

The morphology and affinities of *Geranium* sections *Lucida* and *Unguiculata*

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Descriptions of the external morphology of six species of *Geranium* are presented to match those published by the author previously for the six species of the related sections *Anemonifolia* and *Ruberta*. It is proposed to merge *Anemonifolia* with *Ruberta* and to re-define sections *Lucida* and *Unguiculata*, the first containing *G. lucidum*, *G. glaberrimum* and *G. lasiopus*, and the second *G. macrorrhizum* and *G. dalmaticum*, while *G. cataractarum* is placed in *Ruberta*. *G. lasiopus* is a plant of vertical and overhanging cliffs and has adaptations to keep the seeds within the habitat, whereas *G. glaberrimum*, from the same area of Turkey, occurs on step-crevice and lacks these arrangements. For the species covered earlier, additional notes are provided for most, including reports on variation in *G. robertianum* in England, Taiwan and China. Attention is drawn to the informal term tangle-strands for bundles of long clinging hairs borne by dormant stages of some plants and animals. Scanning electron micrographs of the mericarp surface of all 12 species and a list of specimen citations of interspecific hybrids are presented. © 2004 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2004, 144, 409–429.

ADDITIONAL KEYWORDS: chasmophyte – mericarp surfaces – phytography – tangle-strands.

INTRODUCTION

I have earlier provided detailed descriptions of the six species of *Geranium* constituting sections *Anemonifolia* and *Ruberta* (Yeo, 1973). In doing so I demonstrated the existence of a strong affinity among them, despite their having been placed well apart (as sections 9 and 3, respectively) in the monograph of the Geraniaceae by Knuth (1912). In the same place, I indicated that the other species most closely related to the *Anemonifolia* and *Ruberta* were *G. lucidum*, of section *Lucida* R. Knuth, and *G. cataractarum*, of section *Unguiculata* (Boiss.) Reiche (Yeo, 1973: 287 and 316–320). Detailed descriptions of the external morphology of these two species, and of the remaining four species of section *Unguiculata*, are now given to match those previously published for *Anemonifolia* and *Ruberta*. (Extended descriptions of four of the species have, in fact, been given by me previously (Yeo, 1985, 2002) but more detail is provided here.) Other additional information on the species that were the subject of the 1973 paper is supplied here, using the same numbering as previously. An update on chromosome numbers is provided and the chasmo-

phytic attributes of some of the species are described. Scanning electron micrographs showing the fine details of the mericarps of all species in the four, hitherto recognized, sections constitute Appendix 1. A list of known interspecific hybrids within the group forms Appendix 2.

Before giving extended descriptions of the species of the *Lucida* and *Unguiculata* I have provided short species descriptions of them for use in a discussion of classification in the four sections. This leads to an amended sectional classification, which is used in the main taxonomic part of the paper.

For an account of the basic plan of the cymose inflorescence in *Geranium* see Yeo (1973). The terminology of leaf-division is that of Yeo (1985): the segments of the first order are called divisions, those of the second are called lobes and those of the third are called teeth. If there are only two orders of segmentation, the segments of the second are referred to either as lobes or as teeth, according to which seems the more appropriate. 'Beak of fruit' includes the ovary and remnants of the style.

The later homonyms *G. canariense* Reuter and *G. rubescens* Yeo have been replaced, respectively, by

G. reuteri Aedo & Muñoz Garm. and *G. yeoii* Aedo & Muñoz Garm. (Aedo & Muñoz Garmendia, 1997). The sectional author citations of Yeo (1984) are amended in agreement with Aedo & Muñoz Garmendia (1996).

REVISION OF CLASSIFICATION

The more simply expressed characters of the species in all four of the sections mentioned above are shown in Table 1. The remaining main features of the species placed in sections *Lucida* and *Unguiculata* by Yeo (1984) are also presented here (in the text). (Equivalent summaries were provided for the species covered in my 1973 paper (Yeo, 1973: 288 and 289).).

G. lucidum. Small annual with a sessile rosette and flowering branches borne on a central axis of 1–3 extended internodes (as in *G. purpureum*). Main leaves to 6 cm wide, divided as far as two-thirds of the radius into 5 or 7, the divisions flabelliform, glandular-punctate beneath. Flowers to only 10.5 mm in diameter. Outer sepals winged and with transverse keels. Mericarps with longitudinal cristate ribs, pubescent and with rows of hooked hairs bordering the orifice.

G. cataractarum. Perennial with branching woody rootstock and several rosettes. Leaves to 7(–9) cm wide, non-glossy, scarcely succulent, dissected much as in *G. robertianum*. Flowers widely funnel shaped. Petals to 17 mm, with divergent limb and indistinctly bicarinate claws. Stamens slightly exerted. Anthers red or yellow. Mericarps reticulated at apex, vertical ribs predominant in basal half.

G. macrorrhizum. Creeping perennial of rocky habitats, with non-glossy, usually heavily glandular and aromatic leaves to 12(–20) cm wide with rounded lobes and teeth in an arrangement suggestive of *G. robertianum* and *G. cataractarum*. Inflorescence few-branched, ending in tight flower-clusters. Flowers slightly zygomorphic (corolla, androecium, style). Calyx inflated. Petals 15–18 mm long, broadly clawed. Stamens and style well over twice as long as sepals, far exerted. Mericarps pinnately veined distally, the lateral veins weakly branched.

G. dalmaticum. Rhizomatous like *macrorrhizum* but rhizomes longer and thinner. Leaves small (to 4.5 cm wide), subglabrous, with smooth surface, cut more deeply than in *macrorrhizum* and with few, less obtuse, teeth. Inflorescence like that of *macrorrhizum* but of more limited growth. Flowers like those of *mac-*

Table 1. Attributes of *Geranium* species in the sections accepted by Yeo (1984) (sections relevant to the present work)

	Palmarisect leaf	Hairiness of flower			Hairiness of fruit		Chromosome number	Separate nectar passages ^a
		Petal claw	Stamen filament	Style	Rostrum	Carpels		
<i>Anemonifolia</i>								
<i>maderense</i>	+	–	–	+	–	–	(32 + 36) = 68	+
<i>palmatum</i>	+	–	–	+	–	–	68	+
<i>Ruberta</i>								
<i>reuteri</i> (<i>canariense</i>)	+	–	–	+	–	+/–	128	+
<i>yeoi</i> (<i>rubescens</i>)	+	–	–	+	–	–	128	+
<i>robertianum</i>	+	–	–	+	–	+/–	64	+
<i>purpureum</i>	+	–	–	+	–	+/–	32	+
<i>Lucida</i>								
<i>lucidum</i>	–	–	–	+	–	+	20, 40, 60	+
<i>Unguiculata</i>								
<i>cataractarum</i>	+	–	–	–	–	–	36	–
<i>macrorrhizum</i>	–	+	–	– ^b	+	–	46, c. 92	–
<i>dalmaticum</i>	–	+	– ^c	– ^d	+	–	46	–
<i>glaberrimum</i>	–	+	–	–	–	+	30	+
<i>lasiopus</i>	–	+	–	–	–	+	?	±

^aThat can be probed successively, formed from petal claws and outer filaments (Yeo, 1973).

^bDiscounting apparent 'overflow' from pubescent rostrum, see discussion following species-description, p. 425.

^cA wisp of hair is present on the auricles of the filaments.

^dGlabrous or nearly so, see species-description, p. 426.

rorrhizum but with different opaque pink colouring of petals (at least in Dalmatia (Croatia)), slightly shorter stamens and style, subbasal hairy filament tooth (auricle). Mericarps extensively pinnately ribbed.

G. glaberrimum. Compact saxatile perennial with glossy succulent aromatic leaves (to 6.5 cm wide); leaf-divisions flabelliform. Calyx uninflated; outer sepals winged and keeled as in *G. lucidum* but less prominently. Flowers *c.* 23 mm in diameter. Petals with patent blades. Filaments moderately exerted; anthers red. Mericarps variously sculptured.

G. lasiopus. Like *G. glaberrimum* in habit, leaves and flowers, except that the leaves are no more than 3.5 cm wide and the sepals are apparently not keeled and cross-ribbed. Leaves densely clothed with fine, slightly curled hairs. Mericarps densely covered with crisped hairs that conceal a sculpture of weak ribbing.

Leaf shapes of *Geranium* are shown in Figure 1.

Taken together the 12 species constitute a polyploid complex of advanced morphology and specialized biology. They comprise widespread annual and biennial herbs and mostly narrowly endemic longer-lived plants.

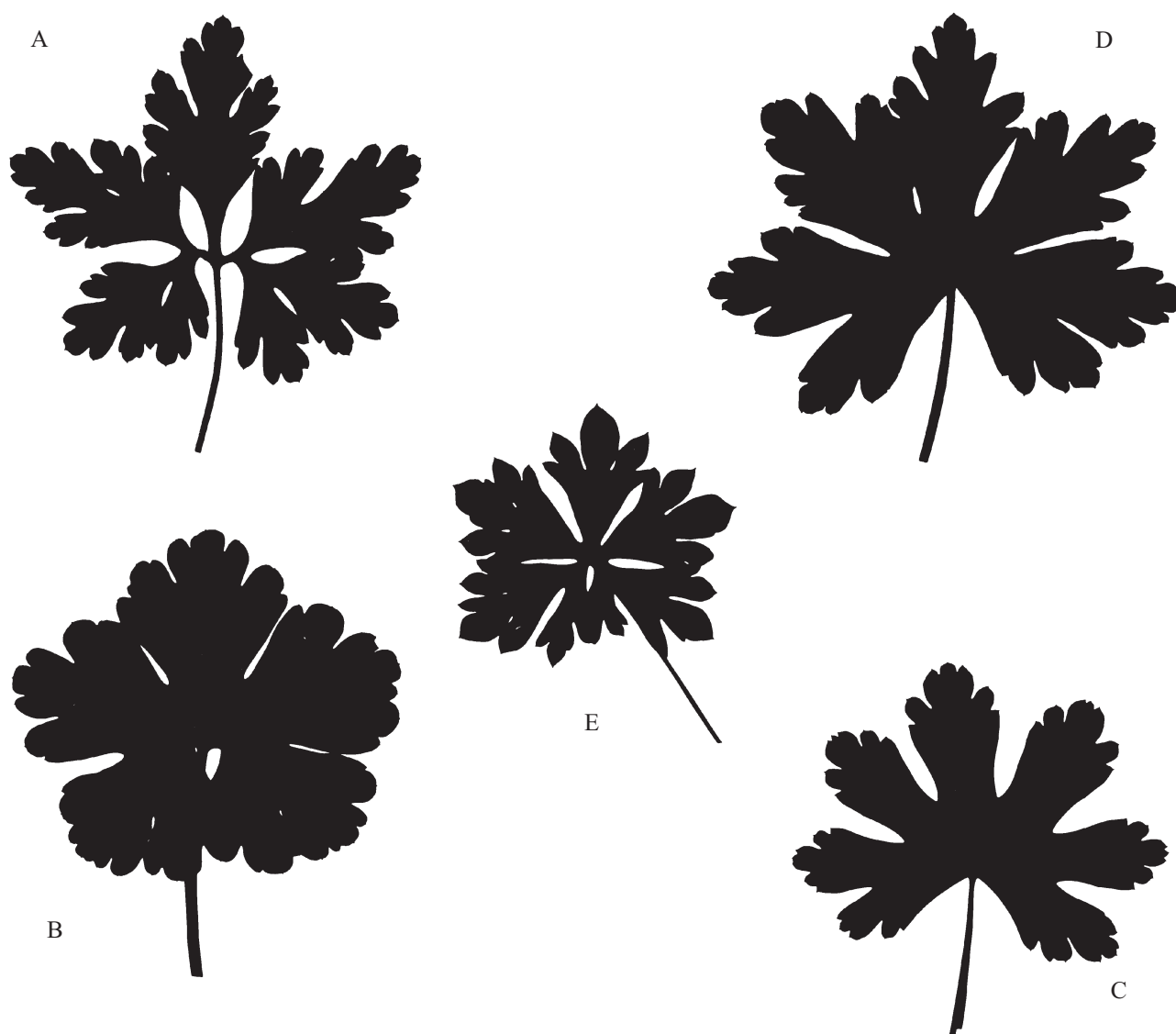


Figure 1. Leaf-silhouettes in *Geranium*. Basal leaves of: A. *G. cataractarum* (from southern Spain, coll. R. C. Barneby, Cambridge University Botanic Garden entry no. 240-70), B. *G. lucidum* (old Cambridge Botanic Garden stock), C. *G. glaberrimum* (G. G. Guittoneau 73.06.26.03, Cambridge University Botanic Garden entry no. 169D-76, coll. Mersin, Turkey), D. *G. macrorrhizum* (horticultural selection: 'Bevan's Var.'), E. *G. dalmaticum* (horticultural selection, unnamed). Actual width of leaves shown is, respectively, 5.5, 6, 5.5, 10 and 4 cm.

