

S. Bm 1010

ISSN 0968-04

# Bulletin of The Natural History Museum

## Botany Series



VOLUME 32    NUMBER 2    28 NOVEMBER 2002

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**The *Bulletin of The Natural History Museum* (formerly: *Bulletin of the British Museum (Natural History)*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology.**

The Botany Series is edited in the Museum's Department of Botany  
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World list abbreviation: *Bull. nat. Hist. Mus. Lond.* (Bot.)

ISSN 0968-0446

The Natural History Museum  
Cromwell Road  
London SW7 5BD

Botany Series  
Vol. 32, No. 2, pp. 61-156  
Issued 28 November 2002

Typeset by Ann Buchan (Typesetters), Middlesex  
Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

# Studies in the genus *Hypericum* L. (Guttiferae)

## 4(2). Section 9. *Hypericum* sensu lato (part 2): subsection 1. *Hypericum* series 1. *Hypericum*

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THE NATURAL  
HISTORY MUSEUM

17 SEP 2003

### CONTENTS

|   |     |
|---|-----|
| Introduction .....  | 61  |
| Sect. 9. <i>Hypericum</i> .....   | 61  |
| Subdivision .....   | 61  |
| Characters and variation .....  | 61  |
| Distribution and evolution .....  | 62  |
| Sect. 9. <i>Hypericum</i> subsect. 1. <i>Hypericum</i> series 1. <i>Hypericum</i> ..... | 62  |
| Characters and variation .....  | 62  |
| Hybrids .....   | 64  |
| Distribution and evolution .....  | 65  |
| Systematic treatment .....  | 66  |
| Sect. 9. <i>Hypericum</i> .....   | 66  |
| Sect. 9. <i>Hypericum</i> subsect. 1. <i>Hypericum</i> series 1. <i>Hypericum</i> ..... | 67  |
| References .....  | 119 |
| Systematic index .....  | 121 |

**SYNOPSIS.** The subdivision of the large sect. 9. *Hypericum* and four of its segregated sections having been treated in Part 4(1), Part 4(2) is concerned with those members of sect. 9, viz. *Hypericum* sensu stricto, in which the stem internodes have glandiferous raised lines – subject. *Hypericum* series *Hypericum*. The series comprises 11 species and can be divided into (i) a group centred in Europe and the Mediterranean (4 species) and (ii) one centred in north-east Asia (6 species), one species of which is confined to western North America and another has spread westward into Europe. The remaining species (*H. perforatum*) is morphologically and geographically intermediate between two taxa, one from each group, and behaves as an allotetraploid hybrid. It is divided into four subspecies: subsp. *perforatum*, *songaricum* (Ledeb. ex Rchb.) N. Robson **stat. nov.**, *veronense* (Schrank) H. Lindb. and *chinense* N. Robson **subsp. nov.** The hybrids of *H. perforatum* are treated in detail and include *H. × desetangsii* nothosubsp. *balkanicum* N. Robson, **nothosubsp. nov.** (*H. maculatum* subsp. *immaculatum* × *perforatum*). Other new hybrids proposed are: *H. × laschii* nothoforma *froelichii* N. Robson, **nothoforma nov.** (*H. maculatum* subsp. *obtusiusculum* × *tetrapterum*), *H. undulatum* × *tetrapterum* and *H. elegans* × *perforatum*.

### INTRODUCTION

In Part 4(1) the relationships of sect. 9. *Hypericum* sensu lato were discussed and it was shown that, although the whole group is apparently derived from sect. 7. *Roscyna*, it consists of six independently derived sections, one from each of the three subspecies of *H. ascyron* and three from *H. przewalskii* (Robson, 2001: fig. 2). The latter three and sect. 9a. *Concinna* (related to *H. ascyron* subsp. *gebleri*) were treated in Part 4(1), this part is concerned with most of sect. 9. *Hypericum* (related to *H. ascyron* subsp. *ascyron*), and Part 4(3) will contain the remainder of Sect. 9 and the American sect. 9b. *Graveolentia* (related to *H. ascyron* subsp. *pyramidatum*).

### Sect. 9. *Hypericum*

#### Subdivision

Sect. 9. *Hypericum*, which is distributed from the Azores through Europe, the Mediterranean and western and northern Asia to China, Japan and western North America, comprises two subsections:

subject. 1. *Hypericum* and subject. 2. *Erecta*. The latter is almost confined to Japan, Taiwan and eastern China, whereas subject. *Hypericum* is widespread. In subject. *Hypericum* the stems are almost always lined and the base is stoloniferous, whereas in subject. *Erecta* the stems are terete and the base is woody or fibrous. Subject. *Hypericum*, in turn, can be divided into two series: series 1. *Hypericum* (with stem lines persistent and bearing dark glands) and series 2. *Senanensia* (with stem lines weak and eglandular or absent). Series 1 is widespread, series 2 confined to northern and central Japan.

#### Characters and variation

The two subsections of sect. *Hypericum* each have primitive characters that clearly relate them individually to *H. ascyron* subject. *ascyron*, but neither can be derived from the other. Thus the primitive species of subject. *Hypericum* (*H. maculatum*), along with the closely related *H. undulatum* and *H. tetrapterum*, has markedly 4-lined stem internodes, like *H. ascyron*; but the group as a whole is advanced in that the stem lines are glandiferous and the stems have creeping bases (i.e. they are stoloniferous). In contrast, the primitive

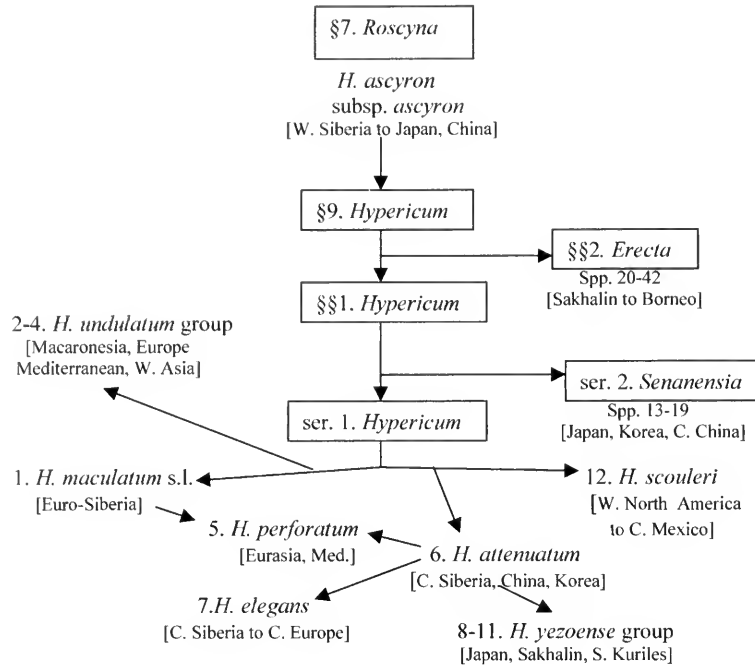


Fig. 1 Section 9. Relationships and distribution.

taxa of subsect. *Erecta* (*H. yamamotoi* var. *riparium* Y. Kimura and *H. ovalifolium* Koidz.) have a branching woody stem base, like *H. ascyron*, but the stem internodes are slightly 2-lined or terete, the lines being eglandular. Also, the leaves in the *H. yamamotoi* and *H. erectum* groups of subsect. *Erecta* are frequently triangular-lanceolate, like those of *H. ascyron* subsp. *ascyron*, whereas a comparable form of leaf occurs only apomorphically in subsect. *Hypericum*, i.e. only in some of the more advanced species.

#### Distribution and evolution (Fig. 1)

The distributions of subsect. 1 series 2 and subsect. 2 are wholly north and east Asian, but that of subsect. 1 series 1 extends from the Azores to Mexico. The latter series comprises a western group, based in south-eastern Europe on 1. *H. maculatum* and extending west to the Azores and east to central Siberia, and an eastern group with two centres, one in eastern Siberia and the other in western North America. The North American centre consists only of 12. *H. scouleri*, which has its most primitive form in the south-eastern United States and shows trends northward to central British Columbia and southward to Michoacán in central Mexico. The basic species of the east Asian centre is 6. *H. attenuatum*, which has its most primitive form in eastern Siberia and a range that extends westward to the Altai region and southward to south-central China. The basic species of the derivative Japanese *H. yezoense* group (*H. tosaense*) is morphologically very near *H. attenuatum* and has been included in it (Kitamura & Murati, 1962), but in my opinion it is specifically distinct. *Hypericum elegans*, a western derivative of *H. attenuatum*, extends the distribution of the eastern group as far as western Germany.

The remaining species in series 1, 5. *H. perforatum*, does not fit easily into the above scheme. Morphologically it is intermediate between 1. *H. maculatum* and 6. *H. attenuatum*, and the areas of these species almost overlap in western Siberia (Maps 1, 16). Each of them is diploid ( $2n=16$ ), whereas *H. perforatum* is tetraploid ( $2n=32$ ); so it is conceivable that *H. perforatum* is an allotetraploid

derivative of a cross between them, especially as *H. perforatum* behaves cytologically as a hybrid (see p. 64). However, the nearest subspecies of *H. maculatum* to *H. perforatum* morphologically is not the one that occurs in Siberia today (subsp. *maculatum*) but subsp. *immaculatum*, which is now confined to the Balkan region. The hypothesis must therefore be that subsp. *immaculatum* at some time was present in Siberia, where it hybridized with *H. attenuatum*. The chromosomes of the resultant diploid hybrid then doubled, giving rise to an allotetraploid species that is partially fertile (see p. 88). Subsequently the area of *H. maculatum* subsp. *immaculatum* became greatly reduced; but that of subsp. *maculatum*, which is apomorphic to it and thus a likely derivative of it, extended eastward into Siberia.

#### Sect. 9. *Hypericum* subsect. 1. *Hypericum* series 1. *Hypericum*

##### *Characters and variation* (Figs 2, 3)

**MORPHOLOGY.** The two main divisions of series *Hypericum* could be separated on whether or not the subsidiary stem lines were present, i.e. whether the stem internodes were 4- or 2-lined, were it not for (a) 4. *H. triquetrifolium*, which has 'lost' them in the 4-lined group and (b) 5. *H. perforatum*, which, as has been explained, appears to be a hybrid with one parent from each group. Figure 3 shows that the 4-lined state is primitive in this series, as indeed it is in the whole genus. Intermediate states occur in hybrids of *H. perforatum*, but not in the species.

The laminar leaf glands are absent or more rarely sparse in 1. *H. maculatum* but more or less dense in the more advanced species. They are all or mostly pale except in 6. *H. attenuatum*, in which black glands often predominate.

The sepals are broad with a rounded apex in 1. *H. maculatum* and usually in 12. *H. scouleri*, as they are in the ancestral (?) *H. ascyron* subsp. *ascyron* (sect. 7. *Roscyna*). In all the other species they are acute and narrow (Spp. 2, 3 and 5) or acute and broad (6. *H.*



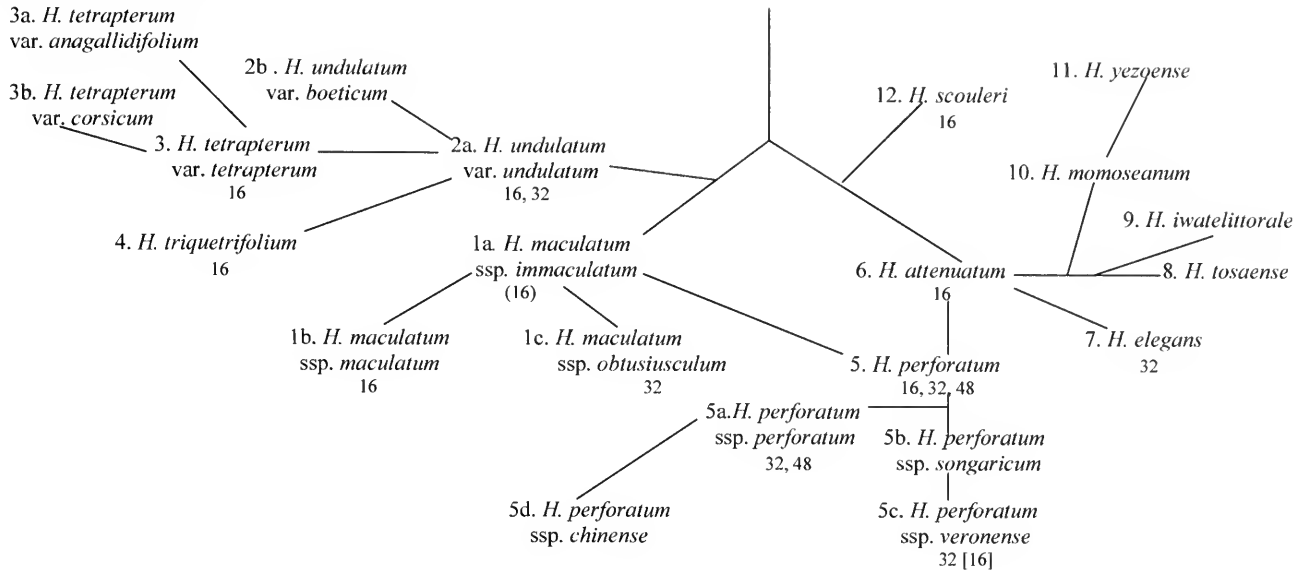


Fig. 2 Section 9, subject. 1, series 1. Relationships and 2n chromosome numbers.

*attenuatum*) or acuminate and broad (Japanese spp.) except 4. *H. triquetrifolium*, in which the more reduced forms have (secondarily) small rounded sepals. The apex is entire except in 2c. *H. maculatum* subsp. *obtusiusculum* and *H. × desetangii* (2. *H. maculatum* × 5. *H. perforatum*), where it is usually eroded-denticulate.

The petal laminar glands are primitively pale and linear to striiform (1a. *H. maculatum* subsp. *immaculatum*, 12. *H. scouleri*), as in sect. 7. *Roscyne*, and evolve in two directions: (a) the lines become interrupted, first toward the apex (Spp. 1b, 5, 6, 8–10, 12) and then throughout the lamina (Spp. 2–4, 7, 11) and sometimes disappear altogether (Spp. 2, 3); (b) some pale glands become black, but these usually remain in the minority except in 6. *H. attenuatum* and usually 1b. *H. maculatum* subsp. *maculatum*, where all glands become black.

The vittae of the ovary and capsule are primitively all narrow and longitudinal, as in sect. 7. *Roscyne*; but the lateral vittae become oblique, in 4. *H. triquetrifolium* only sporadically, in others totally (Spp. 6–11). In 5. *H. perforatum* alone the oblique lateral vittae first become enlarged and then break up to form oval to globose vesicles.

CYTOLOGY. Although the diploid chromosome number in sect. 7. *Roscyne* is usually 18, it ranges from 22 to 16 (Robson, 2001); and 2n=16 appears to be the basic number for the whole of sect. 9. *Hypericum*. In series 1. *Hypericum* (Fig. 2), Spp. 1b, 2–4, 6 and 12 are diploid, Sp. 1a has been shown by indirect evidence from morphology and hybrids to be diploid, and the Japanese species (8–11) seem likely to be so. Tetraploidy (2n=32) has been recorded in 2. *H. undulatum* but without reference to morphology, in 1c. *H. maculatum* subsp. *obtusiusculum*, which appears to be an autotetraploid of 1a. subsp. *immaculatum*, in 7. *H. elegans*, which is possibly a direct derivative of 6. *H. attenuatum*, and in 5. *H. perforatum*, which is apparently an allotetraploid from the cross 1a. *H. maculatum* subsp. *immaculatum* × 6. *H. attenuatum*. Hexaploids (2n=48) have also been recorded in *H. perforatum*, presumably resulting from the fertilization of an unreduced (apomictic) ovule by a normally reduced pollen grain (see p. 88). The diploids reported in this species must be dihaploids resulting from polyhaploidy, i.e. the secondary occurrence of the diploid number as a result of the development of an unfertilized reduced ovule, which is known to

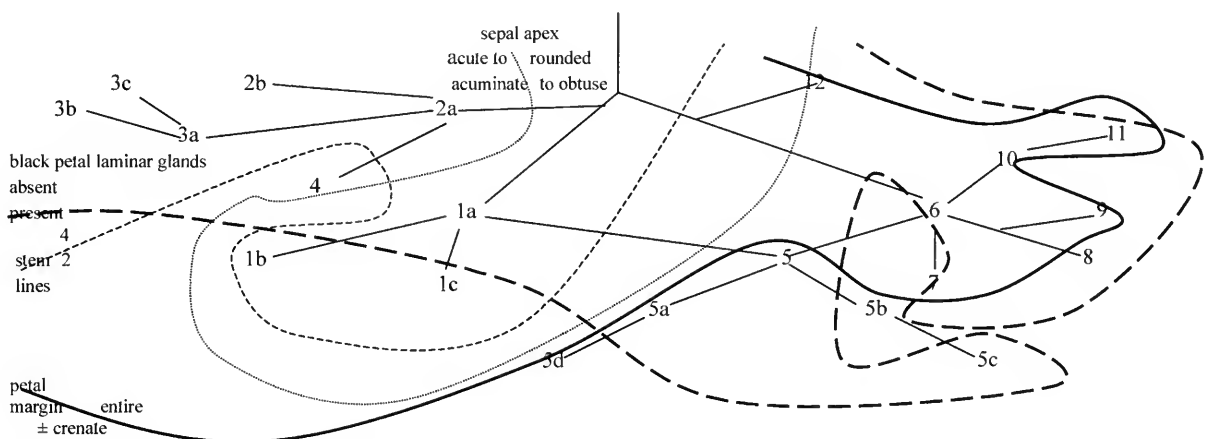


Fig. 3 Section 9, subject. 1, series 1. Limits of some characters.

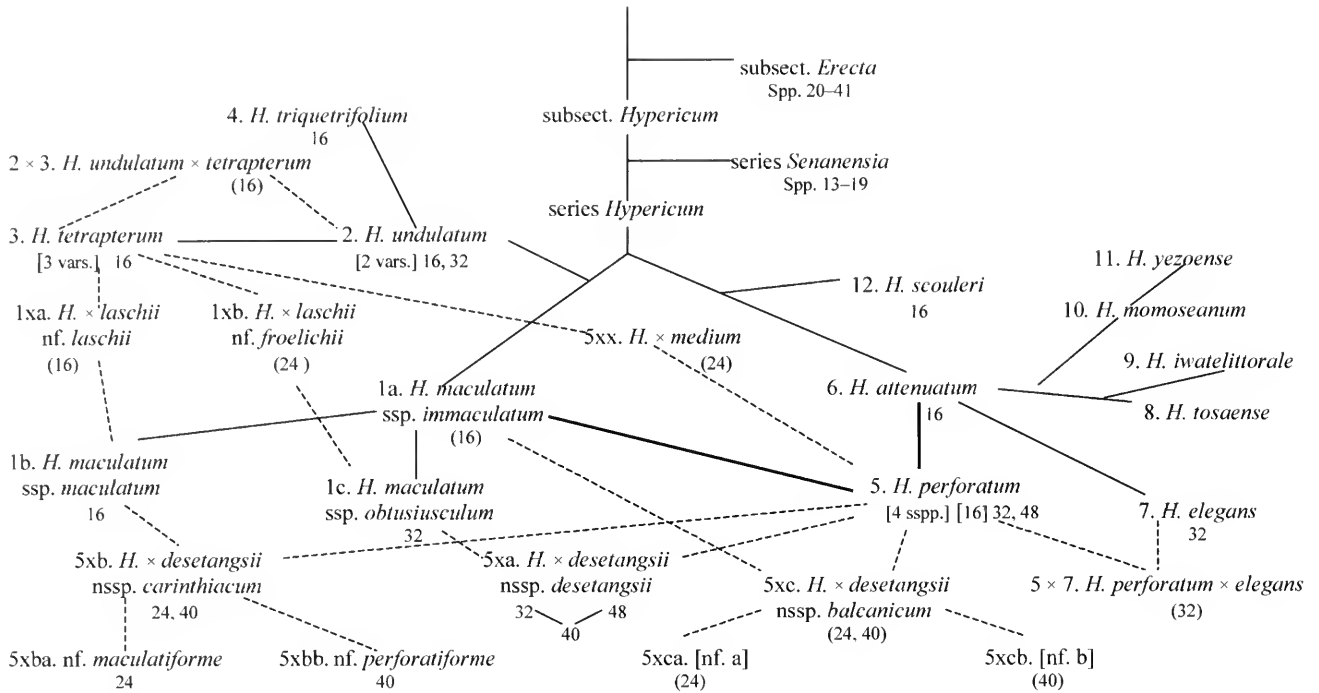


Fig. 4 Section 9, subject. 1, series 1. Relationships (—) and hybrids (---), with  $2n$  chromosome numbers (unverified numbers in parenthesis).

occur in allopolyploids (see p. 88 and Robson, 1998). The report of a triploid number ( $n=12$ ) by Gagnieu & Wilhelm (1965) is likely to be an error for  $n=16$ . A hypoploid number ( $2n=8$ ,  $n=4$ ) has been reported for 2. *H. undulatum* (Guillén et al., 1997), a species which is normally diploid ( $2n=16$ ) or tetraploid ( $2n=32$ ).

#### Hybrids (Fig. 4)

Natural hybridization is relatively rare in *Hypericum* (Robson, 1981: 167, fig. 55) except in series 1. *Hypericum*, where it is quite common largely on account of the floral biology of *H. perforatum* (see p. 88). This species behaves as a hybrid (high pollen sterility, lagging chromosomes at metaphase, 97% apomictic ovule development with pseudogamy). When crossed with diploids, its reduced pollen grains and ovules ( $n=16$ ) produce triploid ( $2n=24$ ) hybrids, while the fertilization of its unreduced ovules by a gamete of a diploid species produces pentaploid ( $2n=40$ ) hybrids. With tetraploids such as *H. maculatum* subsp. *obtusiusculum*, of course, the hybrids are tetraploid ( $2n=32$ ). Figure 4 (modified and expanded from Robson, 1981: fig. 55) shows all the hybrids that have been reported or inferred from series 1. *Hypericum*. The status of some of the hybrids has been inferred from intermediate morphology, while several chromosome numbers have been inferred from those of the parents.

Of the hybrids not involving *H. perforatum*, 2. *H. undulatum*  $\times$  4. *H. tetrapterum*, which is known only from plants with intermediate morphology, appears to be rare. As the tetraploid form of *H. undulatum* has been reported only once, the hybrid is likely to be diploid. 1. *H. maculatum*  $\times$  4. *H. tetrapterum* (*H. x laschii*) was described as intermediate between 1a. subsp. *maculatum* and *tetrapterum* and is known from the area of that subspecies only. It too is therefore likely to be diploid. On the other hand, the cross with (the tetraploid) 1c. subsp. *obtusiusculum*, described by Fröhlich (1911) and named here *H. x laschii* nothoforma *froelichii*, should prove to be triploid.

The hybrids involving *H. perforatum* can be triploid to hexaploid,

depending on the ploidy of the other parent and of the gametes of *H. perforatum* itself. Aneuploid numbers occur in experimental crosses (e.g. those of Lihová et al., 2000), but they have not been reported from wild populations. Noack (1939) found that, in hybrids involving diploids, the triploids were intermediate between the parents whereas the pentaploids could not be distinguished from pure *H. perforatum*. Mártonfi et al. (1996b), however, found that a pentaploid population of *H. maculatum* subsp. *maculatum*  $\times$  *perforatum* from Slovakia did have some intermediate characters as well as the pentaploid number ( $2n=40$ ).

Tetraploid crosses with *H. perforatum* yield intermediates, at least in the first generation. Thus a possible hybrid, 5. *H. perforatum*  $\times$  7. *H. elegans*, is recorded here on the basis of a morphologically intermediate specimen from the Ukraine; and the cross *H. maculatum* subsp. *obtusiusculum*  $\times$  *perforatum* also yields intermediate progeny in the  $F_1$ . The relationship of the parents of this latter cross is very close, however, as subsp. *obtusiusculum* behaves cytologically and morphologically as an autotetraploid of subsp. *immaculatum*, not of subsp. *maculatum*, as I first thought (Robson, 1956; 1958a, 1975). This consanguinity facilitates back-crossing and results in the eventual occurrence of a complete series of intermediates in the wild (cf. Crackles, 1990). Counts of  $2n=48$  and 40 for this hybrid from cultivated plants (Robson, 1956; Robson & Adams, 1968) presumably result respectively from a cross with an unreduced *perforatum* gamete ( $32 + 16$ ) and a backcross of this hybrid to either a 'normal' hybrid or to *H. perforatum* itself ( $24 + 16$ ).

The species 3. *H. tetrapterum* is diploid only, so its cross with *H. perforatum* (*H. x medium*), described as morphologically intermediate, is likely to be triploid; but the cross 1. *H. maculatum*  $\times$  5. *H. perforatum* (*H. x desetangsii*) is much more complicated. The hybrid with the tetraploid 1c. *maculatum* subsp. *obtusiusculum* (5xa. *H. x desetangsii* nothosubsp. *desetangsii*) is also usually tetraploid and has been considered above. That with the diploid 1a. *maculatum* subsp. *immaculatum* (5xc. *H. x desetangsii* nothosubsp. *balcanicum*) and 1b. *maculatum* subsp. *maculatum* (5xb. *H. x*

*desetangsii* nothosubsp. *carinthiacum*) occurs in two forms depending on the sex of the gametes. With *H. maculatum* pollen, triploids ( $2n=24$ ) are produced (e.g. 5xb nothoforma *maculatiforme*) whereas with *perforatum* pollen, the progeny are pentaploid ( $2n=40$ ) (e.g. 5xbb nothoforma *perforatiforme*). The corresponding hybrids with 1a. *H. maculatum* subsp. *immaculatum* have not yet been recognized or named.

