorbia hyberna	–	–	–	–	+
Euphrasia officinalis	–	+	–	–	–
Galium saxatile	–	+	–	–	–
Juncus acutiflorus	–	–	+	+	–
Juncus bulbosus	–	–	+	+	–
Juncus effusus	+	–	–	–	–
Juncus sylvatica	+	–	+	–	–
Luzula multiflora	+	–	–	–	–
Myrica gale	–	–	+	+	–
Narthecium ossifragum	+	–	+	–	–
Parentucellia viscosa	–	–	–	–	+
Pinguicula lusitanica	**–**	**+**	**–**	**–**	**+**
Plantago lanceolata	–	+	–	+	–
Polygala dubia	–	+	–	+	–
Potentilla erecta	+	+	+	+	–
Prunella vulgaris	–	+	–	+	–
Sagina sp.	–	+	–	–	–
Salix aurita	+	–	–	–	–
Salix cinerea ssp. *oleifolia*	+	–	–	–	–
Saxifraga × *Geum*	–	–	–	–	+
Saxifraga spathularis	–	+	–	–	+
Saxifraga umbrosa	–	+	–	–	–
Sisyrinchium bermudiana	+	–	–	–	–
Succisa pratensis	+	+	+	+	–
Viola riviniana	–	+	–	–	–
Agrostis capillaris	–	+	–	–	–
Anthoxanthum odoratum	+	–	–	+	–
Danthonia decumbens	–	+	–	+	–
Festuca ovina	–	+	–	–	–
Holcus lanatus	+	–	–	+	–
Molinia caerulea	+	+	+	+	–
Breutelia chrysocoma	–	–	+	–	–
Brachythecium sp.	+	–	–	–	–
Hylocomium sp.	+	–	–	–	–
Rhytiadiadelphus squarrosus	+	–	–	–	–
Sphagnum papillosum	+	–	+	–	–
Sphagnum rubellum	+	–	+	–	–
Sphagnum subsecundum	+	–	+	–	–
Huperzia selago	–	+	–	–	–

in 1951; personal communication 1965). In the alpine vegetation of the eastern Pyrenees, Braun-Blanquet (1948) noted *P. grandiflora* as constant in the calcareous small-sedge fens (Caricion davallianae). It occurred in the typical Cariceto-Pinguiculetum and also the Cariceto-Pinguiculetum appauvri, whereas it was very scarce in the Caricetum davallianae where *P. vulgaris* ssp. *alpicola* was constant.

IV. Response to biotic factors

In its Irish habitat *P. grandiflora* is much more of an aggressive colonizer than *P. vulgaris* and apparently can compete successfully against other plants because of its spreading, rosette habit during the growing season, and by means of successful vegetative reproduction. However, the plant is shallow rooted and the leaves are delicate and brittle; it does not withstand trampling by stock, being easily uprooted.

V. Response to environment

(A) GREGARIOUSNESS

Pinguicula grandiflora can be an active colonizer of open ground and may form quite dense colonies under favourable conditions – thus in Kerry and Cork it is immensely abundant and profuse where it occurs, whereas *P. vulgaris* is quite rare, being restricted to scattered, often single plants (Praeger in Bot. Irl., Sect. 145); he writes 'one sees over ten thousand *P. grandiflora* for one *P. vulgaris*'). Large patches of *P. grandiflora* are often formed by prolific vegetative reproduction from the original plant, which survives centrally, with clusters of plants of successive generations formed from bulbils, surrounding it. Praeger (Bot. Irl., Sect. 310) described it during May and early June as 'the glory of Kerry … its great purple blossoms nodding in the wind over hundreds of square miles of bog and rocky mountains'. Its abundance here is probably owing to a combination of successful vegetative and seed reproduction coupled with very favourable climatic conditions.

(B) PERFORMANCE IN VARIOUS HABITATS

In south-west Ireland *P. grandiflora* seems to grow luxuriantly wherever it occurs. As with *P. vulgaris* it does not tolerate appreciable water flow, nor immersion whilst in the rosette stage, but can do so in the resting condition. In cultivation plants with access to a continuous supply of insects thrive more than those without, and these then give rise to bigger hibernacula and greater numbers of axillary bulbils at the end of the growing season.

(C) EFFECTS OF FROST, DROUGHT, ETC.

Over 50 hibernacula and their associated bulbils, from Irish sources, in cultivation in a bog garden in Birmingham survived the severe winter of 1962–63 with a continuous snow cover for *c.* 6 weeks, and made vigorous growth and then flowered actively, if sufficiently mature, the following spring. Elsewhere in its range, at high altitudes, the species must obviously also be able to survive frost and snow in the resting condition; however, in its native habitat in south-west Ireland, such extreme conditions never occur.

In cultivation resting buds, both hibernacula and bulbils, survive refrigeration at 1.0–2.0 °C for up to 9 months, and then make good vegetative growth when returned to long days/warm nights (see also VI(Eii)); they can also survive short periods (1–2 weeks) of desiccation or total immersion at *c.* 5 °C or less. Rosettes withstand neither drought nor frost. There is some evidence that drier conditions towards the end of the growing season accelerate dormancy, as in *P. vulgaris*; this may be an adaptation to summer drought in parts of its range.

VI. Structure and physiology

(A) MORPHOLOGY

The morphology of *P. grandiflora* corresponds in the main with that of *P. vulgaris* but differs in details of leaf shape and form of floral parts (see individual species accounts). The root system also resembles that of *P. vulgaris*, consisting, whilst there is active vegetative growth of the rosette, of a tuft of fine, short fibrous roots that do not persist over the winter; new ones replace the old ones when growth of the hibernaculum is resumed in the following spring.

The hibernaculum differs slightly in shape and form from that of *P. vulgaris* (Fig. 7d,e), and also in the way that it opens on resumption of spring growth (see account of *P. vulgaris*, VI(A)). In *P. grandiflora* the hibernaculum consists of (10–)12–15(−17) members upon an abbreviated stem; the outer 5–6 are modified to form protective, indurated, scales swollen with starch, followed by *c.* 3 members intermediate between scales and foliage leaf primordia, in their turn followed by the true leaf primordia, the inner ones bearing axillary flower primordia (Heslop-Harrison 1962; Fig. 7a–c).

As in all species of *Pinguicula* the leaf surface glands are adapted to the trapping and digestion of prey, 'fed' plants in any habitat appearing more robust compared with those unfed. There are some, slight, morphological differences between the leaf glands of *P. grandiflora* and *P. vulgaris*, of taxonomic rather than ecological interest. The head cells on the stalked glands on the upper leaf surface usually number *c.* 16 (15.5 ± 0.36) as is also characteristic of *P. vulgaris*, but occasionally there may be 32. The number of head cells in the sessile glands is 7.9 ± 0.06 (Heslop-Harrison & Heslop-Harrison 1981). Sessile glands number *c.* 120 mm^{-2} in the main leaf area, stalked glands *c.* 16 mm^{-2}, but both types become less common towards the leaf margin and the midrib (the density and distribution of the sessile and stalked glands from a whole leaf mount are shown in figure 16 of Heslop-Harrison & Knox 1971). Comparisons

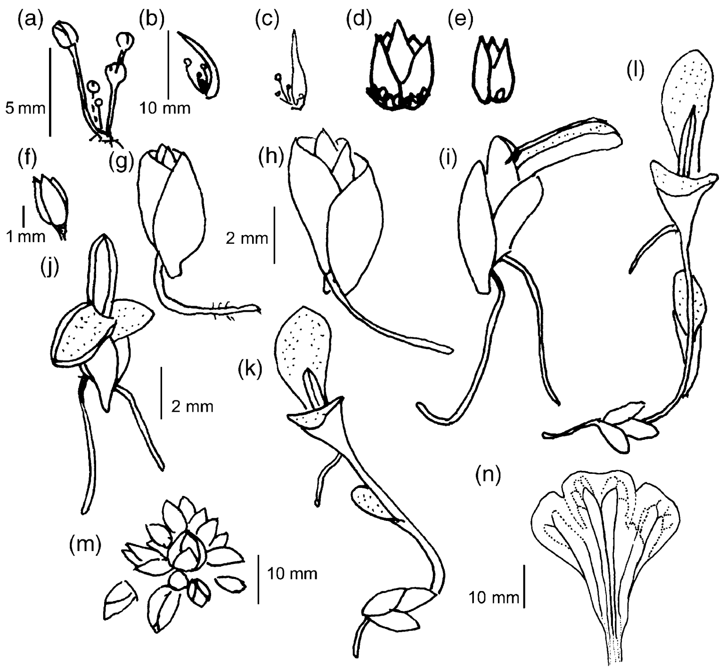

Fig. 7 Features of *Pinguicula grandiflora* from south-west Ireland. (a–c) Flower primordia, dissected from centre of hibernacula, with masking leaf primordia removed. (d) and (e) Comparisons of shapes of hibernacula of *P. grandiflora* (d) and *P. vulgaris* (e). Typical associated bulbils are shown at the foot of the outer scales. (f–j) Development of bulbil to form rosette in Spring. (k–l) Where there is competition from associated vegetation, the opening bulbils may show internodal extension before a rosette is produced. (m) A parent hibernaculum (at centre, from Pyrenean stock) with associated daughters of differing generations clustered around it. (n) The lower lip of the corolla, torn from the upper lip, and flattened to show the venation pattern leading into the spur.

between the dimensions of the gland heads and the endodermal cells of the sessile glands are given in Table 6. The number of cells forming the heads of the hydathodes on the lower leaf surface is usually four, the hydathode density being *c.* 20 mm^{-2}. Stomatal density on both surfaces is *c.* 40 mm^{-2}.

The corolla shape differs markedly from that in *P. vulgaris* (see species descriptions and Fig. 7n for *P. grandiflora*). The trichomes, of three main types, on the corolla, also differ somewhat in their distributions from those of *P. vulgaris*: Type 1 hairs (see *P. vulgaris*, VI(A)) occur less frequently on the lateral lower corolla lobes than the central lobe. Type 2 hairs (intermediate between Types 1 and 3) with heads of 5–7 uniseriate cells tapering to the apex, and a stalk of 2–3 cells, all translucent, occur on the cuneate white area of the central lobe. Type 3 hairs occur at the back of the white area towards the corolla throat, are more abundant than in *P. vulgaris*, and extend into the spur itself for at least half its length (Y. H.-H., unpublished; Casper 1962). These differences may be associated with differences in pollinating insects between the two species.

(B) MYCORRHIZA

Not known (Harley & Harley 1986).

(C) PERENNATION, REPRODUCTION

A hemicryptophyte perennating as a rootless hibernaculum which lies in a pocket formed by the decay of the previous season's rosette leaves, *c.* 0.5–1.0 cm below ground level.

In Ireland, *P. grandifolia* propagates by means of bulbils (Heslop-Harrison 1962); these develop in the axils of the last formed foliage leaves at the end of the growing season. Up to 9 bulbils, grouped as a main axillary and accessory buds, are produced at each of the last 6–7 nodes and total up to *c.* 55 per plant ($\bar{x}$ = 27.7, n = 25, Fig. 7d). Pyrenean stocks produced even more ($\bar{x}$ = 79.2, n = 25), by having larger numbers of accessory buds clustered around the main one. A brood bud, 2–3 mm in length, consists of tightly packed scales, the outer 1–2 serving as protective scales which, as in a hibernaculum, are swollen with starch, so also providing an immediate source of nutrients when growth is resumed. The scales enclose 2–3 leaf primordia.

Pyrenean plants, cultivated in Britain, may produce daughter rosettes from axillary buds during the summer because not all are inhibited from development by apical dominance. By the end of the growing season, what was originally a single plant may also possess 3–4 daughter hibernacula, each with its own cluster of bulbils. This very active formation of daughter plants was not characteristic of Irish stocks cultivated under the same conditions (Fig. 7m, and Y. H.-H., unpublished).

Plants in cultivation survived for at least 10 years and normally flowered and set seed annually. Seed germination is usually *c.* 100% under test conditions, but seedling survival and establishment in the wild is hazardous except when favourable open ground can be colonized. By far the most common method of

Table 6 (a) Dimensions of gland heads, and cell numbers per gland head in the three existing species of *Pinguicula* in the British Isle; part data from Heslop-Harrison & Heslop-Harrison (1981), and those for *P. lusitanica* from Y. H.-H. (unpublished). (b) Estimates of the flow rate through the digestive glands of *P. grandiflora* after stimulation of the leaf with BSA; flow observed over 3 h. (Data from J. H.-H., unpublished)

(a)	Gland head diameter (µm)		Gland head cell number		Gland number mm^{-2}
Species	Stalked	Sessile	Stalked	Sessile	Stalked/Sessile
P. grandiflora	63.7 ± 1.44	37.8 ± 0.52	15.50 ± 0.36	7.9 ± 0.06	16/120
P. vulgaris	59.8 ± 1.7	46.6 ± 0.72	14.75 ± 0.75	*c.* 8	8/112
P. lusitanica	23.5 ± 0.71	33.8 ± 0.91	*c.* 8	6.2 ± 0.52	24/152

(b)
Average flow rate = 1.72×10^4 $\mu m^3\ s^{-1}$.
Flow per gland = 143 $\mu m^3\ s^{-1}$.
Mean area of endodermal cell = 508.4 μm^2.
Flow rate through endodermal cell = 0.28 $\mu m^3\ \mu m^{-2}\ s^{-1}$.

reproduction is by vegetative means when large colonies of the species can arise (see also account of *P. vulgaris*).