The biology and evolution of sections *Anemonifolia* and *Ruberta* were thoroughly discussed by Yeo (1973). Subsequently, trends in subgenus *Robertium* (Picard) Rouy & Fouc. were discussed (Yeo, 1984: 29–30) as were the relationships of chromosome numbers in sections *Anemonifolia*, *Ruberta*, *Lucida* and *Unguiculata* (Widler-Kiefer & Yeo, 1987).

The strong affinity between sections *Anemonifolia* and *Ruberta*, mentioned in the Introduction, is evidenced mainly by the morphology and the interspecific fertility relationships (Yeo, 1973; Widler-Kiefer & Yeo, 1987).

Widler-Kiefer & Yeo (1987: 295) considered that the production of non-germinating seeds and the occurrence of 'some response' by growth on the part of pollinated gynoecia were indicative of a close phylogenetic relationship between *G. macrorrhizum* on the one hand and *G. cataractarum*, *G. robertianum* and *G. yeoi* (*G. rubescens*) on the other. However, in light of the unpublished work of Mr Alan Bremner reported in Yeo (2002: 38–41) such behaviour cannot bear this interpretation. There is still a morphological link among these members of sections *Ruberta* and *Unguiculata*, in that the appearance of the lobes and teeth of the leaves is similar in all four species, although the leaf of *G. macrorrhizum* is palmatifid and that of the other species is palmatisect. The flower, however, is dramatically different.

That *G. dalmaticum* is particularly closely related to *G. macrorrhizum*, in spite of the very different leaves, is shown by the production of mature hybrids (Widler-Kiefer & Yeo, 1987: 290; Yeo, 1985) as well as by almost identical flower-morphology and a shared and unique chromosome number.

Morphological characters common to *G. lucidum* and *G. glaberrimum* are the truncate leaf-divisions and longitudinal and transverse ribbing of the calyx. Finally, *G. glaberrimum* and *G. lasiopus* are similar to one another in leaf-shape, flower-form and the presence of hairs on the mericarps. Thus there are links among all 12 species.

The information assembled in the present paper does not encourage postulating any new phylogenetic pathways (cf. Widler-Kiefer & Yeo, 1987) but it does invite reconsideration of the classification. In particular, it prompts one to question whether it is necessary to have four sections to accommodate 12 species.

I therefore now propose firstly that section *Anemonifolia* should be included in section *Ruberta* (as foreseen in Yeo, 1973: 321). Next, *G. glaberrimum* and *G. lasiopus* only resemble *G. macrorrhizum* and *G. dalmaticum* in the palmatifid leaf and the presence of hairs on the petals; by contrast, they resemble *G. lucidum* also in the palmatifid leaf and in the relatively truncate leaf-divisions and the glabrous rostrum, so I secondly propose to place them in section

Lucida. *G. lasiopus* further resembles *G. lucidum* in the presence of large hairs on the mericarp and *G. glaberrimum* does so slightly in the form of the sepals. (Section *Lucida* was reduced to the single species, *G. lucidum*, by Yeo (1984), the others being mostly transferred to section *Trilopha*.) In making this change, I am playing down the significance of the annual habit.

G. cataractarum is clearly in some ways intermediate between *G. robertianum* and *G. macrorrhizum* but it has a palmatisect leaf and a strong chromosomal relationship with *G. maderense* and *G. palmatum*. Knuth (1912) himself was doubtful about the inclusion of *G. cataractarum* in section *Unguiculata*, as he had never seen the plant. He gave no diagnosis of the section. My third proposal therefore is to accept Van Loon's (1984b) assignment of it to section *Ruberta*. Section *Unguiculata* is thus reduced to two species. The resulting new classification is incorporated in the diagnostic key (p. 414); it may be compared with the old classification in Table 1 (p. 410).

CHROMOSOME NUMBERS

A new chromosome count for *G. lucidum* of $n = 30$ has been reported (Löve, 1983); $2n = 20$ and $2n = 40$ were known for this species previously. Van Loon (1984b) confirmed the euploid number of $2n = 40$ for many European samples of *G. lucidum*, in the majority of which up to three dysploid numbers from 41 to 44 were also found (in root tips). For *G. purpureum* and *G. robertianum* Van Loon (1984b) reported, respectively, $2n = 32$ and $2n = 64$. As there were, respectively, 51 and 143 populations with these numbers, and as Baker (cited in Yeo, 1973: 309) found $2n = 64$ in 57 samples of *G. robertianum*, I think reports of other numbers for this species may be discounted.

Polyploidy in *G. macrorrhizum*, found previously by Gauger and covered in my earlier papers by reference to the compilation by Bolkhovskikh *et al.* (1969), was found again by Van Loon (1984a). *G. dalmaticum* from Albania has been found to have $2n = 46$, like the diploid variant of *G. macrorrhizum* (Baltisberger, 1984). British cultivated material, presumably from the type locality in Dalmatia (see p. 427), was found by me in 1974 to have $n = 23$ in pollen mother cell meiosis (see specimen citation later for details of voucher).

The derivations of most of the chromosome numbers found in this group (Table 1, p. 410) are quite obscure, bearing in mind that $x = 14$ and $2n = 28$ are by far the commonest in the genus. Polyploidy and amphidiploidy are clearly evident in section *Ruberta* (as revised), but other numbers in the group appear unrelated. There is still scope for further chromosome studies and inter-fertility experiments, but molecular studies on this interesting group (e.g. Price & Palmer, 1993; cf. Pax,

Price & Michaels, 1997) seem to have good possibilities for further exposure of its evolutionary history.

INTERSPECIFIC HYBRIDIZATION

One hybrid in the alliance under consideration, namely *G. maderense* × *G. palmatum*, was described by Yeo (1973: 312) and another, that between *G. purpureum* and *G. robertianum*, was mentioned (Yeo, 1973: 314). The latter had been raised and studied by H. G. Baker (as reported by Hughes, 1954). Baker found that the triploid F1 was not completely sterile, and that complete fertility was restored in some plants in the F3 generation (H. G. Baker, pers. comm., before 1973). Synthesis of the latter hybrid was accomplished in both directions by P. M. Benoit (D. McClintock in Stace, 1975) and by Van Loon (1984a). The existence of *G. cataractarum* × *G. maderense* (♀) was mentioned by Yeo (1973: 318) and this hybrid was described later (Yeo, 1985), as was *G. dalmaticum* × *G. macrorrhizum* (♀). The latter has occurred spontaneously in gardens and has also been found in nature (see later, under *G. dalmaticum*, p. 427). A further four hybrids were obtained by Kiefer (Widder-Kiefer & Yeo, 1987), and one more, *G. reuteri* (*G. canariense*) × *G. palmatum*, by Mr Alan Bremner (Yeo, 2002: 214).

Under the classification now proposed, all these hybrids are intrasectional. As might be expected, the hybrids whose parents differ in chromosome number are sterile, though surprisingly there is one exception, *G. reuteri* (*G. canariense*) × *G. palmatum*. The other fertile hybrids are *G. maderense* × *G. palmatum* and *G. reuteri* (*G. canariense*) × *G. yeoi* (*G. rubescens*).

The hybrids are listed in Appendix 2 (p. 429) in alphabetical order of the parent species, the egg donor being indicated by the female sign '♀'.

SEED LONGEVITY

Seed viability up to 7 years has been reported for species of this group (Yeo, 1973). I now have records of seed viability after 15 years for one sample of *G. palmatum*, of 9 years for one sample of *G. glaberrimum* and one of 11 or 12 years for a sample of *G. cataractarum*.

GERANIUM SPECIES AS CLIFF PLANTS (CHASMOPHYTES)

Before I had been to Turkey, I was puzzled by the existence of two saxatile species of *Geranium* in the south-west of the country (cf. the information on Heldreich's type specimens: *in fissuris montis Ghei Daghi* (for *G. glaberrimum*), *in fissuris rupium Lycaoniae* (for *G. lasiopus*). When I visited Turkey in 1989 I found

one population of each and they grew in different habitats. *G. glaberrimum* grew on broken ground at the top of a small nearly vertical cliff facing north-west, which itself formed the upper limit of a hard limestone outcrop. The few other plants present included some Brassicaceae. The colony of *Geranium* probably comprised fewer than 50 plants. The last few flowers of the season were open but imperfect. Plants were 20–35 cm tall and were developing a fresh crop of rather small leaves (19 June). *G. lasiopus* grew on a vertical to slightly overhung north-facing cliff of ochre-coloured and relatively smooth hard limestone. The cliff, 11 m long and 3–4 m high, was situated at the base of an outcrop that formed a mound in a wide hollow opening out on to a plateau and from which a gorge descended northwards. There were between 55 and 60 plants of *G. lasiopus* (including small ones that had not flowered), probably growing in solution hollows. The only associated species were *Parietaria judaica* L., *Galium* sp. (a common one on limestone outcrops) and a crucifer (*Alyssum*?). Flowering was over, there being one or two petals still showing colour (*Geranium pusillum* L. grew at the base of the cliff). Some inflorescences were already dried out but still contained a few seeds. Other seeds were found in inflorescences that had not dried out, and all of these had the pedicels bent towards the rock face. The inflorescences did not stand clear of the foliage as do those of *G. glaberrimum* and the rostrum is very short. Thus it seems that the seed discharge mechanism is weak. The mericarps are densely covered with short-stalked or sessile glandular hairs and longer, very slender eglandular hairs with curled tips. Loose mericarps tend to stick together or adhere to bits of debris because of the long hairs.

Although I saw only one colony of each of these species, I would expect the difference in habitat observed here to be general, because *G. lasiopus* is clearly adapted not to despatch its seeds far but to bring them close to the rock, and to give them a chance of adhering to anything projecting from a hole or crevice.

Davis (1951) wrote a detailed account of cliff vegetation, centred on his studies in Palestine. He recognized six habitats in the profile of a cliff; on these definitions *G. glaberrimum* occupies step-crevice where the ground begins to slope away from the cliff-top, and *G. lasiopus* the overhanging rock near the base of the cliff, and perhaps the vertical face that comes between step-crevice and overhang (diagram in Davis, 1951: 67). Davis states that the species of vertical and overhanging rock are seldom found in other types of rock habitat. He listed a number of massive herbs, such as *Ferula* spp. and *Michauxia campanuloides* Aiton, as inhabitants of step-crevice, but these were absent from the reported *Geranium* sites, and

perhaps are more likely to be found in the Mediterranean climatic region.

Because of the restricted availability of cliff habitats and the obstacles to gene-flow between sites, chasmophytes may be rare and also locally variable (Davis, 1951). Both the Turkish *Geranium* cliff-plants seem to be rare, and in *G. glaberrimum* two considerably different mericarp sculptures are known. Further study of these species is desirable.

Other species that are the subject of the present paper are also chasmophytes. *G. macrorrhizum* favours cave entrances and damp overhangs, shaded stream banks (Schwarz, 1936), shaded rock ledges (Leslie, 1993) and pavement or debris at the cliff-base, especially if damp (pers. observ.). *G. dalmaticum* is found in fissures and screes of calcareous rocks, and is at its best in the *Pinus nigra* zone (von Beck, 1896). It seems to have two isolated and differing populations. *G. cataractarum* of the West Mediterranean is probably a species of vertical or overhung cliffs. As suggested by the specific epithet and some of the herbarium labels, they sometimes grow in stream gullies and might thus depend partly on water for seed-dispersal.

TAXONOMIC ACCOUNT OF SECTIONS *LUCIDA* AND *UNGUICULATA* WITH ADDITIONAL INFORMATION ON SECTION *RUBERTA*

These three sections form part of subgenus *Robertium* (Yeo, 1984), which is defined by the method of fruit dehiscence: the mericarps are thrown off forcibly with the single seed inside, while the elaters (awns) fall away, leaving a naked rostrum (Yeo, 1973, 1984). Sec-

tions of the subgenus not treated here are *Divaricata* Rouy, *Polyantha* Reiche, *Batrachioidea* W. D. J. Koch and *Trilopha* Yeo.