### Distribution and evolution (Fig. 5)

As has already been explained (p. 61), sect. *Hypericum* is most closely related to *H. ascyron* subsp. *ascyron* (Sect. 7. *Roscyna*), and subsect. *Hypericum* is distributed over most of the Palearctic Region from the Azores to Mexico. The distribution of series *Hypericum* occupies most of this area except south-eastern China and south Japan. It is divided into two groups (i) mainly western and (ii) mainly eastern.

Group (i), which extends from the Azores to central Siberia, includes the nearest taxon morphologically to series 2, 1a. *H. maculatum* subsp. *immaculatum*, which is restricted to the central Balkan region but differs little from the north Japanese *H. kamtschaticum* var. *pibairense* Miyabe & Y. Kimura (series 2), mainly in having constantly 4-lined gland-bearing stem internodes. Subsp. *immaculatum* appears to have given rise northward (group iii) to two subspecies: (a) by vicariance to 1b. subsp. *maculatum* (Atlantic coast to central Siberia) and (b) by autotetraploidy to 1c. subsp. *obtusiusculum* (= *H. dubium* Leers) (north-west Europe). Southward there is a derivative (group iv) that divided into a western (damp habitat) subgroup (Spp. 2–3) and an eastern (dry habitat) one (Sp. 4). In group (iii) the stems are 4-lined, the leaves broad and plane and the sepals broad and rounded (entire or not); in group (iv) the stem lines become broad (3. *H. tetrapterum*) or the subsidiary pair disappear altogether (4. *H. triquetrifolium*), the leaves become undulate (2a. *H. undulatum* var. *undulatum*) and narrow (4. *H. triquetrifolium*) or remain broad but revert to plane (2b. *H. undulatum* var. *boeticum*, 3. *H. tetrapterum*), whilst the sepals become narrow and acute but, in *H. triquetrifolium*, revert to rounded when small.

Although a Portuguese specimen of *H. undulatum* was observed to have a habit and narrow leaves that approach those of *H. triquetrifolium*, these characters would seem best interpreted as a parallel development within *H. undulatum*. The first division in group (iv) would then have been between the western Mediterranean/Atlantic wet-habitat *H. undulatum* and the east Mediterranean/W. Asian dry habitat *H. triquetrifolium*. The species 3. *H. tetrapterum*, with broad stem lines, broader plane leaves and a more congested inflorescence of smaller flowers subsequently evolved (in the south-western Mediterranean?) from *H. undulatum* and spread north as far as Scotland, Denmark and southern Sweden, north-east to Poland, Latvia and the western Ukraine, and east to Iran.

Group (ii) divides immediately into an eastern, Old World subgroup (v) and a western, West American subgroup (vi), both of which start with a single species, respectively the eastern Siberian and Chinese 6. *H. attenuatum* and the British Columbia to Mexican 12. *H. scouleri*. Whilst none of the variation in *H. scouleri* has resulted in speciation, *H. attenuatum* has speciated eastward and westward. To the west it gave rise to 7. *H. elegans*, which inhabits steppe regions as far into Europe as south Germany (Saxony, with isolated stations further west). Eastward there is a group of species in Japan of which the two southern, 8. *H. tosaense* (Shikoku) and 9. *H. momoseanum* (C. Honshu) have at one time been included in *H. attenuatum*. They both occur in isolated localities, as does a close relative of *H. tosaense*, 9. *H. iwateiittorale*, in northern Honshu. On the other hand, the northern relative of *H. momoseanum*, 11. *H. yezoense*, is widely spread in Hokkaido and northern Honshu and also occurs in southern Sakhalin.

As we have seen, 5. *H. perforatum* has apparently resulted from a cross between one taxon from group (iii) (1a. *H. maculatum* subsp. *immaculatum*) and one from group (v) (6. *H. attenuatum*). It was suggested that the cross occurred in western Siberia, and the present distribution and variation of *H. perforatum* supports this suggestion. Both parents have sessile herbaceous leaves, and the first division (vii) is between 5a. subsp. *perforatum*, with shortly petiolate herbaceous concolorous leaves and 5b. subsp. *songaricum*, with sessile, often subcoriaceous and discolorous leaves. Subsp. *perforatum* has

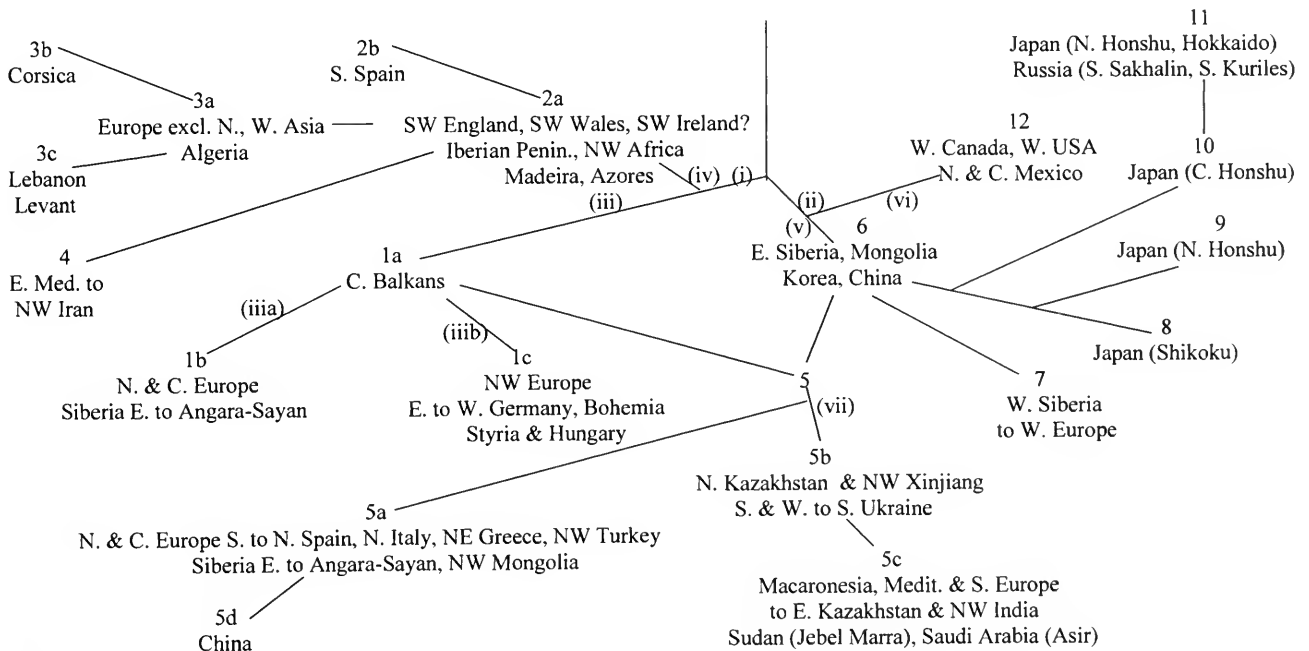


Fig. 5 Section 9, subject 1, series 1. Distribution.

spread westward throughout northern and north-western Europe and eastward into central Siberia. Beyond Siberia it recurs, morphologically scarcely altered, in China to the south-east of the Mongolian desert and steppe region and is transformed gradually south-eastward into a narrow-leaved form with long branches and congested inflorescences (subsp. *chinense*). Subsp. *songaricum* is present in the mountains of north-eastern Kazakhstan and adjacent Kyrgyzstan and Xinjiang (China); then, after a gap of over 2500 km, it recurs in southern Russia (Astrakhan, Ciscaucasus) and Krym. There, with a small transitional zone, it is replaced by 5c. subsp. *veronense*, which appears to have spread through Turkey westward into southern Europe, the Mediterranean and Macaronesia, south to Saudi Arabia and the Sudan Republic (Jebel Marra – if truly native there, see Wickens, 1976a, 1976b: 98), and east to the western Himalaya and Central Asia.

Distributions of species and species groups in series *Hypericum* show few wide disjunctions, but those that do occur are remarkable. The widest is in group (ii), where the eastern Siberian centre of variation (i.e. primitive form) of *H. attenuatum* is now separated from that of *H. scouleri* in Arizona and New Mexico by the north Pacific Ocean. This distribution would seem to support the inference by Hui-lin Li (1952) that plants with eastern Asia – western North America disjunctions are predominantly herbaceous; and it is thus also likely to support his other inference, that such disjunctions are more recent than those involving eastern North America. *Hypericum scouleri* is a member of the Arcto-Tertiary element of the Californian flora (Axelrod, 1959; Raven & Axelrod, 1978), where it occurs in the Yellow Pine (*Pinus ponderosa* Dougl. ex P. & C. Lawson) forests of the Sierra Nevada (Munz & Keck, 1959). It is possible, therefore, that *H. scouleri* has been in western North America since the Miocene.

The other notable disjunction has already been mentioned. It would appear that *H. maculatum* subsp. *immaculatum*, now confined to the central Balkans, once had a distribution extending into western (or even central) Siberia, where it crossed with *H. attenuatum* and gave rise to *H. perforatum*. Its close resemblance to *H. kamtschaticum* var. *pibairense*, of northern Japan, implies that subsp. *immaculatum* (or its immediate ancestor) migrated south-westward (without differentiating?) and eastward with minimal differentiation. It has so far not been possible to estimate the geological age of these disjunctions.

## SYSTEMATIC TREATMENT<sup>1</sup>

### Sect. 9. HYPERICUM

*Perennial herbs or very rarely suffrutices* up to 1.2 m tall, with stems erect to prostrate, glabrous, without or with dark (black or very rarely reddish) glands; branching lateral, from upper or most nodes. *Stems* 4–2-lined or -winged when young, remaining so or becoming terete, eglandular or with glands confined to the lines or not. *Leaves* opposite or abnormally 3-whorled, decussate, sessile to shortly pseudopetiolate, free, persistent; lamina entire with venation pinnate, closed, with tertiary reticulation dense to lax and obscure; laminar glands punctiform or rarely shortly striiform, equal or unequal; intramarginal glands black or occasionally also pale; ventral glands absent. *Inflorescence* 1-c. 70-flowered with branching dichasial-monochasial from 1–4 nodes, often with subsidiary branches from lower nodes; bracts and bracteoles foliar or reduced,

persistent. *Flowers* stellate, homostylous. *Sepals* 5, free or united at base, persistent, erect to recurved in fruit, with margin entire or denticulate to glandular-ciliate; veins 3–5(–7); laminar glands pale and/or dark, linear to punctiform; marginal and/or intramarginal glands dark and/or very rarely pale or rarely absent. *Petals* 5, persistent, erect but not twisting after flowering, without apiculus; margin entire to crenate or eroded-denticulate to ciliate; laminar glands linear to punctiform, pale and/or dark; marginal glands dark, immersed to ± prominent, or absent. *Stamen fascicles* '3' (i.e. united 2+2+1), persistent, with stamens totalling 20-c. 100; filaments basally united; anther gland dark or rarely amber; pollen types IV?, X. *Ovary* with 3(4) completely or almost completely axile placentae, each ∞-ovulate; styles 3(4), divergent from discrete bases; stigma narrowly capitate or narrow. *Capsule* 3(4)-valved, chartaceous, with valves longitudinally vittate or sometimes ± laterally vittate to vesiculate, pale. *Seeds* cylindrical, not carinate or appendiculate; testa scalariform-reticulate to finely foveolate.

BASIC CHROMOSOME NUMBER (X). 8; ploidy 2, 4 (rarely 3, 5, 6).

HABITAT. Various; 0–3150 m.

DISTRIBUTION. Macaronesia, Europe (except extreme north), north-west Africa, south-west Asia (mesophytic regions) east to north-west India (Uttar Pradesh), central Asia, southern Siberia, north-west Mongolia, Korea, China (except the south-east, Tibet, Qinghai and E. Xinjiang), Japan, western Canada, western U.S.A., north-west to central Mexico. Represented in many other parts of the world by *H. perforatum* as an introduction.

42 species in 2 subsections, one with 2 series (for infraspecific taxa and hybrids, see subsectional descriptions).

### Key to subsections and series of sect. 9. *Hypericum*

- 1 Rootstock herbaceous, stoloniferous; stems persistently 2–4-lined or -winged, with glands on the lines and occasionally elsewhere or eventually terete and eglandular; black laminar leaf glands few or none (sometimes numerous in Sp. 6); capsule valves sometimes with lateral oblique vesicles (subsect. 1. **Hypericum**) ..... 2  
 Rootstock woody or fibrous, not stoloniferous; stems always eventually terete, eglandular (sometimes except Sp. 39); black laminar leaf glands usually present; capsule valves always longitudinally vittate ..... subsect. 2. **Erecta**
- 2 Stems persistently 2–4-lined, lines glandiferous, at least one pair prominent (sometimes weak and eglandular in Sp. 12) .....  
 ..... series 1. **Hypericum**  
 Stems eventually terete (except Sp. 13), eglandular, lines weak ...  
 ..... series 2. **Senanensia**

Subsect. 1. **Hypericum**. Type: *H. perforatum* L.

*Stem internodes* persistently 2–4-lined or narrowly 4-winged, the lines and sometimes elsewhere black- or rarely reddish-gland-dotted (very rarely terete and often eglandular in 12. *H. scouleri*). *Leaves* with laminar glands all pale or a few (sometimes more in 6. *H. attenuatum*) black, punctiform, or absent. *Bracts and bracteoles* entire. *Petals* with laminar glands pale to black, linear to punctiform, or absent; marginal glands immersed or sessile. *Capsule valves* (i) longitudinally vittate or with (ii) dorsal and lateral vittae or (iii) vesicles with or without dorsal vittae. *Seeds* linear-foveolate to finely foveolate. Species 1–19.

<sup>1</sup>An asterisk (\*) before a locality or after a herbarium specimen symbol indicates that the specimen has not been seen by me. Type material seen by me is indicated by an exclamation mark (!).

Series 1. *Hypericum*

*Hypericum* sect. *Euhypericum* subsect. *Homotaenium* series *Attenuata*, series *Kamtschatica* pro parte quoad *H. yezoënsis*, series *Acuta*, series *Quadrangula*, series *Elegantia*, series *Crispa* Gorschk. in Shishkin & Bobrov, *Fl. URSS* 15: 236–244 (1949), nom. invalid. omnia sine descr. lat.

*Hypericum* sect. *Euhypericum* subsect. *Heterotaenium* series *Perforata* Gorschk. in Shishkin & Bobrov, *Fl. URSS* 15: 247 (1949), nom. invalid. sine descr. lat.

*Hypericum* sect. *Homotaenium* series *Quadrangula* Y. Kimura in Nakai & Honda, *Nova Fl. Jap.* 10:136 (1951). Type: *H. quadrangulum* L., nom. rejiciendum (= *H. tetrapterum* Fr.).

*Hypericum* sect. *Homotaenium* series *Crispa* Y. Kimura, loc. cit. (1951). Type: *H. crispum* L. (= *H. triquetrifolium* Turra).

*Hypericum* sect. *Homotaenium* series *Bilineata* Y. Kimura, loc. cit. (1951). Type: *H. attenuatum* Fisch. ex Choisy.

Stems persistently 2–4-lined, lines glandiferous, at least one pair prominent (sometimes weak and eglandular in Sp. 12). Spp. 1–12.

Key to sect. 9. *Hypericum* subsect. 1. *Hypericum* series 1. *Hypericum*

- 1 Stem internodes completely 4-lined or 4-winged; capsule valves longitudinally vittate (rarely interrupted to vesiculate in Sp. 4) ..... 2
- Stem internodes partially 4-lined or 2-lined; capsule valves longitudinally vittate to vesiculate ..... 9
- 2(1) Sepals unequal, apex rounded to obtuse or subacuminate, entire to eroded-denticulate; leaves with venation ± densely reticulate and laminar glands absent or scattered, relatively large (*1. maculatum*) ..... 3
- Sepals subequal to equal, apex acute to acuminate, entire; leaves with venation ± laxly reticulate; laminar glands always present, varying in size ..... 5
- 3(2) Stem internodes always with complete subsidiary lines; inflorescence branches making narrow angle (c. 30°) with stem; sepals with apex entire; petals entire, with laminar glands black and dots to short streaks or linear and pale ..... 4
- Stem internodes with complete or incomplete subsidiary lines; inflorescence branches making a broad angle (c. 50°) with stem; sepals with apex usually finely eroded-denticulate; petals usually distally unilaterally crenate, with laminar glands black, mainly lines to streaks ..... 1c. *maculatum* subsp. *obtusiusculum*
- 4(3) Sepals and petals with only pale glands; petal glands lines to streaks ..... 1a. *maculatum* subsp. *immaculatum*
- Sepals and petals with mostly black glands; petal glands dots and short streaks ..... 1b. *maculatum* subsp. *maculatum*
- 5(2) Stem internodes ± equally narrowly 4-winged; leaf margin usually crisped-undulate; inflorescence lax; flowers 12–17 mm in diam.; sepals nearly always with 3–28 laminar black glands; petals bright yellow, nearly always red-tinged dorsally (*2. undulatum*) ..... 6
- Stem internodes ± broadly 4-winged, the principal lines wider; leaf margin nearly always plane; whole inflorescence or partial inflorescences dense; flowers 10–15 mm in diam.; sepals without or rarely with 1–2 laminar glands; petals rather pale yellow, not red-tinged (*3. tetrapterum*) ..... 7
- 6(5) Petals tinged red dorsally; leaves elliptic to ovate, margin crisped-undulate; plant erect ..... 2a. *undulatum* var. *undulatum*
- Petals not tinged red; leaves broadly elliptic to orbicular, margin entire; plant erect to decumbent ..... 2b. *undulatum* var. *boeticum*

- 7(5) Inflorescence 10–c. 70-flowered from 1–4 nodes; stems erect ..... 3a. *tetrapterum* var. *tetrapterum*
- Inflorescence 1–3-flowered from terminal node; stems procumbent to ascending ..... 8
- 8(7) Leaves elliptic to orbicular, mostly 0.5 mm petiolate, margin plane; inflorescence without flowering branches ..... 3b. *tetrapterum* var. *corsicum*
- Leaves elliptic to triangular-ovate, subsessile to 0.5 mm petiolate, margin undulate; inflorescence sometimes with flowering branches from up to 5 nodes below ..... 3c. *tetrapterum* var. *anagallidifolium*
- 9(1) Leaf margin crisped-undulate, lamina usually triangular-lanceolate; stem widely branched for most of its length, forming broad pyramid; sepals 1–3 mm long ..... 4. *triquetrifolium*
- Leaf margin plane, lamina ovate or oblong or elliptic to linear; stem narrowly branched rarely below middle, forming at most narrow pyramid; sepals (2.5)3 mm or more long ..... 10
- 10(9) Stem lines (at least) with black glands, principal lines always present; petal margin usually distally black-glandular-crenate ..... 11
- Stem lines eglandular or very rarely with a few reddish glands, principal lines rarely absent (i.e. rarely terete); petal margin entire to distally black-glandular-suberentate ..... 12. *scoleri*
- 11(10) Subsidiary stem lines nearly always ± developed; sepals often eglandular-denticulate; other characters to varying degrees intermediate between 1. *H. maculatum* and 5. *H. perforatum* (see key, p. 101) ..... 5x. × *desetangii*
- Subsidiary stem lines absent; sepals entire; other characters not so intermediate ..... 12
- 12(11) Capsule valves with lateral vittae or vesicles and often dorsal vittae (*5. perforatum*) ..... 13
- Capsule valves with longitudinal vittae only ..... 16
- 13(12) Leaves (at least on main stem) sessile; petal laminar glands usually all pale ..... 14
- Leaves all petiolate; petal laminar glands pale and/or black ..... 15
- 14(13) Capsule valves with lateral vittae linear or slightly swollen overall, not interrupted; sepals finely acuminate; leaves oblong to oblong-ovate, base ± shallowly cordate-amplexicaul ..... 5b. *perforatum* subsp. *songaricum*
- Capsule valves with lateral vittae swollen at base and/or interrupted to short and irregular (vesicular); sepals acute; leaves usually narrowly triangular-lanceolate to linear or, if broader, then short (c. 5–10 mm long), base rounded to cuneate ..... 5c. *perforatum* subsp. *veronense*
- 15(13) Inflorescence and/or partial inflorescences not usually congested, branches relatively short, straight; leaves usually oblong to ovate or elliptic; at least some petal laminar glands pale ..... 5a. *perforatum* subsp. *perforatum*
- Inflorescence and/or partial inflorescences congested, branches relatively long, curved-ascending; petal laminar glands all black or absent ..... 5d. *perforatum* subsp. *chinense*
- 16(12) Sepals black-glandular-ciliate or with sessile black marginal glands ..... 7. *elegans*
- Sepals entire or with apical black gland only, without or with immersed black marginal glands ..... 17
- 17(16) Sepals and petals with pale and black laminar glands; stem often with scattered black or reddish glands; sepals acute to subacuminate ..... 6. *attenuatum*

- Sepals and petals with pale laminar glands only; stem with black glands confined to raised lines or near them; sepals acute to abruptly acuminate ..... 18
- 18(17) Leaves without black laminar glands; inner petal margin crenulate (unknown in *9. iwatelitorale*); stems usually erect, rather woody ..... 19
- Leaves usually with a few black laminar glands; inner petal margin  $\pm$  plane; stems usually  $\pm$  ascending, herbaceous ..... 20
- 19(18) Leaves all sessile, mostly elliptic or oblong-elliptic to narrowly oblong; flowers 15–18 mm in diam.; sepals 2.5–3 mm long, gradually to abruptly acuminate, intramarginal glands always present, spaced ..... 8. **tosaense**
- Leaves on lateral branches petiolulate, elliptic to oblanceolate; flowers 9–10 mm in diam.; sepals 3–4 mm long, acute to subacuminate, intramarginal glands few or absent ..... 9. **iwatelitorale**
- 20(18) Stems single, 0.25–0.65 m, erect or basally ascending; inflorescence 7–11-flowered from 2–3 nodes, usually with 1–4 flowering branches below ..... 10. **momoseanum**
- Stems usually caespitose, 0.1–0.35 m, erect to procumbent; inflorescence 3–7(–9)-flowered from 1–2 nodes, with 0–1 flowering branches below ..... 11. **yezoense**

1. ***Hypericum maculatum*** Crantz, *Stirp. austr.* 2: 64 (1763), 2nd ed. 2: 98 (1769); Allioni, *Fl. pedem.* 2: 45 (1785), 3: t. 83 f. 1 (1785) pro parte, excl. syn. *H. androsaemifolium* Vill.; Schinz & Keller, *Fl. Schweiz*, 3rd ed., 1: 358 (1909); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 538 (1911), in *Oesterr. bot. Z.* 63: 18 (1913); Thellung in *Allg. Bot. Z. Syst.* 18: 19 (1912); Hayek, *Prodr. Fl. Pen. balc.* 1: 534 (1925); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 517 pro parte, excl. f. 2004 (1925); N. Robson in *Bot. Soc. Brit. Isles Proc.* 2: 237 (1957), in op. cit. 3: 99 (1958), in Davis, *Fl. Turkey* 2: 400 (1967) in adnot., in Tutin et al., *Fl. Europ.* 2: 268 (1968); Zelený et al. in Futák & Bertová, *Fl. Slovinska* 3: 302, t. 37 f. 1 (1982); A. Ramos in *Trab. Dept. Bot. Univ. Complut. Madrid* 12: 49, t. 3 f. 1 (1983), in *Acta Bot. Malac.* 11: 167, f. 6e (1986), in Castroviejo et al., *Fl. Iberica* 3: 168 (1989); Hagemann in *Flora* 173: 112–115, tt. 12–14, 39 (1983); N. Robson & Strid in Strid, *Mtn Fl. Greece* 1: 607 (1986); N. Robson in Cullen et al., *Europ. Gdn Fl.* 4: 60 (1995); in Wisskirchen & Haeupler, *Standardliste Farn-u. Blütenpfl. Deutschl.*: 269 (1998). Type: Austria, 'alpen', 1760 (fl), *Breyñ* in Crantz 828 (BP!-lectotype, N. Robson, selected here).

Fig. 6. Maps 1, 2.

*Perennial herb* 0.2–0.6 m tall, erect or ascending from creeping and rooting base, with stems numerous to few, initially unbranched below inflorescence, later branched above for c. 2/3 of their length. *Stems* 4-lined, the subsidiary ones (decurent between leaves) often less prominent or even partially absent<sup>2</sup>, usually with black glands on the lines; internodes 10–50 mm, shorter than to exceeding leaves. *Leaves* sessile; lamina 15–40 × 10–20 mm, broadly to narrowly elliptic, paler beneath, chartaceous; apex rounded, margin plane, base rounded; venation: 3(2) pairs of main laterals from lower quarter to base of midrib, tertiary reticulation dense; laminar glands absent or rarely pale, scattered, sometimes also black, few, punctiform; intramarginal glands black,  $\pm$  close, irregular in size. *Inflorescence* (2–)3-c. 15-flowered, from 1–3 nodes, with flowering branches narrowly or curved ascending from up to 5 nodes, the whole cylindrical to broadly pyramidal or subcorymbiform; pedicels 1.5–4 mm; bracts and bracteoles up to 5 mm long, narrowly triangular-ovate to narrowly

elliptic, entire. *Flowers* (15–)20–25(–35) mm in diam., stellate to reflexed; buds broadly ellipsoid, rounded to obtuse. *Sepals* 5,  $\pm$  unequal, 3.5–4.5(–5) × 2–2.7(–3) mm, broadly elliptic to broadly ovate or  $\pm$  broadly oblong, rounded to obtuse or subacuminate (varying in same flower), entire to eroded-denticulate, erect to recurved in bud, recurved in fruit; veins 5(–7), not or slightly branched; laminar glands pale and sometimes also black, punctiform and sometimes striiform; intramarginal glands pale or occasionally black or often absent. *Petals* 5, golden yellow, not tinged red in bud, (8–)10–15 × 4–7.5 mm, c. 3 × sepals, broadly elliptic to obovate or more rarely symmetrically oblanceolate, distally crenate or entire; laminar glands pale and/or black, punctiform and sometimes proximally striiform to linear (in subsp. *immaculatum* almost all linear); intramarginal glands few, distal or usually absent. *Stamens* 50–80(–100), '3'-fascicled, longest 7–10 mm, c. 0.65–0.9 × petals; anther gland black. *Ovary* 3-locular, 2–4 × 1.5–2.5 mm,  $\pm$  broadly ovoid to ovoid-ellipsoid; styles 3, free, 3–4 mm, 1–1.5(–2) × ovary, rather narrowly spreading; stigmas narrowly capitate. *Capsule* 6–10 × 4–6 mm, c. 2–2.5 × sepals, ovoid-ellipsoid to  $\pm$  broadly ovoid; valves with longitudinal vittae, linear to striiform. *Seeds* dark brown, 0.8–1.2 mm, cylindrical, not carinate or appendiculate; testa finely linear-foveolate. 2n=16, 32 (see under subspecies).