(D) CHROMOSOMES

Pinguicula grandiflora (from Vallée de la Forge at 1300 m a.s.l., Vercours, France) possesses the chromosome number $2n = 32$ (Doulat 1947); this agrees with counts by Contandriopoulos (1962) from plants from Corsica, by Zamora *et al.* (1996) from the Iberian peninsula, and by Casper (1963), site not known. Godfrey & Stripling (1961), again site unknown, give the number as $2n = 64$, which is the same as that of *P. vulgaris*. For discussion on the hybrid between these two species (*P.* × *scullyi*) see under *P. vulgaris*, VIII(B).

Random amplified polymorphic DNA (RAPD) analyses of two newly described *Pinguicula* species endemic to the east and south of the Iberian peninsula in comparison with the putatively most closely related species, which includes *P. grandiflora*, are given by Zamora *et al.* (1996).

(E) PHYSIOLOGICAL DATA

(i) Leaf gland physiology

The leaf gland physiology, in connection with the insectivorous habit, is essentially the same for all species of *Pinguicula* examined (Heslop-Harrison & Knox 1971; Heslop-Harrison & Heslop-Harrison 1981), and is described under *P. vulgaris*. Estimates of the flow rate through the sessile glands of *P. grandiflora*, after stimulation with bovine serum albumen (BSA), and observed over a period of 3 h are given in Table 6(b) (J. H.-H. & Y. H.-H, unpublished).

(ii) Developmental physiology

Dormancy of the hibernaculum Under natural conditions in south-west Ireland the dormant phase lasts for about half the year, but can be extended by refrigeration at *c.* 1–2 °C. With refrigeration beyond 9 months the hibernacula tend to 'bolt', even whilst kept in a refrigerator (Y. H.-H., unpublished). Irish hibernacula two or more years old do not break dormancy when in cultivation, unless they experience a period of *c.* 4–5 weeks at *c.* 1–2 °C (Heslop-Harrison & Heslop-Harrison 1972). If maintained for a year in a glasshouse, with warm nights but natural daylength, they never open and eventually die. In their native habitat in Ireland perhaps oscillating relatively low winter temperatures may be sufficient to simulate true vernalization, but no experiments using oscillating day and night temperatures have been made; however, survival of the mature hibernaculum without some chilling must be marginal. In contrast, it was found that Pyrenean hibernacula do not require a period of vernalization, and survive several years in a heated glasshouse with natural daylength, the breaking of dormancy being stimulated by increasing daylength alone (Y. H.-H., unpublished). Both in Pyrenean and Irish stocks, with appropriate continuous chilling, dormancy can be curtailed to as little as 3 months immediately after its onset, and normal development and flowering will then follow when the hibernacula are returned to long days and warm nights. Kinetin treatment, in standard doses, can replace vernalization of Irish hibernacula (Y. H.-H., unpublished), but led to some anomalous forms. Gibberellic acid (in 2.5-mg doses applied by pipette, in solution, three times weekly over the hibernaculum surface) did not break the dormancy of unchilled hibernacula, however, but this may be due to lack of penetration of the solution through the hibernaculum scales – of nine plants treated only one opened to produce a small rosette which bore a single abortive flower on an abbreviated scape (Y. H.-H., unpublished).

Dormancy of bulbils and 1-year-old plants (hibernacula) Both Irish and Pyrenean stocks do not require prechilling to break dormancy, but their development is normally prevented throughout the winter by low temperatures and short days until favourable growing conditions in the spring. Products, acting as inhibitors, from the decaying rosette leaves of the previous season also reinforce this dormancy (Y. H.-H., unpublished). A period of chilling for 3 weeks, or applications of kinetin or gibberellic acid in standard doses, all accelerate the breaking of dormancy in bulbils. Without any prechilling treatment, 1-year-old hibernacula will break dormancy after *c.* 5 months if maintained at a minimum temperature of *c.* 10–12 °C in long days (Y. H.-H., unpublished).

VII. Phenology

Pinguicula grandiflora resembles *P. vulgaris* in that, under natural conditions, renewed growth of the hibernaculum starts with rising night temperatures and lengthening days, usually in Ireland shortly after the vernal equinox; the hibernaculum scales open and extension of the enclosed leaf primordia to produce a rosette follows during April and early May, accompanied by the development of a tuft of short, fibrous roots anchoring the rosette to the substratum. In Ireland flowering occurs from mid-May to early June, the flowers opening in succession from primordia developed the previous autumn (Heslop-Harrison 1962). In Spain flowering begins earlier than in Ireland, in March, and continues into October (Blanca *et al*. 1999), suggesting that rising temperatures here are critical for early growth, as well as increasing day length. The fruits mature 3–4 weeks after pollination and the seeds are shed in late June to early July Seed germination in nature has not been observed, but in cultivation seedlings are normally produced only in the following spring, suggesting there is an initial period of dormancy. Irish plants become dormant in late summer as a response to shortening day-length and decreasing night temperatures (Heslop-Harrison 1962), hibernacula being fully formed before the autumn equinox; given a mild autumn, however, the last rosette leaves of the season survive into September or early October, before finally withering, their reserves being stored as starch in the associated developing bulbils and outer scale leaves of the hibernacula. Bulbils remain dormant usually until the following spring, probably as a result of inhibitors released from the old, decaying rosette leaves (Y. H.-H., unpublished); occasionally they do, however, make some growth into young plants in a mild autumn (possibly if the surrounding old leaves and their decomposition products, in the form of inhibitors, have been removed).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

The distinctive dark purple venation pattern on the corolla lobes leading towards the white corolla throat form prominent honey guides (Fig. 7n). The pollination mechanism of *P. grandiflora* is essentially as in *P. vulgaris*, and presumably the flower is bee pollinated; however, the spur, containing the nectar, is longer than in the latter species, so a different species of pollinator may be involved. It is not known what the role of the trichomes on the inner corolla lobes is; they may allow the pollinating insect to gain more purchase whilst collecting the nectar. In the Pyrenees the beetle *Anthobium atrum* Heer was frequently observed in the spur, but no other possible pollinators (MacLeod ex Muller 1881, p. 466).

In cultivation self-pollination does not appear to occur; of eight flowers on eight plants (from Irish stocks) left unpollinated and covered to exclude pollinators only one set seed. Of 45 flowers from Irish stocks crossed artificially, either with pollen from plants of 'Irish' or 'Pyrenean' origin, all set seed successfully. The first indication that pollination has occurred is within 24 h when the corolla is shed whilst still fully turgid, indicating that an abscission zone has formed at the junction of the corolla with the receptacle. In flowers that remain unpollinated the corolla stays firmly attached to the receptacle, withering, along with the other floral parts, in 5–7 days (Y. H.-H., unpublished).

There are no records of either cleistogamy or apomixis.

(B) HYBRIDS

Pinguicula grandiflora occasionally hybridizes with *P. vulgaris* to give the hybrid *P.* × *scullyi* Druce in the Cork–Kerry area and it also occurs in the Val d'Eyne in the east Pyrenees (Casper 1962); see account of *P. vulgaris*, VIII(B)).

It has not been recorded which species was the maternal parent. The natural hybrid between *P. grandiflora* and *P. longifolia* ssp. *longifolia* was found in 1969 in the French Pyrenees (below the Cirque de Gavarnie at 1800 m) by J. F. Steiger (and photographed in cultivation in 1981, personal communication).

The crossing of the tetraploid *P. grandiflora*, genetically closest to *P. submediterranea* Blanca, Jamilena, Ruiz-Rejon, Zamora (a hexaploid, with $2n = 48$) with an unknown diploid species, followed by the subsequent duplication of the chromosome number, may be the origin of this latter, newly described species, endemic to the Iberian peninsula (Zamora *et al*. 1996); the possibility that it has arisen from a cross between *P. grandiflora* and *P. vulgaris* is also discussed. Possible backcrosses of the hybrid *P.* × *scullyi*, to either of the potential parents, may give the variations in intermediate forms in Ireland that have been noted by Praeger (Bot. Irl.), but their permanence and chromosome numbers have not been recorded. A comparison between the Irish forms of *P.* × *scullyi* that have been observed and *P. submediterranea* would be of interest.

As mentioned above (VI(Eii)) the Irish and Pyrenean ecotypes kept under cultivation over a number of years were not morphologically separable, in either vegetative or floral characters; when grown together under glasshouse conditions, the Pyrenean plants appeared more luxuriant in their growth. Hybrids raised between Pyrenean and Irish ecotypes also seemed to show some degree of hybrid vigour, having larger hibernacula and a greater number of bulbils than either of the parents. Two-year-old hibernacula of this cross behaved in the same way as the Pyrenean stock, and did not require vernalization to break dormancy (Y. H.-H., unpublished).

(C) SEED PRODUCTION AND DISPERSAL

Although there are minor differences in seed size and capsule form, many of the features described in the account of *P. vulgaris* apply to *P. grandiflora* also.

(D) VIABILITY OF SEEDS: GERMINATION

Pot-sown seeds overwintered in an unheated glasshouse do not normally germinate until the following spring, when germination is usually *c.* 90–100%, indicating there is an in-built dormancy period. Samples from Irish stocks (i) stored dry at room temperature after being shed until sown the following spring or (ii) pre-chilled at 2–3 °C (after sowing fully imbibed) in a refrigerator for 3–4 months) before introduction in long days/warm nights showed no differences in germination rate, indicating that, as with *P. vulgaris*, there is no vernalization requirement for breaking seed dormancy in *P. grandiflora*. The germination tests were carried out by sowing the seeds on filter paper, permanently moistened with distilled water in Petri dishes, in the standard manner. Germination occurred within 2–3 weeks.

(E) SEEDLING MORPHOLOGY

All seeds of the genus examined are small and bow-shaped, with a brown, reticulate testa, varying slightly in patterning with the species. In *P. grandiflora* they are (0.6–)0.85(–1.1) mm long × (0.2–)0.3(–0.4) mm wide, slightly larger than those of *P. vulgaris*. In *P. grandiflora* the number of cells of the reticulum (or alveoli, Casper 1962) along the long axis of the seed is *c.* 15, and along the short axis *c.* 8–9, about the same number as in *P. vulgaris*. However, each alveolus tends to be roughly isodiametric in *P. grandiflora*, but rather longer than wide in *P. vulgaris* (Y. H.-H., unpublished).

As in *P. vulgaris*, germination is epigeal, and the radicle emerges through a slit in one end of the testa. Only a single cotyledon is apparent and this bears both sessile and stalked glands on its upper surface. Seedling development in *P. grandiflora* is not distinguishable from that of *P. vulgaris.* For other details such as the postulated fusion of two cotyledons to give the single one, see the account of *P. vulgaris*.

(F) EFFECTIVE REPRODUCTON

The most effective method of reproduction is by the bulbils (which are both organs of perennation and propagation) and in the west of Ireland this must be responsible for the dense swards of the species encountered; and bulbil production can be very prolific (see VI(C)). Water currents may dislodge some of the bulbils from the parent plant during the winter and also be effective in dispersal over a wider area. The Irish form of *P. grandiflora* has become adapted singularly well to the climate encountered in south-west Ireland, with its varying degrees of winter harshness, so that, whatever the conditions, the survival of the species is ensured – a mild winter allowing large numbers of bulbils to develop the following spring, even though the parent hibernaculum is killed. Seedlings have not been observed in the wild, but the light-weight seeds would allow effective dispersal over a wide area, the limitation then being their transport to a suitable habitat. Bulbil development is recorded in Fig. 7f–j; Fig. 7k–l also illustrate how a developing bulbil may show a limited amount of internodal extension, overcoming competition of other species for light before forming the typical rosette habit.

IX. Herbivory and disease

(A) ANIMAL FEEDERS AND PARASITES

No information.

(B) AND (C) PLANT PARASITES AND DISEASES

None recorded.

X. History

The original description is that of Lamarck based on material collected in the Alps in 1789 (ex Casper 1962). Although it was first recorded for the British Isles ‘definitely’ by James Drummond in 1809 (More *et al.* 1898; Bot. Irl., Sect. 145), according to Praeger the ‘Butterwort is mentioned in Smith’s History of Kerry, p. 85 (1756) as abundant on islands at the head of Kenmare River, and no doubt this species is intended’.