As previously (Yeo, 1973), I give specimen citations only for species of small geographical area. All descriptions contain some input from living material, most of which has been grown at Cambridge University Botanic Garden (CUBG) and is represented in the herbarium there (CGG) as dried specimens and colour transparencies. Species-numbering has been carried over from Yeo (1973); note that information under nos. 1–6 is merely supplementary to what was in that publication. In my descriptions mericarp colour given is that of the fully ripe but not decaying specimens.

Most of our species (perhaps all) have submicroscopic trichomes that seem to consist of one minute stalk-cell and a considerably larger glandular head (Appendix 1, Fig. 12). These are the 'minute yellowish incurved glandular hairs' described by Yeo (1973); they are probably universal in *Geranium* and will not be mentioned again. Other hairiness will be described if present.

Dimensions of plant parts collected by me have been extended with data supplied by Dr Carlos Aedo from his database of *Geranium* at the Real Jardín Botánico, Madrid.

SECTION *RUBERTA* DUMORT. (INCLUDING SECTION *ANEMONIFOLIA* R. KNUTH)

Annual to perennial herbs. Leaves palmately compound. Petal claws and stamen-filaments glabrous. Rostrum (other than stylar part) glabrous. Note that all but *G. cataractarum* have nectar-passages and a hairy style, that stamen-length ranges from slightly

KEY TO SPECIES AND SYNOPSIS OF CLASSIFICATION

Leaves palmatisect (section *Ruberta*)

Style hairy; stamens and petal-claws arranged to form 5 nectar-passages six species, keyed and described in Yeo (1973): 322

Style glabrous; stamens and petal-claws not arranged to form 5 nectar-passages (7) *G. cataractarum*

Leaves palmatifid

Stamens not much longer than sepals (section *Lucida*)

Annual; flowers 8–10 mm in diameter; petals to 10.5 mm long 8. *G. lucidum*

Perennial; flowers more than 20 mm in diameter; petals 17–19 mm long

Leaves glossy, glandular-puberulent; mericarps puberulous on the ribs (9) *G. glaberrimum*

Leaves more or less densely clothed with fine, slightly curled hairs; mericarps densely

covered with crisped hairs 10. *G. lasiopus*

Stamens more than twice as long as sepals (section *Unguiculata*)

Leaf-blades usually more than 4.5 cm wide; leaf-divisions more or less rhombic,

freely lobed and toothed; filaments simple 11. *G. macrorrhizum*

Leaf-blades not more than 4.5 cm wide; leaf-divisions obtrullate, 3-lobed,

lobes occasionally toothed; filaments with a pair of small, hair-tipped

auricles near the base 12. *G. dalmaticum*

longer than sepals to nearly twice as long, that flowers are zygomorphic in *G. palmatum* and that mericarps may be glabrous or puberulous.

Seven species.

(1) *G. maderense* Yeo.

Now transferred from section *Anemonifolia* to section *Ruberta*.

Mericaip (Appendix 1, Figs 2–4): 4–4.5 mm long, dark brown, evenly reticulate with bold veins dorso-laterally, the network looser at sides but sometimes reaching the ventral border, with 1–3 annular keels at apex; ventral suture gaping widely. Similar overall to that of *G. palmatum* q.v.

(2) *G. palmatum* Cav.

Now transferred from section *Anemonifolia* to section *Ruberta*.

Mericaip (Appendix 1, Figs 5–7): differing from that of *G. maderense* in being 3.2–3.4 mm long, light brown, slenderly veined, with the network largely fading out towards the ventral suture and sometimes with short unconnected pieces, and in having only one or two apical annular keels and a slit-like ventral suture.

(3) *G. reuteri* Aedo & Muñoz Garm. (*G. canariense* Reuter).

This was transferred from section *Anemonifolia* to section *Ruberta* by Yeo (1984).

Mericaip (Appendix 1, Figs 8, 9): 3.2–3.5 mm long, more slender than those of the two preceding species, light brown, reticulum honeycombed at extreme apex, elsewhere rather slenderly veined; veins becoming loose and finally fading out laterally towards the ventral suture, leaving a rather wide unsculptured area; apical annular keels 1–2(–3), not especially deep; suture gaping; apex sometimes pilose.

(4) *G. yeoi* Aedo & Muñoz Garm. (*G. rubescens* Yeo).

Mericaip (Appendix 1, Figs 10–12): sometimes differing from that of *G. reuteri* (*G. canariense*) in being greyish, also differing from it in having stronger venation and a denser reticulum and in having one or two very deep apical annular keels, the second partitioned within by one or two walls at right angles to it; ventral suture narrower; body glabrous.

(5) *G. robertianum* L.

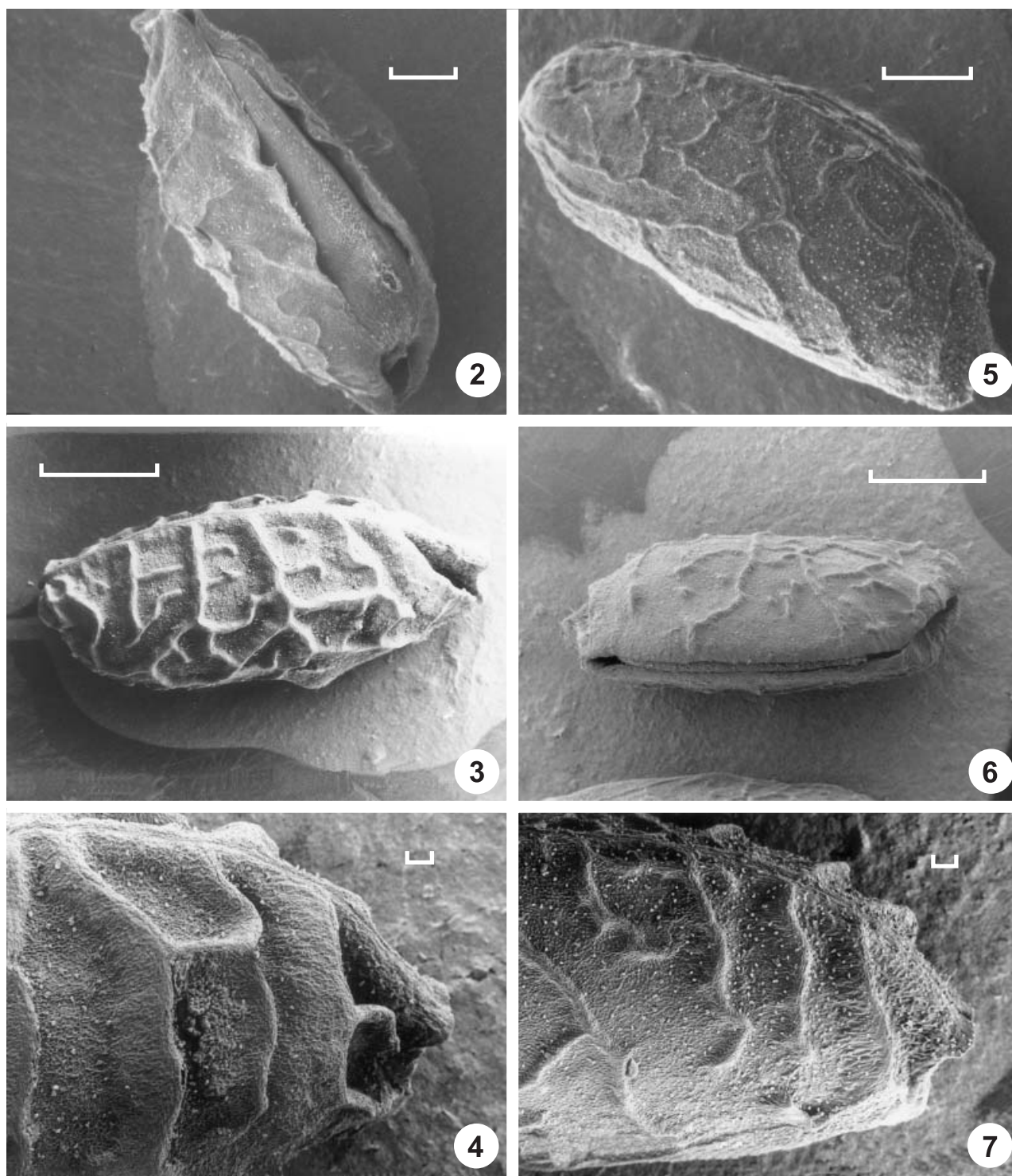
Mericaip (Appendix 1, Figs 13, 14): 2–2.8 mm long, from light to dark brown, pilose distally or sometimes glabrous, provided with tangle-strands (see next paragraph), reticulate, with moderately prominent veins, sparse and scarcely anastomosing in the basal half to form large vertically elongated alveolae, denser above and forming at the apex 1–3 collar-like keels; laterally with an unsculptured margin; suture closed or narrowly open.

I have previously (Yeo, 1973) compared the mericaip dispersal arrangements of *G. robertianum* and *G. purpureum* with the dispersal of peridioles of *Cyathus*, of the basidiomycete family Nidulariaceae. I suggested that the suspension of these fungal propagules from vegetation by fine filaments may be of value in helping them to escape the attentions of some invertebrate animals that might crawl on the leaves. This idea could apply to *Geranium* species too. The same suggestion was made by Askew (1971: 153–154) for the pupae of some Braconidae and Ichneumonidae (Hymenoptera) that are suspended from vegetation on long silken cords. At the suggestion of Dr S. A. Corbet I have proposed the descriptive term ‘tangle-strands’ for this kind of structure in any organism (Yeo, 1985: 158b). Dr Corbet told me that there are dragonflies (Odonata) whose eggs have a similar structure that functions similarly in flowing water, but here presumably to prevent the eggs from being carried to another habitat.

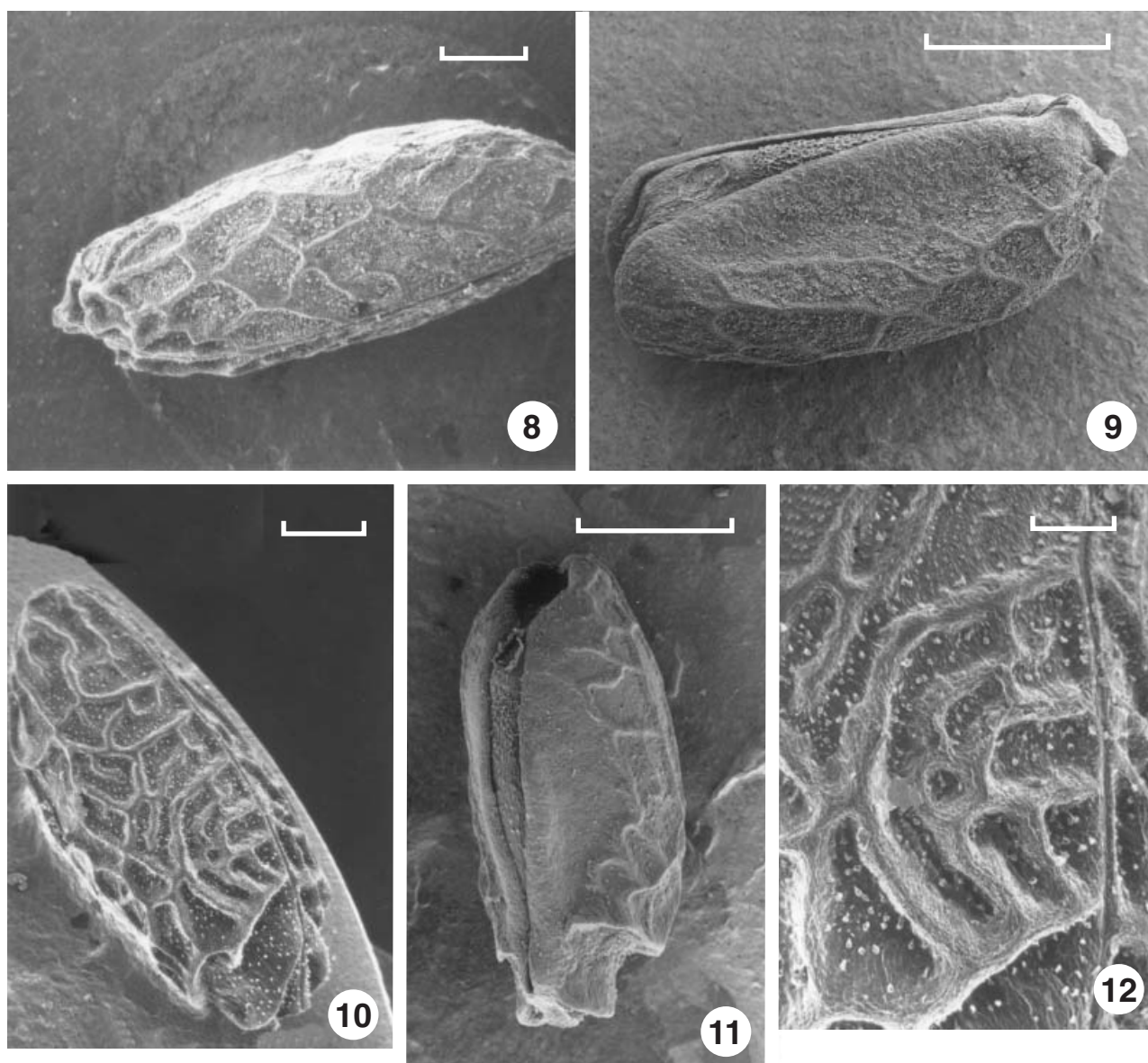
I reported that this species was absent from Madeira but I found it growing there myself in 1990: by a levada near Comacha, 25.iii.1990 (colour transparency in my personal collection). The species is listed for Madeira by Eriksson, Hansen & Sunding (1979). These authors also report it from Gomera, Gran Canaria and Hierro, whereas I gave only Hierro for the Canary Isles. Dr Carlos Aedo informs me that it is represented also from the islands of Tenerife and La Palma in the herbarium of the Real Jardín Botánico, Madrid (MA).