In usually rather damp habitats – woods, scrub, grassland, moorland, meadows and ditches; 0 (W. Scotland) – 2650 m (SE Switzerland).

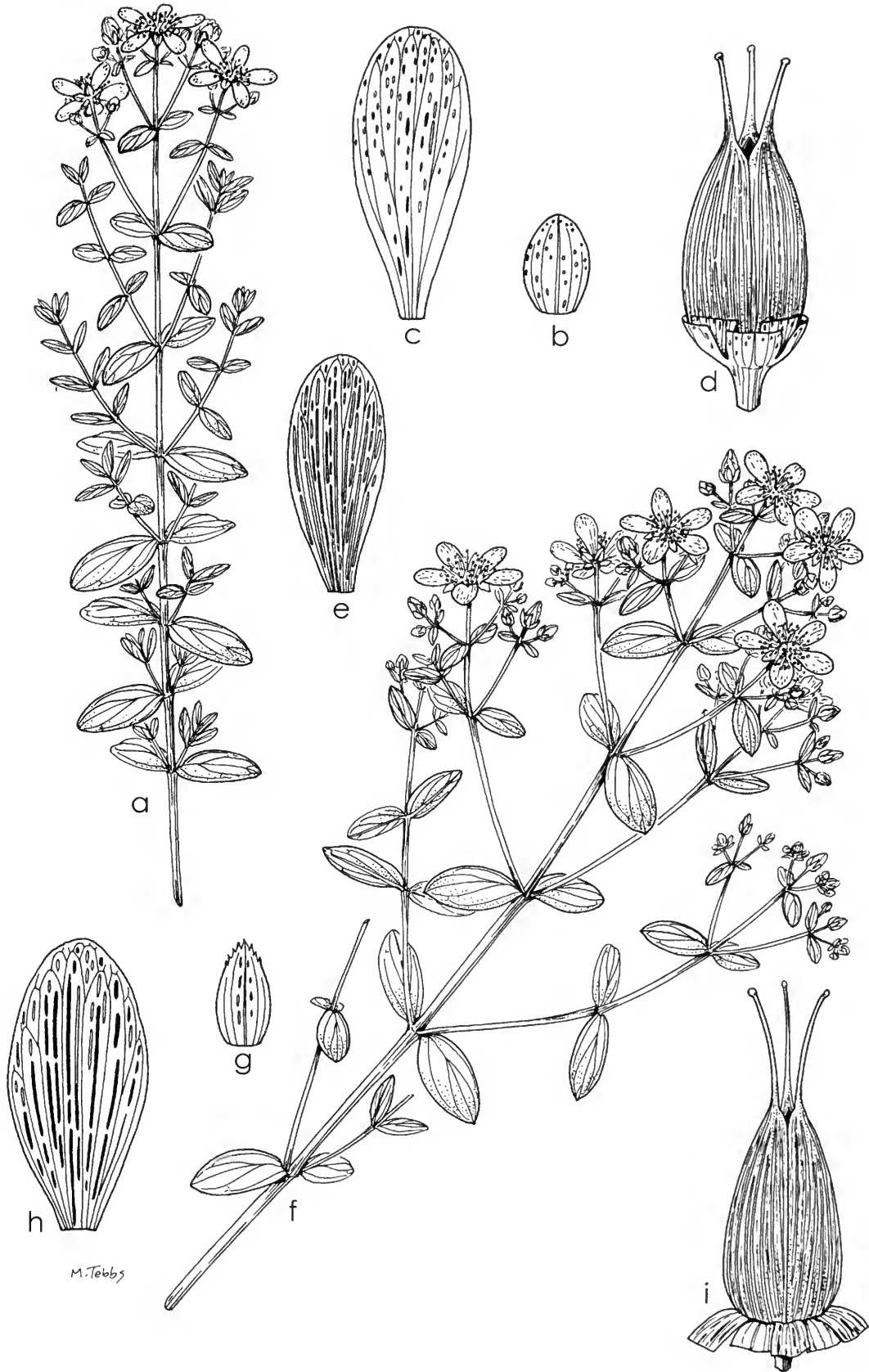
Europe from Scotland (Ross-shire), northern Scandinavia (to Hinnoya (Lofoten Is.), 68°22' N), northern European Russia and western Siberia, south to northern Spain, northern Italy, northern Greece and the central Ukraine, and east to south-western Siberia (R. Ob) with eastern outlier near Krasnoyarsk). Introduced into Canada (British Columbia).

*Hypericum maculatum* is the most primitive species in the (mainly European) series *Hypericum*, its nearest relative in the (eastern) series *Senanensia* (Spp. 13–19) being 13. *H. kamtschaticum* var. *pihirensis* from Hokkaido (N. Japan). It comprises two diploid subspecies (subsp. *maculatum* and *immaculatum*) and a tetraploid subspecies (subsp. *obtusiusculum*) that, from chromosome morphology and synthesis by colchicine doubling of subsp. *maculatum* (Robson, 1958a), would appear to be autotetraploid. The latter has sometimes been treated as a species (*H. dubium* Leers); but (i) the autotetraploidy and (ii) the occasional difficulty in assigning a plant to one or other taxon indicate that subspecies is the most appropriate rank, *pace* Mártonfi et al. (1999) (see p. 75).

The diploid subspecies of *H. maculatum* comprise two populations overlapping in distribution. One (subsp. *immaculatum*) is confined to the south Balkans and lacks black glands on the petals, the pale ones being linear and the leaves usually pale-gland-dotted. Its chromosome number has not yet been counted, but morphologically it is very similar to subsp. *maculatum*, less so to subsp. *obtusiusculum*. The other population (subsp. *maculatum*), which is widespread and slightly overlaps in area that of subsp. *immaculatum* in a zone from Bosnia to southern Bulgaria, has petals with punctiform to shortly striiform black glands, the pale (punctiform) glands being few, and the leaves usually lack pale gland dots.

1a. ***Hypericum maculatum*** subsp. ***immaculatum*** (Murb.) A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 547, f. 8 (1911), in *Oesterr. Bot. Z.* 63: 18 (1913), in *Mitt. Naturwiss. Vereines Steiermark* 51: 223 (1915); Hayek, *Prodr.*

<sup>2</sup> Partial or complete absence of subsidiary lines may possibly indicate hybridization with *H. perforatum* (cf. *H. × desetangii*, p. 75).



**Fig. 6** A. *H. maculatum* subsp. *maculatum*: (a) habit; (b) sepal; (c) petal; (d) capsule. B. *H. maculatum* subsp. *immaculatum*: (e) petal. C. *H. maculatum* subsp. *obtusiusculum*: (f) habit; (g) sepal; (h) petal; (i) capsule (a, f  $\times 2/3$ ; rest  $\times 4$ ). A. (a) *Duvigneaud 77*; (b, c) *Meinertzhagen s.n.*; (d) *Lacaita 6402*.



*Fl. Pen. balc.* 1: 534 (1925); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 518 (1925); Stjep.-Vesel. in Josifović, *Fl. Srbije* 3: 116 (1972). Type as for *H. quadrangulum* var. *immaculatum* Murb.

Fig. 6, Map 1.

*H. quadrangulum* var. *immaculatum* Murb. in *Acta Univ. Lund.* 27(5): 152 (1891); Beck in *Ann. K. K. Naturhist. Hofmus.* 10: 182 (1895). Type: Bosnia, Hercegovina, Velež planina, c. 1500 m, 27 July 1889, Murbeck s.n. (LD!-lectotype, selected here).

*H. quadrangulum* subsp. *immaculatum* (Murb.) Wettst., *Beitr. Fl. Alban.*: 36 (1892). Type as for *H. quadrangulum* var. *immaculatum* Murb.

*H. immaculatum* (Murb.) Vierh. in *Mitt. Naturwiss. Vereins Univ. Wien* II, 4: 62 (1906), *Aufz. Simony Pfl.*: 27 (1906).

*H. maculatum* subsp. *immaculatum* var. *punctatum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math. Naturwiss. Kl.* 120(1): 549 (1911). Type: not seen, no specimen cited.

*H. maculatum* subsp. *immaculatum* var. *epunctatum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 549 (1911). Type: not seen, no specimen cited.

*H. maculatum* var. *immaculatum* (Murb.) Guşul. & Nyár. in *Sävul., Fl. R. P. Roman.* 4: 33 (1956); Stoj., Stef. & Kitanov, *Fl. Bulg.* 2: 721 (1967); Jordanov & Kož in Jordanov, *Fl. R. P. Bulg.* 4: 260 (1970); Robson & Strid in Strid, *Mtn Fl. Greece* 1: 608 (1986); N. Robson in Cullen et al., *Europ. Gdn Fl.* 4: 60 (1995), in Wisskirchen & Haeupler, *Standardliste Farn-u. Blütenpfl. Deutschl.*: 269 (1998). Type as for *H. quadrangulum* var. *immaculatum* Murb.

*H. fallax* subsp. *immaculatum* (Murb.) O. Schwarz in *Drudea* 5: 63 (1965).

*Stems* always with complete subsidiary lines. *Leaves* with densely reticulate tertiary venation; laminar gland dots pale, usually  $\pm$  dense, occasionally with a few black. *Inflorescence* branches narrowly

ascending, making an angle of c. 30° with stem. *Flowers* 15–35 mm in diam. *Sepals* broadly ovate, rounded to obtuse or somewhat acute, entire or minutely denticulate; laminar glands pale, striiform and punctiform. *Petals* entire, without or rarely with 1–3 black marginal glands; laminar glands pale, linear to striiform. *Styles* equalling ovary.  $2n=16?$  (see p. 63)

Subalpine meadows; (500-)1000-c. 2200 m.

Southern Romania (Carpathians), western and southern Bulgaria, northern Greece, Makedhonia, southern Serbia, Bosnia, Montenegro, Kosovo.

**ROMANIA.** Guşuleac & Nyárady (1956: 33) record 'var'. *immaculatum* from SE Transylvania (Odorhei, Codlea and Sibiu regions).

**BULGARIA.** **Mikhaylovgrad:** Predbalkan, Ostabhang des Midshur [Midzor], 4 September 1958 (fl), *K. Meyer* 1140 (JE). **Sofia:** Cherni Vrúkh [Mt Vitoša], c. 1440 m, 23 July 1952 (fl), *Vyhodčevski* s.n. (H). **Blagoevgrad:** Rila Planina, in valle Ristriza, c. 1000–2000 m, 20 August 1907 (fl), *Schneider & Bergmann* 878 (BM, K); Pirin, above Bansko, above L. Okoto, 2130 m, 27 July 1993 (fl), *Jury* 12071 (BM, RNG\*); Rhodopen, Snežanka, 1900 m, 8 October 1958 (fr), *K. Meyer* 1985 (JE).

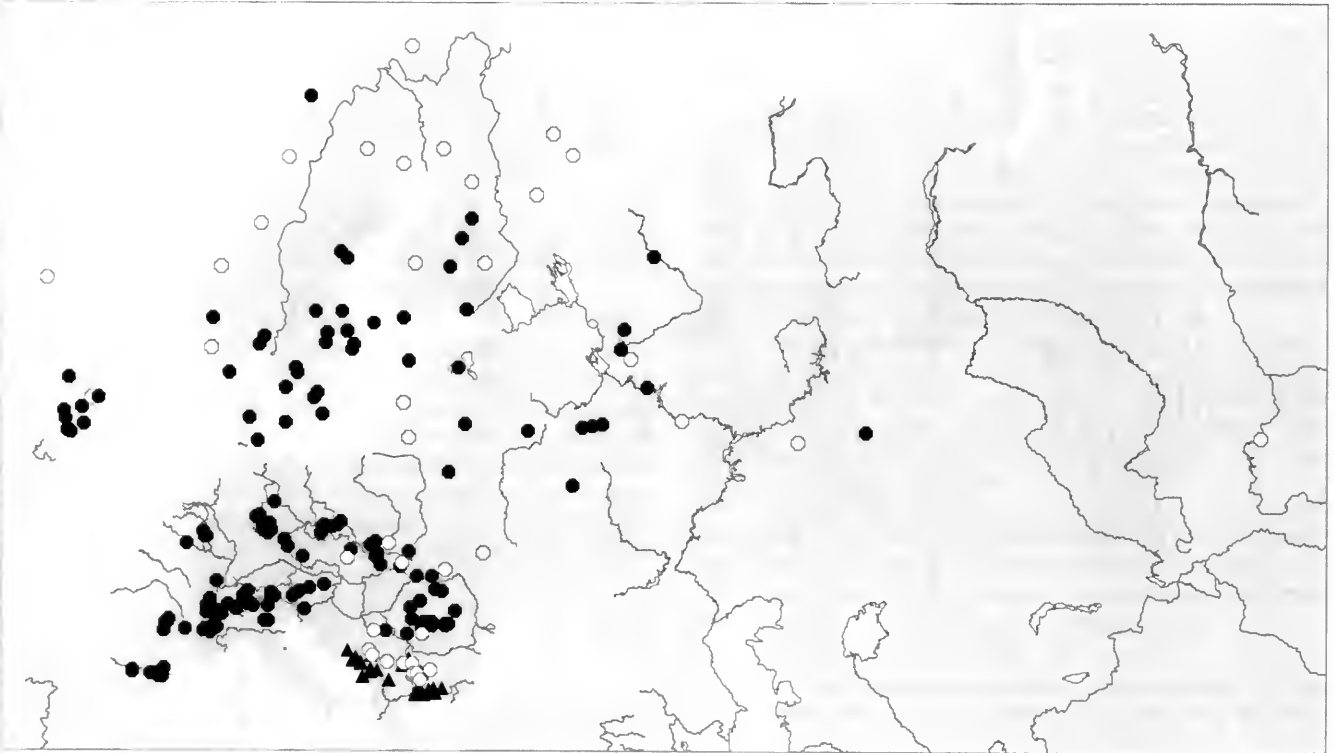
**GREECE.** **Makedhonia:** Drama, in monte Tsalakou ad septentriones ditionis 'Elatia', 1800 m, 18 August 1978 (fl), *Greuter* 16532 (BM, C); Serron, Mt. Vrontous, NE of summit, 1600 m, 27 July 1981 (fl), *Farsakoglou, Franzén & Strid* 19538 (C).

**MAKHEDONIA.** Šar Mtns, Mt. Scardos, 2000 m, 29 May 1983 (o. fr), *McClintock* s.n. (BM).

**SERBIA.** Niš: ad [R.]Vlasina, July 1895 (fl), *Adamovič* s.n. (K). **Kosovo:** Bertiscus, in valle rivuli Dočanska Bistrica, 1200–1300 m, 17–19 July 1933 (fl), *Rechinger f. & Scheffer* 1338 (BM).

**BOSNIA.** Sarajevo, Trebevic, 1600 m, 30 June 1931 (fl), *Gilliat-Smith* 2922 (K); Velež Planina, 5 July 1912, *Sagorski* s.n. (JE).

**MONTENEGRO.** Vasovavići [Vasojevički], sub Varda, 19 July 1898 (fl), *Baldacci* It. Alban. VI 181 (BM, K); prope monast. Piva, July 1905, *Rohlena* s.n. (JE).



**Map 1** 1. *H. maculatum*. a. subsp. *immaculatum* ▲; b. subsp. *maculatum* ●; other records ○. Widespread in Germany, but the records do not differentiate subspecies.



Of the two diploid subspecies of *H. maculatum*, subsp. *immaculatum* would seem to be the more primitive and to constitute a relict Balkan population that has given rise to both subsp. *maculatum* and (by autotetraploidy) to subsp. *obtusiusculum*. It is also the nearest taxon morphologically to the *H. tetrapterum* group (Spp. 2–4) and would appear to be one parent of the allotetraploid 5. *H. perforatum*. The linear pale petal glands and usually glandular-punctate leaves both lead to the above conclusions, as do the punctate leaves and linear to striiform petal glands in *H. perforatum* (q.v.). A sheet from Greece (Makedonia, Drama, Mt. Falakron, *Stamatiadou* 10131 (C)), with one plant with characters of subsp. *maculatum* among four plants of subsp. *immaculatum*, may indicate an independent development of punctate black laminar glands in the sepals and petals.

#### 1b. *Hypericum maculatum* subsp. *maculatum*

Fig. 6, Map 1.

- H. fallax* Grimm in *Nova Acta Phys.-Med. Acad. Caes. Nat. Cur.* **3**, App.: 362 (1767); O. Schwarz in *Drudea* **5**: 62 (1965). Types: Germany, Sachsen, Eisenach, vor Winterstein, Grimm s.n. (JE?-syntype), auf der Schlotwiese, Grimm s.n. (JE?-syntype), unten dem Inselberg, Grimm s.n. (JE?-syntype), um Mosbach, Grimm s.n. (JE?-syntype). Syntypes not found in JE.
- H. delphinense* Vill., *Prosp. Hist. pl. Dauphiné*: 44 (1779), *Fl. delph.*: 81 (1785), *Hist. pl. Dauphiné* **1**: 281, 294, t. 44 (1786), **3**: 497 (1789). Type: France, Isère, Oisans [Oisans], La Moncherolle, 1789 (fl), Villars MNHGr 1837. 28503 (GRM-photograph!-lectotype, selected here).
- H. tetragonum* Fr., *Fl. hall.*: 124 (1818). Type: Sweden, Halland, 'copiose in pratis, aliud in Suecia non reperitur', Fries s.n. (UPS-holotype). Fries rejected the name *H. dubium* for his plant.
- H. dubium* sensu Mauri, *Roman. pl. cent. xiii*: 27 (1820).
- H. quadrangulum* var. [γ] sensu Choisy, *Prodr. monogr. Hypéric.*: 47 (1821).
- H. quadrangulum* sensu Fr., *Novit. fl. suec.*: 94 (1823); Spach, *Hist. nat. vég.*, Phan. **5**: 386 (1836), in *Ann. Sci. Nat. Bot.* **5**: 357 (1836); Lamotte in *Bull. Soc. Bot. Fr.* **21**: 122 (1874); Lange in Willk. & Lange, *Prodr. fl. hispan.* **3**: 591 (1878); J.D. Hooker, *Student fl. Brit. Isles*, 3rd ed.: 73 (1884); Schinz in *Bull. Herb. Boissier* **II**, **3**: 15 (1902), in *Vierteljahrsschr. Naturf. Ges. Zürich* **49**: 231–241 (1905); Tourlet in *Bull. Soc. Bot. France* **50**: 307 (1903); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.*, 2nd ed. **21**: 179 (1925); Druce, *List Brit. pl.*, 2nd ed.: 64 (1928); Stefanoff in *God. Agr. les. Fak. Univ. Sofiya* **10**: t. 2 f. 18, t. 4 f. 30 (1932), **11**: 175, 177 (1933), **12**: 88 (1934), in *Pflanzenareale* **4**: Karten 6a, 8 (1933); Gorschkova in Shishkin & Bobrov, *Fl. U.R.S.S.* **15**: 242, t. 12 f. 3 (1949), et auct.; non L.
- H. quadrangulum* var. [γ] *maculatum* (Crantz) Choisy in DC., *Prodr.* **1**: 548 (1824). Type as for *H. maculatum* Crantz. Choisy cited '*H. maculatum* Allioni', but Allioni (1785) cited Crantz.
- H. commutatum* Nolte, *Novit. fl. holstat.*: 69 (1826); Rchb., *Fl. germ. exc.*, **II**: 837, no. 5180 (1830–1832), *Icon fl. germ. helv.* **6**: t. 345 (1844); Bonnet in *Bull. Soc. Bot. France* **25**: 276 (1878), qua hybr.; Rouy in Rouy & Fouc., *Fl. France* **3**: 335 (1896) qua hybr. Type: Germany, Schleswig-Holstein, in Duc Lauenburg prope pagum Büchen ad fl. Stechnitz, Nolte s.n. (B†-holotype). Fröhlich (1911: 547) saw Nolte's type and identified it as *H. maculatum* subsp. *typicum* var. *punctatum* (Schinz) A. Fröhl.
- H. quadrangulum* var. [b] *subcorymbosum* Schur, *Enum. pl. Transsilv.*: 132 (1866). Type as for *H. commutatum* Nolte.
- H. quadrangulum* var. [c] *macrophyllum* Schur, *Enum. pl. Transsilv.*: 132 (1866). Type: Romania, Transylvania, Kronstadt, July–August, Schur s.n. (BRNU? or LW?).
- H. umbellatum* Miel. ex Wohlf. in W.D.J. Koch, *Syn. deut. schweiz. Fl.*, 3rd ed. **1**: 429 (1892); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. I*, **120**(1): 557 (1911), pro syn.; nomen.
- H. quadrangulum* var. *genuinum* Schinz in *Bull. Herb. Boissier* **II**, **3**: 21 (1902), in *Vierteljahrsschr. Naturf. Ges. Zürich* **49**: 240, 241 (1905) sub subsp. *quadrangulum*, pro parte excl. typum. Type as for *H. quadrangulum* auct. non L., i.e. *H. maculatum* Crantz.
- H. quadrangulum* var. *punctatum* Schinz in *Bull. Herb. Boissier* **II**, **3**: 20, 22 (1902), in *Vierteljahrsschr. Naturf. Ges. Zürich* **49**: 240, 241 (1905) sub subsp. *quadrangulum*. Type: Switzerland, Graubünden, Oberengadin, Fornogletscher, Hegi s.n. (BR?-holotype).
- H. quadrangulum* subsp. *quadrangulum* sensu Tourlet in *Bull. Soc. Bot. France* **50**: 307 (1903); Schinz in *Vierteljahrsschr. Naturf. Ges. Zürich*, **49**: 231–241 (1905), pro parte excl. typum.
- H. maculatum* subsp. *eu-maculatum* Schinz & Thell. in Schinz & Keller, *Fl. Suisse*: 381 (1909); Thellung in *Allg. Bot. Z. Syst.* **1912**: 24 (1912); A. Fröhl. in *Oesterr. Bot. Z.* **63**: 18 (1913), in *Mitt. Naturwiss. Vereines Steiermark* **51**: 223 (1915); Hegi, *Ill. Fl. Mitt.-Eur.* **5**(1): 517 (1925). Type as for *H. maculatum* Crantz.
- H. maculatum* subsp. *typicum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. I*, **120**(1): 540 (1911). Type as for *H. maculatum* Crantz.
- H. maculatum* subsp. *typicum* var. *genuinum* (Schinz) A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. I*, **120**(1): 545 (1911). Type as for *H. quadrangulum* var. *genuinum* Schinz.
- H. maculatum* subsp. *typicum* var. *punctatum* (Schinz) A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. I*, **120**(1): 545 (1911). Type as for *H. quadrangulum* var. *punctatum* Schinz. Fröhlich (p. 546) names forms *glabrum* and *subnervosum* (based on nervation) as well as *rotundifolium* and *angustifolium* (based on leaf shape) for both vars *genuinum* and *punctatum*; but giving the same epithet to infraspecific taxa within the same species is inadmissible (I.C.B.N. Art. 24, note 2). The epithet f. *luteum*, however, was given to subsp. *typicum* as a whole and would therefore appear to be valid.
- H. maculatum* subsp. *typicum* forma *luteum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. I*, **120**(1): 546 (1911). Type: Austria, Styria, Puntigamer Güns (bei Graz), 16 July 1910 (fl), Fröhlich GZU 16228 (GZU!-lectotype, selected here).
- H. maculatum* subsp. *quadrangulum* sensu Hayek, *Prodr. Fl. Pen. balc.* **1**: 534 (1925). Hayek cited '*H. quadrangulum* Tourlet', i.e. *H. maculatum* Crantz not *H. quadrangulum* L.
- H. quadrangulum* subsp. *maculatum* (Crantz) Goday & Carbonell in *Anales Inst. bot. Cavanilles* **19**: 380 (1961).
- H. fallax* Grimm subsp. *fallax*, O. Schwarz in *Drudea* **5**: 63 (1965).
- H. fallax* subsp. *fallax* Grimm var. *fallax*, O. Schwarz in *Drudea* **5**: 63 (1965).
- H. fallax* subsp. *fallax* var. *fallax* forma *punctatum* O. Schwarz in *Drudea* **5**: 63 (1965). Type not cited (JE).
- H. fallax* subsp. *fallax* var. *quadrangulare* sensu O. Schwarz in *Drudea* **5**: 63 (1965) pro parte, quoad descr. Schwarz cited '*H. quadrangulare* L. (1776)' as basionym.
- H. maculatum* subsp. *maculatum* forma *punctatum* (Schinz) Stjep.-Vesel. in Josifović, *Fl. Srbije* **3**: 116 (1972).
- Icons: Rchb., *Icon fl. germ. helv.* **6**: t. 343 f. 5178 (1842–44); Gorschkova in Shishkin & Bobrov, *Fl. U.R.S.S.* **15**: 188, t. 12 f. 3 (1949); Zelený et al. in Futák & Bertová, *Fl. Slovenska* **3**: t. 37 f. 1 (1982).