See account of *P. vulgaris* for possible uses, but none has been recorded specifically for *P. grandiflora*.

Neither seeds nor pollen grains of *P. grandiflora* have been identified in Quaternary deposits held in the Natural History Museum, London, nor in the Palynology Department of the Royal Botanic Gardens, Kew. The Postglacial history of the species, as part of the Lusitanian element in the British Isles, is likely to be linked with the other species in this group, notably *P. lusitanica* (see that account).

List Br. Vasc. Pl. (1958) no. **441**, 1

Pinguicula lusitanica L.

Pale butterwort. Subgenus Isoloba Barnhart. An insectivorous perennial consisting in summer of a rosette of 5–12(–15) leaves, horizontal and lying close to the ground, shallowly anchored by a tuft of fine, fibrous roots. Usually overwintering as a rosette, but occasionally behaving as an annual. Leaves oval or oblong-oval (0.6–)1.0–2.5(–3.0) cm long, 0.3–0.8(–1) cm wide, apex slightly emarginate, subpetiolate, the short petiole fringed with hairs before flaring out into the lamina. Sometimes the leaf margins are inrolled to expose little of the lamina which is pale green-'grey' or yellowish, with dark red veins, the upper surface bearing red-headed glands. Plant flowering successively over a period of months usually from June until August, sometimes to October in the British Isles, a single flower produced per leaf axil. Scapes 1–6(–12) in number, 3–15 cm long and lengthening as the fruit develops; slender, erect and glandular. Flowers small, calyx bilabiate, the upper 3-lobed, the lobes ovate-oblong diverging, 0.2–0.4 cm long, the lower 2-lobed for up to 1/3 of its length, the outer surface covered with red-headed glands. Corolla pale lilac (pastel lilac of BCC 437) or very pale crimson, the lobes subequal, emarginate and not overlapping, 0.15–0.3 cm long; corolla tube longer than the limb, yellow internally with red veins, laterally compressed. Palate is velvety surfaced (hairy) and continues as a ridge inside the corolla throat which bears very fine hairs and yellow-tipped glands. Spur 0.2–0.45 cm long, subcylindrical, deflexed, yellowish. The stigma at the entrance to the corolla throat is white, and unequally bilobed, the lower lobe forming a conspicuous flange closing the entrance and protecting the two anthers at each side and behind it. Capsule subglobose, 0.25–0.45 cm long, scarcely larger than the calyx; seeds ellipsoidal, 0.5–0.65 mm long by 0.2–0.25 mm wide, with a reticulate testa and 1–4 distinctive transverse bars within the elongated alveoli.

Very uniform throughout its area of distribution and no morphological variants have been described. *Pinguicula lusitanica* is a member of the Lusitanian element of the flora of the British Isles, occurring also in France, the Iberian peninsula and the extreme north-west of Africa. Unlike the other species of *Pinguicula* in Europe (except for *P. hirtiflora* Ten. and *P. crystallina* Sibth., Casper 1962) it belongs to the subgenus Isoloba and its morphological affinities are closer to those centred in the Gulf of Mexico than the other European ones.

A native of bogs, wet heaths and in flushes where water oozes out of the ground.

I. Geographical and altitudinal distribution

Pinguicula lusitanica has a highly restricted western distribution in the British Isles but is local or even absent in some of these areas (Fig. 8). In Scotland it is found mainly in the west from Kirkudbright to Orkney (the northern limit here being 58°58′ N (Bennett 1923) and the Outer Hebrides; it is most abundant in the western parts of Ross and Sutherland, and fairly abundant throughout the north of Scotland (except Caithness), extending south approximately as far as the railway from the Kyle of Lochalsh to Strathpeffer; south of this it is found mainly in the west, with a few isolated colonies elsewhere. South of Loch Lomond it continues along the coasts of Renfrewshire, Ayrshire and Galloway. In England it occurs in the west to Cornwall, Wiltshire and as far east as Hampshire; it also grows in Pembroke and the Isle of Man. It is most common in Ireland being found in 33 of the 40 vice-county divisions into which the island was divided; and, although rare in the lowland centre, it is widely distributed in the coastal districts (More *et al*. 1898; Bot. Irl.).

Elsewhere in Europe (Fig. 9) it has a westerly, fringing distribution from France (with its easterly limit in France at *c.* 5° E and its northerly limit at *c.* 51° N) and southwards into Portugal and Spain and thence just into north-west Africa, in Morocco, and in one locality in Algeria (Casper 1962). It is classified as Oceanic – or sub-Oceanic – Temperate by Preston & Hill (1997).

In the British Isles it extends from close on sea level to *c.* 450 m in the Mourne mountains (Stewart & Corry 1888), and to 300 m in Scotland (Slack 1966) with a maximum of 487 m on Dartmoor in Britain (Alt. range Br. Pl.). In continental Europe it is found from 10 m to 1200 m (Blanca *et al*. 1999); its maximum altitudinal limits are approximately only half those of *P. alpina*, *P. grandiflora* and *P. vulgaris*, almost certainly because of its habit and distinctive method of perennation as compared with these species.

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

In Britain the species is restricted to the oceanic, relatively frost-free areas wherever the substratum is favourable and sufficient moisture is available. In Scotland there appears to be a correlation between the occurrence of *P. lusitanica* and the 400 line for Meyer's Precipitation Saturation Deficit Quotient (Slack 1966); to the north and west of this line the species is common, but in the fringing areas it becomes less common. Here presumably habitat factors, particularly the availability of ground water, rather than climatic factors, may come into operation (see Section II(B), below). In the west of Ireland also it decreases in abundance rather suddenly east and south of the 400 Meyer's line (Slack 1966). Areas in Great Britain and Ireland where the species occurs at lower humidities include Galloway, the Isle of Man, the Mourne mountains, the Wicklow mountains, Pembroke, Devon, Cornwall and the Hampshire basin – and in the latter the Meyer quotient is down to 200. This may be misleading, however, because it is such a small plant and is present only in localized pockets where the relative humidity immediately above the wet substratum is obviously more significant than any general measure of precipitation. In the British Isles there appear to be no marked summer temperature limitations,

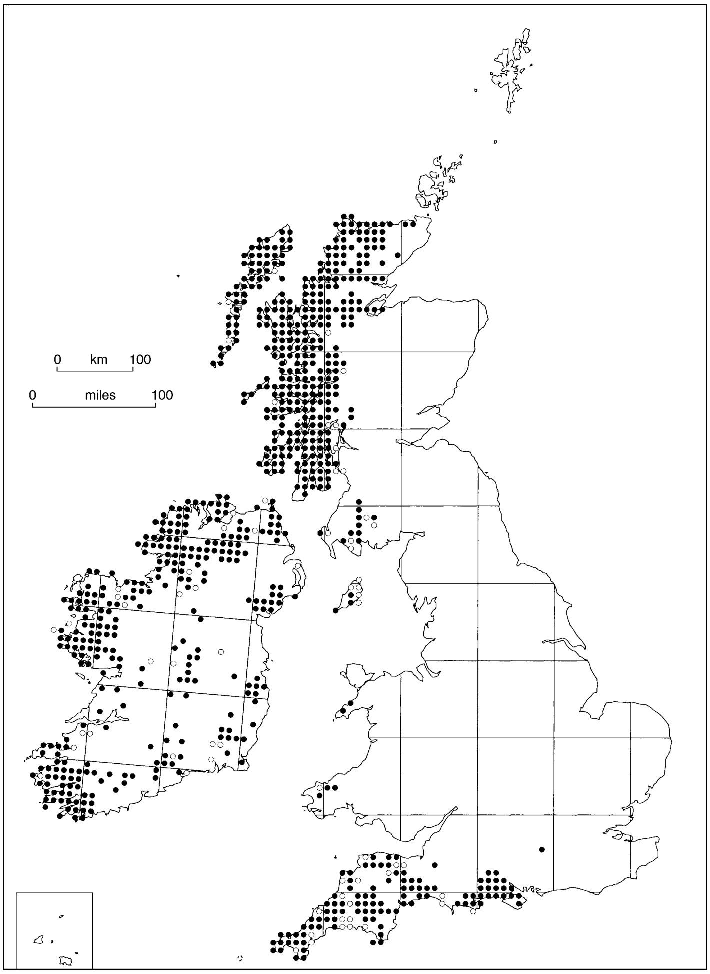

Fig. 8 The distribution of *Pinguicula lusitanica* in the British Isles: (○) Pre-1950, (●) 1950 onwards. Each symbol represents at least one record in a 10-km square of the National Grid. Mapped by Henry Arnold, using the DMAP programme, mainly from records collected by members of the Botanical Society of the British Isles.

with the possible exception of a minimum July mean of 12 °C; this could account for its absence in the Shetlands and its rarity in Orkney and parts of Caithness (Slack 1966).

In mild conditions *P. lusitanica* may survive the winter in the vegetative state, as a rosette, but it can also behave as an annual; the length of the growing season then becomes a limiting factor, and, if favourable, may allow the plant to complete its life cycle in a few months (Y. H.-H., unpublished). Slack (1966), however, states that 'low winter temperatures down to a February mean minimum of about 0 °C do not destroy the plant which at that time is in the condition of a resting bud'; a possible interpretation of his observations is that he was referring to very small rosettes protected from frost in a sheltered south-facing bowl; a low winter temperature must be an important constraint on its survival in any area. However, there seems to be no particular reason why *P. lusitanica* does not occur in many of the seepage mires beyond its present range of distribution, were low temperatures a limiting factor – for their groundwater has a minimum temperature of 8–9 °C, and 'a feature of many groundwater-fed mires is that they rarely, if ever, freeze, at least in the permanent seepages, where one would expect *P. lusitanica*)' (B. D. Wheeler, personal communication). If frost is prolonged the parent plant dies and survival depends on the success of seed germination and seedling establishment (see also VI(E)).

In an analysis of the microclimates in the fringing areas in Scotland, Slack (1966) noted that *P. lusitanica* occurred in 'suntrap' habitats which were flat, or sloping to the south or south-west. However, according to Preston & Hill (1997), it may also grow in shaded microclimates. That it can indeed tolerate summer shade was indicated when B. D. Wheeler (personal communication) found it in winter 'amongst quite dense stands of *Molinia* in sites where it had possibly been overlooked during summer field work, indicating that it may function as a hiernal or vernal species'.

(B) SUBSTRATUM

There appears to be some correlation between type of substratum from which drainage is taking place in any particular flush and the occurrence of *P. lusitanica*; it is

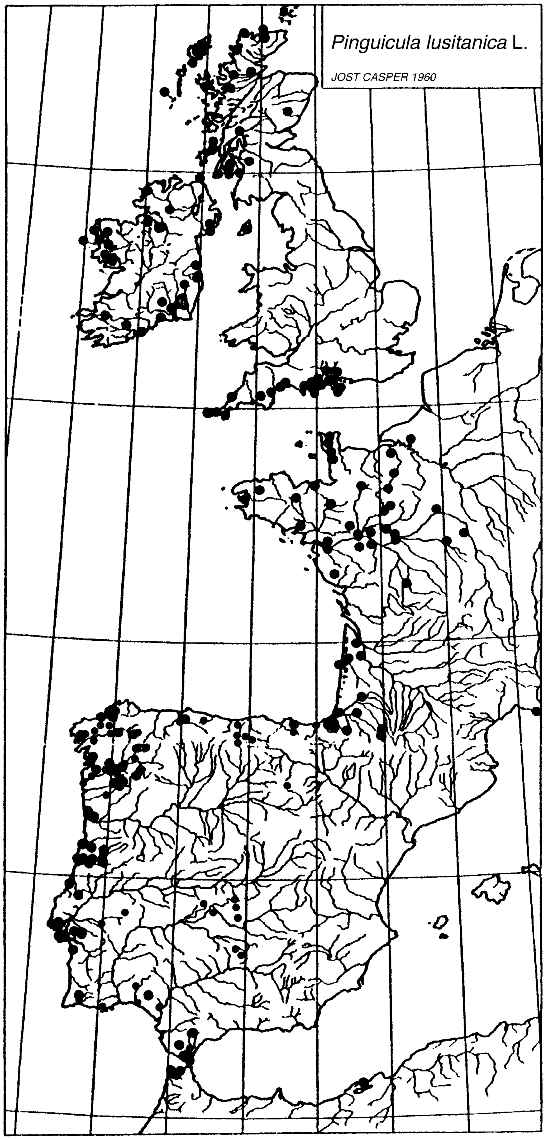

Fig. 9 The distribution of *Pinguicula lusitanica* in Europe. Data from Casper (1962) and modified (for Spain and Portugal) after Blanca *et al*. (1999).

found in flushes emerging from such substrata as basalt, gabbro, epidiorite, schistose grits and blown sand; more rarely on sandstone and granite, and more rarely still (as at Glencoe) with drainage from calcareous rocks (Slack 1966). It seems to be absent from chalk and limestone areas, but 'whether this is because it is intolerant of highly calcareous water seems still open to question and investigation, partly because of the possible confounding effects of climate on its distribution' (B. D. Wheeler, personal communication). On the Lizard in Cornwall, where *P. lusitanica* has its highest recorded frequency, the distinctive lithology is of serpentine and some gabbro, the soils being moderately base-rich but notably calcium poor; the serpentine here is made up of ferromagnesian silicates which give rise to soils where magnesium predominates over calcium and is rich also in other minerals such as chromium and nickel, but poor in aluminium, potassium and phosphorus (Rodwell 1991b). The species is described as being silicolous by Blanca *et al*. (1999). Why *P. lusitanica* and *P. vulgaris* do not often occur together in any one habitat, climatic tolerances and origins apart, remains uncertain (see also under *P. vulgaris*). In Devon it is absent from calcareous soils (Keble Martin & Fraser 1939). In the New Forest area, in Hampshire, it is recorded as frequent and often plentiful on both acid peat, as well as on peat over calcareous marl (Brewis *et al*. 1996). In Scotland, near sea level, the species grows in small, flat, rather stony flushes washed by oozing, peaty water, but at higher altitudes it occurs in steeper areas on black peat with relatively few stones (Slack 1966). In Ireland it never occurs in bare drainage channels nor on wet rock faces where both *P. grandiflora* and *P. vulgaris* can be found; perhaps, being a smaller plant than either of these species, it is not able to obtain nor retain, adequate purchase on bare rock accompanied by some surface water flow. It does not survive total inundation, or only for very short periods.