Below are cited cultivated specimens from England, mainland China and Taiwan, on which I now make comment. All were grown in a greenhouse at Cambridge.

The English sample is from a dune/shingle habitat; it resembled the Chesil Beach sample (Yeo, 1973) in being compact, slow-growing and small-leaved (lamina to 4.5 cm wide on young plants) and the stems were firmly appressed to the substratum. The flower-size was very uniform, with a diameter of only 12–13 mm and petal lamina 6.5–7.5 mm. The leaves were quite strongly hairy, the stems less so than in inland shade forms. I visited the Winchelsea site with Dr Rose in June 1993; flowers were mostly 11–12 mm in diameter, but down to 8.5 mm. Otherwise the plants were exactly like those growing in Cambridge. A similar form was seen the previous day on the Hampshire coast in the North Solent National Nature Reserve about 100 km to the west. (These populations were treated by Baker (1956) as *G. robertianum* ssp. *maritimum* (Babington) H. G. Baker, but I have reservations as to the distinctness and constancy of this taxon (Yeo, 1973).) Baker (1956) was wrong in attributing the varietal name to Babington, 1851: 62; it had already been used by T. H. Cooper in 1834 (see Allen,



Figures 2–7. Figs 2–4. *G. maderense*. Fig. 2. Whole carpel, ventral view. Scale bar = 500 μ m. Fig. 3. Whole carpel, oblique side view, apex to left, dorsal rib along upper edge. Scale bar = 1000 μ m. Fig. 4. Apex of carpel. Scale bar = 100 μ m. 2–4: 310-65 Talbot (the late Lord Talbot de Malahide, Dublin). Figs 5–7. *G. palmatum*. Fig. 5. Whole carpel, dorsal rib along lower edge to left, apex of carpel right foreground. Scale bar = 500 μ m. Fig. 6. Whole carpel, ventral suture on lower side, apex to left. Scale bar = 100 μ m. Fig. 7. Apex of carpel. Scale bar = 100 μ m. 5: 284-64 Stephens (the late Mr Jan Stephens, Tring, Hertfordshire); 6, 7: 191-74 Kew, coll. Madeira.

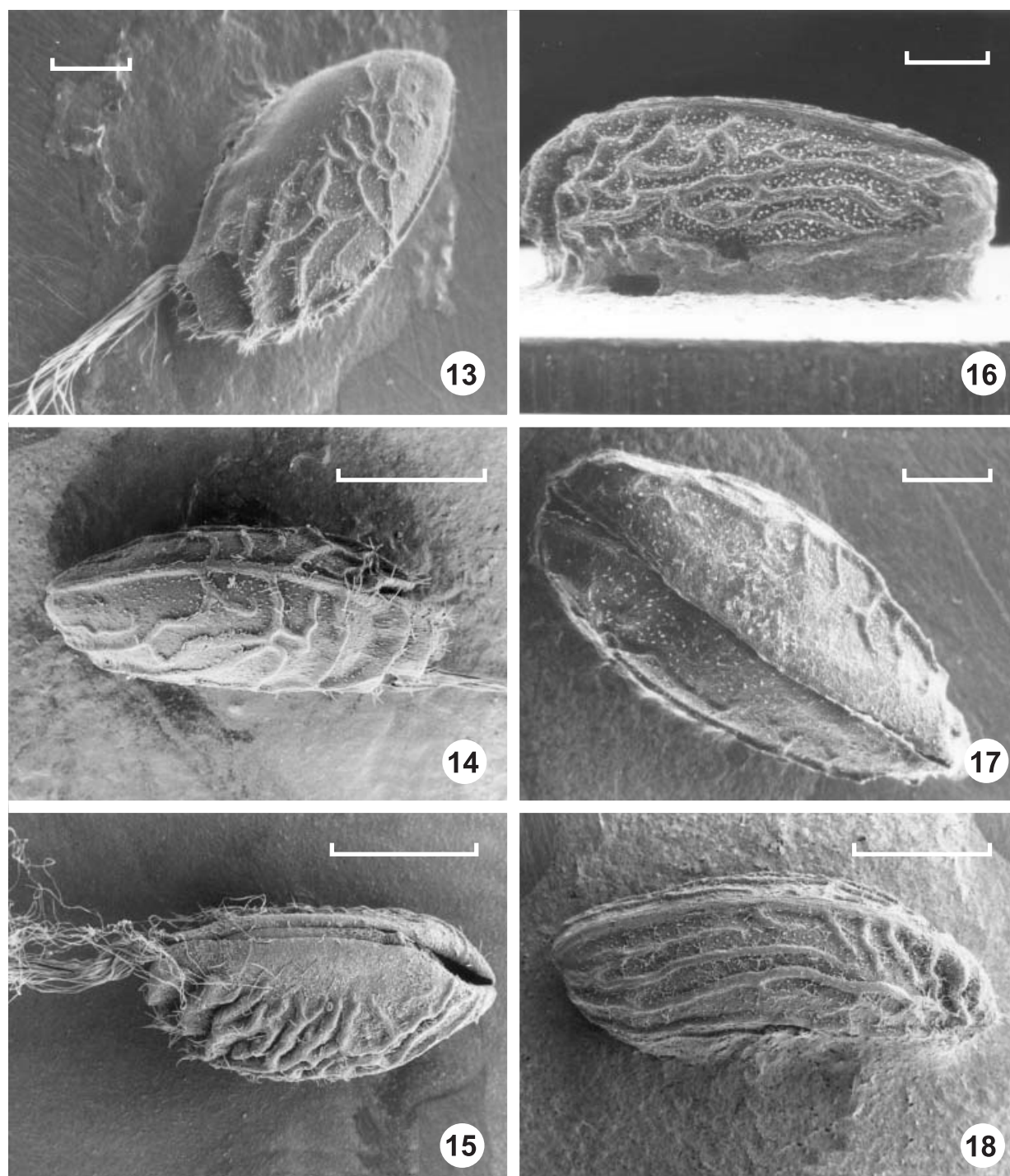


Figures 8–12. Figs 8, 9. *G. reuteri* (*G. canariense*). Fig. 8. Whole carpel, apex at left, ventral suture along lower edge. Scale bar = 500 μ m. Fig. 9. Whole carpel, apex to right, ventral suture along upper edge. Scale bar = 1000 μ m. 8: either 192-66 Barcelona (seeds from La Orotava Bot. Gdn., Tenerife) or 192B-69 Tenerife, La Orotava Bot. Gdn. (seeds collected on Gomera, Canary Isles); 9: 192B-69 Tenerife, as preceding. Figs 10–12. *G. yeoi* (*G. rubescens*) all with apex pointing downwards. Fig. 10. Whole carpel, dorsal rib along upper edge. Scale bar = 500 μ m. Fig. 11. Whole carpel from side, ventral suture at left. Scale bar = 1000 μ m. Fig. 12. Enlarged detail of apical area, showing submicroscopic trichomes. Scale bar = 200 μ m. 10, 12: origin uncertain (one of three, none direct from natural habitat); 11: old CUBG stock, origin unknown.

2001) and by G. Don in 1831 (*Gen. Hist.* 1: 721) as kindly pointed out to me by Dr C. Aedo. Typification of these names is still to be done.

In both the Far Eastern samples the flower-size maximum is also well below that for European plants from mesophytic habitats (13.5 mm diameter instead of 16.5 mm) and the petal-colour is paler. In the Taiwan stock the coloured area is marked by a faint pale

mid-vein part-way whereas the basal third of the limb of the petal is white, with no darker veins. In the Sichuan specimen, anthocyanin pigmentation of leaves and stems is rather weak. The Taiwan specimen is vigorous but apparently water-stressed; it is very bristly. Otherwise there are no noticeable differences from normal European material. The mericarps are glabrous in both samples.



Figures 13–18. Figs 13, 14. *G. robertianum*. Fig. 13. Whole carpel seen from beyond the apex showing apical collar-like keels and tangle-strands arising from apex. Scale bar = 500 μ m. Fig. 14. Whole carpel in obliquely dorsal view, with tangle-strands. Scale bar = 1000 μ m. 13: 104B-74 Kiefer, spontaneous in CUBG, presumably local native stock; 14: 289–86 Yeo, collected by the author in the Burren, western Ireland. Fig. 15. *G. purpureum*. Whole carpel in obliquely ventral view, showing ventral suture and apical tangle-strands. Scale bar = 1000 μ m. 178–77 Yeo, collected by the author on Cap Corse, Corsica. Figs 16–18. *G. cataractarum*. Fig. 16. Whole carpel from side with apex at left. Scale bar = 500 μ m. Fig. 17. The same from ventral side showing closed ventral suture. Scale bar = 500 μ m. Fig. 18. Whole carpel, obliquely dorsal view, apex at right. Scale bar = 1000 μ m. 16, 17: 240-70 Barneby, collected by the late R. C. Barneby in Sierra de Cazorla, Prov. Jaén, Spain. 18: 169B-76 Guittonneau, Moroccan stock, see p. 420, Cultivated specimens.

Cultivated specimens: ENGLAND: Rye Harbour National Nature Reserve, Winchelsea Beach, vice-county 14, East Sussex, 1991, *Dr Francis Rose*. CUBG entry no. 1259–91: 16.vi.1992, 7.v.1993 (CGG) (and transparencies, 26.viii.1992). *CHINA.* Sichuan: between Luding and Kangting, *Dr A. C. Leslie 33/81*, CUBG entry no. 488–81: 11.ii.1983, 22.iii.1983, 4.xi.1986, CGG (and transparencies). *TAIWAN:* approx. 11 km east of Taiuling, Taroko National Park, Hualien Prov., 2430 m alt., north-east side of the island, in a wall, 30.x.1992, *B. S. Wynn-Jones (BSWJ) 194*, CUBG entry no. 374–96: 24.iv.1997, CGG (and transparencies).

(6) *G. purpureum* Vill.

Mericaip (Appendix 1, Fig. 15): 2.3–3 mm long, with similar proportions to *G. robertianum*, glabrous or pilose, provided with tangle-strands as in *G. robertianum* (see preceding species), ribbed or more or less reticulate in the basal half, sometimes sparsely, the lowest ribs curving down towards the base, sulcate or closely ribbed in the distal half, with 3–5 overlapping collar-like keels or contiguous circumferential ridges at the apex; body sculpture ending abruptly at the sides, leaving a large unsculptured area. Suture narrowly open.

Previously (Yeo, 1973) I have given evidence that variation in the colour of the mericarps and the form of the veins of the reticulum depends on the level of maturity achieved by the carpel before the specimens were collected. Weakness of the sculpture in mericarps that matured in adverse summer weather or on dying plants has been noted by Mr Tony O'Mahony (pers. comm.) in Ireland.

With regard to the function of the fruit-dispersal arrangements, see above (second paragraph on *G. robertianum*).

Corrigendum: figure 5D in Yeo (1973) shows the sepals with a uniform clothing of rather short glandular hairs; other types of indumentum are covered by the species description on p. 340 of that publication, as should have been pointed out in the caption to the figure.