*Stems* always with complete subsidiary lines. *Leaves* with densely reticulate tertiary venation; pale glands usually absent but some-

times few to numerous. *Inflorescence* branches narrowly ascending, making an angle of c. 30° with stem. *Flowers* 15–25 mm in diam. *Sepals* broadly ovate to broadly elliptic or elliptic-oblong, entire or more rarely slightly eroded-denticulate; laminar glands pale and black, punctiform. *Petals* entire, without or rarely with 1–3 black marginal glands; laminar glands all or mostly black, punctiform or proximally shortly striiform. *Syles* equalling ovary.  $2n=16$  (Noack, 1939; Robson, 1956, 1957; Schwarz, 1965; Reynaud, 1975; Dmetrieva, 1986; Parvenov & Dmetrieva, 1987),  $n=8$  (Nielsen, 1924; Winge, 1925; Robson, 1956, 1957, 1981; Laane, 1969).

Subalpine and alpine regions of the Pyrenees, Alps and Balkans; hilly regions further north (Massif Central, Vosges, Ardennes, Scotland); 0–2650 m (lowland in the north).

Distribution of the species except for lowland NW Europe (but with enclaves in the Ardennes and western and central Scotland) and valleys of the Alps east to Styria.

**SCOTLAND.** **W. Ross:** Ullapool, by Ullapool R., 16 August 1996 (fl & e.fr), *Kitchener* s.n. (BM). **Westerness:** Sunart, Strontian, 13 July 1966 (bud), *Cannon & Kendrick* s.n. (BM). **Argyll:** Dunadd area, between Lochgilphead and Kilmartin, July 1958 (fl), *Kenneth* s.n. (K). **Arran:** Lamblash, 10 August 1937, *Mackechnie* s.n. (BM).  **Lanark:** Glenhove near Airdrie, 22 August 1951 (fl), *Mackechnie* s.n. (BM). **Mid Perth:** between Lawers and Fearnan, 3 September 1913 (fr), *Marshall* in B.E.C. 3787 (BM, K). **S. Aberdeen:** Aboyne, 9 August 1968 (fl), *Robson* s.n. (BM).

**ENGLAND** (introduced). **Herts.:** Gaddesden, The Hoe, 11 August 1962 (fl), *J. & C. Dony & Allen* s.n. (BM).

**THE NETHERLANDS.** Very rare. Records from Gelderland (1954), south of Limburg (1917), and near Nijmegen (1924), *vide* Mennema, Quené-Broterrenbrood & Plate (1980).

**BELGIUM.** **Liège:** Recht, 10 August 1977 (fl), *Duvigneaud* 77 B 737 (H). **Namur:** Cul-des-Sarts, Le Marais, 5 August 1977 (fl & fr), *Duvigneaud* 77 B 704 (BM, H). **Luxembourg:** Vielsalm, bord de la Salm, 28 August 1935 (fr), *Mosseray* s.n. (BM, BR\*).

**FRANCE.** **Ardennes:** près de Hulle, rive gauche de la Hulle, 14 August 1970 (fl), *Duvigneaud* 70 F 41 (H). **Vosges:** Ventron, Gerbamont, August 1880 (l. fl), *Pierrat* (BM, K). **Doubs:** Mont d'Or, 6 August 1851 (fl), *Grenier* s.n. (BM). **Jura:** Noirmont, près de Rousses, 6 August 1856 (fl), *Michalet* fam. 2, 67 (K). **Haute-Savoie:** Vallée de l'Arve, Vallon de Flaine/Cluses, 1700 m, 16 July 1964 (fl), *F. & J.-D. Berstier* 517 (G\*, H). **Savoie:** Lanslebourg, 9 July 1884 (fl), *Willmott* (K). **Isère:** L'Oursière, près de Uriage, 1500–1600 m, 26 August 1880 (fl), *Tillet* (BM). **Hautes-Alpes:** Lauteret, 18 July 1931 (fl), *Pugsley* s.n. (BM). **Alpes-de-Haute-Provence:** Goudéissant, près Barcelonnette, 11 August 1854 (fl), *Willmott* s.n. (K). **Loire:** Mont Pilat, 1400 m, 14 July 1881 (fr), *Glastien* s.n. (BM). **Puy-de-Dôme:** le Mont-Doré, plateau de Durbise, 20 August 1928 (fl), *Fiton* in *Duffour* 5662 (BM). **Cantal:** Puy Mary, NW of Murat, 12 September 1966 (fl), *Summerhayes* 4202 (K). **Haute-Garonne:** Luchon, 14 July 1889 (fl), *Murray* s.n. (BM). **Ariège:** Ax, chemin d'Orgeix, n.d. (fl), *de Martrin* s.n. (K). **Pyrénées-Orientales:** Mont-Louis, Ostrand der Wald von Font-Romeu, 7 August 1926 (fl), *Ronniger* s.n. (W). **Hautes-Pyrénées:** Gavarnie, 1350–1500 m, 30 August 1932 (fl), *Meinertzhagen* s.n. (BM).

**ANDORRA.** Ordino, 1250 m, 14 July 1962 (fl), *Edwards & Perry* 9 (BM).

**SPAIN.** **Gerona:** [Santuario de] Nuria, Via Crucis, 3 August 1934 (fl), *Dauder Rodés* s.n. (BM). **Lérida:** Gorges de Llo, 1450 m, 29 August 1929 (fr), *Sennen* s.n. (BM). **Teruel:** Bronchales, Sierra Alta, 11 June 1962 (st), *Kjellqvist & Löve* N588 (RNG).

**ITALY.** **Val d'Aosta:** Val Ferret, SE of Mont Blanc, 12 July 1854 (fl), *Hort* s.n. (BM). **Novara:** Val Formazza, Discesa da C. Cavala e S. Michele, 1827–1250 m, 3 August 1918 (fl), *Boggiani* s.n. (BM). **Verona:** Monte Baldo, 1000 m, June 1902 (fl), *Rigo* s.n. (H). **Bolzano:** Pusteria med., 1860–1950 m, 29 August 1871 (e. fr), *Huter* s.n. (BM). **Treviso:** Bosco Cansiglio (?), 1000 m, 10 July 1922 (fl), *Fiori* Fl. Ital. Exs. III 2664 (BM, K).

**SWITZERLAND.** **Vaud:** Alpen über Bex, 1832 (fl), *Thomas* in *Reichenbach* 1500 (BM, H, JE, WAG). **Valais:** Col du Lein, 1720 m, 29 July 1979 (fl), *Lawalrée* 21846 (BM, BR\*). **Bern:** Mürren, 1590 m, 2 September 1923 (fr), *Lester Garland* s.n. (K). **Graubünden:** Tachitta Valley, near Preda,

Albula, 20 July 1928 (fl), *Pugsley* s.n. (BM). **Glarus:** Glärnisch Mtn, Glüterbach, 1150 m, 19 September 1963 (fr), *Robson* 1826 (BM). **Appenzell:** am Gäbris ob Gais, July–August (fl), *Schneider* s.n. (BM).

**AUSTRIA.** **Vorarlberg:** Rätikon, 19 July 1952 (fl), *Jacobs* 3577 (L). **Tirol:** prope Trins in valle Gschnitz, c. 1100 m, n.d. (fl), *Kerner* in Fl. Exs. Austr.-Hung. 3647 (BM, H, JE, K). **Salzburg:** Radstadter Tauernpasshöhe, 1700–1300 m, 13 August 1932 (fl), *Hübl* s.n. (BM). **Kärnten:** Weissenfels Krain, September 1913 (st), *Meebold* s.n. (K). **Steiermark:** Schlading, 750 m, 3 July 1994 (fl), *Townsend* 94/34 (K). **Niederösterreich:** Montes Rax in valle Höllenthal, 600 m, August 1953 (fl), *Patzak* s.n. (H, W\*).

**GERMANY.** **Bayern:** Kampenwald, above Steinlinghütte, 26 July 1934 (fl), *Willmott* s.n. (BM); Oberostrod, 25 July 1927 (fl), *Mann* s.n. (FR). **Hessen:** Wasserkuppe gegen den Pferdskopf, c. 900 m, 9 August 1903 (fl), *Goldschmidt* s.n. (FR). **Thüringen:** Erfurt, bei Oberhof, Schmücke, c. 900 m, 16 July 1952 (fl), *Launert* s.n. (BM); Suhl (?), Neuhaus (Reunsteig), 1950, *K. Meyer* s.n. (JE). **Sachsen:** bei Dresden, n.d. (fl), *Horn* in Reichenbach, Exs. Fl. Germ. 1397 (BM, H, JE). **Sachsen-Anhalt:** Harz, Minfra nach Harlingerode, 1858, (*Collector?*) (JE); Magdeburg, Werningerode, July 1860 (fl), (*Collector?*) (FR). **Brandenburg:** *vide* Ascherson (1864: 113). **Berlin:** Spandau, Finkelhang, 28 July 1867 (l. fl) *Wagner* s.n. (K). **Mecklenburg-West Pomerania:** Schwerin, prope Gustrowiam, 1830, *Jahn?* s.n. (JE); Rügen l., 1958, *Inst. Excurs.* s.n. (JE).

**DENMARK.** **Jylland:** Frederikshavn, Pikkerbakken, 26 July 1968 (fl), *Jensen, Nielsen & Pedersen* in Fl. Jtl. Exs. 465 (BM, H, TAI). **Fyn:** Dyreborg Skov, Faaborg, 24 July 1952 (fl), *Young* 4482 (BM). **Sjælland:** Dyrhavn, Klampenborg, 15 August 1947 (fl), *Price* 307(?) (K).

**FAEROE ISLANDS.** Streymoy, Vágur (*vide* Jóhansen, 2000).

**NORWAY.** **Akershus:** As, near Ski, c. 48 km S. of Oslo, 29 July 1961 (fl), *Goodfellow* 61.1600 (BM, LIV\*). **Vestfold:** Åsgårdstrand, 31 August 1934 (fr), *Williams* s.n. (BM). **Vest Agder:** Vigeland, Kristiansand, August 1909 (fl), *Gamble* 29773 (K). **Rogaland:** Stangaland, Eide, 14 August 1930 (fl), *Rosseland* s.n. (H). **Hordaland:** Hardanger Fjord, Utne, S. Bergenhus, 16 August 1934 (fr), *Williams* s.n. (BM). **Nordland:** Holandsfjord, c. 200 m, 22 July 1950 (fl), *Boyd* in Durham U. Exped. 346 (BM); Lofoten Is., Svolveaer, Svolveaerigeita, 27 July 1939 (fl), *Blake* 73 (K).

**SWEDEN.** **Blekinge:** Rödeby, Rödebyholm, 11 July 1989 (fl), *Hult* s.n. (H). **Gotland:** Öland l., Bredsåtra sn., Bredsåtra by, 15 August 1957 (fl), *Saarsoo* 7684 (H). **Kronoberg:** Sörabý s. n. ö. om Stavsåkra, 4 August 1957 (fl), *Saarsoo* 7684 (H). **Jönköping:** Korsberga, Mölebo, 3 August 1908 (fl), *Stalin* s.n. (H). **Skaraborg:** Skara, 15 July 1908 (fl), *Jacob & Jacobson* s.n. (BM). **Ålvsborg:** Skene, c. 700 m, nordlich Berghem station, 13 August 1965, *Butler & Gaubl* 7941 (FR). **Örebro:** Närke, Svennevad, Gropen, c. 75 m, 4 August 1950 (fl), *Kjellmart* s.n. (H). **Stockholm:** Stockholm, 23 July 1858 (fl), *Nynan* s.n. (BM). **Uppsala:** prope Upsallem, July 1869 (fl), *Ahlberg* s.n. (BM). **Västmanland:** Arboga, Hamnen, 19 July 1951 (fl), *Fridell* s.n. (H). **Kopparberg:** Leksands sn., Björkberg, 17 September 1956 (fl & fr), *Norrmann* s.n. (BM). **Gävleborg:** Gävle, Lovudden, 20 August 1964 (fl & fr), *Nannfeldt* s.n. (BM). **Västernorrland:** Ålno, 15 September 1909 (fl & fr), *Rönnblad* s.n. (H).

**FINLAND.** **Oulu:** Kn. Kajaania, Likapuro, n.d., *Heikkinen* s.n. (JE). **Keski-Suomi:** Laukaa, Leppävesi Linnaasaari, 30 July 1965 (fl), *Valovirta* s.n. (H). **Kuopio:** Savonia borealis, Iisalmi, Iimäki, 6 August 1975 (fl), *Tallgrén* s.n. (BM). **Pohjois-Karjala?:** Karelia austr., par. Vehkalahti, Pyhäntö, 7 July 1961 (fl), *Fagerström* s.n. (BM). **Turku Pori:** Turku, Ruissalo, Laurila, 18 July 1968 (fl), *Tallgrén* s.n. (BM). **Åland:** Hammarland, Näfsby, 20 July 1968 (fl), *Haakana* s.n. (BM).

**RUSSIA.** **Ladoga-Ilmen:** Leningradsky obl., Lupskiy r-n., Merabush-Lupeska, 13 July 1969 (fl), *Nepli* 18 (K). **Dvina-Pechora:** Archangelsk, Beresink, 1919 (fl), *Grantham* s.n. (BM). **Upper Volga:** Prov. Mosqua, prope urbe Noginsk, 30 June 1968 (fl), *Sanozvon* 158A (H). **Volga-Kama:** Prov. Kostroma, distr. Kineshma, prope Pawlowskoje, 4 July 1903 (fl), *Klementz* 1970 (H). **Upper Dnieper:** Smolensk obl., Dukhovshchina distr., prope pag. Ovsianka (10 km NW of Preczistoe), 8 August 1974 (fl & fr), *Makarov & Bazhenova* s.n. (H). **Middle Dnieper:** *vide* Gorschkova (1949: 243). **Volga-Don:** Orël obl., Orlovsk, Ostrovakami, n.d. (l. fl), *Tarachkova & Poganki* 317 (H). **Transvolga:** *vide* Gorschkova (1949: 243). **Upper Tobol:** Chelyabinsk, Ural, in vallibus montis Jurma, July 1844 (fl), [*Buhse?*] (Herb. Buhse). **Ob:** south, *vide* Gorschkova (1949: 243). **Angara-Sayan:** Ibryul' village, *vide* Gorschkova (1949: 243).

**ESTONIA.** Ingrida, Hietamäki, Nütty, 20 July 1915 (fl), *Jamalainen* s.n. (H); Dagö I. [Hüümaa], Emmaste, 1872, *Winkler* 335 (JE).

**LATVIA.** Krashavskiy r-n., Zabludovka, 13 July 1967 (fl), *Makarova* s.n. (H).

**LITHUANIA.** Throughout the Territory (Vilkevičiūtė, 1971).

**BELOARUS.** Njadrkóv, distr. Nowogródek [Novogrudok], 28–1898 (fl), *Dybowski* in *Woloszczak*, Fl. Polon. Exs. 715 (BM).

**UKRAINE.** \***Rossia Subcarpatia:** montes Vysoké Poloniny, polonina Rovná, c. 1300 m, 8 July 1938, *Jirásek* s.n. (PR). \***Carpatorossia:** Čorná Hora, in ... montis Hoverla, 1800–2056 m, July 1935, *M. Deyl* in PR 164845 (PR). **Bucovina:** in summis alpinis ... alpis Tschumaled, July 1833 (fl), *Herbich* s.n. (W).

**POLAND.** **Jelenia Góra:** Sudet, Hirschberg, 1 July 1958, *Köhler & Zippold* s.n. (JE). **Walbrzych:** Śląsk Dolny, Spalona pow. Bystrzyca Kł. 25 July 1958 (fl), *Gołowin* 157 (H). **Wrocław?:** Breslau, Strachate, 28 July 1888, *Kionka* s.n. (JE). **Bielsko Biala:** distr. Wadowice, infra cas. Potrójna, 24 July 1938 (fl), *Łancucka* in Pl. Pol. Exs. 329a (BM, K). **Tatry:** Tatra, Zakopane, Dol. Maty Zaly, 11 July 1958, *Köhler & Zippold* s.n. (JE). **Krosno?:** E. Carpath., Breskul, ± 1450 m, 29 August 1938 (fl), *Kosij* in Pl. Pol. Exs. 329b (BM, K).

**CZECH REPUBLIC.** **Bohemia:** Montes Šumava, p. p. Hamny, 3 August 1962 (fl), *Hostička* s.n. (H); \*distr. Cheb, in valle R. Libocký potock sub vico Opatov, ad Dolní mlýn, c. 560 m, 18 September 1950, *Klásterský* in PR 165161 (PR). **Moravia:** Weisskirchen bei Hrubuska, July 1911 (fl), *Petrak* 1142 (BM); \*chalet Bunč near Salaš, 6 July 1987, *Mártonfi* 459 (KO).

**SLOVAKIA.** Michalovec, Vihorlat, oberhalb Remetske Hamre, c. 500 m, 23 July 1974 (fl), *F.K. & J. Meyer* 11006 (JE); \*Bukovské vrchy Mts, near Runina, 31 July 1995, *Mártonfi* 2022 (KO); \*pasture 'Voniarky' near Dobšiná, c. 915 m, 13 August 1991, *Mártonfi* 976 (KO).

**HUNGARY.** Absent?

**SLOVENIA.** Bled [Veldes], 1924 (fl), *Leathes* s.n. (BM).

**CROATIA.** Widespread (Schlosser & Vukotinovi, 1869: 382).

**SERBIA.** **North:** Fruška Gora. **Central:** Suva planina, Stara planina, Tara planina, Zlatibor, Kopaonik (Stjepanovi-Veseliči, 1972).

**ROMANIA.** **Transsilvania:** Crișana, Bihor, ad Balneas Stăna de Vale, c. 1100 m, July 1936 (fl), *Borza* in Pl. Exs. Rom. 1520c (H, K); in monte Butka-Kandrenulni ad Dorna-Kandreni [Dornișoara], July 1838 (fl), *Herbich* s.n. (W); \*Munții Bihorului Mts., above Scărișoara, c. 1400 m, 16 July 1995, *Mártonfi* 1985 (KO). **Moldavia:** Comm. Dărmănești, monte Nemira, c. 1500 m, 14 July 1970 (fl), *Barabaș & Șova* 158 (H); \*Distr. Turda-Arieș, Valea Morii prope oppid. Cluj, c. 600–650 m, 28 July 1923, *E.I. Nyárády* in CL 444000 (CL). **Walachia:** Oltenia, distr. Gilort, mont. Paring, ad Mușatoiu, c. 1540 m, 30 September 1960 (e. fr), *Buia* et al. in Fl. Olten. Exs. 52 (BM, H).

**BULGARIA.** Jordanov & Kozhukharov (1970: 260) record var. *maculatum* from N. and W. Stara planina, the Znepolski region (Golo birdo), W. Granichni planina, the Vitoša region (Vitoša), Slavianka and Rila.

1c. ***Hypericum maculatum* subsp. *obtusiusculum*** (Tourlet) Hayek, *Sched. fl. stiriac.* 23–24: 27 (1912); Thellung in *Allg. Bot. Z. Syst.* 1912: 24 (1912); A Fröhl. in *Oesterr. Bot. Z.* 63: 13, 18 (1913), in *Mitt. Naturwiss. Vereines Steiermark* 51: 223, 224 (1915); Schinz & Keller, *Fl. Schweiz*, 4th ed. 1: 451 (1923); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 517 (1925); N. Robson in *Bot. Soc. Brit. Isles Proc.* 2: 237 (1957), in op. cit. 3: 99 (1958), in Tutin et al., *Fl. Europ.* 2: 268 (1968), in *Wisskirchen & Haeupler, Standardliste Farn- u. Blütenpfl. Deutschl.*: 269 (1998). Type as for *H. quadrangulum* subsp. *obtusiusculum* Tourlet=*H. desetangsii* var. *imperforatum* Bonnet.

Fig. 6, Map 2.

*H. dubium* Leers, *Fl. herbörn.*: 165 (1775); Sm., *Engl. Bot.*: 296 (1796), *Fl. brit.* 2: 802 (1800); Bab. in *Trans. Bot. Soc. Edinburgh* 1: 88 (1841), *Man. Brit. bot.*: 57 (1843); Belynk, *Fl. Namur*: 52 (1855); Syme, *Engl. Bot.*, 3rd ed. 2: 151 (1864); Schinz in *Vierteljahrsschr. Naturf. Ges. Zürich* 49: 231–241 (1905); Mártonfi et al. in *Preslia* 71: 337 (1999). Types: Germany, Hesse, 'ad sepes am Sieghaus', *Leers* s.n. (?-syntype); 'am Homberg', *Leers* s.n. (?-syntype). According to Stafleu & Cowan (1979), *Leers'* herb-

arium was taken to Russia (early in the nineteenth century?) and subsequently partly destroyed and partly lost. His description (apart from the ovate entire sepals) and the location of Herbörn are both consistent with his plant's belonging to subsp. *obtusiusculum*; and broad entire sepals are not unknown in subsp. *obtusiusculum*, having been found in Kirkcudbrightshire, SW Scotland (see record, p. 75), and they were recorded by Tourlet (1903). They also occurred in a plant of subsp. *maculatum* in which the chromosomes had been doubled by colchicine treatment (Robson, 1956, 1957, 1981). Schinz, in the paper cited above, discussed the name *H. dubium* but treated it as a synonym of *H. quadrangulum* in his sense, i.e. *H. maculatum* Crantz. Fröhlich (1911) also regarded *H. dubium* as a synonym of *H. maculatum* (i.e. subsp. *typicum*).

*H. obtusum* Moench, *Methodus*: 129 (1794), nom. illegit. Type as for *H. dubium* Leers.

*H. leersii* C.C. Gmel., *Fl. bad.* 3: 253 (1808); 5: 575 (1826), nom. illegit. Type as for *H. dubium* Leers.

*H. quadrangulum* var. [β] sensu Choisy, *Prodr. monogr. Hypéric.*: 47 (1821).

*H. quadrangulum* var. [β] *dubium* (Leers) Choisy in DC., *Prodr.* 1: 548 (1824), pro parte excl. syn. *H. delphinense* Vill.

*H. dubium* var. [β] *maculatum* sensu Bab., *Man. Brit. bot.*, 3rd ed.: 58 (1851), i.e. sensu *H. dubium* Bab. in *Trans. Bot. Soc. Edinburgh* 1: 88 (1841), *Man. Brit. bot.*: 57 (1843), 2nd ed.: 60 (1847).

*H. dubium* var. [α] *genuinum* Syme, *Engl. Bot.*, 3rd ed. 2: 151 (1864).

*Holosepalum dubium* (Leers) Fourr. in *Ann. Soc. Linn. Lyon, N.S.* 16: 352 (1868).

?*Hypericum quadrangulum* var. [b] *ambiguum* Schur in *Verh. Naturf. Vereins Briinn* 15(2): 158 (1877). Type: Czech Republic, Moravia, oberhalb der Mazocha bei Blansko, August 1871, *Schur* s.n. (BRLU? or LW?).

*H. desetangsii* var. [β] *imperforatum* Bonnet in *Bull. Soc. Bot. France* 25: 277 (1879); Schinz in *Bull. Herb. Boissier* II, 3: 14 (1902), in *Vierteljahrsschr. Naturf. Ges. Zürich* 49: 241 (1905). Type: France, Seine-et-Oise, Meudon, 11 August 1878 (l. fr), *Bonnet* in Soc. Dauphinoise 1998 (P-lectotype, selected here; CLF!, FR!, K!-isolecotypes). My preliminary selection of lectotype for this variety, Lloyd's specimen from Loire-Inférieure [Loire-Atlantique], was published by Mártonfi et al. (1999: 339) as 'Robson, in prep.'. Neither they nor I have seen this specimen, and the more widely distributed Bonnet exsiccata cited above would seem to be a more appropriate choice.