The soil pH arising from the breakdown of serpentine in the Lizard area is given as between 5.5 and 7.5 (Rodwell 1991b), and in the subcommunity in which *P. lusitanica* is found the range is limited to (6.5–)6.7 (–7.1); however, a soil pH of (4.08–)4.99 – 6.55(–7.2) and a water pH of (4.66–)5.11–6.49(–7.07) has been noted by B. D. Wheeler & S. C. Shaw (1992, personal communication). Comparisons between the pH of soil and water, and water level, in cm (from FenBASE) for *P. vulgaris* and *P. lusitanica* habitats are given in Table 7. The basic tolerance seems to be higher in *P. vulgaris* than in *P. lusitanica.*

III. Communities

Pinguicula lusitanica is restricted essentially to wet flushes in bogs, seepage mires and heaths but it does not

Table 7 Comparisons of soil and water pH, and water levels in cm in UK habitats for *Pinguicula lusitanica* (n = 39) and *P. vulgaris* (n = 120). FenBASE data from B. D. Wheeler (University of Sheffield)

	P. lusitanica				*P. vulgaris*			
	Min.	Mean	SE	Max.	Min.	Mean	SE	Max.
Water pH	4.5	5.7	0.05	7.1	4.1	6.4	0.03	8.4
Soil pH	4.1	5.7	0.05	7.2	3.9	6.5	0.03	7.56
Water level	−6	0.3	0.7	9.2	−34.5	−2.6	–	8.4

grow in the most acid of conditions where *Trichophorum cespitosum* is found. The Corine biotopes, as listed in The Ecological Flora of the British Isles (Fitter & Peat 1994) are northern wet heaths (Code 31.11), Atlantic *Erica–Ulex* heaths (31.23), bog-hollows (51.12), purple moor-grass bogs (51.2), and brown bog-rush fens (54.22); the first and last noted habitats here are also shared with *P. vulgaris* (see also below).

Its typical associates in Scotland are *Carex hostiana*, *Drosera anglica*, *D. rotundifolia*, *Eleocharis pauciflorus*, *Pinguicula vulgaris. Rhynchospora alba*, *Saxifraga aizoides*, *Schoenus nigricans*, and *Utricularia minor* (Slack 1966). Associated species listed by Slack, and where *P. lusitanica* was abundant (at the highest point between Acharacle and Kinlochmoidart, altitude *c.* 150 m, on a hillside concave to the south-west) were: *Carex viridula* ssp. *oedocarpa*, *C. echinata*, *C. hostiana*, *Drosera anglica*, *D. rotundifolia*, *Juncus bulbosus*, *Molinia caerulea*, *Myrica gale*, *Narthecium ossifragum*, *Pinguicula vulgaris*, *Rhynchospora alba*, *Schoenus nigricans*, *Selaginella selaginoides*, *Triglochin palustre* and *Utricularia intermedia*. The only heath community where *P. lusitanica* is listed by Rodwell (1991b, p. 420) with a frequency as high as IV (Domin value (1–3)) is an *Erica vagans–Schoenus nigricans* heath (*Eleocharis multicaulis* subcommunity) which is restricted to the Lizard in Cornwall (Table 8); *P. vulgaris* is absent from this area. However, *P. lusitanica* is a relatively rare and uncompetitive plant, and it is not necessarily significant that it should be reported with high constancy only in this community. Table 9 also lists those communities where *P. lusitanica* is occasional, or scarce, as well as new records.

Pinguicula lusitanica is found with *P. grandiflora* in the pass behind Glengariff, Co. Kerry (see *P. grandiflora* account). In the Burren, Ireland, *P. vulgaris* and *P. lusitanica* occur in the same 2 × 2 m quadrat (M. C. F. Proctor, personal communication). It also occurs with *P. vulgaris* east of Erigal, Co. Donegal, although rare here (Colgan & Scully 1898) and in some other localities (see *P. vulgaris* account). All three species of *Pinguicula* were found to occur on a moor near Brandon, Co. Kerry, Ireland (personal archival letter from A. W. Stelfox, undated but *c.* 1950s) along with 'many sedges' and *Schoenus nigricans*.

Table 8 Floristic table for *Pinguicula lusitanica*, as part of the *Eleocharis multicaulis* subcommunity of the *Erica vagans-Schoenus nigricans* heath from the Lizard in Cornwall; this is the only subcommunity in which the species has been recorded in 61–80% of the stands sampled ($n = 9$). The numbers in brackets give the range of Domin values. The vegetation height was 29 cm (17–45 cm), the vegetation cover 91% (65–100%) and the slope 1° (0–4°). Data from Rodwell (1991b)

Species	Subcommunity details
Schoenus nigricans	V(1–8)
Erica tetralix	V(2–8)
Serratula tinctoria	V(2–5)
Molinia caerulea	IV(4–7)
Anagallis tenella	V(1–3)
Campylium stellatum	V(2–5)
Succisa pratensis	V(2–4)
Carex pulicaris	IV(1–3)
Festuca ovina	III(1–3)
Potentilla erecta	III(2–3)
Ulex gallii	III(1–6)
Genista anglica	I(1–3)
Fissidens adianthoides	I(1–2)
Platanthera bifolia	I(2)
Carex flacca	IV(3–4)
Eleocharis multicaulis	V(1–4)
Eriophorum angustifolium	V(1–5)
Pinguicula lusitanica	**IV(1–3)**
Drosera rotundifolia	IV(1–3)
Phragmites australis	III(1–3)
Dactylorhiza incarnata	III(1–2)
Riccardia multifida	III(1–2)
Riccardia sinuata	III(1–3)
Sanguisorba officinalis	III(1–4)
Carex hostiana	III(2–3)
Juncus acutiflorus	III(1–2)
Polygala vulgaris	III(1–3)
Scorpidium scorpioides	II(2–3)
Gymnadenia conopsea	II(2–3)
Hypericum pulchrum	II(1)
Stachys officinalis	II(1)
Galium uliginosum	II(1)
Ulex europaeus	I(2)
Angelica sylvestris	I(2)
Eupatorium cannabinum	I(1)
Eurhynchium praelongum	I(1)
Juncus maritimus	I(4)

As with other rosette-forming plants, butterworts may not always tolerate much shade from taller, summer vegetation, and it is not found in association with *Juncus acutiflorus*; however, it does occur in gaps between taller plants such as *Myrica gale* and *Pteridium aquilinum*, perhaps receiving some protection from them. It occurs in woodland clearings, particularly in alder woods, but it was also found in the quite dense shade of a birch-alder wood in one locality on the north shore of Loch Leven, Inverness-shire (Slack 1966). Rankin (ex Tansley, Br. Isl.) noted that in the New Forest 'spring' and 'valley' bogs the dominant *Sphagnum* spp. matrix was made firm in some areas by the rhizomes and roots of *Eriophorum angustifolium*, *Eleocharis multicaulis* and *Juncus acutiflorus*, and it was here that *P. lusitanica*, along with two species of *Drosera*, and *Narthecium ossifragum* occurred. On Dartmoor (Devon) *P. lusitanica* is very conspicuously a plant of the Carboniferous rocks of the metamorphic aureole rather than of the blanket peat or base-poor flushes on the granite. It is usually not on *Sphagnum*, contrary to the statement made by Keble Martin & Fraser (1939, p. 506), but may occur on peat at the sides of *Sphagnum* clumps. If it occurs on *Sphagnum* it is not known how it can keep up with the upward growth of this moss, as can the sundew.

Pinguicula lusitanica withstands little water flow, mainly occupying the fringes of a flush; in a locality in west Inverness the species listed in a flush by Slack (1966) were: *Carex hostiana*, which occupied the

Table 9 NVC communities in which *Pinguicula lusitanica* is occasional, scarce, or, as yet, unrecorded (FenBASE data from B. D.Wheeler, University of Sheffield)

Pinguicula lusitanica is occasional in the *Schoenus nigricans–Narthecium ossifragum* community (M14), found very locally in Cornwall and in east Devon, south-east Dorset and the New Forest. It is also occasional in the *Carex hostiana–Ctenidium molluscum* variant of the *Carex viridula* ssp. *oedocarpa–Juncus bulbosus/kochii* subcommunity of the *Pinguiculo–Caricetum dioicae* community (M10).

Pinguicula lusitanica is scarce in the subcommunity M10a. It is also scarce in the *Rhynchospora alba–Drosera intermedia* subcommunity of the *Erica tetralix–Sphagnum compactum* wet heath (M16), the *Narthecium ossifragum–Sphagnum papillosum* valley mire (M21) and its subcommunity *Rhynchospora alba–Sphagnum auriculatum*; and in the *Erica vagans–Schoenus nigricans* wet heath community (H5) and its typical subcommunity.

New records for *P. lusitanica*, from the FenBASE database, from southern England include five from the M10 subcommunity *Carex viridula* ssp. *oedocarpa–Juncus bulbosus/kochii*, and a single record in the *Briza media–Primula farinosa* subcommunity of M10. *Pinguicula lusitanica* is also present in the *Angelica sylvestris* subcommunity of the *Molinia caerulea–Potentilla erecta* mire (M25). Also several records for *P. lusitanica* in this database have not yet been allocated to a particular NVC community. These include seven records of its occurrence in the typical subcommunity of M14, and one record each of its occurrence in the CM and F10 *Cladio–Molinietum*.

central area, with *Drosera anglica*, *Rhynchospora alba*, *Pinguicula lusitanica* and *Drosera rotundifolia* at progressively further distances up the slope on either side. In profile transects between *Molinia caerulea* tussocks and permanent water channels in Somerset, *P. lusitanica* was also found above the level of the water flow, accompanied by *Narthecium ossifragum*, *Drosera anglica* and *Rhynchospora alba* (Watson ex Tansley, Br. Isl.).

In south-west Europe (Polunin & Smythies 1973) it is described as an inconspicuous plant of *Sphagnum* bogs and wet heaths.

IV. Response to biotic factors

As with *P. vulgaris* and *P. grandiflora*, *P. lusitanica* does not withstand trampling by stock because of the brittle and very thin nature of its leaves and the weak anchorage afforded by its short and shallow fibrous root system. Slack (1966) noted that it is even more vulnerable than the other two species because it flowers and sets seed later than they do, at a time when man and stock are more active. It is mainly restricted to areas which have never been cultivated, and recent drainage and other man-made operations have resulted in the destruction of many of its previously existing sites (Fig. 8). In the Lizard area of Cornwall it has been suggested that a thin upper layer of peat may have been removed either as domestic fuel, or as a fuel during early tin-mining operations, and the remaining heath vegetation may be secondary, with the runnels and pans representing 'surface irregularities produced by such activities' (Rodwell 1991b, p. 416); the effect of fire in this area is not fully known, but, if not too prolonged, it prevents the invasion and subsequent shading of taller vegetation in the vicinity. Ratcliffe (1964b, p. 541) has described a *Carex–Saxifraga aizoides* flush near Braemar, Aberdeenshire, in open places between birch–alder woods, and a low level facies 'nearly always occurring in deforested country' where the more characteristic montane species are replaced by others, including *P. lusitanica*; perhaps it is protected here by trees in the vicinity, but has colonized the open ground after deforestation. Seed setting and germination are usually good, in plants under cultivation, so spread to surrounding, favourable, relatively open, sites in the vicinity could be rapid.