The description (Yeo, 1973) applies to ssp. *purpureum*, for which I gave a maximum leaf-width of 8.5 cm; now, plants with basal leaves 14.5 cm wide have been found (in a sparse self-sown colony in mulched soil in the open in the University Botanic Garden, Cambridge, in 1998). Baker's (1955) account of the occurrences of this subspecies in the British Isles was updated to 1984 for Ireland by O'Mahony (1985). At that time its survival seemed precarious and since then some colonies have succumbed, but the species has survived near the previous sites (in and near Cork, vice-counties H4 and H5, Mid and East Cork) and by 1996 it existed at 23 sites (O'Mahony, 1997). The species has also now been

refound at Dungarvan, Co. Waterford, vice-county H6 (by Paul and Ian Green – Tony O'Mahony, pers. comm.). Mr O'Mahony disagrees with Baker's suggestion that hybrids with *G. robertianum* occur here; however, this hybrid does occur in the Cork area (O'Mahony, 1996). Additionally, *G. purpureum* has been found on shingle in vice-county H3, West Cork (Akeroyd, 1996).

A variant of *G. purpureum* with a modified habit grows on the south coast of the counties of Hampshire and Sussex in England and in Guernsey in the Channel Islands. Attention was drawn to it by A. J. Wilmott (1921) and it was further investigated by Baker (1955) who gave it the rank of subspecies, as *G. purpureum* ssp. *forsteri* (Wilmott) H. G. Baker. It is rare and local and my observations on it in the field and in cultivation are given elsewhere (Yeo, 2003a, b).

The adventive geographical distribution now includes New Zealand, North Island, 'naturalized' (Webb, Sykes & Garnock-Jones, 1988) as well as temperate South America.

(7) *G. cataractarum* Cosson, Not. Pl. Crit. 3: 99 (1851). *G. occitanicum* Batt. & Pit., Contr. Fl. Maroc, 8 (1918) [effectively published in mimeographed handwriting; the epithet refers to the Languedoc and is therefore inappropriate (Maire, l. c., infra)].

G. cataractarum ssp. *pitardii* Maire, Bull. Soc. Hist. Nat. Afr. Nord 15: 96 (1924).

G. cataractarum ssp. *cossonii* Maire, Bull. Soc. Hist. Nat. Afr. Nord 15: 98 (1924) (nom. illeg. pro subspecie typico).

Cotyledons entire; seedlings with long fine pluricellular glandular hairs. Perennial to 30 cm tall, aromatic (smell resembling that of *G. robertianum*), forming a caulorhiza to 2 cm high and 1.2 cm thick that bears several rosettes. Petiole of basal leaves 2–4 times as long as lamina, densely clothed with red-tipped pluricellular glandular hairs up to 2 mm long. Stipules sheathing for up to 1.2 cm, with a pair of acute lanceolate lobes at apex, glandular-hairy. Lamina 1.5–5 cm long and 2–7(–9) cm wide, divided to the base into 3, of which the middle division is petiolulate and the laterals shortly petiolulate and cut to the base or nearly so by one incision, so that the lamina is pedately 5-partite. Divisions lobed to half or two-thirds their length, the lobes obtusely or acutely toothed and mucronulate; indumentum as on the petioles but less dense distally; surface matt. Stems, peduncles and pedicels with the same glandular clothing as the petioles and with a furrow filled with eglandular hairs; peduncles and pedicels green, lower internodes flesh-pink.

Inflorescence a cyme, with pairs of unequal branches at 4 or 5 successive nodes and pairs of unequal stem leaves. Stem leaves similar to the basal, decreasing

upwards. First one or two internodes sometimes short, otherwise 6–8 cm long, decreasing upwards.

Inflorescence above the 3rd to 5th pair of leaves merely bracteate. Cymules two-flowered, arising at 2nd or 3rd node and onwards.

Flower buds nodding, ovoid. Flowers upwardly inclined, 17–19 mm in diameter. Sepals 5.5–7 mm long, outer with the intermediate veins keeled, green with membranous red-flushed borders, inner with their median rib the most prominent, largely membranous and red-flushed; mucro *c.* 0.5 mm long. Petals 12–17 mm long, glabrous; claw *c.* 5.5 mm long, pale pink, at most obscurely 2-ridged on either side of a furrow that is closed distally and then opens again at the angle between the claw and the limb; lamina 7–10.5 × 5.5–8 mm (slightly unequal within the flower), rounded to subtruncate, divergent rather than patent, bright or deep pink, sometimes pale towards the throat, sometimes with faint darker veins here. Stamen filaments 8.5–9 mm long, gradually but feebly dilated towards the base, glabrous, proximal part nearly white, exerted part pink, this initially pressed outwards against the petals, then straight at dehiscence, finally *c.* 3.5 mm long. Anthers scarlet to orange-red, with yellow sutures, or yellow, *c.* 2 × 1.25 mm; pollen yellow. Stigmas *c.* 1 mm long, pink on back, white or nearly so on receptive surface. Style *c.* 9 mm long, pale pink, straight.

Fruit 18–22 mm long overall; rostrum glabrous. Mericarps (Appendix 1, Figs 16–18) 3–3.7 × 1.5–1.8 mm, obovoid, orange-brown, glabrous or pilose, heavily veined throughout; veins at apex reticulate or pinnately arranged and slightly wavy, areoles becoming strongly elongated towards the base. Seeds *c.* 2.2–2.5 mm long.

South-east Spain (selected specimens): ALBACETE (MURCIA in schedis): in rupib. irrigatis & umbros ad los Chorros et in Sierra Padrón de Bienservida, 1000–2000 m, 2–4.vii.1891, *Porta et Rigo, Iter III. Hispanicum*, 278 (BM, K); Prov. JAÉN: Sierra de Cazorla, above Cazorla, towards/near Fuente de Rechitas, 14.vi.1927, Wilmott & Lacaita, *Lacaita 31143*, *Wilmott loc. 3b* (BM, 3 sheets in all); Sierra de Cazorla, al Puntal del Aire, 15.vi.1928, *Lacaita 32454, 32449* (BM), *Lacaita 448/29* (K); Sierra de Cazorla, cañada de las Fuentes or Las Cabañas, 1.vii.1948, *Heywood 426* (BM); Sierra de Cazorla, Cortado del Háza, 1250 m, *Heywood 1686* (BM); Sierra de Cazorla, Cerro Gilillo, 1450 m, *Heywood 1433A* (BM).

North-west Africa (Morocco) (selected specimens): MOYEN ATLAS: Jimdighas, au-dessus du lac, 1550 m, 16.v.1925, *Jahandiez-Plantes Marocaines* 298 (K); Ras-el-Ma prope pag. Azrou, *c.* 1600 m, 27.vi.1926, *Lindberg, Iter Moroccanum 4359* (K);

c. 34 km from Azrou, on road to Midelt, Lat. 33°12'N, long. 5°4'W, 1880 m, loc. 17, 12.vi.1992, *Optima Iter V, 704* (BM); van Ifrane naar Midelt, 1900 m, 21.vi.1954, *Van Steenis 19332* (BM).

Cultivated specimens: Prov. JAEN: Sierra de Cazorla, near source of Río Guadalquivir, viii.1967, *R. C. Barneby*, CUBG entry no. 240-70, 19.xi.1970, 31.v.1971, 13.ix.1971, 27.iii.1972 (*n* = 18, R. Finch, on pmc) (CGG), and Royal Botanic Gardens, Kew, entry no. 080.71.00948, 22.v.1972 (K, 2 sheets) (2*n* = 36, C. A. Brighton). MOYEN ATLAS: falaise du Senoual à 1 km E. de Bekrit, *G. G. Guittonneau 72.07.10.05* (embodying date 10.vii.1972), CUBG entry no. 169B-76, 13.ii.1979, 9.iv.1979, 1.vi.1979 (CGG).

The leaves of this saxatile perennial are cut to the base, as in all species of former section *Anemonifolia* and section *Ruberta*, their closest resemblance being with those of *G. robertianum*. However, there are no well-formed floral nectar passages. The exertion of the stamens is intermediate between the extremes shown by this section.

Maire considered that the principal differences of ssp. *pitardii* from ssp. *cataractarum* were a deeper dissection of the leaf and a greater length of the claw of the petal. He admitted that ssp. *pitardii* was very little different from ssp. *cataractarum* but filled 3½ pages describing and discussing the taxon.

Of the two stocks that I have cultivated (see above) the Spanish one is larger in all parts, with the flowers less crowded, and the petal-limbs deeper purplish pink, but lacking a pale basal median zone. The Moroccan stock's dimensions do not reach the maxima that I give for the species; the smaller flowers are more numerous and more crowded and the petal-limb is paler, shading gently to paler still in the basal median area. Previously I have assumed that these differences might characterize the plants of the two areas and have treated them as subspecies (Yeo, 2002). However, in refereeing this paper Dr Carlos Aedo tells me that the populations show notable variability in many characters but that he has found no constant feature supporting division into two taxa. I have therefore combined them.

Habitats of the species in both areas (from herbarium labels) are faces and crevices of limestone rocks, and river gulleys on limestone.

SECTION LUCIDA KNUTH

Annual or perennial herbs. Leaves simple, palmatifid, with more or less truncate divisions. Flowers actinomorphic, with nectar-passages. Stamens slightly longer than sepals. Note that *G. lucidum* and *G. lasiopus* have large hairs on the mericarps and

G. glaberrimum and *G. lasiopus* have hairy petal-claws.

Seven species were assigned to this section by Knuth (1912) but Yeo (1984) recognized only one, most of the others being removed to section *Trilophia* Yeo. Here, three species are accepted.

(8) *G. lucidum* L. *Sp. Pl.* 682 (1753).

Annual germinating in autumn or spring. Cotyledons shallowly asymmetrically bilobed, up to 7 mm long and 11 mm wide, glandular-pilose, bright green (with shorter petioles than in *G. robertianum* and *G. purpureum*). Stem a caudex up to c. 10 mm long bearing a rosette of crowded leaves and terminated by an inflorescence. Stipules of the rosette up to c. 3×1.5 mm, deltoid or ovate-lanceolate, green or reddish. Petioles of the rosette up to 8 cm long and c. 1.5 mm thick, terete, greenish, flushed with red, ascending, reflexed in age. Lamina of the rosette up to 5 cm wide, bright green, sometimes red-edged, fleshy, turning red when dying, suborbicular, divided half-way to the base or a little more into 5 or 7, the divisions with more or less closed sinuses between them, flabelliform, coarsely and shallowly lobed for one-third to one-half their length, few-toothed, teeth and tips of lobes rounded or subtruncate, mucronate, upper surface with large tapering colourless glandular hairs, veins eglandular-villous above, margins weakly ciliate with minute eglandular as well as glandular hairs. Rosette leaves dying soon after beginning of flowering in over-wintered plants. Leaves of the inflorescence paired, resembling those of the rosette, but at least the distal part of the upper petioles villous-pubescent along the upper side, and the lamina glandular-punctate beneath, up to 6 cm wide, more or less reniform, divided c. two-thirds its length into 5.

Inflorescence terminal, up to c. 50 cm tall, consisting of a central axis of 1–3 internodes with 2 or 3 equal or unequal branches at the terminal node and sometimes smaller branches at the preceding one. Internodes to 10 cm long. Axes green with red nodes, or dark red, the upper internodes also with a band of eglandular villosity. Branches erect, with the lower internodes up to 18 cm long and 5 mm thick, leafy, the two branches of each dichotomy increasingly unequal upwards. Peduncles terminal, 1–7 cm long (1–)2-flowered. Pedicels divaricate, 2–15 mm long.

Flowers salverform, c. 8–10 mm in diameter, more or less erect. Sepals 5–7 mm long, including mucro c. 1 mm, tapered to an acute apex, connivent, 3 outer with the vein on either side of midrib raised to form a green wing with transverse green ridges or flaps on either side of it, otherwise colourless and translucent, two inner smaller with veins only slightly raised, greenish, otherwise colourless and translucent, with

a tuft of villosity at the base of the mucro. Petals 7.5–10.5 mm long, glabrous; lamina $3\text{--}3.5 \times 2\text{--}2.5$ mm, cuneate with rounded apex, upper surface distally bright rose-pink, proximally with pale edges, a pale central depression and a darker-coloured ridge on either side of the depression, lower surface with a whitish cast, claw 4.5–5 mm long, with white wings and pink twin keels that diverge and fade out at the base. Petal claws and stamen filaments together forming nectar passages of circular cross-section. Stamens 6–7 mm long, slightly exerted, filaments glabrous, white or pink-tipped; nectaries small. Style 6.5–7.5 mm long (including stigmatic branches), minutely bristly; stigmatic branches pink, divergent but not recurved.