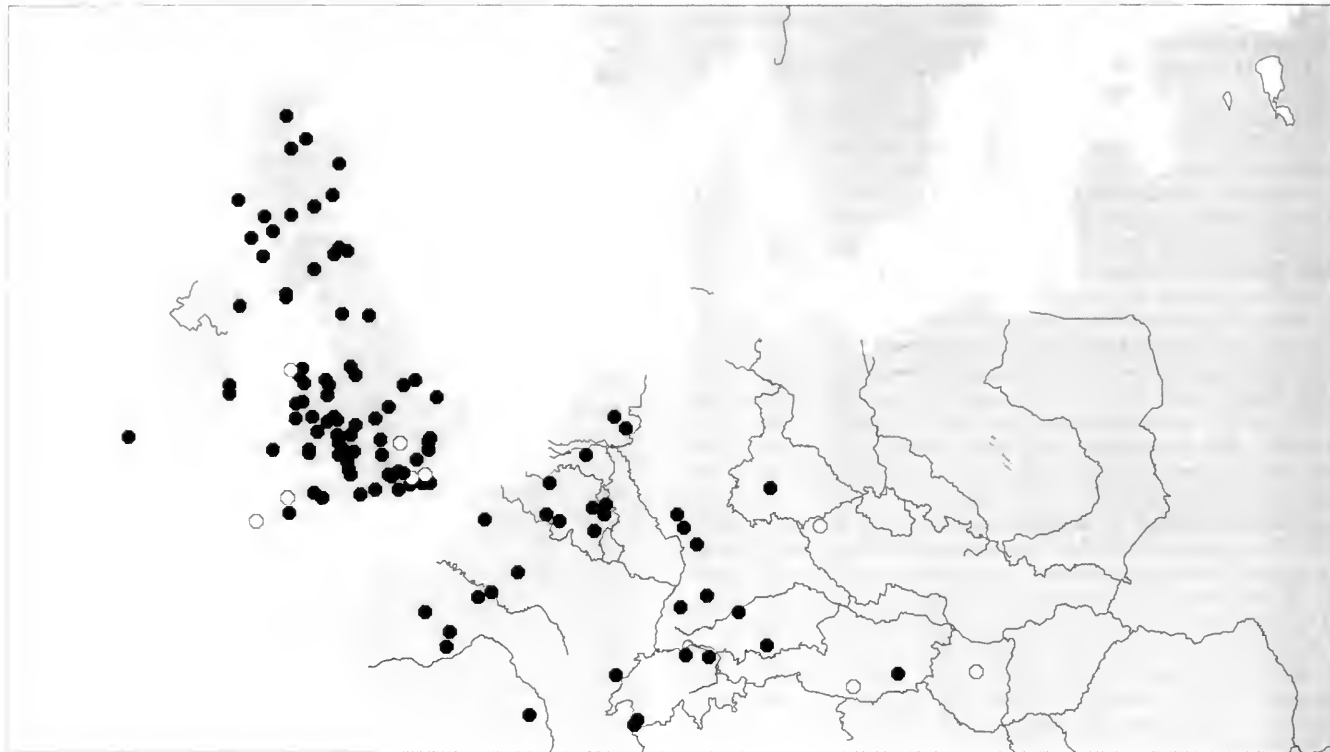
*H. quadrangulum* var. *occidentale* Franch., *Fl. Loir-et-Cher*: 97 (1885); Rouy in Rouy & Fouc., *Fl. France* 3: 335 (1896). Types: France, Loir-et-Cher, environs de Mondoubleau, 16 July 1867 (fl), *Legué* s.n. (P!-lectotype, selected here); bois de Roquelane, August 1864 (fl), *Legué* s.n. (P!-syntype); Onzain, petit bois de Mare, *Monin* s.n. (?-syntype, not lectotype as cited in Mártonfi et al., 1999: 339). The last specimen has not been found in P.

*H. acutum* subsp. *desetangsii* var. *imperforatum* (Bonnet) Rouy in Rouy & Fouc., *Fl. France* 3: 337 (1896), comb. illegit. Type as for *H. desetangsii* var. *imperforatum* Bonnet.

*H. quadrangulum* subsp. *obtusiusculum* Tourlet in *Bull. Soc. Bot. France* 50: 307 (1903). Type as for *H. desetangsii* var. *imperforatum* Bonnet. Tourlet describes *H. quadrangulum* subsp. *quadrangulum* on the same page in the sense of *H. tetrapterum* Fr.

*H. quadrangulum* subsp. *obtusiusculum* var. [α] *imperforatum* (Bonnet) Tourlet in *Bull. Soc. bot. France* 50: 308 (1903). Type as for *H. desetangsii* var. *imperforatum* Bonnet, i.e. this is subsp. *obtusiusculum* Tourlet var. *obtusiusculum*.

*H. quadrangulum* subsp. *obtusiusculum* var. [β] *perforatum* Tourlet



Map 2 1c. *H. maculatum* subsp. *obtusiusculum* ●, other records ○. French and German records probably incomplete, as are the Irish ones.

in *Bull. Soc. Bot. France* **50**: 308 (1903). Type: France, Indre-et-Loire, vallon de la Desmée, [Les] Hermites, Doucet s.n. (G?-holotype).

*H. maculatum* var. [β] *babingtonii* H. & J. Groves, *Man. Brit. bot.* 9th ed.: 74 (1904). Type as for *H. dubium* var. *maculatum* sensu Bab., i.e. *H. dubium* Leers.

*H. quadrangulum* subsp. *erosum* var. *epunctatum* Schinz in *Vierteljahrsschr. Naturf. Ges. Zürich* **49**: 240, 241 (1905), nom. illegit. (Art. 52.1). Type as for *H. desetangii* var. *imperforatum* Bonnet. Schinz, in order not to provide an unnecessary synonym and in support of the Rules of Nomenclature, named this form [sic] *epunctatum*.

*H. quadrangulum* subsp. *erosum* var. *punctatum* Schinz in *Vierteljahrsschr. Naturf. Ges. Zürich* **49**: 240, 241 (1905), nom. illegit. (Art. 52.1). Type as for *H. quadrangulum* subsp. *obtusiusculum* var. *perforatum* Tourlet.

*H. maculatum* subsp. *erosum* sensu Schinz & Keller, *Fl. Suisse*: 381 (1909); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.*, **120**(1): 550 (1911).

*H. maculatum* subsp. *erosum* var. *imperforatum* (Bonnet) A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 553 (1911). Type as for *H. desetangii* var. *imperforatum* Bonnet.

*H. maculatum* subsp. *erosum* var. *perforatum* (Tourlet) A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss. Math.-Naturwiss. Kl.* **120**(1): 553 (1911). Type as for *H. quadrangulum* subsp. *obtusiusculum* var. *perforatum* Tourlet.

*H. maculatum* subsp. *erosum* var. *imperforatum* forma *latisepalum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 554 (1911), in *Mitt. Naturwiss. Vereines Steiermark* **51**: 221 (1915). Type: Austria, Styria, bei Doblbad, 22 August 1909 (fr), Fröhlich GZU16202 (GZU!-lectotype, selected here). Note: none of Fröhlich's combinations of his formae under subsp. *obtusiusculum* in 1915 (p. 221) were effective.

*H. maculatum* subsp. *erosum* var. *imperforatum* forma *latisepalum* [sub]forma *nigrum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 554 (1911), in *Mitt. Naturwiss. Vereines Steiermark* **51**: 221 (1915). Type: Austria, Styria, Ragnitz bei Graz, July 1909 (fl), Fröhlich GZU16194 (GZU!-lectotype, selected here).

*H. maculatum* subsp. *erosum* var. *imperforatum* forma *latisepalum* [sub]forma *lucidum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 554 (1911), in *Mitt. Naturwiss. Vereines Steiermark* **51**: 221 (1915) sub var. *imperforatum* (Bonnet) Fröhl. Type: Austria, Styria, bei Stattegg, nach Graz, 10 July 1910 (fl), Fröhlich GZU16200 (GZU!-lectotype, selected here).

*H. maculatum* subsp. *styriacum* A. Fröhl. in *Mitt. Naturwiss. Vereines Steiermark* **51**: 222, 224 (1915); Hegi, *Ill. Fl. Mitt.-Eur.* **5**(1): 518 (1925). Type: Austria, Styria, ad vicum Maria-Trost prope urbem Graz, c. 430 m, July 1911 (fl), Fröhlich in Hayek, *Fl. Stir. Exsicc.* 1198 (GZU!-lectotype, selected here, BM!, GB!, H!, K!-photographs; see also Mártonfi et al., 1999: 340).

*H. maculatum* subsp. *obtusiusculum* var. *perforatum* (Tourlet) A. Fröhl. in *Mitt. Naturwiss. Vereines Steiermark* **51**: 243 (1915). Type as for *H. quadrangulum* subsp. *obtusiusculum* var. *perforatum* Tourlet.

*H. maculatum* subsp. *obtusiusculum* var. *imperforatum* (Bonnet) A. Fröhl. in *Mitt. Naturwiss. Vereines Steiermark* **51**: 243 (1915). Type as for *H. desetangii* var. *imperforatum* Bonnet.

*H. dubium* var. *perforatum* (Tourlet) Pugsley in *J. Bot.* **78**: 35 (1940). Type as for *H. quadrangulum* subsp. *obtusiusculum* var. *perforatum* Tourlet.

*H. erosum* (Schinz) O. Schwarz in *Drudea* **5**: 63 (1965) pro parte excl. typum.

Icons: Syme, *Engl. Bot.*, 3rd ed. **2**: t. 269 (1864); Ross-Craig, *Draw. Br. Pl.* **6**: t. 8 (1952).

*Stems* with subsidiary lines present or sometimes partly (or wholly?) absent. *Leaves* with rather dense tertiary venation (somewhat laxer than in subsp. *maculatum*); laminar gland dots pale, dense to very sparse or absent. *Inflorescence* branches widely ascending, making an angle of c. 50° with stem. *Flowers* 25–30 mm in diam. *Sepals* broadly to narrowly ovate, with apex finely eroded-denticulate or rarely entire. *Petals* usually distally unilaterally crenate with marginal black glands in depressions?; laminar glands pale and black or rarely only pale, linear to striiform and sometimes punctiform. *Styles* 1–2 × ovary. 2n=32 (Robson, 1956, 1957, 1958a).

Montane regions and valleys in the Alps, lowland further north, in meadows, rough pasture and damp woods; 0–c. 850 m.

North-west Europe east to western Germany and Bohemia (except most of western Scotland), valleys of the Alps east to Styria, western Hungary. Introduced into Canada (British Columbia).

**SCOTLAND.** **E. Sutherland:** Lairg, 24 July 1961 (fl), *McCallum Webster* 5726 (K). **Easternness:** Inverness, Clashnaharry, 3 October 1975 (fr), *McCallum Webster* 18700 (BM). **Moray:** Brodie Castle, 3 August 1961 (fl), *McCallum Webster* 5848 (K). **S. Aberdeenshire:** Drum, R. Dee by Old Manse, 15 August 1956 (fl & fr), *Robson* s.n. (BM). **W. Perth:** Callander, 16 July 1989 (fl), *N.F. Stewart* s.n. (BM). **Mid E. B.:** Mull, between Glen Forsa Lodge entrance and Forsa bridge, July 1984 (fl), *Stirling* s.n. (BM). **Kintyre:** near Fairy Isles, 28 July 1979 (fl), *Kenneth* s.n. (BM). **Selkirk:** banks of R. Ettrick near Selkirk, July 1926 (fl), *Hayward* s.n. (BM). **Renfrew:** near Gourrock, 17 July 1899 (fl), *Pugsley* s.n. (BM). **Dumfries:** Applegarth, Perchall, 8 August 1957 (fl), *Bangerter & Collett* 381 (BM). **Kirkcudbright:** Rockcliffe, August 1999, *Tregale* s.n. (Herb. Tregale).

**ENGLAND.** **Westmorland:** Tebay, Low Borrowbeck, 31 July 1991, *Halliday* 72/91 (BM). **N.B.** The records of subsp. *maculatum* in Cumbria (Halliday, 1997: 578) all proved to be subsp. *obtusiusculum*. **NW Yorks.:** near Richmond, 22 August 1842 (fl & fr), *J. Ward* s.n. (BM). **W. Lancs.:** near Whittingham, Coney Garth Lane, September 1982 (fr), *L. & P. Livermore* s.n. (LIV). **Cheshire:** below Overton Scar, 15 July 1909 (fl), *Wolley Dod* s.n. (BM). **Leicester:** Ulverscroft, 10 August 1890 (e. fr), *A.B. Jackson* s.n. (BM). **N. Lincs.:** Woodhall Spa, 6 August 1945 (fl), *Alston* s.n. (BM). **Shropshire:** near Ludlow, Bringwood Chase, August 1935 (e. fr), *Ross* s.n. (BM). **Warwicks.:** Brandon, 17 July 1925 (fl), *Riddelsdell* s.n. (BM). **Hereford:** near Ross, Chase Wood, 19 July 1915 (fl), *Adamson* s.n. (BM). **E. Gloucs.:** Brimscombe, 3 August 1953 (e. fr), *Townsend* s.n. (K). **Bedford:** Potsgrove, 7 July 1945 (fl), *Dony* s.n. (BM). **W. Norfolk:** Dersingham, 16 July 1949 (fl), *Libbey* 3229 (BM). **Oxford:** near Hempton, 30 October 1930 (fr), *Riddelsdell* s.n. (BM). **N. Essex:** near Quendon, 25 July 1942 (fl), *Pugsley* s.n. (BM). **W. Kent:** near Ide Hill, 13 July 1939 (fl), *C.E. Britton* 4322 (BM). **W. Sussex:** Midhurst, West Lavington, 7 July 1934 (fl), *N.D. Simpson* 34220 (BM). **Dorset:** between Crendell and Daggins, 2 August 1934 (e. fr), *Good* 484 (BM). **E. Cornwall:** near Rilla mill, 6 September 1948 (fl), *Alston* s.n. (BM).

**WALES.** **Glamorgan:** near Lisvane, 3 July 1968 (fl), *Pinkard* s.n. (H). **Pembroke:** Caneston wood, 11 August 1931 (fl), *Alston* s.n. (BM). **Merioneth:** Dolgelly, Bontnewydd, 8 August 1923 (fr), *Barton* s.n. (BM). **Radnor:** Llangullo station, 5 August 1956 (fl), *P.C. & J. Hall* s.n. (BM). **Denbigh:** Llanrwst, 9 August 1930 (fl), *Holder* 464 (LIV). **Anglesey:** Benllech, 5 July 1911 (fl), *Cooper* s.n. (BM).

**IRELAND.** **Kerry:** Killarney, 30 July 1885 (fl), *Linton* s.n. (BM). **Clare:** 0.8 km W. of Ballynalacken Castle, 1 August 1962 (fl), *Moore* 459 (BM). **Galway:** Co. Galway, July 1854 (fl), *More* s.n. (BM). **Wicklow:** near Roundwood, 31 August 1962 (fl), *McCallum Webster* 7981 (K). **Antrim:** Belfast, Shaw's Bridge, 24 August 1872 (fr), *Stewart* (BM). **Fermanagh:** Inver Lough, 19 July 1957 (fl), *Meikle* 2127 (K).

**NETHERLANDS.** **Overijssel:** near Mokkalengoor, S. of Ijpele, 14 June 1947 (fl), *van Royen* s.n. (H). **Gelderland:** s' Hertogenbosch, Meteren, Tienenwaard, 22 July 1974 (l. fl), *Hekking* s.n. (BM).

**BELGIUM.** **Oost Vlanderen:** Hamme Mille (?), 11 July 1953 (fl), *Pierart* s.n. (K). **Liège:** Spa, September 1876 (fr), *C.H. Wright* s.n. (K). **Hainault:** bois d'Obourg, 4 July 1867 (e. fr), *Martinis* in Pl. rar. crit. Belg. VI, 269 (BM). **Namur:** Crupet, près du confluent du Crupet et du Bocq, 8 August 1978 (fl), *Lawalrée* 21100 (BM, \*BR). **Luxembourg:** La Roche [-en-Ardenne], August 1960 (l. fl), *Dubois* 1635 (BM, \*BR).

**FRANCE.** **Pas de Calais:** Hersin[-Coupigny], 15 July 1917 (l. fl), *G.C. Brown* s.n. (BM). **Aisne:** la forêt de Retz près Villers-Cotterêts, 3 September 1878 (e. fr), *Bonnet* s.n. (K). **Seine-et-Oise:** Bois de Meudon, près l'Étang de Colm Porche, 19 August 1877 (fl), *Delacour* s. n. (K). **Loire-Atlantique:** bord de la Divatte, 5 August 1886 (fl & e. fr), *Lloyd* s.n. (BM). **Orne:** Alençon, route de Fresnay, 19 July 1891 (l. fl), *Beaudoin* in Soc. Dauph. II 599 (BM). **Allier:** Cresset, bord du Sichon, 27 July 1867 (e. fr), *Gaevier* s.n. (BM). **Doubs:** Mouthier, 15 July 1927 (fl), *Williams* s.n. (BM).

**GERMANY.** **Hessen:** Königstein/Taunus, NW der Stadt, 20 August 1961 (fl), *Schaarschmidt* 257 (FR); Kreis Limburg-Weilburg, Weilburger Lahntal, Weilburg, 260 m, 22 July 1978 (fl), *Kalheber* 78–527 (H). **Thüringen:** Weimar, Ettersburg, September 1923, *Bormüller* s.n. (JE). **Baden-Württemberg:** Schwarzwald, Heselbach, 9 August 1931 (fr), *Williams* s.n. (BM). **Bayern:** Schwaben, Leipheim/Donau, Donauried, 7 July 1961 (fl), *Doppelbaur* 488 (H); Oberbayern, nahe dem Westufer des Staffelsees, 650 m, 11 August 1957 (fl), *Launert* s.n. (BM).

**SWITZERLAND.** **Valais:** Col de Balme, 30 August 1868 (fr), *G. Engelmann* s.n. (WIS). **Zürich:** oberhalb Oberglatt, c. 420 m, 3 September 1936 (fr), *W. Koch* s.n. (H). **St. Gallen:** Fürstenland, Gem. Waldkirch, Tannenren, c. 850 m, 31 July 1948 (fl), *W. Koch* 48/473 (H).

**AUSTRIA.** **Steiermark:** ad vicum Maria-Trost prope urbem Graz, c. 430 m, July 1911 (fl), *Fröhlich* in Hayek, Fl. Stir. Exs. 1198 (BM, GB photograph, GZU, H, K photograph). **Kärnten:** *vide* Fröhlich (1915: 223).

**CZECH REPUBLIC.** **Bohemia:** \*Doupovské Hory Mts, E. from Karlovy Vary, near Bražec, c. 685 m, 12 July 1996, *Mártonfi* 2125 (KO).

**HUNGARY.** **Veszprém:** \*Montes Bakony, inter stationem ferroviae Porvacsesznek ad pagum Borzavár, c. 400 m, 9 July 1934, *Polgár* in BP 261467 (BP); \*in fossis Nádaser pr. villa Dobospuszta iuxta pag. Sáska, 27 July 1954, *Szalay* s.n. (ZIRC).

**CANADA** (introduced). **British Columbia:** Prince Rupert, September 1939 (fl), *King* UBC 21544 (UBC); Burnaby Mountain, 1 August 1990 (l. fl), *Lomer* UBC 202196 (UBC); Pemberton, 2 August 1946 (fr), *Eastham* UBC 14970 (UBC); North Vancouver, Capitano R. estuary, 8 August 1990 (fl), *Lomer* UBC 202195 (UBC).

The presence of linear glands (sometimes pale) in the petals and the greater frequency of pale glands in the leaves suggest that subsp. *obtusiusculum* has evolved from subsp. *immaculatum*, not, as I thought from my own observations and experiment, from subsp. *maculatum*. The plant obtained by colchicine doubling of the chromosomes (Robson, 1957, 1958a) had broad leaves, broad entire sepals and black petal laminar glands, as was to be expected starting from var. *maculatum*; but the inflorescence branching was wide and the petal glands (as far as I can remember in the absence of a specimen) were mostly linear. The presence of broad entire sepals in this experimental plant, in Leers's (lost) type of *H. dubium* and in a collection from Applegarth, Dumfries, SW Scotland (*Bangerter & Collett* 381 (BM)), suggests that the frequent occurrence today of narrow oblong sepals and incomplete subsidiary stem lines may have resulted from recent introgression from *H. perforatum*.

Schwarz (1965) recorded 2n=16 for '*H. erosum*' (= subsp. *obtusiusculum*) and 2n=24 for its hybrid with *H. perforatum*, adding that all his material gave the diploid number. Unless his results are duplicated in the future (which would necessitate a revision of the view adopted here), one must assume that his material was misidentified.

1x. *Hypericum* × *laschii* A. Fröhl. in *Mitt. Naturwiss. Vereines Steiermark* 51: 244, 245 (1915), in *Preslia* 32: 97–99, ff. 1, 2 (1960); Guşul. & Nyár. in *Sävul., Fl. R. P. Roman.* 4: 46 (1956). Type as for *H. tetraptero-quadrangulum* Lasch.

1. *H. maculatum* Crantz × 3. *H. tetrapterum* Fr. *H. tetraptero-quadrangulum* Lasch in *Linnaea* 4: 414 (1829). Type: Germany, Brandenburg, Driesen, 1829 (fl & fr), *Lasch* s.n. (B†-holotype).

*H. maculatum* Crantz × *H. acutum* Moench sensu A. Fröhl. in



*Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 584 (1911).

In comparison with *H. tetrapterum*: *Stems* relatively narrowly 4-winged. *Leaves* usually rather densely veined, with pale glands numerous, some large and some small. *Sepals* relatively broad, obtuse to rather acute. *Flowers* about twice as large.

For distribution see under nothoformae.

The name *H. × laschii* applies to all hybrids between *H. tetrapterum* and *H. maculatum*, but only crosses involving subspp. *maculatum* and *obtusiusculum* are recorded. It therefore occurs in diploid (2n=16) and triploid (2n=24) forms, depending on which subspecies of *H. maculatum* is involved. Nearly all records are of crosses involving subspp. *maculatum* (diploid), but Fröhlich (1911) described one that appears to involve subspp. *obtusiusculum* (i.e. it would be triploid). The syntype populations of *H. × desetangii* Lamotte from near Troyes (Aube, France) appear to be an example of this latter cross (nothoforma *froelichii*), not, as all authors after Bonnet (1879) have assumed, of *H. maculatum* × *perforatum*. Bonnet, himself, stated that it was 'intermédiaire entre la suivante [*H. tetrapterum*] et l'*H. quadrangulum* [*H. maculatum*]'. In the interests of nomenclatural stability, however, I have retained the current usage. The type of *H. intermedium* Belynyck has also proved to belong to *H. × laschii* nforma *froelichii*. A proposal to conserve the name *H. × desetangii* with a new type will therefore have to be made. Such a proposal would also conserve it against possible threats from *H. mixtum* Du Moulin and *H. commutatum* Nolte (see p. 104).

#### 1xa. *Hypericum × laschii* nothoforma *laschii*

1a. *H. maculatum* subsp. *maculatum* × 3. *H. tetrapterum* Fr.  
*H. maculatum* Crantz subsp. *typicum* A. Fröhl. × *acutum* Moench sensu A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 582, f. 12 (1911).

Icon: Rchb.,  *Ic. fl. germ. helv.* **6**: t. 344, no. 5178 (1842–1844) [*quadrangulo-tetrapterum*].

Intermediate in height and habit between the parents. *Leaves* with tertiary venation usually relatively densely reticulate. *Sepals* c. 0.5–0.75 × petals, obtuse to acute, with pale striiform laminar glands. *Petals* entire, with pale or pale and black punctiform and striiform laminar glands.

**FRANCE.** Cher: Achères, 20 July 1909 (fl), *Imbault* s.n. (FR). **Rhône**: Arnas, August, 1878 (fl), *Gandoger* Fl. Gall. Exs. 407 (H). **Tarn**: Anglès, 23 July 1911 (fl & fr), *d'Alleizette* s.n. (CLF).

**SWITZERLAND.** Schwyz (Einsiedlen), Zürich? (Geissboden), *fide* Fröhlich (1911).

**AUSTRIA.** Salzburg (Salzburg), **Oberösterreich** (Ischl), *fide* Fröhlich (1911).

**CZECH REPUBLIC.** Moravia: Bad Luhaovice, *fide* Fröhlich (1960).

**SLOVAKIA.** Bad Kovaová (near Zvolen), *fide* Fröhlich (1960).

**GERMANY.** Bayern: Kreis Augsburg, östlich Reinhartshausen, 5 August 1966 (fl), *Petermann* s.n. (H). **Thüringen**: Feun (with parents), August 1977 (fl), *Schulze* s.n. (FR). **Berlin**: Bredower Forst bei Berlin, August 1864 (fr), *O. Kuntze* (BM).

**POLAND.** Jelenia Góra: Schoenu [Zwierzawa], Polnisch-Hundorf, 4 June 1897 (fl), *Scholz* s.n. (H). Zielona Góra: Grünberg [Zielona Góra], Lindenbusch, 31 August 1892, *Hellwig* in *Callier* 576 (JE).

**DENMARK.** Fyn: Svendborg Fioniae, July 1872 (l. fl), *Lange* s.n. (K).

**SWEDEN.** Malmöhus: Helsingborg, 1 September 1897 (fl & fr), *Strandmark* s.n. (H); also several other collections from extreme SE Skåne.

This hybrid may be expected to occur anywhere within the wide area of overlap of the distributions of the parents; but, on account of the differing habitat requirements of the parents, it is rare.

1xb. *Hypericum × laschii* nothoforma *froelichii* N. Robson, **hybr. nov.** Type: Austria, Styria, Ragnitz bei Graz, c. 400 m, 31 July 1909 (fl & fr), *Fröhlich* GZU16255 (GZU!-holotype).

1c. *H. maculatum* subsp. *obtusiusculum* × 3. *H. tetrapterum* Fr.  
*H. quadrangulum* sensu Des Étangs in *Mém. Soc. Agric. Dép. Aube* **10**: 24 (1841).

?*H. tetrapterum* var. [β] *intermedium* Coss. & Germ., *Fl. descr. anal. Paris*: 64 (1845). This variety is described as intermediate between *H. tetrapterum* and *H. quadrangulum* (i.e. *H. maculatum*), of which the only subspecies in the Paris region is subsp. *obtusiusculum*.

*H. intermedium* Belynyck, *Fl. Namur*: 31 (1855); Gren., *Fl. jurass.* **1**: 154 (1863); Nyman, *Consp. fl. eur.*: 133 (1878); non Steud. (1847). Type: Belgium, Namur, Wépion, *Dave* s.n. (BR!-holotype).

*H. maculatum* Crantz subsp. *erosum* sensu Schinz & Keller. × *H. acutum* Moench sensu A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 588, f. 13 (1911).

Intermediate in height (c. 0.6 m) and habit between the parents. *Leaves* with tertiary venation laxly reticulate. *Sepals* c. 0.5 × petals, broadly to narrowly oblong or narrowly elliptic (sometimes in same flower), obtuse to acute or subacuminate, entire to apiculate-eroded, with pale punctiform and striiform and single black linear laminar glands.