Pinguicula lusitanica is insectivorous and responds to the capture and digestion of insects on its leaves, growing, flowering and fruiting more prolifically when insects are available (see VI(Ei)).

V. Response to environment

(A) GREGARIOUSNESS

Isolated plants occur only occasionally, small populations of some 10–20 plants being most usual (but varying in number in any habitat from year to year depending on the temperature, rainfall and humidity of any particular season). Larger populations of one thousand or more may be found in more extensive flushes, as at Glen Falloch, but these are broken into subgroups of some hundred to two hundred plants, with drier ridges where it is absent in between (Slack 1966). It rarely forms pure stands of any appreciable extent.

(B) PERFORMANCE IN VARIOUS HABITATS

In bogs or seepage channels, particularly on south-facing slopes, *P. lusitanica* grows well, flowering and setting seed over several months. It does not tolerate inundation which could damage the rosette and dislodge its roots. Because of this it is rarely found besides larger flushes and streams, being confined to smaller, sloping courses or where the water oozes out of the ground. In cultivation in a glasshouse it grows well on a 2 parts peat : 1 part washed sand mixture, pH *c.* 4.7–5.3, with distilled water supplied constantly from below; it does not tolerate top-watering, and benefits from a supply of small insects for the provision of micronutrients. These conditions mirror the optimum conditions in the wild, and, if not as favourable, flowering does not occur, or fewer flowers are produced.

(C) EFFECTS OF FROST, DROUGHT, ETC.

Individual plants do not survive either frost or drought (see VI(E)). Since summer drought tends to dry up flushes in the lowland areas of its range, it occurs more often in mountainous or coastal areas where the general humidity is more constant.

It is most frequent on south, south-west or west-facing slopes (Slack 1966), perhaps as a protection against frost.

VI. Structure and physiology

(A) MORPHOLOGY

Pinguicula lusitanica differs from *P. grandiflora* and *P. vulgaris* in many vegetative and floral characteristics, sufficiently so for it to be included in a different subgenus (Isoloba Barnhart) rather than the subgenus Pinguicula which includes the two other existing British and Irish species. (*P. alpina*, once occurring in a few sites in Scotland, but now extinct, belongs to another subgenus again, subgenus Micranthus Casper; see that account). *Pinguicula lusitanica* does not form an overwintering resting bud (hibernaculum) at the end of the growing season, although the leaves produced later in the season may be smaller, forming a denser cluster; when conditions remain relatively mild the plant overwinters as a rosette. The leaves are tinier than in our other two species, often with pink-tinged veins; the lamina margins are often strongly involute, and the tip emarginate (Fig. 10). The leaves are very thin, almost pellucid, without a palisade tissue, and subpetiolate. The petiole, *c.* 0.5 cm wide, is usually about 1/4–1/2 the length of the lamina; non-glandular trichomes, up to 0.75 mm in length and consisting of about six uniseriate cells each, fringe the petiole but cease where the lamina flares out; they are also present along the length of the midrib (which is slightly depressed) and here they criss-cross one another. Stalked and sessile glands, of significance for its insectivorous habit, are well distributed over the upper leaf surfaces but thin out towards the midrib and leaf margins. The gland heads of both types of gland contain anthocyanin. The sessile gland heads consist of 4–8 cells, those of the stalked of 8–12. Hydathodes on the lower leaf surface have a two-celled head. Stomata occur on both leaf surfaces, more being present on the lower and are of the anomocytic type. No records of their density are available.

Seedlings initially have a single primary root up to 2 cm in length (Fig. 10), but this is later replaced by a tuft of short, adventitious, fibrous roots which rarely exceed 15–20 in number.

The flower is small and the corolla has emarginate lobes which scarcely overlap one another; its tube is longer than the lobes and the spur is deflexed. There is a white, velvety surfaced, pronounced palate on the centre of the lower lobe leading into the corolla throat, and this continues as a prominent ridge within the corolla tube (Fig. 10). Whilst the flower is in bud, the tip of the pedicel is bent over, but becomes more or less erect or only slightly curved at anthesis, holding the tube of the flower in a horizontal position and more readily available for insect pollinators.

The capsule is small, erect, 2.5–4.5 mm long, scarcely longer than the calyx lobes, and subglobose.

(B) MYCORRHIZA

Not examined (Harley & Harley 1986).

(C) PERENNATION: REPRODUCTION

A hemicryptophytic perennial herb, usually overwintering as a rosette, but occasionally behaving as an

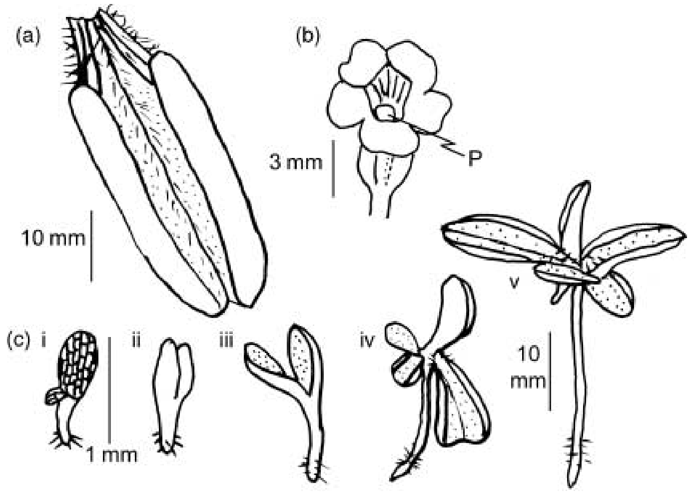

Fig. 10 (a) A typical, mature leaf of *Pinguicula lusitanica* showing the involute leaf margins, emarginate apex, and the distribution of hairs on petiole and midrib. Gland distribution on the upper leaf surface is indicated by dots. (b) Flower of *P. lusitanica*, front view, showing the prominent palate (p) in the throat entrance, and veined corolla throat. (c) Stages in the germination of *P. lusitanica* seed collected the previous year, stored dry, in the dark at 10 °C; then vernalized, fully imbibed, for 8 weeks at 0–5 °C before sowing in February on moist germination paper in a Petri dish at room temperature (*c.* 20 °C) with natural daylength. (i) after 3 days, before and after shedding of testa, (ii) after 7 days, (iii) after 25 days, (iv) after 30 days, and (v) young plant.

annual. It does not reproduce vegetatively, as do the other existing species of *Pinguicula* from the British Isles, which produce bulbils in the leaf axils towards the end of the growing season. A single plant does not persist for longer than 2–3 years, and flowering is usually annual, although in unfavourable conditions flowering may be delayed until the following year. It has a long period of flowering, lasting up to 3 months or more, when flowers are produced singly, in succession, from the leaf axils. After pollination the flowering scape extends significantly to carry the developing fruit above the level of the rosette. Seed set is very good, and large numbers of the small seeds are released from the capsules; in wet weather the valves on the capsules close, but the seeds can be carried some distance in the wind in dry weather. Seedlings have not been observed in the wild. Quite dense colonies of plants, however, are sometimes found (see V(A)), the result of seedling development around the parent plant. Establishment is limited because seedlings do not withstand competition.

(D) CHROMOSOMES

The number $2n = 12$ for *P. lusitanica* from Slepe Heath, Dorset, has been recorded by Hollingsworth *et al*. (1993), and, elsewhere in Europe, from the Loire Valley and Corsica (Contandriopoulos 1962; Casper 1963; Kondo 1969; Schotsman 1970; Contandriopoulos & Quezel 1974). Although the species belongs to the subgenus Isoloba, and has closer relatives in the Gulf of Mexico area than most of its counterparts in Europe, the chromosome number is rather distinctive; the diploid numbers recorded for its nearest relatives in south-eastern USA (for *P. pumila* and *P. ionantha*) are 22, and (for *P. caerulea* and *P. lutea*) 32 (Godfrey & Stripling 1961).

(E) PHYSIOLOGICAL DATA

No experimental data seem available on response to shade, water relations, gas exchange, nor to mineral nutrients which are relevant to the ecology of *P. lusitanica* and which might affect its microclimatic limitations; however, evidence reported in field observations on some of these aspects are discussed in Sections II(A), II(B), III and V(B).

(i) Response to nutrients and the significance of insectivory

When grown in axenic culture, plants of *P. lusitanica* showed significant increases in numbers of leaves and flowers when fed with live *Drosophila*, egg yolk, ammonium phosphate or even pine pollen; the plants also grew successfully on a nutrient medium, but without supplementary feeding to the leaves (Harder & Zemlin 1968). These authors suggested that, in the wild, as well as deriving benefit from the trapping of insect prey, pollen 'rain' from the surrounding vegetation could provide a source of nutrients.

As in all species of *Pinguicula* so far examined, there are two types of gland on the upper leaf surface, sessile and stalked, both connected with the insectivorous habit. The gland heads of both sessile and stalked glands resemble in methods of enzyme storage, secretion and absorption of the products of digestion those of *P. grandiflora* and *P. vulgaris* (Heslop-Harrison & Knox 1971; Heslop-Harrison 1975, 1976b; Heslop-Harrison & Heslop-Harrison 1980, 1981). The smaller leaf surface area, and characteristic inrolling of the lateral margins means that the surface area exposed for the capture of insects is more limited in *P. lusitanica*; the size and type of prey trapped in this species have not been described, but the distinctive red colour of the gland heads may serve as an attractant to small flying insects different from those attracted by the two other native species of *Pinguicula*.

The relative photosynthetic area is increased during flowering by the extension of the scapes after pollination and fruit development. The individual leaf surface area is small; the leaves overlie one another in the rosette, and only the last-formed four to five are fully exposed to light, the surface exposed being further reduced when the leaf margins are rolled after prey entrapment.

(ii) Conditions for growth

Experiments conducted in a phytotron under a range of thermo- and photoperiodic conditions showed that *P. lusitanica* differs from both *P. grandiflora* and *P. vulgaris* in its developmental physiology (Heslop-Harrison 1962, and unpublished).

Sets of glasshouse-grown plants of *P. lusitanica* raised from seedlings (from seeds from an Irish source) were taken at the end of flowering (early August), and exposed to five differing regimes (a–e), as noted in Table 10, for 2 months. At the end of that period all were transferred to LD/22 °C for a further two months. Records of vegetative appearance, after the first two months under conditions (a) to (e), and occurrence of flowering during the second two months, all in LD/22 °C, are given in Columns (2) and (3).

The results indicate (a) that flower primordia are initiated either by short days or temperatures in the region of 8–10 °C., or a combination of both; thus flowering can be resumed in a mild autumn, the result of shortening day length and/or lower night temperatures and (b) that *P. lusitanica* plants do not withstand a prolonged temperature in the region of freezing. The latter observation would account for its mainly westerly fringing distribution within the British Isles and its lower altitudinal tolerances as compared with *P. grandiflora*, *P. vulgaris* and *P. alpina*.

(F) BIOCHEMICAL DATA

No data traced.

Table 10 Vegetative and flowering behaviour of plants of *Pinguicula lusitanica* after treatment under differing thermo- and photo-periodic regimes. First column gives the treatment (a) to (e), of plants at the end of the current flowering season (August), for 2 months. Second column records the vegetative state, number of leaves per rosette and maximum leaf length per rosette at the end of the 2 months' treatments (a) to (e). Third column records the flower production (+) or absence (–) at the end of a further treatment in LD (18 h days) at 22 °C. Number of plants per treatment, 5–10. ND, not determined

Initial treatment at end of flowering	Vegetative state Number of leaves Maximum leaf length	Whether flowering (+) or not (–) after 2 months in LD/22 °C
(a) SD/22 °C	Active rosette Up to 15 2.5 cm	+
(b) LD/8–10 °C	Active rosette Up to 10 1.7 cm	+
(c) SD/8–10 °C	Depauperate 3–5 2.5 cm	+
(d) SD/0.5–1.0 °C	Depauperate, over 50% died ND ND	–
(e) LD/22 °C	Active rosette Up to 11 ND	–

VII. Phenology

In cultivation in a bog garden in the English Midlands new leaves developed in the centre of the rosette of *Pinguicula lusitanica* as early as March in a mild year, and new roots appeared with the renewal of top growth. In a cool spring, growth was delayed until April. *Pinguicula grandiflora* and *P. vulgaris* tend to respond more quickly to milder conditions than *P. lusitanica* when the three species are grown together, probably because food reserves can be drawn on from the hibernacula in the first two species. *Pinguicula lusitanica* is also often later flowering (June), even when the rosette has survived the winter, whereas the other two species may come into flower in May; flowering time, however, overlaps in all the species as the flowers are produced successively over some weeks in all. In *P. lusitanica* the flowering period is quite prolonged. A later flowering (into October, e.g. Fl. Br. Isl.; Casper 1962; Blanca *et al*. 1999) may be the result of a secondary period of flowering induced by shorter days or lower night temperatures during September followed by a mild October (a 'secondary period of flowering' was noted by A. W. Stelfox in Ireland in a personal letter to J. H.-H., and see VI(Eii)). Each flower survives only 3–4 days if unpollinated, and fruit ripening and dehiscence occur some 3 weeks after pollination, from July onwards; the scape extends in length by 2–3 cm as the capsule matures, allowing the capsule to dry out more easily above ground level and to catch the wind.