Beak of fruit, including stigmas and carpels, 15–18 mm long. Mericarps (Appendix 1, Figs 19, 20) 2.2–2.4 mm long, light brown, strongly rounded on the back at the apex, obliquely tapered at the base, with dorsal keel running from apex to base and 4–6 cristate lateral keels parallel to it, these breaking up into a raised reticulum in the basal half, the outermost keels being the shortest; ventro-lateral surfaces very finely obliquely striate. The crests of the apical ridges and the margins of the ventral suture with short stiff hairs that are curled at the top.

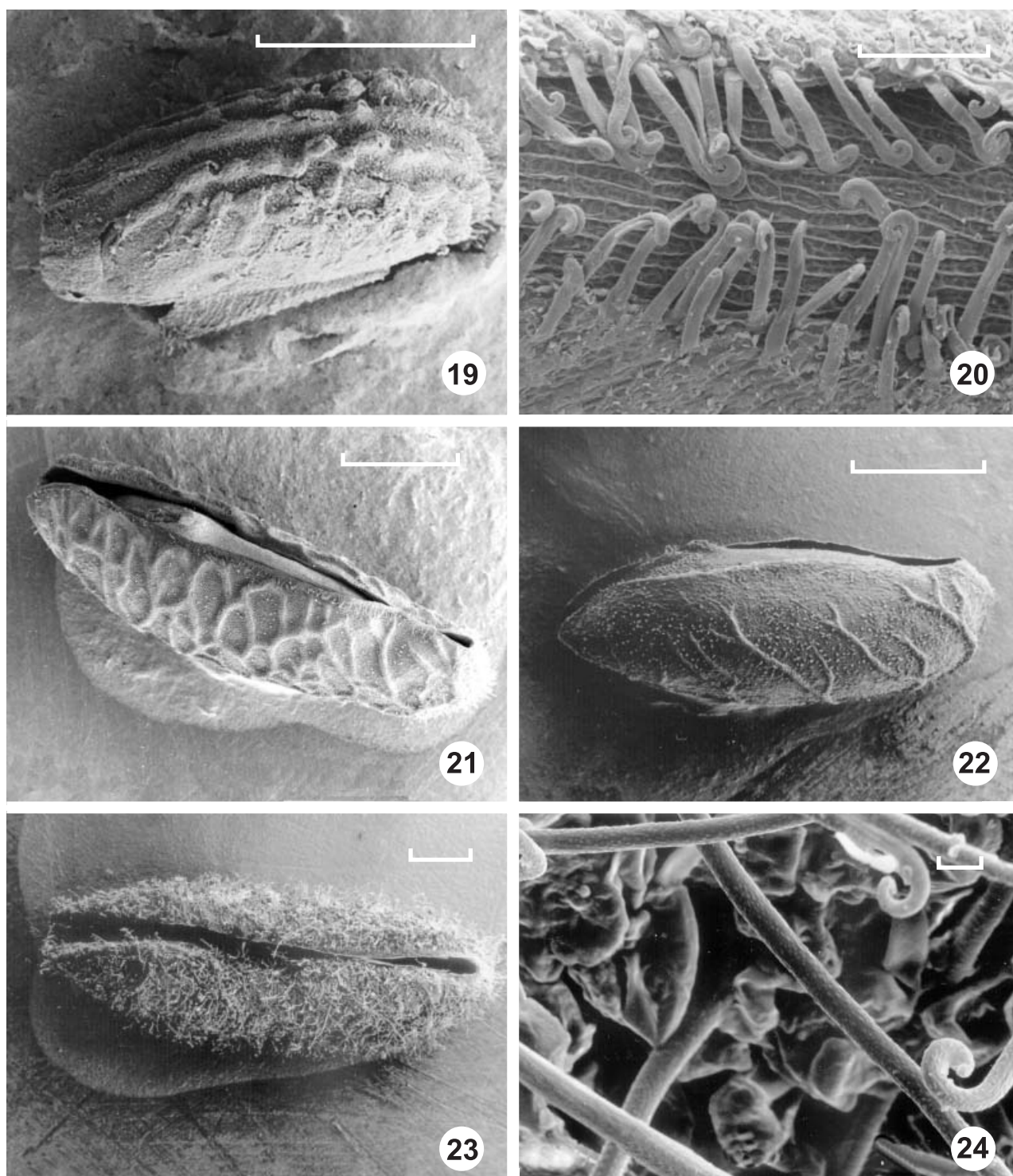
Europe, north Africa, south-west and central Asia. Introduced in North America (Aedo, 2000).

Plants that grow from seed that germinates in the autumn develop fully as described above in spring. Those resulting from spring germination show a truncated development, and may have flowers open before the cotyledons are dead. The plants are very conspicuous in senescence because of the brilliant red colouring of their vegetative parts. The species inhabits rocky ground and seems to prefer limestone in Britain. It easily becomes established in gardens and on paved areas and walls (Oswald, 1996).

The floral nectar accumulates not on the nectaries but between the stamen-bases and the sepals. Although the petal claws form five nectar-passages they are not firmly associated with the stamen-filaments opposite them, as in species 1–5. There is enough nectar to attract small bees, such as small species of *Lasioglossum* (Halictidae), a genus in which the proboscis is rather long and slender in relation to the size of the bee. However, the flowers automatically self, with the stigmas diverging slightly before the flower opens and the dehiscent anthers pushing their pollen up between them.

The species shows the lowest chromosome number known in the genus, $2n = 20$, but $2n = 40$ and $2n = 60$ also occur (see p. 410).

(9) *G. glaberrimum* Boiss. & Heldr. *Diagn. Pl. Or. Nov.* ser. 1, 8: 116 (1849).



Figures 19–24. Figs 19, 20. *G. lucidum*. Fig. 19. Whole carpel, obliquely dorsal view, apex to right. Scale bar = 1000 μ m. Fig. 20. Enlargement of the ventral suture showing mericarp wall, hooked hairs and surface of seed. Scale bar = 100 μ m. 19, 20: old CUBG stock, origin unknown. Figs 21, 22. *G. glaberrimum*. Fig. 21. Whole carpel, obliquely ventral view, seed within, apex to the right (169D-76 Guittouneau). Scale bar = 1000 μ m. Fig. 22. Similar view, 531-89 Yeo. Scale bar = 1000 μ m. 21, 22: see p. 423, 'Cultivated specimens'. Figs 23, 24. *G. lasiopus*. Fig. 23. Whole carpel, slightly oblique ventral view, apex to right. Scale bar = 500 μ m. Fig. 24. Hair-clothing, further enlarged. Scale bar = 10 μ m. 23, 24: see p. 424, specimen citations, Yeo 89.8.

Cotyledons entire, with slightly larger hairs than those of the leaf. Perennial to 40 cm tall, with short, decumbent to suberect, knotted and branched caulorhiza up to 6 cm tall and 1 cm thick, marked with leaf-scars *c.* 1 mm apart. Foliage weakly to strongly aromatic (presumably from the submicroscopic hairs that are especially dense on the abaxial surface of the stipules and on the petioles). Leaves mainly crowded at tips of branches of caulorhiza; a few smaller ones in the inflorescence. Stipules 10–15 × 5.5–7 mm, the free lobes *c.* 1.5–2 mm long, asymmetric (turned away from the petiole), the whole weakly chlorophyllous except for the transparently membranous margins of the lobes. Lamina to 6.5 cm wide, divided two-thirds to three-quarters of the way to the base into 5 or 7, sometimes red-edged. Divisions weakly cuneate, overlapping or with narrow or wide sinuses between them, lobed to *c.* one-fifth to one-quarter their length, the lobes few-toothed; teeth and tips of lobes ovate and acute to wider than long and obtuse, apiculate.

Inflorescence a cyme, usually with paired leaves and paired shoots at the first one or two nodes, and a single leaf (or bract) and shoot at later nodes. Lowest stem leaves very like the basal, with stipules 3–8 mm long; succeeding ones diminishing rapidly upwards in size and complexity. Bracts of pedicels *c.* 2 mm long, ovate. Cymules 2-flowered, the first borne at the first to third node, apparently fewer than ten per inflorescence. Peduncles 0.5–4 cm long; pedicels (0.6–)1.8–2.5 cm long.

Flower buds nodding if not too crowded, ovoid. Flowers indefinitely orientated but upwardly inclined. Sepals erect, with body 5.5–7 mm long, acute to obtuse at apex, the three outer with a strong keel on either side of the weakly keeled midrib, and with elevated cross-veins, not always evident in pressed specimens; ribs and cross-veins green, margins transparent, colourless or pink-tinged. Mucro *c.* 1 mm long. Petals 15–19 mm long; claw 6–7.5 mm long, erect, with a double median distally pink keel, and a wing either side, the flanks of the keel and the edges of the wings front and back being pilose; blade 11–13 × 8–9.5 mm, patent, rounded or truncate at apex, deep pink, hollowed towards the base, and here more or less striated, with a pale cast on the back. Stamen-filaments 11–16 mm long, glabrous, exerted from the throat by 6–7 mm, distally appressed to the petal-blades until anther-dehiscence, white and ribbon-like from base to beyond the throat, apically deep pink and subulate, appressed to the petal claws for part of their length to form five circular nectar-passages. Anthers red; pollen orange-yellow. Style including stigmas 13–17 mm long, glabrous, deep pink except at base (where it is green); stigmas 0.7–1 mm long with pale stigmatic surfaces.

Fruit 19–26 mm long; rostrum glabrous. Mericarps (Appendix 1, Figs 21, 22) 4.5 × 1.8 mm, mid-brown; ventral orifice more or less closed. Two different samples known. (1) Narrow, with a network of raised ribs. Dorsal profile gently and evenly curved. Uniformly reticulate; sculpture extending nearly to the ventral margin. Edges slightly gaping. With eglandular hairs at apex and bordering the ventral orifice (these distinctly larger than the submicroscopic hairs). (2) Seemingly fatter, more tapered in the basal third. Venation very sparse, pinnate with a few slightly branched veins; almost veinless at the base and with a veinless lateral zone. Eglandular hairs slightly longer than the submicroscopic hairs.

Seeds nearly 3 mm long; micropyle *c.* one-quarter the way up from the base.

TURKEY. ANTALYA C3: Bozburun Dağ, 25.vii.1949, 1700 m, *P. H. Davis 15551* (K) and 1900–2200 m, *P. H. Davis 15620* (K) and 1800 m, *P. H. Davis 15695* (K); ANTALYA C4: in monte Ghei Dagh Tauri Isaurica alt. 6000', vii.1845, Herb. de Heldreich (BM); in fissuris rupium montis Ghei Dagh, Tauri Isaurici, alt. 6000', *de Heldreich*, vii.1845 (BM, K, type collection); Gunodoğmus, 12.v.1979, 1400 m, *Mathew, T. Baytop & Sütllüpinar 9613* (K). Further specimens are cited by Davis (1967).

Cultivated specimens: MERSIN (IÇEL) C4, Entre Anamur et Ermenek, sur rochers calcaires à Saray Mahallesi, *G. G. Guittonneau 73.06.26.03* (embodying date 26.vi.1973), CUBG entry no. 169D-76, 20.iv.1978, 13.v.1978, 23.vi.1983 (CGG); KONYA C3, S of Lake Beyşehir, route 695, near sign reading 46 km from Beyşehir, west of road and 100 m higher, limestone outcrop in scrubby woodland, 19.vi.1989, *Yeo 89.1*, CUBG entry no. 531-89, 30.x.1990 (CGG).

Two samples of known wild origin cultivated at Cambridge differ in leaf-shape, density of glandular hairs, intensity of scent and mericarp sculpture. Such variation is not surprising in a cliff-dwelling plant occurring in isolated colonies. Close acquaintance with material from other colonies is likely to reveal further variation, which should be especially obvious in the mericarp surface. The colony that I saw in Turkey occupied broken ground at the top of a small cliff (see p. 413).

Flowering in cultivation is from April to June.

(10) *G. lasiopis* Boiss. & Heldr. Diagn. Pl. Or. Nov, ser. 1, 8: 117 (1849).

Plant *c.* 15 cm high, with a condensed, branched caulorhiza up to 1.2 cm thick. Leaves mainly in rosettes at tips of branches. Stipules to *c.* 1 cm long, with free lobes 2–4 mm long, finely eglandular-pilose as well as glandular-puberulous. Petioles to *c.* 3 times

as long as lamina, densely and finely hairy. Lamina to 3.5 cm wide, divided as far as one-third to three-quarters of the way to the base into 5 or 7, more or less densely fine-hairy, the hairs slightly curled. Divisions contiguous or with open sinuses between them, broadly cuneate, subtruncate or shallowly rounded, with shallow, rounded lobes; lobes entire or with one or two teeth. Lobes and teeth obtuse, minutely mucronate.