Very rare, probably as a result of the differing habitat requirements of the parents. Austria.

**AUSTRIA.** Steiermark: Ragnitz bei Graz, 15 July 1910 (fl), *Fröhlich* GZU 16256 (GZU).

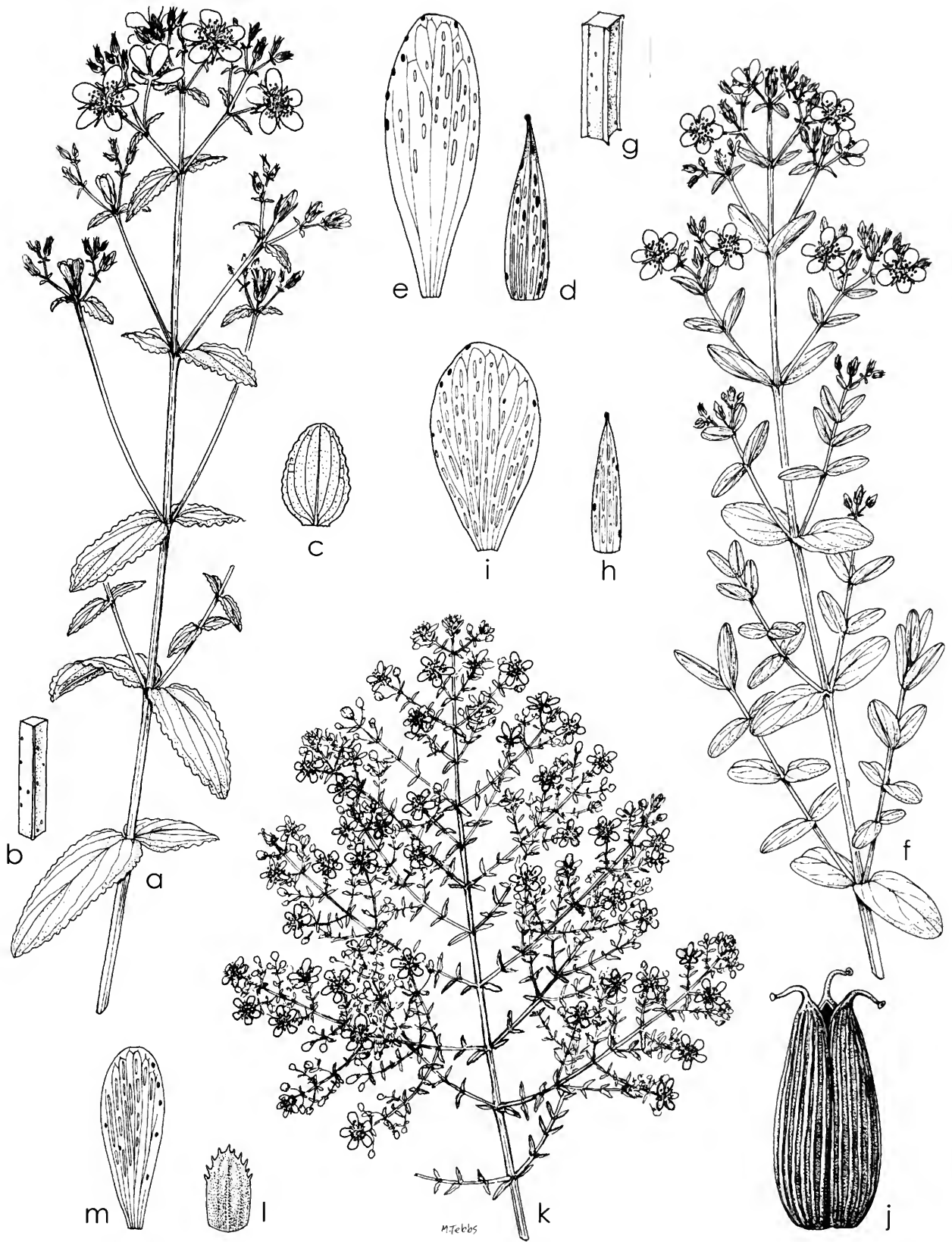
This hybrid was known from the type locality only (but probably includes the types of *H. × desetangii* and *H. intermedium*). Fröhlich (1911) described it as agreeing almost completely with the var. *maculatum* hybrids, but that (i) it was growing crowded together with both putative parents, so that cross-pollination was quite possible, (ii) it had characters intermediate between them, and (iii) its flowering dates were also intermediate. The latest of Fröhlich's collections of this hybrid (26 July 1914) was identified by him as *H. maculatum* subsp. *styriacum* × *acutum*.

1. *Hypericum maculatum* Crantz × 5. *H. perforatum* L. (see 5x, p. 102).

2. *Hypericum undulatum* Schousb. ex Willd., *Enum. pl. Berol.*: 810 (1809); Spach in *Ann. Sci. nat. Bot.* **5**: 357 (1836); Bab., *Man. Brit. bot.*: 67 (1843), in *J. Bot.* **2**: 97, t. 16 (1864); Archer Briggs in *J. Bot.* **2**: 45 (1864); Hance in *J. Bot.* **5**: 299 (1867); Nyman, *Consp. fl. eur.* **1**: 133 (1878); Lange in Willk. & Lange, *Prodr. fl. hisp.* **3**: 591 (1878); Bonnet in *Bull. Soc. Bot. France* **25**: 28 (1879); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 583 (1911); Ross-Craig, *Draw. Br. Pl.* **6**: t. 10 (1952); N. Robson in Tutin et al., *Fl. Europ.* **2**: 268 (1968); Franco, *Nova Fl. Portugal* **1**: 453 (1971); A. Ramos in *Trab. Dept. Bot. Univ. Complut. Madrid* **12**: 49 (1983), in *Acta Bot. Malac.* **11**: 167, f. 6d (1986), in Castroviejo et al., *Fl. Iberica* **3**: 167 (1989); Valdés, Talavera & Galiano, *Fl. Vasc. Andal. Occ.* **1**: 316 + map & fig. (1987); B. Tebbs in Press & Short, *Fl. Madeira*: 222 (1994); N. Robson in Cullen et al., *Europ. Gdn Fl.* **4**: 60 (1995). Type: Morocco, Tangier, *Schousboe* s.n. (C-holotype; G-BOISS!-isotype).

Fig. 7, Map 3.

*H. quadrangulum* var. [ε] *undulatum* (Schousb. ex Willd.) Choisy in DC., *Prodr.* **1**: 548 (1824); Colm., *Apunt. fl. Castillas*: 37 (1849).



**Fig. 7** A. *H. undulatum* var. *undulatum*: (a) habit; (b) stem section; (c) upper leaf; (d) sepal; (e) petal. B. *H. tetrapterum* var. *tetrapterum*: (f) habit; (g) stem section; (h) sepal; (i), petal; (j) capsule. C. *H. triquetrifolium*: (k) habit; (l) sepal; (m) petal (a, c, f, k  $\times 2/3$ ; b, g  $\times 2$ ; rest  $\times 6$ ). A. (a, b) Goyder & Jury 545; (c) Reverchon 238; (d, e) Davis 54961. B. (f, g) Gadecean s.n.; (h, l) Granvik s.n.; (j) Coste 801. C. Davis & Coode 39246.

- H. decipiens* H. Watson in *London J. Bot.* **3**: 588 (1844). Types: Azores, Flores (fl), *H. Watson* s.n. (K!-lectotype, selected here); Fayal (st), *J.C. Hunt* s.n. (K!-syntype).
- H. quadrangulum* sensu Colm., *Recuerd. bot. Galicia*: 10 (1850); Lowe, *Man. fl. Madeira*: 79 (1868) pro parte excl. typum.
- H. boeticum* sensu Syme, *Engl. Bot.*, 3rd ed. **2**: 153, t. 270bis (1864); H. Wats. in Godman, *Nat. hist. Azores*: 143 (1870); Bull in *J. Bot. (Lond.)* **13**: 296 (1875); Trelease in *Rep. Mo. bot. Gdn*, no. 8: 100 (1897); Stefanoff in *God. Agr.-les. Fak. Univ. Sofiya* **10**: t. 4 f. 27 (1932), **11**: 176 (1933), **12**: 88 (1934), in *Pflanzenareale* **4**(1): Karte 6a (1933).
- H. tetrapterum* var.  $[\beta]$  *undulatum* (Schousb. ex Willd.) Cout. in *Bolm Soc. Brot.* **12**: 21–22 (1895), comb. illegit. (Art. 58.2).
- H. acutum* subsp. *undulatum* (Schousb. ex Willd.) Rouy in Rouy & Foucaud, *Fl. France* **3**: 337 (1896); Cout., *Fl. Portugal*: 404 (1913), 2nd ed.: 482 (1939); comb. illegit. (Art. 58.2).
- H. desetangii* sensu Lloyd, *Fl. Ouest France*, 5th ed.: 72 (1898), non Lamotte (1874).
- H. acutum* var. *undulatum* (Schousb. ex Willd.) Pau in *Bol. Soc. Aragonesa Ci. Nat.* **8**: 118 (1909), comb. illegit. (Art. 58.2).
- H. quadrangulum* var. *tetrapterum* forma *undulatum* (Schousb. ex Willd.) Borg, *Descr. fl. Malt. isl.*: 248 (1927).
- H. maculatum* subsp. *undulatum* (Schousb. ex Willd.) P. Fourn., *Quatre fl. France*: 453 (1946).
- H. tetrapterum* subsp. *undulatum* (Schousb. ex Willd.) P. Silva in *Agron. Lusit.* **12**(2): 271 (1951) comb. illegit. (Art. 58.2).
- H. quadrangulum* subsp. *undulatum* (Schousb. ex Willd.) Goday & Carbonell in *Anales Inst. Bot. Cavanilles* **19**: 380 (1961).

Icones: Bab. in *J. Bot. (Lond.)* **2**: 97, t. 16 (1864); Ross-Craig, *Draw. Br. Pl.* **6**: t. 10 (1952).

*Perennial herb* 0.015–0.12 m tall, erect to decumbent from creeping and rooting base, with stems numerous to few, initially unbranched below inflorescence, later branched above. *Stems* narrowly and  $\pm$  equally 4-winged, with black glands on the wings and sometimes elsewhere; internodes 12–65(–80) mm, longer than leaves. *Leaves* sessile; lamina 6–40  $\times$  (3–)7–14(–20) mm, elliptic or narrowly ovate to narrowly oblong or rarely suborbicular, paler beneath, thickly to thinly chartaceous; apex rounded to obtuse or rarely subacute, margin usually crisped-undulate, base rounded to cordate-subamplexical; venation: 3(4) pairs of main laterals from lower quarter of midrib, tertiary reticulation rather dense; laminar glands pale, dense, medium to small; intramarginal glands black, close, irregular in size. *Inflorescence* 7-c. 40-flowered, from 1–3 nodes, with flowering branches ascending to horizontal from up to 6 nodes, the whole cylindrical to subcorymbiform, lax; pedicels 1–2.5 mm; bracts and bracteoles 2–4 mm long, lanceolate, entire, with (0–)2–8 black glands. *Flowers* 12–17 mm in diam., stellate; buds ellipsoid, obtuse. *Sepals* 5, subequal, 3–5.5  $\times$  1–1.8 mm, narrowly elliptic to lanceolate, acute to acuminate, entire, erect in bud and fruit; veins (3)5–7, when 5 the outer pair branched; laminar glands punctiform, all pale or nearly always (3–)6–20(–28) black; intramarginal glands black, few or absent, rarely with terminal black gland. *Petals* 5, bright yellow, nearly always tinged red dorsally, (5–)7–10  $\times$  3–4 mm, c. 2–2.5  $\times$  sepals, obovate-oblanccolate, entire; laminar glands black, punctiform, few or absent; marginal glands black, up to 6, scattered, or absent. *Stamens* c. 25–40, '3'-fascicled, longest (4.5–)5–8 mm, c. 0.75–0.9  $\times$  petals. *Ovary* 3-locular, 2–3.5  $\times$  1–1.5 mm, narrowly ovoid to narrowly ellipsoid; styles 3, free, 3–4 mm, 1–1.3  $\times$  ovary, spreading; stigmas narrowly capitate. *Capsule* 5–8  $\times$  3.5–4 mm, c. 1.65  $\times$  sepals, ovoid; valves with longitudinal linear vittae. *Seeds* yellow-brown, 0.6–0.8 mm, cylindrical, not carinate or appendiculate; testa linear-foveolate.  $2n=16$ ,  $32$  (ploidy apparently

not correlated with morphology). The record of  $2n=8$ ,  $n=4$  for this species by Guillén Oterino et al. (1997) is difficult to interpret. The count appears to be genuine, being vouched for and illustrated by drawings; but no other report of such a hypoploid number has been made elsewhere in the genus.

Non-calcareous marshes, mildly acidic bogs; 0–2700 m.

Extreme western Europe and North Africa: England (Cornwall, W. Devon), Wales (Pembroke, Cardigan, Merioneth), Ireland (W. Cork?, see below), France (W. Brittany, see below), central and W. Spain, Portugal, W. Algeria, N. Morocco, Madeira, Azores.

*Hypericum undulatum* occurs as two very unequal varieties. The vast majority of the species (var. *undulatum*) has relatively narrow undulate leaves and red-tinged flower buds; but a population in the south of Spain (Sierra Nevada) has broader plane-margined leaves and untinged flower buds. This population, which Boissier named *Hypericum boeticum*, appears to be intermediate in some characters between 2. *H. undulatum* and 3. *H. tetrapterum*; and since there are some plants with intermediate characters elsewhere in the Iberian Peninsula, some (particularly Spanish and Portuguese) botanists reduced these taxa to subspecies. The real 'link' between these species, however, would seem to be the plant from southern Italy and Sicily known as *H. neapolitanum* Ten., which is the most luxuriant form of *H. tetrapterum*. *Hypericum boeticum*, on the other hand, has flowers and inflorescence typical of *H. undulatum* in size and shape; and the broad leaves (which are linked in the population with ones more typical of *H. undulatum*) should be interpreted as a development in that species parallel with the broadening of the leaves in more advanced forms of *H. tetrapterum*. The plane margins and plain yellow petals are thus a reversion, not an intermediate condition. Populations that are truly intermediate between these species and apparently hybrid in origin occur in scattered localities in the Iberian Peninsula (see below). It seems appropriate, then, to treat the Sierra Nevada population as a variety (var. *boeticum*).

## 2a. *Hypericum undulatum* var. *undulatum*

*Plant* erect. *Leaves* (3–)4–14(–18) mm broad, elliptic to ovate, margin crisped-undulate. *Petals* red-tinged dorsally.

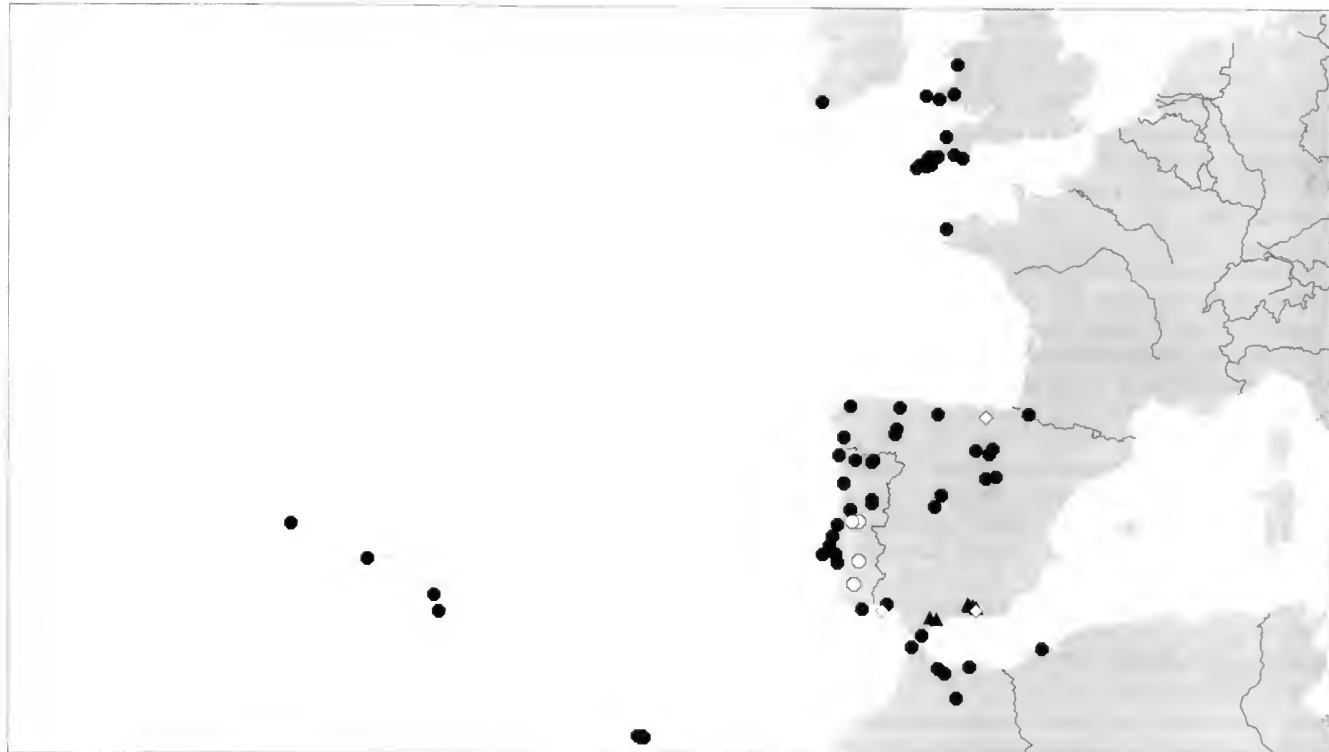
0–1750 m.

Distribution of the species except extreme south Spain. The record for Ireland (Co. Cork) is based on a specimen in K and that for France (Brittany) on specimens of a Lloyd collection in BM and ANG. The former, from Glengarriff, could just possibly be due to mislabelling, but the latter appears to be a correct record. Both collections were misidentified, the former as *H. tetrapterum* and the latter as *H.  $\times$  desetangii*. Lloyd, in *Fl. Ouest France* 5th ed., cites several localities round Brest for *H.  $\times$  desetangii*, his description of which agrees with *H. undulatum*, not *H.  $\times$  desetangii*. It seems, therefore, that the 'Atlantic' distribution of *H. undulatum* includes (or included) the extreme 'Atlantic' part of France and possibly SW Ireland.

**WALES. Merioneth:** Morfa Arthog (Arthog Bog), 2 August 1953 (fl), *Benoit* s.n. (K). **Cardigan:** 0.4 km W. of Trawscoed Station, 1933, *Salter* (Salter, 1935). **Pembroke:** between St. David's and Solva, 8 August 1931 (fl), *Alston* s.n. (BM); near Narberth, 1885 (fl), *Barrett* s.n. (BM).

**ENGLAND. W. Cornwall:** Penzance, Tremethick Moor, 7 August 1911 (fl), *Barton* s.n. (BM, K); N. of Camborne, Reskadinnick, 4 August 1971 (fl), *Murphy* s.n. (BM). **E. Cornwall:** Tywardreath Marsh, 23 July 1935 (fl), *Grose* 1278 (BM); near Falmouth, Penjerrick, August 1871 (c. fr), *T.A. Briggs* s.n. (BM). **S. Devon:** Morwellham, 9 August 1901 (fl), *Hume* 3944 (BM); Egg Buckland, Common Wood, 31 August 1872 (l. fl), *T.A. Briggs* s.n. (BM). **N. Devon:** Torrington, 9 September 1935 (fl & fr), *Chapple* s.n. (BM).





Map 3 *2. H. undulatum*. a. var. *undulatum* ●, other records ○; b. var. *boeticum* ▲. *2. H. undulatum* × *3. H. tetrapterum* ◆.

**IRELAND?** W. **Cork**: Glengariff, 18 August 1908, *C. Bucknall* s.n. (K). See Robson (1958b); but this record is not mentioned by Perring (1996).

**FRANCE. Finistère**: environs de Brest, end July 1886 (fl), *Blanchard* in *Lloyd* s.n. (ANG, BM); cult. du jardin d'un pied de Brest, end July 1890 (fl), *Lloyd* s.n. (ANG).

**SPAIN. Pontevedra**: Pontevedra, 27 July 1930 (fl & fr), *Buch* s.n. (H). **Coruña**: La Coruña, near Coruña, August 1888 (fl), *Guardia* s.n. (BM). **Oviedo**: gorge of Peña de la Paloma, near Tineo, 16 July 1927 (fl), *Wilmott* s.n. (BM). **Cantabria**: Santander, Picos de Europa, Fuente De, 1200 m, 1 August 1969 (fl), *Grimes* 229 (BM). **León**: El Bierzo, Villanueva to San Adrian, 900 m, 10 July 1933, *Rothmaler* 471 (JE). **Soria**: Vinuesa, Santa Inés, in loco Gargantillas, 1450 m, 15 July 1989 (fl), *Segura Zubizarreta* in Soc. Exch. Pl. Vasc. Eur. Bass. Med., Fasc. 23, 14273 (RNG). **La Rioja**: Valle del Río Iregna, between Pantano Ortigosa and Lumbreras, 1 July 1958 (bud), *Sandwith* 5265 (K). **Avila**: 25 km SE of Avila, 3 August 1962 (fl), *Scott* 359 (BM). **Zaragoza**: Catalayud, Sierra de Vicort, 23 July 1910 (fl), *Viciosa* in *Sennen* 1122 (FR, H, JE). **Tarragona**: Cambrils, acequia 'Canaleta del Civil', Partida de l'Ardiaca, 12 August 1926 (fl), *Teodora* s.n. (BM). **Guadalajara**: Aldeanueva de Atienza, 11 September 1965 (fl), *Silvestre* s.n. (RNG, SEV\*). **Huelva**: between Palos de la Frontera and Punta Arenilla, 8 October 1968 (fl & fr), *Bramwell & Valdés* 173 (RNG).

**PORTUGAL**. Throughout, but rarer in SE (Franco, 1971: 453). **Minho**: Viana do Castelo, fl. Minii prope Seixas, 29 July 1938, *Rothmaler* s.n. (JE). **Tras-os-Montes**: Vila Real, Chaves, prope Sapiães, 800 m, 31 July 1938, *Rothmaler* 14002 (JE). **Douro Litoral**: S. of Oporto, Granja, 31 July 1910 (fl), *Johnston* s.n. (BM). **Beira Alta**: Guarda, Serra da Estrêla, 5 km from Pousada de São Lourenço to Gouveia, 1360 m, 20 August 1982 (fl), *Goyder & Jury* 545 (BM, RNG). **Beira Baixa**: fide Ramos (1993). **Beira Litoral**: Coimbra, 20 September 1950 (e. fr), *J. & A. Matos* s.n. (BM). **Estremadura**: Lisboa, Torres Vedras prope Puteiro, 3 July 1936, *Rothmaler* s.n. (JE). **Ribatejo, Alta Alentejo, Baixa Alentejo**: fide Ramos (1993). **Algarve**: Faro, ribeira de S. Cristovão, August 1882 (e. fr), *Peres* in Fl. Lusit. (4<sup>o</sup> anno) 562 (BM).

**MOROCCO. Tanger**: Tetuan, Cap Spartel, 200 m, 3 July 1989 (fl), *Garcia, Silvestre & Talavera* 110/89 (SEV). **Rif**: W. side of Ketama, 1500–1600 m, 8 July 1973 (fl), *Davis* 54961 (BM, E\*). **Moyen Atlas**: Ras Chedaya, Bab Boudir, 1400 m, 2 August 1968 (fl), *Fry* 193 (BM).

**ALGERIA. Oran**: Gambetta, 9 June 1913 (fl), *Faure* s.n. (H).

**MADEIRA**. S. of Ribeiro Frio, 3 km N. of Poiso, 1100 m, 31 July 1979 (fl), *Jarvis & Wild* 820 (MO); Queimadas, 900 m, 17 August 1961 (fl), *Coleridge* 6 (BM; K); Santa Madalena, 4 July 1957 (fl), *Malmberg* s.n. (H); Passa d'Area, 12 August 1855 (fl), *Lowe* s.n. (BM).

**AZORES. Santa Maria**: Ribeira da Vila, 50 m, 2 May 1972 (st), *Gonçalves* 3947 (BM). **São Miguel**: Seara near Sete Cidades, Lagoa Azul, W. bank, 243 m, 26 July 1970 (fl), *Dolman* 329 (BM). **Terceira**: Terreiro dos Prados, 450 m, 10 July 1971 (fl), *Gonçalves* 3148 (BM). **São Jorge**: Camolico do Pinheiro, 400 m, 4 September 1971 (e. fr), *Gonçalves* 3442 (BM). **Pico**: Madalena, 9 July 1938 (fl), *Cederkreutz* s.n. (H). **Faial**: Caldeira, 500 m, 7 October 1971 (fl & e. fr), *Gonçalves* 3652 (BM). **Flores**: Fazenda, Santa Cruz to Lajes, 200 m, 3–8 September 1985 (fl), *Parry* 103 (BM). **Corvo**: Weather station, 200 m, 3 September 1967 (fl), *Pryor* 170 (BM).

2b. *Hypericum undulatum* var. [β] *boeticum* (Boiss.) Lange in Willk. & Lange, *Prodr. fl. hisp.*: 591 (1878); N. Robson in Tutin et al., *Fl. europ.* 2: 268 (1968) in adnot. Type as for *H. boeticum* Boiss.

Map 3.