Seedlings have not been observed in the wild, and germination would probably not occur until the following spring (see VIII(D) below). *Pinguicula lusitanica* can behave as an annual (flowering and fruiting within a single season, Y. H.-H., unpublished), or as a perennial, but of limited duration. In cultivation the first flowers produced from seedlings of the current season appear a week or two later than those from rosettes of the previous year.

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Reproduction in *P. lusitanica* is amphimictic. Neither vivipary nor cleistogamy is known. The flower is adapted to pollination by relatively long-tongued insects probing into the spur, and nectar is stored here. However, insect visitors, if any, have not been recorded. Keble Martin & Fraser (1939) noted that 'the flowers are always fertilized'. In spite of the floral adaptations for insect pollination it is often regarded as being self pollinated (Fl. Br. Isl.), achieved by a rolling inwards of the stigmatic fringe on the large lower lobe to make contact with the anthers behind it.

(B) HYBRIDS

No hybrids known.

(C) SEED PRODUCTION AND DISPERSAL

The seed is 0.5–0.6 mm long and 0.2–0.26 mm wide, and is illustrated by Casper (1962). The powdery seeds are shed when the capsule dehisces by two valves, which can close when wet. Dispersal is by wind when the capsule is shaken; the scape lengthens as the fruit ripens, facilitating the drying process. Several fruits are produced in succession over several weeks providing excellent opportunities for dispersal over a long period.

(D) VIABILITY OF SEEDS: GERMINATION

Precise data on temperature and light requirements for germination are not known, nor is the duration of viability of the seeds. Because mature plants grow best in relatively open ground, freedom from competition must favour seed germination. The first leaves are minute, however, measuring less than 1 mm in length, so seedlings have not been observed in the wild.

Seeds, stored dry, in the dark at *c.* 10 °C after collection, were sown on germination paper, kept damp with distilled water, in Petri dishes in early January. They were kept on a shaded window sill at room temperature. Half had been vernalized previously, fully imbibed, at *c.* 0–5 °C for 8 weeks. Germination occurred within 16 days in both sets, but was 100% for the vernalized and 38% for the unvernalized. The seedlings were transplanted into pots in February, in a 2 : 1 Irish peat : washed sand mixture, and watered from below with distilled water; they were transferred to a glasshouse with natural daylength, but maintained at a minimum temperature of 10 °C, rising in periods of sunshine. The first flower buds were visible by the end of April, and flowering continued into June.

(E) SEEDLING MORPHOLOGY

Germination is epigeal. The primary root emerges first from one end of the black-brown testa, which splits, to allow the emergence of the deeply bifid single cotyledon (Fig. 10, and see also account of *P. vulgaris*). The maximum length of the third leaf is about 1.5 mm. Compared with the seedlings of the other two species described some differences are apparent almost immediately; the red pigment in the gland heads and leaf veins is already observable on the upper surface of the second foliage leaf, and the later ones. The emarginate leaf apex, the rather pronounced inwardly rolled leaf margins, and hairy petioles are also diagnostic features of *P. lusitanica* seedlings. The original primary root extends to no more than 2 cm before a secondary root emerges from near its base; further roots keep pace with the development of new leaves, and the original seminal root dies.

(F) EFFECTIVE REPRODUCTION

Both *P. grandiflora* and, to a lesser extent, *P. vulgaris* have an effective means of vegetative reproduction by bulbils produced in the leaf axils in the autumn; this never occurs in *P. lusitanica*. Neither have adventitious plantlets on the leaf surface been observed, a characteristic of some other species of the subgenus Isoloba. Reproduction is entirely dependent on seed production. Normally seed is produced annually and prolifically, but establishment in a suitable environment must remain critical.

IX. Herbivory and disease

There are no published records for *P. lusitanica* on (A) animal feeders or parasites, or (B) and (C) plant parasites and plant diseases.

X. History

Because the closest relatives of *P. lusitanica* (apart from *P. hirtiflora* and *P. crystallina*, of limited distribution elsewhere in Europe) are all within the subgenus Isoloba (most well represented in the Gulf of Mexico area) its early history may have some affinities with species of the Hiberno-American or north-west European–North American group (Webb 1952a,b ex Irl. Pfl.; Markgraf 1952 ex Casper 1962), and have Miocene origins (Casper 1962).

Species belonging to the Lusitanian group of the flora of the British Isles were well represented during the Hoxnian interglacial in western Ireland, and probably reached England and Ireland 'by coastwise migration during the early Flandrian period' (Godw. Hist.); many of the thermophiles (in this group) were present 'as early as the Late Weichselian' (Mitchell 1952 ex Irl. Pfl.); *P. lusitanica* would be included here. The seeds of *P. lusitanica*, with distinctive cross bars within the alveoli on the testa, would be distinguishable from those of *P. grandiflora* or *P. vulgaris*, in any peat deposits, but there are no such records.

Pinguicula lusitanica was originally named by Linnaeus in 1753, but the first British record of it is earlier still – that of 1666 for *P. minima* fl. *albo* 'in the midway betwixt Oakhampton and Launceston, Cornwall' (Druce 1932; Keble Martin & Fraser 1939, pp. 94 and 769–770, quoting Merrett's *Pinax Naturalium Britannicarum*; it is probable that John Ray contributed to the list of West-country plants, including *P. lusitanica* for Devon). It was recorded from the Mourne Mountains, Northern Ireland in 1794 (Stewart & Corry 1888), and from Orkney between 1774 and 1805 by the Rev. G. Low (ex Spence 1914).

List Br. Vasc. Pl. (1958) no. **441**, 2

Pinguicula alpina L.

Alpine butterwort. Subgenus Micranthus, section Micranthus. An insectivorous perennial consisting in summer of 5–8 leaves in a rosette lying close to the ground, with long perennial, relatively stout, brownish roots. Overwintering as a hibernaculum. Leaves pale, yellowish-green, often red tinged on lower surface, sessile, involute, oblong-elliptic to lanceolate-oblong (1.5–)2.5–4.5(–6.0) cm long by 0.5–1.4 cm wide (description based mainly on Casper (1962) and Blanca *et al.* 1999). Pedicels 1–8 per plant, sometimes reddish, glabrous or sparsely glandular towards the top, 4.0–

11.0(–13) cm long. Calyx glabrescent, lobes of upper lip 2.2–3 mm long, triangular to ovate, obtuse or subacute, scarcely divergent; lower lip lobed for up to one-third of its length, the lobes not divergent, obovate. Corolla 10–16(–21) mm long (spur included), the lips unequal, the upper shorter, with lobes suborbicular, obtuse; the lower lip with lobes not overlapping, the middle one 4–6(–7) mm long, much longer than the lateral ones, with apex obtuse or truncate. Corolla white with one or more yellow spots at the throat; tube short, broadly infundibuliform, glabrescent outside; spur 2–3(–5) mm long, curved, yellowish. Capsule 6–7 mm long, pear-shaped acute, longer than the calyx. Seeds 0.7–0.8 mm long, oblong, rugose-striate or obscurely reticulate. Mean seed weight 15.1 ± 2.5 µg (Karlsson 1986).

The species is relatively constant throughout its range and no subspecies have been described; however, some phenotypic variations of the flower have been reported (Casper 1962).

No longer native in the British Isles, but recorded in East Ross from *c.* 1830–1900 (Druce Com. Fl. 1932, Stace 1997); it was also 'supposed to have been found in Skye in 1794' (Druce Com. Fl. 1932).

Bogs and wet places.

I. Geographical and altitudinal distribution

Pinguicula alpina is classified as Eurosiberian Arctic montane (Preston & Hill 1997).

It was formerly found at Rosshaugh in the Black Isle of Cromarty, eastern Ross-shire, part of which was enclosed by stone walls, and it occurred there until about 1900. Apparently pine seeds blew into the enclosure, they germinated and, as the resulting trees grew up, the bog dried and *P. alpina* was finally lost (Druce 1932). However, according to A. Davy (personal communication, 2004, quoting F. J. Rumsey's *New atlas CD ROM*), there is a suspicion that *P. alpina* may have been planted there. It was picked, in 1831, in the bogs of Auchterflow, in the parish of Avoch and Shannon where it grew in great abundance; by 1845 it was said to 'still exist in the walled-in enclosure of bog amid cornfields under high cultivation', and Duncan (1980) refers to 38 herbarium sheets of specimens collected from that locality during the early 1800s. It has also been recorded from the Isle of Skye, Morarshire in Inverness, and western Ross (Good 1953 and Fig. 11). Elsewhere in Europe it occurs in arctic and subarctic regions, the mountains of Fennoscandia, the mountains and uplands of central Europe (the Alps and the Jura), and eastwards to the Baltic states and its islands; in the Iberian peninsula it is found only in the central Pyrenees. It extends across Siberia into Asia, from Croatia as far east as south-west Szechuan and north-west Yunnan and as far south as the Himalaya (Fig. 12 and Casper 1962).

In the Alps it reaches an altitude of 2600 m, and in the Himalayas 4100 m (Casper 1962). In Norway (at Singsås) the limit is 1150 m (Lid 1979).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

The species is characteristic only of arctic, subarctic and, where it occurs further south, of alpine and subalpine situations; it can withstand a long period of dormancy as a resting bud under snow. During the short growing season the active rosette requires constantly wet conditions. In high altitude populations in the subarctic, climate may restrict growth and reproduction more severely than nutrient availability, and *P. alpina* is better adapted to these conditions than *P. vulgaris* (Thoren & Karlsson 1998). In the Swedish subarctic it is characteristic of frost-heaved soils on solifluction terraces or polygons (Karlsson 1986; Svensson *et al.* 1993; Eckstein & Karlsson 2001), but it can also tolerate less extreme conditions, growing at sites together with *P. vulgaris*. Both species are common at 1510 m in a subalpine bog, Trogenmoos, above Interlaken, Switzerland (J. Steiger, personal communication). In the Pyrenees it is found in 'damp and shady places, waterlogged pastures and banks of streams' (Blanca *et al.* 1999); perhaps in this locality *P. alpina* tolerates more shade than is usual – a characteristic of just a few other species of the genus, notably *P. vallisneriifolia* Webb and *P. longifolia* Ramond ex DC (although both of these have erect to suberect summer leaves, and so expose a greater leaf surface area to available light).

(B) SUBSTRATUM

In northern Sweden (the Abisko area) *Pinguicula alpina* is found, most characteristically, on calcareous soils which may be subject to spring frost heaving at a low altitude (400 m a.s.l.). *Pinguicula vulgaris*, on the other hand, seems to tolerate a variety of soil types which range from ombrotrophic to calcareous, but requires more stable soils (Karlsson 1986; Thoren & Karlsson 1998; Eckstein & Karlsson 2001).

The pH (KCl) of the top 5 cm of the soil where *P. alpina* grew in the Abisko region was 7.2 ± 0.52, whereas that of *P. vulgaris* was 3.9 ± 0.16. The soil-water content (% dry weight) was 34.6 ± 15.6 (Karlsson 1986) for *P. alpina*, compared with 16.4 ± 0.03 for *P. vulgaris*; the soil's ash content (% dry weight) was 93.5 ± 4.8, compared with 97.0 ± 1.2 for *P. vulgaris*. Other characteristics of a locality in northern Sweden where it is found are given by Sonesson (1970a). Oberdorfer (Pfl. Exc.) says *P. alpina* occurs in scattered seepage tracks and spring-fens of the subalpine zone, and the stony-turf in the alpine zone on damp to trickling, 'often open, base-rich, mostly calcareous mild-humus, stony-, or swamp-humus soils'. Thus, on the continent, *P. alpina* seems to be consistently more calcicolous than *P. vulgaris* (Lid 1979). There remains the puzzle that the old Scottish localities are not notably calcium-rich.