Inflorescence a hirsute, few-branched cyme, with leaves similar to the basal at the first one or two nodes. Bracts at higher nodes 4–5.5 mm long, linear with clear membranous margins. Cymules few (up to 4 as far as known). Peduncles hairy. Pedicels hairy, flushed with red, recurved in bud, straight in anthesis and recurved again in fruit (turning towards the substratum).

Buds ovoid to subglobose. Flowers c. 23 mm in diameter, upwardly inclined. Sepal body 4.5–6 mm long. Outer sepals with green lateral keels, inner with three green veins; margins of outer and most of inner membranous, flushed with red, finely hairy (at least on the keels). Mucro very short (0.5 mm). Petals 11–18 mm long, tapered to an indistinct claw 3–5 mm long; claws erect, shorter than calyx, pink, probably a little darker in the throat, pilose at extreme base (at least on the edges), keeled but the keel not appressed to the filament, so that nectar-passages are not clearly defined. Blade 9–12 × 7–9 mm, rich pinkish purple, patent, truncate or sometimes retuse, veined with white towards the throat. Filaments 7–10 mm long, glabrous, exserted from the throat by 3.5–4 mm, rather deep pink, straight during anther-dehiscence. Anthers more or less colourless; pollen orange-yellow. Style glabrous; style-branches 0.5–1 mm long, deep red before opening.

Fruits hidden among the leaves. Rostrum glabrous apart from a few hairs at base (see comment below). Mericarps (Appendix 1, Figs 23, 24) c. 3.5 mm long, densely clothed with crisped hairs and subsessile glandular hairs, under which is a close reticulum of raised veins. Ribs arising towards the apex are slanted upwards as they pass from ventral to dorsal; the areoles often scurfy (waxy secretion?).

TURKEY: MUĞLA C2: Baba Dağ south-east of Fethiye, north slope, crevices in calcareous cliff in steep gully, 17.v.1990, *Turland 354* (BM); ISPARTA B3: In submont. Pisidiae inter Ghelindost & Karagatsch, vi.1845, Heldreich (BM) (type locality, which Davis (1967) incorrectly placed in Konya C4); high road from Gelendost to Sarki-Karaagaç, 4.3 km beyond Balci, vertical limestone cliff, 21.vi.1989, *Yeo 89.8* (CGG-mericarps and colour transparency of cultivated offspring only); Egredir, 2 km south of Yaka köyü (village), rocky places, mixed forest, 1400–

1500 m, 28.v.1974, *Pesmen & Güner 1258* (HUB, teste A. Baytop); ANTALYA C3: Akseki, calcareous rocky places, 9.vi.1970, *A. Pamukçu & Quézel, s.n.* (HUB, teste A. Baytop); KONYA C4: Caramania, in fissuris rupium Karadagh Pisidiae, v.1845, *Heldreich* (K, one sheet with two similar labels); Karaman, Karadağ, east slope of Kartallik tepe, 1700 m, *A. Ünal s.n., s.d.* (KNYA, teste A. Baytop); KONYA C5: Eregli, Aydos Dağı, Kayasaray to Kiraçlı, calcareous places, 12.vi.1988, *S. Erik 2272* (HUB, teste A. Baytop).

Similar to *G. glaberrimum* in flowers, though the stamens are less exserted; it differs mainly in being strongly hairy and in its leaf-shape. The few hairs at the base of the rostrum give an impression of an 'overflow' from the strongly hairy carpels. The plant grows on vertical rock exposures. The fruiting cymules grow towards the rock, disappearing among the leaves, so that the mericarps have a chance of lodging in rock-crevices, or clinging to vegetation growing therein, with the aid of their dense curly hairs (for further details see p. 413).

Unfortunately the chromosome number of *G. lasiopus* is still unknown and morphological data on it are incomplete.

My collection of seed of this species was unfortunately scanty, and as a result of a series of mishaps and cultivation errors, the stock is no longer living. I suspect that an appearance of poor health in the roots may be the normal condition in this species. For cultivation in the future I suggest growing as many plants as possible from seed, transplanting them to a variety of situations and soils and then leaving them until or unless the soil appears to become exhausted.

SECTION *UNGUICULATA* (BOISS.) REICHE

Rhizomatous perennials. Leaves simple, palmatifid. Flowers slightly zygomorphic, without nectar-passages. Petal-claws and rostrum hairy. Style glabrous or slightly hairy at base.

Stamens more than twice as long as sepals. Mericarps glabrous.

Two species.

(11) *G. macrorrhizum* L., Sp. Pl. 680 (1753).

Perennial, with decumbent fleshy rhizomes of indefinite length, usually with the surface concealed by leaf-bases but sometimes penetrating the soil and then with much longer internodes. Foliage aromatic. Leaves borne in clusters at tips of ascending caudices and in pairs on flowering shoots. Petiole 1–3 times as long as lamina, sparsely to densely clothed with long to short pluricellular glandular hairs, often distally closely covered instead or as well as with uniform very short glandular hairs. Lamina to 12 (–20) cm wide, scarcely fleshy, with more or less matt surfaces, some-

times slightly peltate (Schwarz, 1936), divided as far as two-thirds to three-quarters into 7; divisions broadest at or above the middle, 3-lobed for one-sixth to one-quarter of their length; lobes with one or two teeth on either side. Teeth and tips of lobes from more or less truncate and very broad to elliptic and acute, mucronate. Indumentum like that of petioles; very short glandular hairs tending to follow the veins on the adaxial side. Stipules ovate to ovate-lanceolate, mainly free from the petiole. Leaves of the inflorescence in 1–3 unequal pairs, the last (or only) pair greatly reduced compared with the basal; stipules of stem leaves lanceolate.

Flowering stems with two leaves, two axillary branches and sometimes a 2-flowered cymule or a solitary flower at the first 1–3 nodes. Beyond this the leaves are merely bracteal and the axillary branches have shortened internodes, so that clusters of flowers opening in succession are produced.

Flower buds nodding. Flowers facing horizontally at anthesis, slightly zygomorphic. Calyx inflated. Sepals 7–9 mm long, with green veins and translucent membranes flushed with purple or red, glandular-hairy, almost circular in outline but emarginate at the apex and with an often slightly foliaceous mucro one-eighth to one-quarter as long as sepal-body. Petals 15–18 × 8.5–10 mm, with a cuneate claw 4–6.5 mm long; lamina spreading slightly asymmetrically in the flower, rounded, usually purple or pink; claw with two obtuse keels and a central channel, hairy on the back and at the sides on the front, the hairs sometimes extending on to the tops of the ridges and overhanging the channel. Stamen-filaments 18–25 mm long, glabrous or nearly so, slightly to strongly declinate, not or slightly upturned at apex, not pressed between the keels of the petal-claws to form separate nectar-passages. Anthers orange-red to dull red. Style c. 22 mm long, hairy at base, growing rapidly, purplish red, declinate like the stamens; stigmatic branches 1–1.5 mm long, with yellowish receptive surface.

Flowers erect soon after pollination. Rostrum loosely glandular- and/or eglandular-hairy. Mericarps (Appendix 1, Fig. 25) 2.5–3 × c. 1.5 mm, obovoid, glabrous, sometimes not fully enclosing the seed, with a median rib and on either side 5 or 6 wavy horizontal weakly branched veins that may include unconnected short pieces in the distal half. [Tokarski (1972) shows a densely ribbed example resembling *G. dalmaticum*.] Seeds about the same size as the mericarps, which do not fully cover them.

Distribution: French Alps, Italy and Austria eastwards to Carpathians, Romania, Bulgaria and Crimea, and southwards to Greece. (Introduced to Belgium, Germany and, rarely, to Britain.)

G. macrorrhizum is variable in stature, leaf-dissection, density of glandular hairs (and correspondingly in intensity of scent) and flower colour. It has strongly extending rhizomes enabling it to form large colonies. The leaf-lobes and teeth are suggestive of the *Ruberta*, though the blade is not divided to the base. The flowers are strikingly modified in being horizontal in posture and slightly zygomorphic and in having far-exserted stamens and style; these characters are suggestive of adaptation to pollination by Lepidoptera, but in Britain, where the species is commonly cultivated, bumblebees are the principal visitors. The calyx is conspicuously inflated. The few hairs at the base of the style give an impression of an 'overflow' from the pubescent rostrum. *G. macrorrhizum* occurs in rocky places including loose material (see p. 413).

(12) *G. dalmaticum* (Beck) Rech. f., Magyar Bot. Lapok 33: 28 (1934).

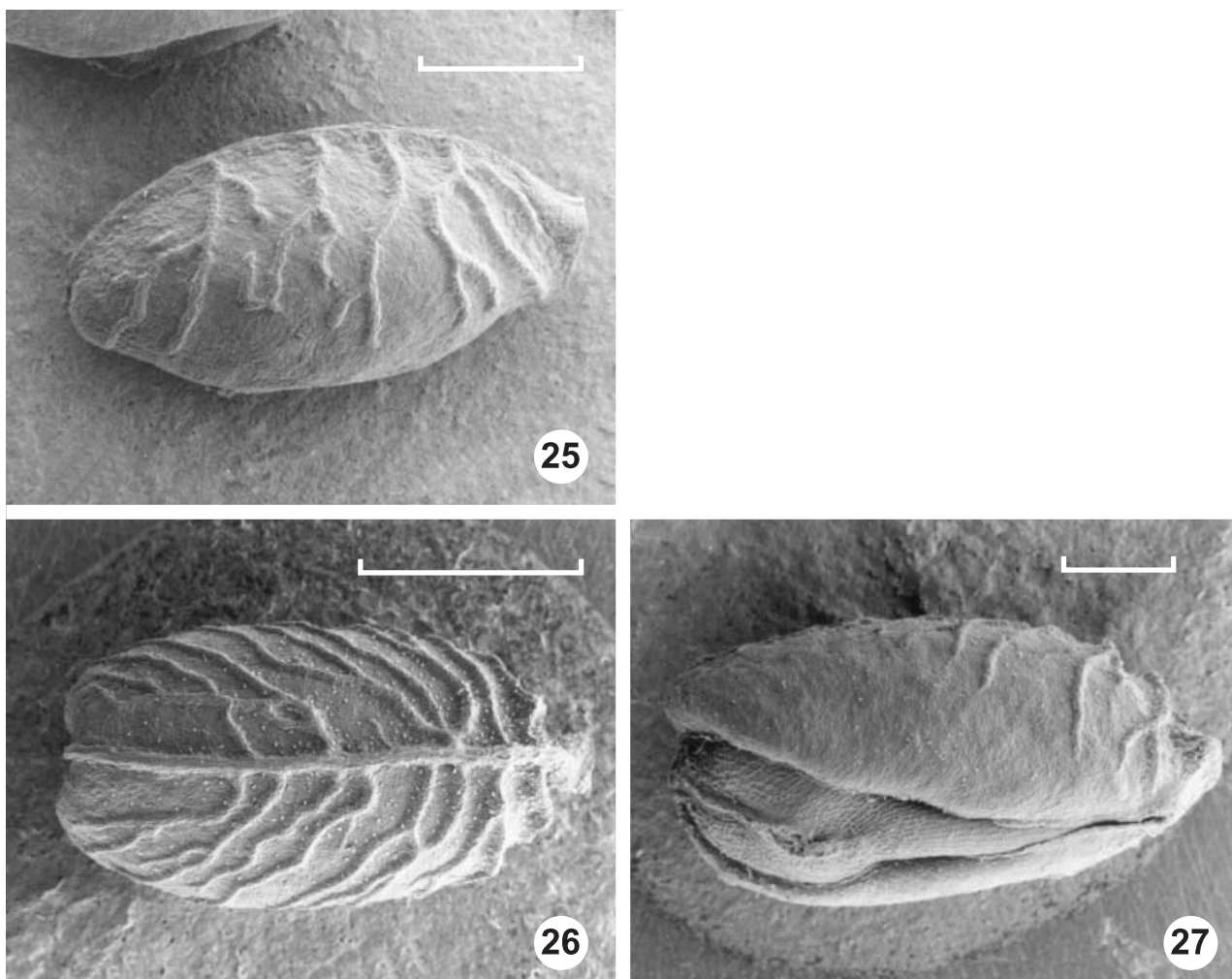
G. macrorrhizum var. *dalmaticum* Beck, Verh. K. K. Zool.-Bot. Ges. Wien, 46: 266 (1896) [*Geranium macrorrhizum* L. var. *G. dalmaticum* G. Beck nov. var.] et in Bot. Centralbl. 69: 55 (1897). Type: Croatia, Dalmatia: in Monte Vipera peninsulae Sabioncello in fissuris et glareis rupium calcareum alt. 700–800 m s.m., florens legit mens. junio, *G. de Beck*. [exact date from protologue is 12.vi.1894; place of conservation unknown; Sabioncello = Peljesac].