*H. boeticum* Boiss., *Elench. pl. nov.*: 25 (1838), *Voy. bot. Espagne* 1: t. 34 (1839), 2: 114 (1839); Nyman, *Consp. fl. eur.* 1: 133 (1878); Burdet, Charpin & Jacquem. in *Candollea* 39: 788 (1984). Types: Spain, Granada, prope Yunquera prov. Malacitanæ, 1837, *Boissier & Reuter* s.n. (G-BOISS!-lectotype, N. Robson, 22 June 1955); prope Alhaurin, Carratraca et thermas Viló, *Boissier & Reuter* s.n. (G-BOISS!-syntype); secus fluvium Jenil inter Granada et Guejar, *Boissier & Reuter* s.n. (G-BOISS!-syntype); inter Berja et Adra in ditone Alpujarras dicta, *Boissier & Reuter* s.n. (G-BOISS!-syntype). 'In humidis mont. Regn. Granat. vulg., Aest. 1837' (fl), *Herb. Boissier* (K) is likely to be a duplicate of one of the above collections.

*H. tetrapterum* var. [β] *rotundifolium* Willk. in Willk. & Lange,

*Prodr. fl. hisp.* 3: 591 (1878). Type: Spain, Granada, Barranco de Gualnon, Dehesa de S. Geronimo, 1800 m, July 1844, *Willkomm* s.n. (G-lectotype, selected here; BM!-isolecotype); *Monachil*, *Funk* s.n. (G-syntype). Willkomm's original (unpublished) name for this taxon would appear to have been var. *nivale*, according to the label on Willkomm, Pl. *Hisp. Exsicc.* 1844-6 no. 358 (BM).

*H. tetrapterum* var. *boeticum* (Boiss.) Cout. in *Bolm Soc. Brot.* 12: 21-22 (1895).

*H. acutum* var. [ $\beta$ ] *rotundifolium* (Willk.) Schinz in *Bull. Herb. Boissier* II, 3: 16 (1902); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120: 582 (1911), comb. illegit.

*H. acutum* subsp. *boeticum* (Boiss.) Cout., *Fl. Portugal:* 404 (1913), 2nd ed.: 482 (1939), comb. illegit.

*H. baeticum* sensu auct. plur., sphalm.

Icon: Boiss., *Voy. bot. Espagne* 1: t. 34 (1839).

Plant erect to decumbent. Leaves (4-)8-20 mm broad, broadly elliptic to orbicular, margin plane. Petals not red-tinged dorsally.

1500-2700 m.

Spain (Andalucia).

**SPAIN. Granada:** barranco del río Segura, 1500 m, July 1906 (c. fl), *Reverchon* 238 p.p. (BM, FR, H); Capileira, c. 1750 m, 18 June 1962 (st), *Rovainen* s.n. (H). **Málaga:** Sierra de Yunquera, 3 July 1890 (fl), *Reverchon* 238 p.p. (JE, K).

When *H. boeticum* is regarded as an extreme development of *H. undulatum*, it becomes evident that Willkomm's var. *rotundifolium* is not part of *H. tetrapterum* but forms an extreme development of *H. undulatum* var. *boeticum*. Indeed there seems to be no break in variation between typical var. *boeticum* and the higher-altitude 'var.' *rotundifolium*, which differs in its decumbent habit, smaller leaves and fewer smaller flowers. Examples of this form (additional to the syntypes cited above) are:

**SPAIN. Granada:** Sierra Nevada, pass between Borreguiles de San Juan and Peñones de San Francisco, 2700 m, 23 August 1948 (e. fr), *Heywood & Davis* 983 (BM); Río Monachil, 2300 m, 28 July 1950 (fl), *Rovainen* s.n. (H).

## 2. *H. undulatum* $\times$ 3. *H. tetrapterum*

Map 3.

The following specimen has characters intermediate between 2a. *H. undulatum* var. *undulatum* and 4a. *H. tetrapterum* var. *tetrapterum* and is assumed to be a hybrid between these taxa:

**SPAIN. Viscaya:** Bilbao mont., 20 July 1905 (fr), *Elias* 801 (BM).

An intermediate specimen from Andalucia, however, is probably a hybrid involving 2b. *H. undulatum* var. *boeticum*:

**SPAIN. Granada:** Andalucia, near Trevezlez, Puerta de Granada, 1260 m, 4 August 1969 (fl), *Brinton-Lee* 940 (BM).

3. ***Hypericum tetrapterum*** Fr., *Novit. fl. suec.*: 94 (1823), ed. altera: 236 (1828); Spach, *Hist. nat. vég.*, Phan. 5: 387 (1836), *Ann. Sci. Nat. Bot.* 5: 357 (1836); W. Koch, *Syn. fl. germ.*: 134 (1837); Rchb., *lc. fl. germ. helv.* 6: t. 344, f. 5179 (1844); Godr. in Gren. & Godr., *Fl. France* 1: 34 (1847); Bellyneck, *Fl. Namur*: 31 (1855); Syme, *Engl. Bot.* 3rd ed. 2: 152, t. 270 (1864); Boissier, *Fl. orient.* 1: 805 (1867); Bab., *Man. Brit. bot.*, 6th ed.: 66 (1867); Lange in Willk. & Lange, *Prodr. fl. hisp.* 3: 591 (1878); Bonnet in *Bull. Soc. Bot. France* 25: 279 (1879); Schinz & Keller, *Fl. Schweiz:* 326 (1900); Coste, *Fl. France* 1: 259 (1901); Stefanoff in *God. Agr.-les. Fak. Univ. Sofiya* 10: t. 4 f. 26 (1932), 11: 175 (1933), 12: 87 (1934), in *Pflanzenareale* 4(1): Karte 6a (1933); Mansfeld in *Repert. Spec. Nov. Regni Veg.* 47: 278 (1939); Pugsley in *J. Bot.* 78: 35 (1940); Ross-Craig, *Draw.*

*Br. Pl.* 6: t. 9 (1952); N. Robson in Davis, *Fl. Turkey* 2: 399 (1967), in Tutin et al., *Fl. Europ.* 2: 268 (1968), in Rech.f., *Fl. Iranica*, Guttif.: 17 (1968), in Townsend & Guest, *Fl. Iraq* 4: 378 (1980); in Cullen et al., *Europ. Gdn. Fl.* 4: 60 (1995), in Wisskirchen & Haeupler, *Standardliste Farn- u. Blütenpfl. Deutschl.*: 270 (1998); Pignatti, *Fl. Italia* 1: 177 (1982); Zelený et al. in Futák & Bertová, *Fl. Slovenska* 3: 306, t. 37 f. 2, map 57 (1982); Hagemann in *Flora* 173: 115, tt. 5B, 15-18, 39 (1983); A. Ramos in *Trab. Dept. Bot. Univ. Complut. Madrid* 12: 49 (1983), in *Acta Bot. Malac.* 11: 167, t. 6c (1986), in Castroviejo et al., *Fl. Iberica* 3: 168, t. 46 (1989); Azadi in *Fl. Iran* 27: 9 + t. + map (1999). Type: Sweden, Skåne, in silva Resten, 1819 (?), *Fries* s.n. (UPS-holotype).

Fig. 7, Map 4.

*H. quadrangulum* L., *Sp. pl.*: 785 (1753); Huds., *Fl. angl.*: 292 (1762); Crantz, *Stirp. austr.* 2: 65 (1763); Leers, *Fl. herborm.*, 2nd ed.: 169 (1789); Vill., *Hist. pl. Dauphiné* 3: 497 (1789); Sm., *Engl. Bot.*: t. 370 (1797), *Fl. Brit.* 2: 801 (1800); DC., *Fl. France* 4: 862 (1805); Choisy, *Prodr. monogr. fam. Hyperic.*: 47 (1821), in DC., *Prodr.* 1: 548 (1824); Bab. in *Trans. bot. Soc. Edinburgh* 1: 83 (1841), *Man. Brit. bot.*: 57 (1843); Syme, *Engl. Bot.*, 3rd ed. 2: 152, t. 270 (1864); Rendle & Britten in *J. Bot.* 45: 436 (1907); Grande in *Boll. Orto bot. Regia Univ. Napoli* 8: 74 (1926); Pugsley in *J. Bot.* 78: 25 (1940); N. Robson in Greuter, Burdet & Long, *Med-Checklist* 3: 271 (1986); nom. rejic. (see N. Robson in *Taxon* 39: 135 (1990) and Brummitt in *Taxon* 43: 114 (1994)). Type: Netherlands (?), *Hort. Cliff.* 380 (BM!-holotype).

*H. quadrangulare* sensu L., *Diss. Hypericum*: 5 (1776), *Amoen. Acad.* 8: 322 (1785); Murray, *Syst. veg.*, 14th ed.: 584 (1784); Lam., *Dict.* 4: 163 (1797); Willd., *Sp. pl.* 3: 1459 (1802), sphalm. Type as for *H. quadrangulum* L.

*H. acutum* Moench, *Methodus*: 128 (1794); Beck, *Fl. Nieder-Österreich* 2(1): 530 (1892); Rouy in Rouy & Fouc., *Fl. France* 3: 335 (1896); Burnat, *Fl. Alpes marit.* 2: 28 (1896); Schinz in *Bull. Herb. Boissier* II, 3: 16 (1902), in *Vierteljahrsschr. Naturf. Ges. Zürich* 49: 241 (1905); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 580 (1911); Thellung in *Allg. Bot. Z. Syst.* 1912: 19 (1912); Coutinho, *Fl. Portugal:* 404 (1913), 2nd ed.: 481 (1939); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.* 2nd ed. 21: 179 (1925); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 520 (1925); Briquet, *Prodr. fl. corse* 2(2): 144 (1936); Gorschikova in Shishkin & Bobrov, *Fl. URSS* 15: 241 (1949); Stjep.-Vesel. in Josifović, *Fl. Srbije* 3: 116, t. 33 f. 2 (1972); nom. illegit. (Art. 52). Type as for *H. quadrangulare* L.

[*H. alatum* Retz., *Obs. bot.*: 18 (1810); Rchb. in *Flora* 5: 530 (1822). Type: ex America septentrionale, *Collector?* (LU). Wahlenberg (*Fl. suec.*: 476 (1826)) makes this a synonym of his *H. quadrilatum* along with '*H. quadrangulare* Sm.' and *H. tetrapterum* Fr.; but the original description (e.g. ... *caule ... subtomentoso, calycibus serrulato-glandulosis*) clearly applies to quite another plant.] *H. quadratum* Stokes, *Bot. Mat. Med.* 4: 99 (1812), nom. illegit. (Art. 52). Type as for *H. quadrangulum* L.

*H. quadrangulum* var. [ $\delta$ ] sensu Choisy, *Prodr. monogr. Hyperic.*: 47 (1821).

*H. quadrangulum* var. [ $\delta$ ] *confertum* Choisy in DC., *Prodr.* 1: 548 (1824). Type unlocalized, *collector* unrecorded (G-DC!-lectotype, selected here); England, 1816, *Dawson Turner* s.n. (G-DC!-syntype). Although Choisy cites only 'Anglia' for the provenance of his var.  $\delta$  in 1821, the Dawson Turner specimen is *H. perforatum*. The other specimen, however, is *H. tetrapterum*, and its dense inflorescence would appear to be the origin of the epithet *confertum*.

- H. quadrangulare* var. [ $\alpha$ ] *humile* Boenn., *Prodr. fl. monast. westphal.*: 227 (1824). Type: Germany, none stated.
- H. quadrangulare* var. [ $\beta$ ] *alatum* (Retz.) Boenn., *Prodr. fl. monast. westphal.*: 227 (1824) pro parte excl. typum. See *H. alatum* Retz. above.
- H. quadrangulare* var. [ $\gamma$ ] *patulum* Boenn., *Prodr. fl. monast. westphal.*: 227 (1824). Type: Germany, none stated.
- H. quadrialatum* Wahlenb., *Fl. suec.*: 276 (1826), nom. illegit. (Art. 52.1). Type as for *H. tetrapterum*.
- H. neapolitanum* Ten., *Ind. Sem. Hort. Neap. ann. 1829*: 19 (1829); Guss., *Fl. sic. syn.* 2: 379 (1843); Lojacono-Pojero, *Fl. sicula* 1(1): 188 (1886–88). Type: Sicily, sine loc., in pratis paludosis, pre May 1830 (fl), Tenore s.n. (NAP-holotype; K!-isotype). Gussone gives a valid description but attributes the name to Tenore. I have not been able to check that Tenore himself provided a valid description.
- H. confertum* (Choisy) G. Don, *Gen. Syst.* 1: 606 (1831), non Moench (1794) nec Choisy (1821), nom. illegit. (Art. 52). Based on *H. quadrangulum* var. *confertum* Choisy.
- H. neapolitanum* var. *confertum* (Choisy) Guss., *Fl. sic. syn.* 2: 379 (1843); Lojacono-Pojero, *Fl. sicula* 1: 188 (1886–1888). Type as for *H. quadrangulum* var. *confertum* Choisy.
- Holosepalum quadrangulum* (L.) Fourr. in *Ann Soc. Linn. Lyon*, N.S. 16: 352 (1868).
- Hypericum rotundatum* Schur in *Verh. naturf. Vereins Brünn* 15(2): 159 (1877). Type: Romania, Transylvania, 'Auf Moorwiesen, an Gräben auf den Burgenwiesen bei Kronstadt [Braşov]', July 1854, Schur s.n. (FR!-holotype).
- H. borbasii* Formáněk in *Verh. naturf. Vereins Brünn* 29: 143 (1891). Type: Turkey: Istanbul (Asia), Alemdağ ('Alemda'), July–August 1890 (fl), Formáněk s.n. (BRNM!-holotype).
- H. quadrangulum* var. *acutum* (Moench) Fiori in Fiori & Paol., *Fl. Italia* 1: 387 (1898), *Nuovo fl. Italia* 1: 521 (1924), comb. illegit. (Art. 58.2).
- H. quadrangulum* subsp. *quadrangulum* sensu Tourlet in *Bull. Soc. Bot. France* 50: 307 (1903); Schinz in *Vierteljahrsschr. Naturf. Ges. Zürich* 49: 231–241 (1905), pro parte uterque quoad typum.
- H. tetrapterum* forma *stigmaphyllum* Woron. in Kuzn., Busch & Fomin, *Fl. Cauc. crit.* 3(9): 43 (1906). Type: Russia, Ciscaucasia, Stavropol, Norman s.n. (LE).
- H. tetrapterum* var. [ $\beta$ ] *neapolitanum* (Ten.) N. Terracc. in *Nuovo Giorn. Bot. Ital.* 14: 135 (1907).
- H. acutum* forma *humile* (Boenn.) Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 521 (1925); Guşul., in Sävul., *Fl. R. P. Roman.* 4: 26 (1956) ['Boenningh. ex Hegi'].
- H. acutum* forma *patulum* (Boenn.) Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 521 (1925).
- H. acutum* subsp. *eu-acutum* Hayek, *Prodr. Fl. Pen. balc.* 1: 534 (1925), nom. illegit. (Arts 21.3, 52, 58.2).
- H. maculatum* subsp. *quadrangulum* (L.) Hayek, *Prodr. Fl. Pen. balc.* 1: 534 (1925), pro parte quoad typum.
- H. quadrangulum* var. *tetrapterum* (Fr.) Borg, *Descr. Fl. Malt. isl.*: 248 (1927).
- H. acutum* subsp. *tetrapterum* (Fr.) Maire in Jahandiez & Maire, *Cat. pl. Maroc*: 483 (1932), comb. illegit. (Art. 58.2).
- H. acutum* var. *typicum* Guşul. in Sävul., *Fl. R. P. Roman.* 4: 885 (1956). Type as for *H. acutum* Moench=*H. quadrangulum* L.=*H. tetrapterum* Fr. On p. 26 this combination is given as 'f. nova', but on p. 885 (with other nomenclatural novelties) as 'var. nova'. The latter would seem to have been intended.
- H. quadrangulum* subsp. *acutum* (Moench) Goday & Carbonell in *Anales Inst. Bot. Cavanilles* 19: 380 (1961), comb. illegit. (Art. 58.2).

*H. fallax* subsp. *fallax* var. *quadrangulare* (L.) O. Schwarz in *Drudea* 5: 63 (1965) pro parte quoad typum.

Icones: see under varieties.

*Perennial herb* (0.15–)0.2–0.7(–1.2) m tall, erect to  $\pm$  decumbent or rarely ascending to procumbent from creeping and rooting base, with stems numerous to few, initially unbranched below inflorescence, later branched above for half to most of their length. *Stems*  $\pm$  broadly 4-winged, the subsidiary wings narrower or rarely with wings equally narrow, with black glands on the lines and sometimes elsewhere; internodes 7–50 mm, shorter than to exceeding leaves. *Leaves* sessile or rarely (especially the lower) up to 0.5 mm petiolate; lamina (6–)9–40  $\times$  (4–)7–24 mm, ovate or elliptic or triangular-ovate to orbicular, somewhat paler beneath, thinly chartaceous; apex rounded to very rarely apiculate-obtuse, margin plane or rarely  $\pm$  undulate, base rounded to cordate-amplexicaul; venation: 1–3 pairs of main laterals from base of midrib; tertiary reticulation dense, rather obscure; laminar glands pale, dense, small; intramarginal glands black, rather close, uniform. *Inflorescence* (1–)10–35(–c. 70)-flowered, from 1–2(–4) nodes, with flowering branches ascending from up to 10 nodes, the whole cylindrical to corymbiform, dense or with partial inflorescences dense; pedicels 1–2 mm; bracts and bracteoles 2–3 mm long, lanceolate to linear, entire, with 0–4 black glands. *Flowers* 10–15 mm in diam., stellate; buds ellipsoid, subacute. *Sepals* 5, equal, 3–5  $\times$  1–1.5 mm, lanceolate to narrowly oblong, acute to acuminate, entire, erect in bud and fruit; veins 3 with outer pair branched or 5 unbranched; laminar glands striiform to punctiform or occasionally basal linear, all pale or 1–2 black; marginal glands absent or rarely up to 7, black, immersed. *Petals* 5, rather pale yellow, not tinged red, 5–8  $\times$  2–3(–4) mm, c. 1.4  $\times$  sepals, oblanceolate, entire or distally unilaterally crenate; laminar glands absent or rarely few, punctiform, black and pale; marginal glands 1–4 or usually absent. *Stamens* 30–40(–60), '3'-fascicled, longest c. 4.5–7.5 mm, c. 0.9  $\times$  petals. *Ovary* 3-locular, 2–2.5  $\times$  1–1.5 mm, narrowly ovoid; styles 3, free, 2–3.5 mm, 0.8–1.4  $\times$  ovary, widely spreading. *Capsule* 5–7(–8)  $\times$  2.4–4 mm, c. 2  $\times$  sepals, narrowly cylindrical-ellipsoid to ovoid; valves with longitudinal linear vittae. *Seeds* dark brown, 0.6–0.8(–1.1) mm, cylindrical, not carinate or appendiculate; testa finely foveolate.  $2n=16$  (Stenar, 1938; Noack, 1939; Pólya, 1950; Robson, 1956; Gadella & Kliphuis, 1966; Zhukova, 1967),  $n=8$  (Nielsen, 1924; Winge, 1925; Chattaway, 1926; Noack, 1939; Sugiura, 1944).

In wet habitats – marshes, streamsides, open ditches, wet meadows, springs; 0–1300 m (Switzerland, Valais), –1900 m (Corsica), –2000 m (Turkey).

Europe from Scotland (Orkney and Sutherland southward), Denmark, S. Sweden (Skåne), Poland, the SW Ukraine and Transcaucasia south to Spain, Algeria, Sicily, Greece, Turkey, N. Israel, N. Iraq and NW Iran.

The variation in *H. tetrapterum* is wide but almost continuous, from a tall, branching, relatively narrow-leaved form in southern Italy and Sicily ('*H. neapolitanum*') to short unbranched forms in northern Europe. In two areas, however, decumbent small-leaved few-flowered high-altitude forms have developed – Corsica and the Levant. Although in neither area have field studies been made to decide how distinct these forms are from the adjacent typical form, they both seem worth recognizing at least until such studies are made.

*Hypericum tetrapterum* is related to 2b. *H. undulatum* var. *undulatum*, differing from it in the more broadly winged stem internodes, the usually relatively broader leaves with plane margin,

and the denser inflorescence with smaller flowers, sepals with fewer black laminar glands, and paler petals that are not tinged red. The form most similar to var. *undulatum* occurs in southern Italy and Sicily ('*H. neopolitanum* Ten.').

### 3a. *Hypericum tetrapterum* var. *tetrapterum*

*H. tetrapterum* subsp. *tetrapterum*, Zangheri, *Fl. Ital.* 1: 396 (1976).

Icones: Rchb.,  *Ic. fl. germ. helv.* 6: t. 344, f. 5179 (1844); Ross-Craig, *Draw. Br. Pl.* 6: t. 9 (1952); Ramos in Castroviejo et al., *Fl. Iberica* 3: t. 46 (1989).

*Stems* erect, to 1.2 m tall. *Leaves* sessile or lowermost to 0.5 mm petiolate, 9–40 mm long, ovate or elliptic to orbicular, margin nearly always plane. *Inflorescence* 10-c. 70-flowered, from 1–4 nodes, with flowering branches from up to 10 nodes below.

Lowland to montane zones; 0–1380 m.

Distribution as for species, except for the alpine zone (1380–2000 m).

**SCOTLAND.** **Orkney:** Hoy, North Walls, Lyness, 16 July 1956 (fl), *Sinclair* 8872 (K). **East Ross:** Dingwall, 25 July 1961 (fl), *McCallum Webster* 5788 (K). **Moray:** near Elgin, Lochinver Farm, 13 August 1960 (fr), *McCallum Wester* 3833 (K). **Kincardine:** St. Cyrus, 6 August 1881, *Nicholson* s.n. (JE). **Mid Perth:** Crieff, near Comrie, July 1880 (fl) *Bennett* s.n. (BM). **W. Lothian:** near Kirkliston, 1 August 1905 (fl), *Bennett* s.n. (BM). **E. Lothian:** Aberlady, 15 August 1933 (fl & fr), *Taylor* s.n. (BM). **Lanark:** Carluke, meeting of Cauldron Gill and Yieldshiel Burn, 11–15 July 1962 (fl), *Phillips* 176 (BM). **Wigtown:** Wigton, July 1895 (fl), *McAndrew* s.n. (BM). **Clyde Isles:** Arran, Whiting Bay, Glenashdale, 26 July 1953 (fl), *Robson* 24 (BM). **Argyll:** near Crarae, 20 July 1936 (fl), *A.B. Jackson* s.n. (BM). **S. Ebuades:** Islay, Bowmore to Laggan Bridge, 28 August 1955 (e. fr), *Hillcoat* s.n. (BM).

**ENGLAND.** **Westmorland:** Arnside, 5 August 1896 (fr), *Worsdell* s.n.

(K). **Durham:** Wynch Bridge, 18 June 1934 (fl), *Taylor* s.n. (BM). **NE Yorks.:** near Scarborough, Trontedale, 20 July 1939 (fl), *Evans* s.n. (BM). **S. Lancs.:** Freshfield Dunes, 26 July 1929 (fl), *Holder* 461 (LIV). **Notts.:** E. of Blaxton on B 1396, 25 July 1963 (fl), *Bowden & Hillman* 359 (BM). **S. Lincs.:** near Fenhouses, 31 July 1945 (fl), *N.D. Simpson* s.n. (BM). **Worcs.:** Wyre Forest, 11 August 1915 (fl), *Rea* s.n. (BM). **E. Gloucs.:** Shuthanger Common, 22 September 1973 (fl), *Fowlers* s.n. (BM). **Huntingdon:** Eynesbury, August 1944 (fl), *Peck* s.n. (BM). **W. Suffolk:** Mildenhall, July 1908 (fl), *Adams* s.n. (BM). **Oxford:** King's Sutton, 1 August 1961 (fl), *Sheasby* 601 (BM). **Middlesex:** Finchley Common, 12 September 1925 (fr), *Moring* 282 (BM). **Surrey:** Horley, Langshott Wood, July 1948? (fl), *Morgan* s.n. (BM). **E. Sussex:** Pett, 12 September 1938 (fl & fr), *Bangerter* s.n. (BM). **Isle of Wight:** Freshwater, 1 August 1953 (fl), *Hancock* s.n. (BM). **S. Wilts.:** Donhead St. Mary, Alec's Shade, 4 August 1947 (fl), *Wihnott* 1102 (BM). **N. Devon:** Braunton Burrows, 15 July 1957 (fl), *Matthews* s.n. (BM). **W. Cornwall:** St. Ives, 17 June 1952 (fl), *Edwards* 57 (BM).

**WALES.** **Glamorgan:** Kenfig Dunes, 15 July 1934 (fl), *N.D. Simpson* s.n. (BM). **Carmarthen:** Pembrey, September 1900 (fl), *Riddelsdell* s.n. (BM). **Pembroke:** Sagerton Common, 18 August 1957 (fr), *Powers* 5 (BM). **Radnor:** near Rhos-goch, 18 August 1885 (fl), *A. Ley* s.n. (BM). **Caernarvon:** Bardsey I., August 1933? (fl), *Butler* (BM). **Flint:** Bodlewyddan Park, 12 August 1941 (fl), *A.B. Jackson* s.n. (BM).

**IRELAND.** **N. Kerry:** Lough Leane, E. side of Ross I., c. 20 m, 20 July 1973 *Jerny* 10391 (BM). **W. Cork:** near Toormore Mizen Head, near Ballyrigode House, 1 July 1961 (fl), *James* 60 (BM). **Waterford:** c. 2.4 km S. of Tramore, near road to Great Newton Head, 18 August 1967 (fl), *Ferguson* 2039 (BM). **Dublin:** How the Hill, August 1877 (e. fr), *Gamble* 26303 (K). **Longford:** 8 km SW of Granard, 17 August 1961 (fl), *Summerhayes* 3599 (K). **S. Donegal:** Ballyshannon, 1992 (fl & fr), *Wyse Jackson* s.n. (Herb. M.W.J.).