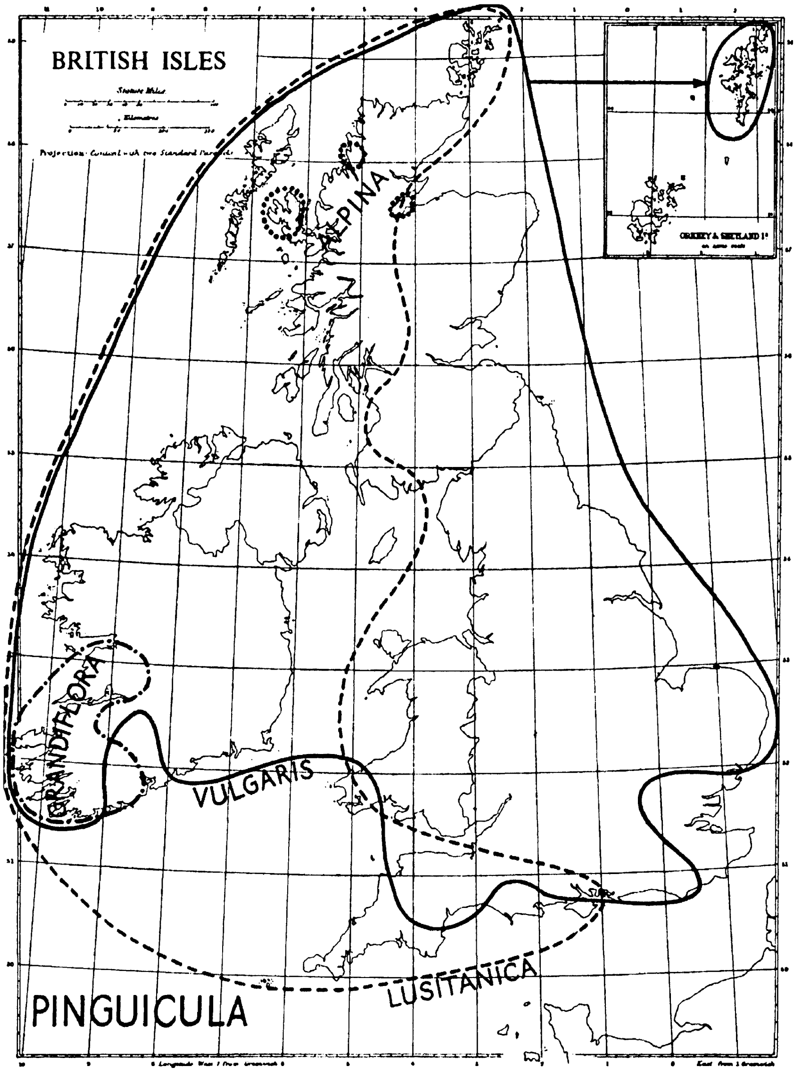

Fig. 11 The distribution of *Pinguicula alpina* until *c.* 1900 as compared with the existing geographical limits of *P. grandiflora* (– · – · –), *P. lusitanica* (– – –) and *P. vulgaris* (——) in the British Isles today. Reproduced from Good (1953).

III. Communities

The species grows in northern Sweden, near Abisko, in wet, open situations intermingled with a mosaic of heath vegetation consisting of small, scattered plants of *Empetrum hermaphroditum*, *Rhododendron lapponicum*, *Tofieldia pusilla* and *Vaccinium* spp., as well as *P. vulgaris* (Karlsson 1986). At another site in this area the main species listed were *Arctostaphylos alpina*, *Betula nana*, *Cladonia* spp., *E. hermaphroditum*, *Loiseleuria procumbens* and *P. vulgaris*. Comparisons of the communities in which *P. vulgaris* and *P. alpina* grow are also made by Hedburg *et al.* (1952) and Svensson *et al.* (1993); see also this Section under *P. vulgaris*. The vegetation at a habitat exclusive to *P. alpina* was characterized by *Bartsia alpina*, *Dryas octopetala*, *Salix reticulata* and *Tomenthypnum nitens* (Karlsson *et al.* 1987). The communities of the poor mires in the Torneträsk area of northern Sweden where *P. alpina* occurs are described by Sonesson (1970b), and in Petsamo-Lappland by Soyrinki (1938, 1939). Species lists, where *P. alpina* is part of the *Sesleria-Anthyllis* community in the Bayern Alps, are given by Soyrinki (1954; pp. 28–29 and 54, and a photograph of it growing alongside *Anthyllis vulneraria*, *Dryas octopetala*, *Polygonum viviparum* and *Rhododendron hirsutum* is given on p. 49). Bauquis & Mirimanoff (1970) found these two species of *Pinguicula* coexisting in abundance, and 'litteralement entrêmelées' in the Vallon de Vernant, Haute Savoie, France. Detailed accounts of the plant communities in Scotland in which *P. alpina* occurred are unfortunately not available, and the local flora may have changed since its extinction.

IV. Response to biotic factors

Any grazing in the habitat where *P. alpina* grows is likely to be detrimental to its survival, and stock are probably most active at the height of the growing season. As with other British species of *Pinguicula*, trampling by stock is also a threat to its existence because of the extreme delicacy of the leaves.

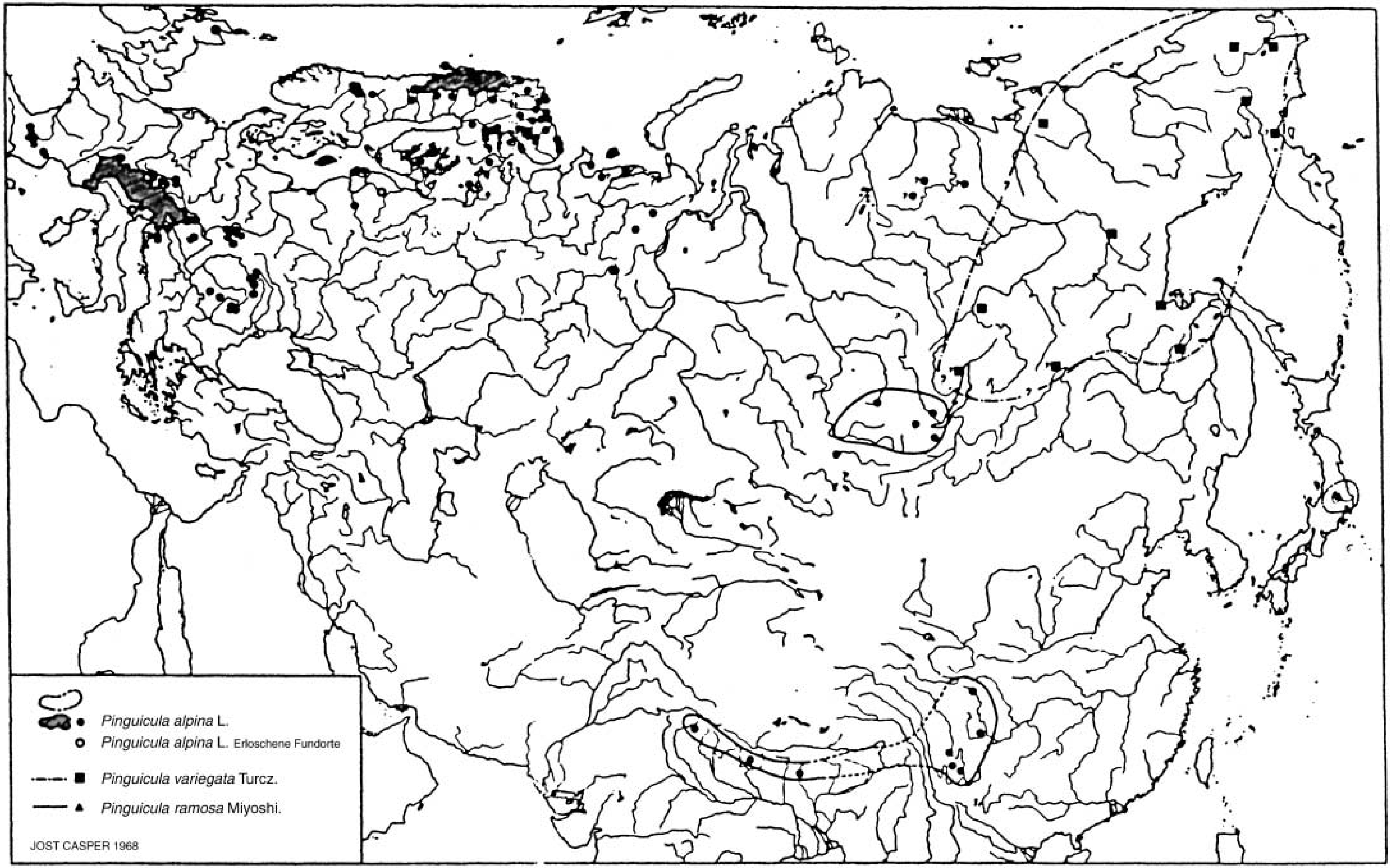

Fig. 12 The distribution of *P. alpina* world-wide. After Casper (1962) and Blanca *et al*. (1999).

The significance of prey capture as a source of supplemental micronutrients for *P. alpina* has been discussed in a series of papers (e.g., Karlsson *et al*. 1994, 1996; Thoren & Karlsson 1998). The largest number of prey attached to leaves per plant (as sampled throughout the growing season of 60–90 days) was found to be in early July for *P. alpina*, though this was smaller than for *P. vulgaris* (range 0–14 compared to 9–69), suggesting that the trapping efficiency is less for *P. alpina* (Karlsson *et al*. 1987, 1994); as expressed by weight at two different sites this represented an average of 21 and 37 µg cm^{-2} day^{-1} for *P. vulgaris* and 14–18 µg cm^{-2} day^{-1} for *P. alpina*. Whereas the seasonal catch studied over a period of 5 years remained fairly constant at *c.* 600 µg plant^{-1} season^{-1} for *P. vulgaris*, it varied much more between the years (means of 89–329 µg dry matter plant^{-1} season^{-1}) for *P. alpina*. The lesser trapping ability of *P. alpina* could be attributed to the difference in leaf colour between it and *P. vulgaris.* The type of prey caught varied with the species (Nematocera *c.* 45%, Collembola *c.* 40% for *P. vulgaris*), Nematocera (*c.* 63%) and Collembola (24%) predominating for *P. alpina* (Karlsson *et al*. 1994; which article also gives the final corrected values for dry mass for Collembola). The potential to benefit from trapped prey according to the amount of soil nutrients appeared to have no correlation in either species (see also under Section VI(E)). Flowering individuals of *P. alpina* captured no more prey than those fully vegetative, whereas in *P. vulgaris* plants with flowers were almost twice as successful as trappers than vegetative ones (Karlsson *et al*. 1987, 1994).

As noted under *P. vulgaris*, the leaves were collected, from plants where it grew in abundance, during the eighteenth and early nineteenth centuries and used to produce a type of yoghurt from reindeers' and cows' milk; they were also used for medicinal purposes by herbalists (see also X); possibly the leaves of *P. alpina* were also collected, and this could be a contributory cause for the diminishing number of sites where this species grows. At its last site recorded in Scotland, the depredations of botanists collecting specimens must have been a severe threat to its survival, as well as the changing ecological conditions in the area (see above).

V. Response to environment

(A) GREGARIOUSNESS

Pinguicula alpina was described as being 'in great abundance in the bog of Auchterflow in 1845' (ex Duncan 1980) in this fully verified Scottish locality, but this did not indicate its gregariousness there. Elsewhere in Europe it is characteristic of open habitats and does not form pure stands. The individual plants remain scattered and survival depends principally on availability of water and adequate temperatures during the short growing season.

(B) PERFORMANCE IN VARIOUS HABITATS

Of the *Pinguicula* species in this account only *P. alpina* has a large, perennial root system which may favour the absorption of a greater amount of micronutrients from the substratum. In northern Sweden the proportion of biomass consisting of roots was several times larger than that for *P. vulgaris* (Karlsson 1986). The extent of its root development in different habitats, however, has not been investigated. An oscillation of freezing conditions followed by thaws, characteristic of some seasons and particular years, could damage the root system. In northern Sweden a maximum of only one flower is produced per plant, and only 20–35% of plants flowered in a season in any population (Karlsson 1986), a reflection of the harshness of the habitat. However, the number of flowers per plant is given as 1–8(–13) by Casper (1962), and 1–4(–5) by Blanca *et al*. (1999), so when conditions and habitat are favourable a plant can obviously flower more prolifically and produce more fruits and seeds. In the central Pyrenees it is said to occur in damp 'and shady places', as well as in more open situations such as waterlogged pastures and banks of streams (Blanca *et al*. 1999).

(C) EFFECT OF FROST, DROUGHT, ETC.

In the dormant condition, the resting bud and associated perennial roots of *P. alpina* can withstand frost and a period of several months under snow; this is indicated from its northerly geographical range across Europe into Asia, and only mountainous areas further south. The species must be most vulnerable in spring during periods of fluctuating temperatures, when growth is renewed. The strong roots can help to anchor the plant in the surrounding soil when there is solifluction, and, during a rapid thaw, resist its uprooting in water currents. In summer the rosette cannot withstand drought because of the delicacy of the leaves.