G. macrorrhizum ssp. *microrrhizon* Freyn, Mém. Herb. Boiss. 13: 4 (1900) [*Geranium microrrhizon* nov. ssp. *Geranii macrorrhizon* L.]. Type: Dalmatia australis, Ragusa: in cacumine montis dicto Monte Vipere, 960 m supra mare, 18.vii.1899, *Brandis* [place of conservation unknown].

G. microrrhizum (Freyn) O. Schwarz, Repert. Spec. Nov. Regni Veg. 40: 352 (1936).

Perennial, producing decumbent branching caudices 3–6 mm thick with long internodes (leaf-bases not overlapping) ending in loose or dense clusters of leaves (internodes shorter). Petioles very slender, 2–4 times as long as lamina, with a band of fine curled hairs on the adaxial side. Lamina to 4.5 cm wide, scarcely succulent but smooth and more or less glossy, divided as far as four-fifths to six-sevenths into 5 or 7; divisions obtrullate, mostly 3-lobed for one-quarter to one-third of their length, with the middle lobe usually the largest; lobes broad, abruptly pointed, entire or occasionally with 1 or 2 small teeth at the sides. Sides of entire part of division concave, straight or convex. Stipules 2–5 mm long sometimes with pluricellular hairs; free portion to c. 2 mm long. Stem-leaves, if present, smaller than the basal.

Inflorescence similar to that of *G. macrorrhizum* but with 0 or 1 leaf-bearing nodes. First internode 10–18 cm long, usually bearing also one 2-flowered cymule and two branches each with a few crowded



Figures 25–27. Fig. 25. *G. macrorrhizum*, whole carpel, side view, apex at right. *G. macrorrhizum* ‘Album’, cult. P. F. Yeo, Cambridge. Scale bar = 1000 µm. Figs 26, 27. *G. dalmaticum*. Fig. 26. Whole carpel, dorsal view, apex at right. Scale bar = 1000 µm. Fig. 27. Whole carpel, obliquely ventral view, apex at left, showing considerable exposure of seed. Scale bar = 500 µm. 26, 27: 546–82 Beanland, Mr F. Beanland, nurseryman.

flowers and many barren bracts. Inflorescence internodes glabrous, villous or tomentose and sometimes with some long pluricellular glandular hairs.

Flower-buds nodding. Flowers facing horizontally at anthesis, slightly zygomorphic. Calyx inflated. Sepals 6–6.5 mm long, ovate (the inner) to broadly ovate (the outer), with 3 green veins and translucent membranes flushed with pink or red, densely long-glandular-hairy, with a mucro c. 0.7–2 mm long. Petals to 12–18 × 12 mm with a cuneate claw 4–6 mm long; blades rounded, patent, almost uniformly pink; claw without central ridges, abaxial surface woolly, adaxial woolly at the sides and across its width in a strip above the base. Stamen-filaments 15–17 mm long, slightly declinate (but not turned up at the tips), each with a pair of long-haired teeth very near the base, otherwise glabrous, not pressed against the petal-claws to form

nectar-passages, distally coloured as the petals, proximally colourless. Anthers red or yellow and flushed with red. Style c. 18 mm long, growing rapidly, glabrous or with a few hairs at base or singly further up, declinate with upturned tip, red; stigmatic branches 1.5–2 mm long, red, with sometimes paler receptive surface. Flowers erect soon after pollination.

Fruit 30–36 mm long, including styler portion of 13–14 mm; rostrum with short to long glandular hairs and a few eglandular ones. Mericarps (Appendix 1, Figs 26, 27) c. 2.2–2.5 mm long, ovoid, glabrous, sometimes not fully enclosing the seed, orange-brown, with median rib and a dense pinnate arrangement of descending, often branched, lateral ribs, effaced well before the axial margin or extending faintly nearly to the base, the uppermost forming a collar round the apex.

Distribution: Croatia, Yugoslavia-Kosovo, Albania.

CROATIA: the type locality, cited above. ALBANIA: in fissuris rupium ad Trijepsi vs. fines Turcorum, distr. Kuci, 3 julio, Baldacci, *Iter Albanicum (Montengrinum) Sextum 110* (BM, K); in rupestribus Skala Rapsa, distr. Hoti, 26 junio, Baldacci, 1900, *Iter Albanicum Septimum 8* (BM, K). [On the specimens in BM Baldacci reports finding it at other sites, thus on *Iter Sextum 110* he writes 'et ad "Katrini" m. Hum Orahovski' (Orahovac is a town in Kosovo) and on *Iter Septimum 8* he writes 'm. Hum, m. Veličiko (now Veličiqut, 1275 m alt.), m. Kara Brojs (presumably Brojë), supra Tamara (vidi!)'. All these additional sites, except apparently mount Hum, are north of Shkodër and near the Montenegrin frontier – compare citation of Baltisberger's specimens below.]

Cultivated specimens: Cult. W. T. Stearn, Kew, Surrey, 26.vi.1951 (BM), 18.vi.1952 (BM), 30.vi.1953 (BM, K), 13.vi.1961 (BM). CUBG entry no. 449-58 Savory (a horticultural source), 27.vi.1984 (CGG); 372-57 Finnis (a horticultural source), 25.vi.1970, 23.vii.1971, 10.vi.1975 ($n = 23$, P. F. Yeo, pmc, counted 1974) (CGG). ALBANIA: c. 40 km north of Shkodër and der Strasse Shkodër-Vermosh, in der Schlucht des Flusses Cem, 300 m, Baltisberger 83/1001, 83/1002, CUBG entry no. 217-84: 18.vi.1987, 17.vii.1989 (CGG).

Both Freyn and Beck wrote intended infraspecific names in binary form; these have therefore to be altered to agree with the authors' intentions (ICBN, Art. 24.4). *G. macrorrhizum* var. *microrrhizon* Freyn ex Knuth, Pflanzenreich IV.129: 90 (1912), appeared only in synonymy and is therefore not validly published.

The literature of this species has suffered somewhat from authors' ignorance of the work of others. Freyn re-published the taxon in ignorance of its having been named by Beck. O. Schwarz took up Freyn's epithet at specific rank in ignorance of Reehinger's having done the same with Beck's epithet two years earlier; also he did not know of the occurrence of the species in Montenegro [Albania] except from a bare mention by von Hayek (1925: 575).

G. dalmaticum was introduced into cultivation from the type locality by W. Liebmann of Arnstadt in Germany and was given by him to O. Schwarz for the Berlin Botanic Garden (Schwarz, 1936). It was found to seed freely in Liebmann's garden. It is presumably this stock that reached Britain in 1947, having been given to the distinguished nurseryman W. E. Th. Ingwersen by Dr Wilhelm Schacht of the Munich Botanic Garden (note by W. T. Stearn on specimen in BM). Baltisberger's introduction from Albania is of a more robust and erect form. Baldacci's Albanian material shows the same characters, suggesting that this species has a bipolar distribution with possible subspecific differentiation between the two. The Albanian

stock of three clones died out after some years in the Cambridge Botanic Garden. Colour transparencies (CGG) show a less attractive flower colour than that of the presumed Monte Vipere plant. Plants from both origins have similar mericarp sculpture.

Although in Croatia *G. dalmaticum* is still known only from the type locality, a very interesting find of the sterile hybrid *G. dalmaticum* \times *G. macrorrhizum* was made some time before 1985 by Dr Hans Simon, in the Biokovo mountains. The site was almost due east of Makarska and is perhaps 40 km due north of Monte Vipera and at an altitude of 1600–1650 m. It was assumed at the time to be a variant of *G. macrorrhizum*. No other *Geranium* was noticed and no search was made on a hasty motor trip from Makarska. (Unexpectedly, this plant has white petals, and it has become a popular garden plant under the name *G. \times cantabrigiense* Yeo 'Biokovo'.)

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APPENDIX 1

SURFACE CHARACTERS OF THE MERICARPS

Explanations

Mericarp structure in *Geranium* has been extensively studied by Tokarski (1972) in a monograph on the fruits and seeds of 42 European and Caucasian species. This publication includes a key and is superbly illustrated by line drawings. Four of these species were included in a later study by Dr Helen Kiefer (1980). This comprises written descriptions and scanning electron micrographs of the carpellary surface

sculpture of nine species, covering the sections with which we are here concerned: the then-recognized *Anemonifolia*, and the *Ruberta*, *Unguiculata* and *Lucida*. As her some-time academic supervisor I have permission to use her observations in the present paper and have used her descriptive data for certain characters and some of the scanning electron micrographs (SEMs). (There are practical obstacles to taking in the whole of her work on this topic.) I have also used amplified data from Yeo (1973) and some additional SEMs of my own.

Kiefer examined additional material (including herbarium specimens) with a stereo dissecting microscope to look for variation among different individuals, different years and different accessions. Such variation was found to be always within limits that permitted determination of the species on the basis of the sculpture and indumentum of the mericarps. By contrast, she found so much overlap in size that she did not include measurements in her dissertation. For the surface sculpture Dr Kiefer devised a set of descriptors and applied these to the making of detailed descriptions of the mericarps and the writing of a dichotomous key to the nine species.

Apart from the conspicuous character of the raised venation, Kiefer's descriptors give particular emphasis to the dorsal (abaxial) and ventral (adaxial) profiles and to the state of the keel or suture, which is formed where the edges of the mericarp meet axially provided the seed is not so prominent as to prevent the closure of the suture.

The legends to the figures include Cambridge University Botanic Garden entry numbers where available; they include a hyphen followed by two digits for the year and then the donor's name.

APPENDIX 2

INTERSPECIFIC HYBRIDS

The appendix lists the hybrids and their raisers. For each parental combination the CUBG entry numbers and donor-names are given followed by the dates of

specimens in CGG, the herbarium of the University Botanic Garden, Cambridge (CUBG). Some of the entry numbers are batch numbers. The hybrids are listed in alphabetical order of the parent species and the egg donor is indicated by the female sign '♀'.

cataractarum × *maderense* ♀ – Yeo, Kiefer

190B-71 Yeo, 13.x.1971, 2.xii.1971, 15.ii.1972, 2.iv.1972, 29.iii.1973, 20.iv.1974; 232-74 Kiefer, 17.xii.1985, 22.v.1986.

dalmaticum ♀ × *macrorrhizum* ♀ – (either sp. in female role) Kiefer, Bremner

232-74 Kiefer, 22.vi.1983 (HOLOTYPE and two ISOTYPES of *G.* × *cantabrigiense* Yeo).

maderense ♀ × *palmatum* – Yeo, Kiefer

187B-67 Yeo (F1), 24.vi.1968, 23.x.1968, 28.i.1969, 29.v.1969, 20.iv.1970, 29.iii.1973, 17.xii.185; 201E-69 Yeo (F2), 14.xi.1969; 232-74 Kiefer, 22.v.1986, 18.vi.1987.

maderense × *robertianum*-Kiefer

232-74 Kiefer, 20.iv.1978.

palmatum × *reuteri* ♀ (*G. canariense*)-Bremner.

Specimen raised by Bremner in Orkney, no CUBG accession number, 11.v.1999.

purpureum ♀ × *robertianum* ♀ – (either sp. in female role) Baker, Benoit, Kiefer, Van Loon, Yeo.

Kiefer A6 (no accession no.), *G. robertianum* as seed parent, 26.i.1978; 625-79 Yeo, *G. purpureum* as seed parent, 7.v.1980, 14.viii.1980.

reuteri (*G. canariense*) × *robertianum* ♀ – Kiefer, Bremner.

No specimens.

reuteri (*G. canariense*) ♀ × *yeoi* (*G. rubescens*) ♀ – (either sp. in female role) Kiefer, Baker.

288-75 Kiefer (F1), 10.vi.1978; 26A-1977 Baker (F2), 10.vi.1978, 4.vii.1978.

robertianum × *yeoi* (*G. rubescens*) – Kiefer.

none from Kiefer preserved; spontaneous out-of-doors in CUBG, 15.viii.1980.