VI. Structure and physiology

(A) MORPHOLOGY

Root growth is initiated in early spring as soil temperatures rise. The roots of an actively growing plant of *Pinguicula alpina* comprise some 50% or more of its total biomass, whereas those of *P. vulgaris* make up only *c.* 5–10%. The average total root length of a plant (in northern Sweden) was *c.* 30 cm, whilst that from an equivalent plant of *P. vulgaris* was rather less than one-third of this (Karlsson 1986). The duration of the perennial roots is not known. After active growth of the rosette during the summer, a hibernaculum is formed in the autumn and the relative amounts of resorption of nutrients from leaves before abscission in the Swedish species of *Pinguicula* were studied by Karlsson (1988); compared with arctic graminoids, where 50% of the above-ground nutrient content can be lost as litter

(Chapin ex Karlsson 1986), he concluded that the species of *Pinguicula* he studied, including *P. alpina*, 'probably had a more efficient nutrient recycling system'. In the winter condition, the hibernaculum of *P. alpina* represents only a small proportion of the total biomass of the plant, and is smaller than in *P. vulgaris* – suggesting that root storage is used in *P. alpina* (Karlsson 1986), rather than expansion of the hibernaculum to accommodate the swelling of the outer scales and their starch reserves (Y. H.-H., unpublished). Stomatal frequency has not been determined.

(B) MYCORRHIZA

Absent (Harley & Harley 1986).

(C) PERENNATION: REPRODUCTION

A semi-rosette hemicryptophtye. *Pinguicula alpina* perennates as a hibernaculum, with reserves stored mainly in the stout perennial roots, rather than in the hibernaculum scales (which become characteristically swollen in both *P. vulgaris* and *P. grandiflora*, see above and these accounts). Axillary buds (brood buds and bulbils) may develop in *P. alpina* in the last formed leaves of the season, sometimes reaching a length of *c.* 3 mm, but the average numbers are not given (Casper 1962). Soyrinki (1939) noted that although Schröter (Schröter 1923 ex Soyrinki, p. 366) said that bulbils were produced in localities in the Alps, he had seen none either in the Bayern Alps or in Lapland. Where bulbils are not produced reproduction depends entirely upon seed production. When weather conditions are not favourable, as may occur in northern Sweden, the plant does not necessarily flower and set seed every year; the low frequency of seed production may also be attributed to other factors, e.g. low levels of N and P (Karlsson 1986). According to Svensson *et al.* (1993), *P. alpina* had a higher frequency of flowering than had *P. vulgaris* in a similar environment, but its seed output 'was strongly resource limited' and supplementary insect 'feeding' led to a major increase in production of seeds (Thoren & Karlsson 1998). The population half-life for *P. alpina* is 7.5 years, as for *P. vulgaris* (Svensson *et al.* 1993; Thoren & Karlsson 1998).

(D) CHROMOSOMES

The numbers recorded have been consistently $2n = 32$ from root tips, and $n = 16$ after meiosis within anthers; the chromosomes of *P. alpina* are illustrated at meiotic metaphase/diakinesis, and mitotic metaphase by Casper (1962). The material sampled has been from a wide range of sources including Sweden (Löve & Löve 1944), Poland (Skalinska *et al.* 1959), France (Doulat 1947), Austria (Casper 1960 ex 1962, 1963; Dobes *et al.* 1997), Slovakia (Murin 1976a), Iceland (Löve & Löve 1956), Russia (Sokolovskaya & Strelkova 1960), and Mongolia (Murin *et al.* 1980).

(E) PHYSIOLOGICAL DATA

Klein (1883) found that *P. alpina* was insectivorous, in common with other species of *Pinguicula* as had been established by Darwin (1875). Other experimental work on this species has been carried out by Karlsson and colleagues, in its natural habitat, in sites in the Abisko region of northern Sweden. These have included comparisons between the photosynthetic performances of the four carnivorous species, including *P. alpina*, growing there (Mendez & Karlsson 1999), as well as comparisons between these and some other subarctic non-carnivorous plants, of a variety of growth forms, in the vicinity. The photosynthetic rates were lower in the carnivorous species, agreeing with previous work on species of other genera of carnivorous plants. The possible explanation was that *Pinguicula* leaves have a very simplified anatomy lacking a palisade layer (see Fig. 3 in account for *P. vulgaris*), a lower mesophyll conductance and also that there is a conflict between combining carnivorous devices with the photosynthetic functions of a normal leaf. The mean values of leaf-area-based and mass-based photosynthetic rates, respiration rates, photosynthetic nitrogen-use efficiency, and nitrogen content were determined for *P. alpina* and compared with the other *Pinguicula* species in northern Swedish localities by Mendez & Karlsson (1999); these showed that *P. alpina* had an increased photosynthetic capacity when reproducing, thus partially compensating for the cost of reproduction. The results also showed a higher cost of reproduction for *P. vulgaris* compared with *P. alpina* (Karlsson *et al.* 1990).

The trapping efficiency of the north Swedish *Pinguicula* species, the types of prey caught, and the effects of supplementary insect-feeding were also studied (Karlsson *et al.* 1987, 1994, 1996; Thoren & Karlsson 1998). Fed plants increased in size relative to controls, but only for the first 2 years of the experiment, presumably until they reached a limiting size, and the effect of feeding was rather less for *P. alpina* than for *P. vulgaris*. When feeding was stopped the rosette size decreased. The dry weight of the resulting winter buds was also greater in the fed plants. These differences were constant irrespective of the site and altitude from which the plants were taken (Thoren & Karlsson 1998).

The seasonal patterns of nitrogen, phosphorus and potassium utilization (Karlsson 1988) and the effects of flowering/seed production on nitrogen use have been investigated (Eckstein & Karlsson 2001). The principal anion in the mucilage of the stalked glands on the leaves (as determined with a laser microprobe analyser, LAMMA) was chloride. The most prevalent divalent cations were Mg^{++} and Ca^{++}, whilst K^+ and Na^+ were present in smaller amounts (Heinrich 1984).

Since *P. alpina* flowers early in spring, as soon as temperatures rise and growth is resumed, it is likely that flowers are initiated in the previous autumn under shortening day lengths and lower night temperatures, and that flower primordia are already present in the hibernaculum, as in *P. grandiflora* and *P. vulgaris* (Heslop-Harrison 1962); nutrients available for early growth are most likely to be stored in the perennial root system in this species, however, rather than in the hibernaculum (as in *P. vulgaris* and *P. grandiflora*).

(F) BIOCHEMICAL DATA

The carotenoids lutein, B-carotene, cryptoxanthin, violaxanthin, and neoxanthin (and their quantities) have been identified in the leaves of *P. alpina* and lutein-ester, B-carotene and violaxanthin-ester in its flowers (Neamtu & Bodea 1972); this work was part of a more general chemotaxonomic study. As with *P. vulgaris* (see that account for more detail) the leaves of *P. alpina* contain *trans*-cinnamic acid in free form, and as heterosides, and benzoic acid is absent.

VII. Phenology

Reserves stored in the perennial root system of *P. alpina* enable early spring growth to take place as soon as conditions become favourable; flower primordia must be already present in the centre of the hibernaculum, initiated the previous autumn (see above). Five or so outer leaf primordia expand first to form the first rosette leaves of spring. This is followed by the rapid extension of the flowering scape(s) in the centre and then the opening of the flower bud(s). Because *P. alpina* occupies markedly northerly regions, or mountainous areas further south, the flowering season is often relatively late, i.e. June to July. However, the flowering time is given as early as April to June (to August) by Casper (1962), and July to August by Blanca *et al.* (1999). In the subalpine bog, at Tragenmoos, near Interlaken, Switzerland, at an altitude of 1500 m it is said to flower always ‘three to five weeks earlier than *P. vulgaris*’ where both species are common (J. F. Steiger, personal communication). The relatively early flowering of *P. alpina* compared with the other *Pinguicula* species (*P. vulgaris* and *P. villosa*) in the vicinity has also been noted by Molau (1993), and this helps to lower the risk of seed set failure in the short growing season that is available (Thoren & Karlsson 1998). Seeds are usually released from the pear-shaped capsule after it dries out and dehisces in mid- to late August, as compared with some weeks later for *P. vulgaris* – in which seeds may not mature until mid-September when the first snows may fall (Thoren & Karlsson 1998).

Seedling establishment was found to vary between the years, never being greater than 15%. The overall population at the site studied remained relatively stable over 7 years of observation, and survival of individual plants appeared more important than reproduction for the maintenance of the population (Svensson *et al.* 1993).

The rosette leaves persist in northern Sweden until late August or early September (Karlsson 1986). Where several flowers are produced in succession per plant, the flowering season is prolonged for some weeks. The roots of plants remaining purely vegetative developed earlier in the season than those producing flowers (Karlsson 1986).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Reproduction is amphimictic and cleistogamy and vivipary are not known. The flowers are hermaphrodite and adapted for insect pollination mainly by flies but also bees, although selfing may occur if there is no cross pollination. Molau (1993) concluded that the differences in pollination biology, flowering phenology and breeding systems were sufficient to keep the populations of the three Nordic species of *Pinguicula* reproductively isolated (see also below under Hybrids).

(B) HYBRIDS

No hybrids between *P. alpina* and *P. vulgaris* have been reported in the areas in Scotland where they once, perhaps, coexisted. However, elsewhere in Europe this hybrid (*P.* × *hybrida* Wettst.) does occur (see account of *P. vulgaris*).

(C) SEED PRODUCTION AND DISPERSAL

The number of seeds per capsule in *P. alpina* from near Abisko, northern Sweden, was 113 ± 43 (Karlsson 1986), fewer than *P. vulgaris* which had 140 ± 62 in the same locality. As with the other species described in this account, seeds are dispersed by wind currents when the dry, dehiscing capsule is shaken. The seeds are lighter in weight than those of *P. vulgaris* (15.1 ± 2.5 µg, compared with 23.8 ± 3.6 µg).

(D) VIABILITY OF SEEDS: GERMINATION

Seedling frequencies were positively correlated with late-summer temperatures the previous year, suggesting that seeds of *P. alpina* germinate in the autumn in northern Sweden (Karlsson *et al.* 1996). Seedling survival was low, however, with an establishment rate of *c.* 0–15% (Svensson *et al.* 1993).

(E) SEEDLING MORPHOLOGY

The seedlings are minute, the first leaves measuring only 1 mm across; and so difficult to detect in the wild (Svensson *et al.* 1993).

IX. Herbivory and disease

(A) AND (B) ANIMAL FEEDERS OR PARASITES, PLANT PARASITES

It is unlikely that grazing stock led to the extinction of the species in Scotland. Where *P. alpina* grows elsewhere, often on the margins of any vegetation at all, there is a possibility that grazing by wild or domesticated animals, as part of their summer diet, may be detrimental to its survival, but this has not been reported. Neither are there any records of insect attacks, either in the mature or larval stages. However, mites (Acarina) may live on the leaves – and make up to 8% of the total arthropod catch in this species (R. J. Antor and M. B. Garcia, unpublished ex Karlsson *et al*. 1994) but have not been reported to do any damage. Robbery of prey initially caught by the leaves is unlikely because the prey is usually too small to attract gross feeders. Ants have been observed associated with the leaves of *P. alpina* in northern Sweden, but they do not appear to influence the general nutrition of the plant (Karlsson *et al*. 1994), although they are a feature of some *Pinguicula* species endemic to Spain (Zamora 1995). Neither has kleptoparasitism of the prey (trapped initially by the leaf glands, and used as a food source secondarily by slugs) been reported in this species, although again occurring in the Spanish *P. vallisneriifolia* (Zamora & Gomez 1996).

No plant parasites have been reported.

(C) PLANT DISEASES

The anthers of *P. alpina* are often infected by *Ustilago pinguiculae* Rostrup (Casper 1962).

X. History

The species was first described by Linnaeus in *Flora Lapponica* (1737), and it is also illustrated there. The original specimen is in poor condition and this illustration has been selected as the lectotype (Blanca *et al*. 1999). The *Flora Lapponica*, edited by J. E. Smith (1792), also contains this illustration (Fig. 13). Although first reported from the Isle of Skye in 1794 (see I above) it is not mentioned by Withering (edn 6, 1818); in Hooker's flora of 1870 (Hooker 1870) it is said to occur both on the Isle of Skye and at Rosehaugh in Ross-shire. However, its occurrence in these areas does suggest it was once more widespread in Scotland, and so would belong to the arctic-alpine element of the British Isles. If sufficiently prolific in other areas, apart from the British Isles, its possible use for therapeutic or culinary purposes may have paralleled that of *P. vulgaris*, but no records of such use are recorded.

Fig. 13 The illustration of *Pinguicula alpina* in Linnaeus's *Flora Lapponica* of 1737 (and reproduced in the English edition of 1792), selected as the lectotype by Blanca *et al*. (1999).

As with the other British *Pinguicula* species, there are no records of either pollen or seeds of *P. alpina* in Quaternary, or later, peat deposits.

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