**CHANNEL ISLANDS.** **Guernsey:** Petit Bot Bay, 22 July 1950 (fl), *F. Balfour-Browne* s.n. (BM). **Sark:** near harbour, 10 July 1953, *Sowerby* 134 (BM). **Herm:** N. of island, 13 August 1952 (fl), *Hancock* s.n. (BM). **Alderney:** Clanque Bay, 16 August 1932 (fl), *A.B. Jackson* 579 (K). **Jersey:** no loc., 21 July 1900 (fl), *Lester-Garland* s.n. (K).



Map 4 3. *H. tetrapterum*. a. var. *tetrapterum* ●, other records ○; b. var. *corsicum* ▲; c. var. *anagallidifolium* ■ (among the Lebanon records).

**THE NETHERLANDS. Zuid-Holland:** Rozenburg I., 'De Beer', 26 August 1948 (e. fr), *Maas Geesteren* 4321 (K, L\*). **Utrecht:** N. of Utrecht, Molenpolder, 19 August 1953 (fr), *Leeuwenberg* s.n. (H).

**BELGIUM. Antwerpen:** entre Lierre [Lier] et Emblehem, 25 July 1920 (e. fr), *Lambert* s.n. (BM). **Namur:** Wavreille, June 1914 (fl), *Boullenger* s.n. (BM).

**FRANCE Oise:** près Senlis, Fôret de Hallare, 18 August 1834 (fl), *Bentham* s.n. (K). **Seine:** bois de Meudon, 26 August 1889 (fl & fr), *Gadeceau* s.n. (BM). **Finistère:** Morlaix, August 1883 (fl), *Miciol* s.n. (BM). **Loire-Atlantique:** ruisseau d'Escoublac, 1887 (fr), *Gadeceau* s.n. (BM). **Deux-Sèvres:** Saint-Genard, près de Chancelles, August 1951 (fl), *Contre* in Soc. Fr. Exch. Pl. Vasc. B. de Retz 5 (K). **Cher:** Saulzait-le-Potier, 22 July 1859 (e. fr), *Déséglise* s.n. (BM). **Haut-Rhin:** Pfetterhausen, 9 August 1869 (fl & fr), *Gadeceau* 217ter (BM). **Doubs:** Besançon, marais de la Malcombe, n.d. (fl), *Grenier* 2036bis (BM, JE). **Ain:** Cascade de Glossdieu, 9 August 1891 (fl). **Borel s.n. (K). **Rhône:** ad Ainas, 6 August 1874 (e. fr), *Gandoger* 407 (BM, K). **Savoie:** Saint Bezon, 7 August 1892 (fl), *Borel* s.n. (K). **Puy-de-Dôme:** Puy St Gulunier?, 7 August 1928 (fl), *Eluss?* 355 (BM). **Cantal:** Ydes, 8 August 1874 (fr), *Héribaud-Joseph* s.n. (BM). **Aveyron:** Saint-Paul-des-Forêts, August 1904 (fr), *Coste* s.n. (BM). **Basses-Pyrénées:** Harambez, vid Chapelle St Nicolas, 15 August 1968 (fl), *Sonck* s.n. (H).**

**SPAIN. Guipuzcoa:** Vascongadas, San Sebastián, M. Castelli, 80 m, September 1940, *Rothmaler* 16415 (JE). **Huesca:** Castejon de Sos, valley of Río Esera, c. 950 m, 27 July 1955 (fl), *Sandwith* s.n. (K). **Barcelona:** Montserrat, 24 August 1941 (fl & e. fr), *Collector?* (RNG). **Zaragoza:** Catalayud, 17 July 1912 (fl), *Vicioso* s.n. (BM). **Avila:** Sierra de Gredos, Río Alberche S. of St. Martin del Pimpollar, c. 1450 m, 23 July 1974 (fl), *Brenan* 13036 (K). **Castellón:** Segorbe, 18 July 1922 (fl), *Pau* in *Sennen* Pl. Esp. 4620 (BM, RNG). **Almería:** Laujar de Andarax, 8 August 1978 (fl), *Roivainen* s.n. (H, RNG).

**ALGERIA. Atlas Tellien:** Médéa, gorges de la Chiffa ((fide Quézel & Santa, 1963: 682); près Blidah [Blida], Ravin de l' Oued-el-Kebir, 13 July 1854 (fl), *Cosson* s.n. (G-BOISS). **Petite Kabylie:** Djurdjura (fide Quézel & Santa, 1963: 682).

**CORSICA.** Stagno di Palo, 20 July 1933 (fl), *Aellen* 1655 (K).

**SARDINIA.** Tempio, 7 August 1882, *Reverchon* s.n. (JE).

**SICILY.** Messina: Messina, *Haeckel* s.n. (JE). *Collector?* : [Boscovi Pennzubaltone della] Castagnera, July 1879 (fr), *Tacono* s.n. (FR). **Palermo:** Palermo, June 1900 (fl & fr), *Ross* s.n. (BM).

**ITALY. Venezia Giulia:** bei Trieste, Monfalcone, September 1921 (fr), *Meebold* s.n. (K). **Trentino-Alto Adige:** Bozen [Bolzano], pre 1877 (fl), *Hausmann* 1377 (BM). **Piemonte:** Casale Masferrato, 15 July 1957 (fl), *Ulla & Cedercreutz* s.n. (H). **Massa-Carrara:** Massa, August 1952, *Pellegrini* s.n. (H). **San Marino:** Carrepa, 7 September 1920 (e. fr), *Pampanini* s.n. (K). **Campania:** between Majori [Maiori] and Capo d'Orso, 29 June 1883 (fl), *Lacaita* 6400 (BM).

**SWITZERLAND. Genève:** Geneva, July 1859, *Huet de Pavillon* s.n. (JE). **Vaud:** Nyon ad pagum Trilia, 9 August 1876 (fl), *Elfvig* s.n. (H). **Bern:** Radelfingen, 1 August 1879 (fl), *de Rutte* s.n. (K). **Luzern:** Lucerne, Sonnenberg, 24 July 1930 (fl), *Rathbone* s.n. (BM). **Appenzell:** am Gäbris ob Gais, July–August, *Schneider* s.n. (BM).

**AUSTRIA. Tirol:** Oberinntal, Vols bei Innsbruck, c. 600 m, 8 August 1980 (fl), *Polatschek* s.n. (BM). **Salzburg:** near Salzburg, Gaisberg, n.d. (e. fr), *Hinterhuber* s.n. (K). **Kärnten:** Klagenfurt, 1864 (fl), *Kokeil* s.n. (K). **Steiermark:** Lemsitz, Rössegg Ettendorf bei Stainz, 14 August 1924 (fl & fr), *Troyer* s.n. (H). **Oberösterreich:** bei Aishersheim, August 1861, *Keck* s.n. (JE). **Niederösterreich:** Mödling, Vorderbrühl, August 1919 (fr), *Fenz?* 82 (K). **Burgenland:** Podersdorf, Zitzmandorfer Wiesen, 1–9 August 1966 (fl), *Excurs. Bot. Inst. Ffm.* s.n. (FR).

**GERMANY. Baden:** Baiert hab, 18 August 1883 (fl), *Druce* s.n. (BM). **Württemberg:** Oberamt Reutlingen, Kirchentellinsfurt, 31 July 1991?, *Lindberg* s.n. (H). **Bayern:** Oberbayern, Haspelmoor, 17 July 1918? (fl), *Oberneder* 3261 (BM). **Hessen:** Bickenbach, bei Darmstadt, 10 September 1961 (fl & fr), *Schaarschmidt* 96 (FR). **Thüringen:** Souder bei Schlobheim, 25 July 1952 (fl), *Lauert* s.n. (BM). **Brandenburg:** Lychen, bei Küstmichener Bach, 20 July 1900 (fl), *Heiland* s.n. (H). **Schleswig-Holstein:** Kaltenhöfer, 25 July 1893 (fl), *Simmons* s.n. (H).

**DENMARK. Jutland:** between Lönstrup and Hirtshals, 17 July 1967 (fl), *Hohm-Nielsen & Jeppesen* in Fl. Jutl. Exs. 347 (BM, H, TA); **Fünen:** Potenden to Söndersö, 6 August 1883 (fl), *Mortensen* s.n. (H). **Falster:**

Hannenv Skov, D. 37, 17 July 1942 (fl), *Dahl* s.n. (BM). **Zealand:** W. of Vrangskov, N. of Ringsted, 24 July 1969 (fl), *Jacobsen & Svendsen* in Pl. Dan. Exs. 93 (H).

**SWEDEN. Skåne:** Benstadt, 2 October 1899 (fr), *Sjöshol* s.n. (H); Par. Everöd, Lyngby, 31 August 1933 (fl), *Haslow* s.n. (BM).

**POLAND. Siedlce:** Sedletz, ad pag. Jagodne prope urbem Łuków, 28 July 1902 (fl), *Puring* 1971 (H). **Wrocław:** Stawno apud Milicz, ad ripam stagni 'Golica', 5 August 1963 (fl), *Kotowicz & Koziol* 857 (H). **Bielsko-Biala:** Wadowice, prope Andrychów, 6 August 1938 (fl), *Łańcucka* Pl. Polon. Exs. 330 (BM, JE).

**UKRAINE.** West and south-west regions (fide Karnaukh, 1955: 307); Krym: Oreanda, 29 July 1987 (fl), *Golde* s.n. (LE).

**CZECH REPUBLIC. Moravia:** bei Schnobolin n. Olmütz, June 1908 (fl), *Laus* s.n. (BM, JE, K); Brno, Bilovice, ad Ricmanice, c. 230 m, 27 July 1925 (l. fl), *Mrkos* 243a (H, K).

**SLOVAKIA.** Throughout (see Zelený et al., 1982: map 57).

**ROMANIA. Transylvania:** Cluj, ad pagum Feleac super oppidum Cluj, c. 650 m, 28 July 1923 (fl & fr), *Gürtler & Nyárády* 1521b (H); Oreada, inter oppida Bucea et Grossi, 900 m, 30 July 1971 (fl), *Černoch* 22232 (BM, H). **Walachia:** Muntenia, distr. Prahova, Prahova rly stn, 5 August 1923 (fl & fr), *Grintescu* 1521a (H). Also in Moldavia (fide Guşuleac & Nyárády, 1956: 26).

**BULGARIA. Sofia:** prope Sofia, ad radicem m. Vitoša [Cherni Vrhkh], 5 August 1939 (fl), *Lindberg* s.n. (H).

**SLOVENIA.** Bled [Veldes], 1924 (fl), *Leathes* s.n. (BM); Carniolia, ad pagum St. Margarethen prope Rudolfswert, 200 m, August (l. fl), *Paulin*, Fl. exs. Carniol. 326 (BM).

**SERBIA.** bei Bor, June 1917, *Koppe* s.n. (JE).

**BOSNIA.** Sarajevsko Polji, prope Ilidža, c. 500 m, 5 August 1902 (fr), *Malz* s.n. (K).

**MAKEDONIJA.** \*L. Ochrid [Ohrid]. W. of Ochrid, 25 July 1976, *Akeroyd, Mellors & Preston* (CGE).

**ALBANIA. North:** Tepalens [Toplane?] bei Luzat, c. 250 m, 9 September 1964 (fr), *Meyer* 6029 (JE); Dardha, Weg zum Qani i Dardhes, c. 800 m, 1 August 1959 (fl), *Meyer* 4569 (JE). **South:** Berat, c. 60 m, 16 August 1935 (fr), *Alston & Sandwith* 2514 (BM, K).

**GREECE. Thrace:** Emirli, 100 m, 24 June 1931 (fl), *Tedd* 742 (K). **Makedonia:** Dramas, vill. Katafyton (SE foot of Mt. Orvilos), road to Ano Vrontou, 740 m, 23 July 1977 (fl & fr), *Strid & Georgiadou* 13052 (C); Grevenon, Mt. Smolikas, 2–3 km S. of Samarina towards Armata, 1275–1350 m, 27 August 1975 (l. fl), *Hartvig & Seberg* 4816 (C). **Ipiros:** Pindus, Smokovo to Rentino, 4 August 1937 (fl), *Balls & Gourlay* B. 3711 (BM, K). **Corfu:** Limni Korisson, near Linia, 17 July 1972 (fl), *Davis* 54547 (BM). **Thessalia:** Mt. Olympos, S. side, Leptokarya to Karya, 22.8 km, 770 m, 27 August 1975, *Strid & Hansen* 9555 (C). **Stereá Ellas:** Attica, prope Kephissiam [Kifisiá], ad radices montis Pentelici, 195–300 m, August (l. fl). *Heldreich* s.n. (BM). **Akhaía:** Ep. Kalavryton, Mt. Chelmos (east), c. 2 km SSW of Zarouchla, 1400–1450 m, 22 August 1982 (fl), *Hartvig, Franzén & Cristensen* 10296 (C). **Argolos:** prope Lerni, 13 July 1930 (fl), *Guiol* 1518 (BM). **Arkhadia:** Kinouria/Lakedhemonia, Mt. Parnon, Ajos Petros, Vitilithra, 1300 m, 13 July 1971 (fl), *Samatiadou* 13225 (BM). **Evvoia:** Mt. Dirphys, 24 July 1932 (l. fl), *Guiol* s.n. (BM). **Karpathos:** 0.25 km SW of Avlona, 300 m, 8 April 1992 (st), *Chilton & Turland* 285 (BM). **Lesvos:** Agios Anagari, c. 3 km S. of Sikounta, 100–150 m, 9 September 1992 (e. fr), *Hansen & Nielsen* 8030 (C).

**TURKEY. Istanbul (Europe):** Belgrad Forest, 31 July 1959 (fl), *Yaltirik* ISTO 1351 (E). **Istanbul (Asia):** Aydos, 20 September 1950 (fr), *Baytop (& Berk)* 3603 (BM, ISTE\*). **Kocaeli:** Izmit, Izmit to Sapanca, c. 20 km, Masukiey, 20 July 1981 (fl), *Kurtto* 3088 (H). **Kastamonu:** N. side of Ilgaz Dağ 1500 m, 28 July 1962 (fl), *Davis, Coode & Yaltirik* D. 38288 (E, K). **Giresun:** above Giresun, 900 m, 24 August 1962 (fl), *Furse* 4137 (K). **Trabzon:** Of, s.l., 5 August 1957 (fl & fr), *Davis & Hedge* D.20823 (BM, E, K). **Çoruh:** Chope [Hopá], 6 August 1917 (fr), *Shishikin* s.n. (LE). **Manisa:** Manisa, 3 September 1932 (fl), *Kotte* 319 (K). **Kutahya:** Gediz, Şaphane, 1200 m, 27 August 1950 (fl), *Davis* 18505 (E). **Afyon:** Afyon to Sandıklı, 3 km from Sinkanlı [Sinanpaşa], 28 August 1971 (fl), *Fraser Jenkins* 2164 (BM, E). **Sivas:** 11 km N. of Sivas, 1300 m, 10 September 1977 (fr), *Sorger* 77–109–8 (Herb. Sorger). **Antalya:** SW of Elmali, W. of Gömbe, 1200 m, 10 July 1968 (fl & e. fr), *Sorger* 68–25a–2 (BM); Gebiz, Bosburun Dağ at Panargazu yayla, 600 m, 23 July 1949 (fl), *Davis* 15492 (K). **Hatay:** Amanos dağı, Dörtüyl Pinarbaşı, 22 September 1967 (e. fr), *Akman* 136 (ANK, BM).

**SYRIA.** Damascus, n.d. (fr), *Gaillardot* 910 (JE); Mt. Hermon, in valle Ormy 1500 m, 2 July 1855 (fl), *Kotschy* 218 (BM, K, UPS).

**LEBANON.** Coast: Saïda, au dessus du moulin de l'Emir, 4 August 1854 (fl), *Gaillardot* 911 (G, JE). **Lower mountains:** Becharre [Bcharré], 18 August 1945 (fr), *Davis* 10087 (K). **Al Biqâ:** Bekâa, Mâlaka, July 1853 (fl), *Gaillardot* s.n. (JE).

**IRAQ.** **Amadiyah:** Sersang, 1050 m, 14 July 1955 (fl), *Haines* W.534 (K). **Rawanduz:** Pusstashan, 15 km NE of Rania, Qandil Range, 1150 m, 29 July 1957 (l. fl), *Rawi* NHI 23897 (K). **Sulaymaniya:** in Mt. Avroman humid., 1200–1800 m, July 1867 (fr), *Hausknecht* s.n. (JE).

**IRAN.** **Gilan:** Deylaman to Lanak, 600–1600 m, 9 July 1972 (fl & fr), *Terné* 34320 E (BM, EVIN). **Mazanderan:** Astara to Bandar-Pehlevi, 15 km, 18 August 1963 (fl & fr), *Jardine* 921 (E, W). **Arak:** in monte Raswend, August 1989 (fl), *Strauss* s.n. (JE). **Gorgan:** Ketul, June 1948 (fl), *Sharif* in Herb. Min. Agr. 359 (W).

**AZERBAIJAN.** Lenkoranskiy rayon, Port Il'ish, 17 July 1963 (fl), *Bobrov & Tzelev* 284 (LE).

**ARMENIA.** **South-east:** recorded from Dzhermuk, Shake and Goris (*fade* Takhtajan, 1966: 13).

**GEORGIA.** Batumi, Strandpromenade, 5 August 1977 (fl), *Marsteller* s.n. (JE); Sukhumi, E. of the town, 27 August 1957 (fr), *Meyer, Lippold & Köhler* 835 (JE). Gudauta, NW bei Xirmema, 13 July 1969 (fl), *Lepper, Fischer* et al. 5299 (BM, JE).

**RUSSIA.** **Stavropol:** Nevinnomyssk, bei der Kuban-Brücke, 18 August 1957 (fr), *Meyer, Lippold & Köhler* 18 (JE).

3b. **Hypericum tetrapterum** [var.]  $\gamma$  **corsicum** (Steud.) Boiss., *Fl. orient.* **1:** 816 (1867) pro parte quoad typum. Type as for *H. corsicum* Steud.

Map 4.

*H. tenellum* Tausch in *Flora* **14:** 211 (1831); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120:** 584 (1911), non Solander ex Clarke (1812). Type: Corsica, in montibus Corsicae, *Tausch* s.n. (PRC-holotype).

*H. corsicum* Steud., *Nomencl.* 2nd ed., **1:** 787 (1840); Godr. in Gren. & Godr., *Fl. France* **1:** 315 (1847); Bonnet in *Bull. Soc. Bot. France* **25:** 280 (1878); Rouy, *Ill. pl. Eur.*, fasc. 5: 35, t. 106 (1896). Type as for *H. tenellum* Tausch.

*H. repens* Duby ex Nyman, *Consp. fl. eur.* **1:** 133 (1878), nomen.  
*H. tetrapterum* var.  $[\beta]$  *tenellum* (Tausch) Parlat., *Fl. ital.* **5:** 518 (1875); Cesati, Passerini & Gibellini, *Comp. fl. ital.*: 758 (1884).

*H. acutum* subsp. *corsicum* (Steud.) Rouy in Rouy & Fouc., *Fl. France* **3:** 338 (1896); Hayek, *Prodr. fl. Pen. balc.* **1:** 534 (1925) pro parte quoad typum; Briquet, *Prodr. fl. Corse* **2(2):** 145 (1936); comb. illegit. (Art. 58.2).

*H. quadrangulum* subsp. *corsicum* (Steud.) Fiori in Fiori & Paol., *Fl. Italia* **1:** 387 (1898).

*H. insulare* Foucaud & Mandon in *Bull. Soc. Bot. France* **47:** 89, t. 2 (1900). Types: Corsica, entre le col de Sorba et Ghisoni, *Mandon & Foucaud* s.n. (?); Cascade de la fontaine de Puzichello, près de Ghisoni, *Mandon, Rotgès & Foucaud* s.n. (?).

*H. acutum* var. *corsicum* (Steud.) Halácsy, *Consp. fl. graec.* **1:** 281 (1900). comb. illegit. (Art. 58.2).

*H. acutum* var. *insulare* (Foucaud & Mandon) Briq. in *Annuaire Conserv. Jard. Bot. Genève* **5:** 95 (1901), comb. illegit. (Art. 58.2).

*H. acutum* subsp. *corsicum* var. *rotundifolium* sensu Briq., *Prodr. fl. Corse* **2(2):** 143 (1936), non *H. acutum* var. *rotundifolium* (Willk.) Schinz (= *H. undulatum* var. *boeticum*).

*H. tetrapterum* subsp. *corsicum* (Steud.) Zangh., *Fl. Ital.*, **1:** 196 (1976).

Icones: Rouy, *Ill. pl. Eur.*, fasc. 5: t. 106 (1896); Foucaud & Mandon in *Bull. Soc. Bot. France* **47:** t. 2 (1900).

Stems procumbent to ascending, up to 0.2 m long. Leaves mostly 0.5

mm petiolate, 6–12 mm long, elliptic to orbicular, margin plane. Inflorescence 1(2–3)-flowered.

Montane to alpine zones; 1000–2000 m.

Corsica. The Cretan record (Bonnet, 1879) is an error (see Greuter, 1974: 156). Bonnet's record from Spain (loc. cit.) would appear to refer to small plants of 2b. *H. undulatum* var. *boeticum*.

**CORSICA.** Monte d'Oro, 2000 m, 6 August 1826? (fl), *Soleirol* 112 (BM, K, WAG); Licano, 12 July 1912 (fl), *Lacaita* s.n. (BM); Bastelica, Monte Renoso, 25 August 1878 (fl & fr), *Reverchon* s.n. (BM).

3c. **Hypericum tetrapterum** var.  $[\beta]$  **anagallidifolium** Boiss., *Fl. orient.* **1:** 806 (1867); Rech.f. in *Ark. Bot.* **5:** 294 (1960). Type as for *H. anagallidioides* Jaub. & Spach.

Map 4.

*H. anagallidioides* Jaub. & Spach, *Ill. pl. orient.* **1:** 47, t. 24 (1842), non *H. anagalloides* Cham. & Schldtl. (1828). Type: [Turkey (Amanus)], in oriente, *Labillardière* s.n. (FI-holotype, photograph!).

*H. anagallidifolium* Boiss., *Fl. orient.* **1:** 806 (1867), in synonym.

*H. acutum* var. *anagallidifolium* (Boiss.) Post, *Fl. Syria*, 2nd ed. **1:** 233 (1932), comb. illegit. (Art. 58.2).

*H. acutum* var. *anagallidioides* (Jaub. & Spach) Zohary, *Fl. Palaestina* **1:** 223 (1966), comb. illegit. (Art. 58.2).

Icon: Jaub. & Spach, *Ill. pl. orient.* **1:** t. 24 (1842).

Stems ascending, slender, c. 0.15 m long (habit of *Anagallis arvensis* L.). Leaves subsessile to 0.5 mm petiolate, c. 7–12 mm long, elliptic to triangular-ovate, margin undulate. Inflorescence 1–3-flowered, from one node, sometimes with flowering branches from up to 5 nodes below, then totalling 20–25 flowers.

Stream banks; 1300–2000 m.

Turkey (Amanus), Lebanon, Israel.

**TURKEY.** **Hatay:** Ziairetdag, 18 September 1884 (l. fl), *Post* s.n. (BM); Monts Amanus, 1200–1800 m, September 1913 (fl), *Haradjian* 4635 (E, G).

**LEBANON.** **Lebanon:** montagne entre Saïda et Deir Mekhalta près du Djoûme, n.d. (fl), *Gaillardot* s.n. (JE); Tripoli, Vallée de Hasroun, 7 July 1866 (fl), *Blanche* s.n. (JE).

**ISRAEL.** Upper Galilee (*fade* Zohary, 1966: 223).

4. **Hypericum triquetrifolium** Turra, *Farsetia:* 12 (1765); Post, *Fl. Syria*, 2nd ed. **1:** 233 (1932); Briquet, *Prodr. fl. corse* **2(2):** 148 (1936); Blakelock in *Kew Bull.* **3:** 404 (1948); Quézel & Santa, *Nouv. Fl. Algérie:* 682 (1963); Zohary, *Fl. Palaestina* **1:** 233, t. 328 (1966); N. Robson in Davis, *Fl. Turkey* **2:** 400 (1967), in Tutin et al., *Fl. Europ.* **2:** 269 (1968), in Meikle, *Fl. Cyprus* **1:** 300, t. 16 (1977), in Townsend & Guest, *Fl. Iraq* **4:** 379 (1980); Mouterde, *Nouv. Fl. Liban Syrie* **2:** 527, t. 228 (1970); Täckholm, *Students' Fl. Egypt*, 2nd ed.: 150 (1974); Ali & Jafri, *Fl. Libya* **2:** 2, f. 1 (1976); Pott.-Alap., *Fl. Tunisie:* 508 (1979); Hagemann in *Bot. Jahrb. Syst.* **102:** 247, f. 9 (1981), Hagemann & Meusel in *Flora* **175:** 385–405, ff. 1A, 2–8, 9B, 9C, 10A, 11 (1984), Hagemann in op. cit. **183:** 284, f. 57 (1989); Demiri, *Fl. Ekskurs. Shqipërisë:* 314 (1981?); Pignatti, *Fl. Italia* **1:** 350 (1982); Ramos in *Acta Bot. Malac.* **11:** 167, f. 6b (1986), in Castroviejo et al., *Fl. Iberica* **3:** 167 (1993); Boulos, *Fl. Egypt* **2:** 156 (1999). Type: 'Habitat in Grecia, Sicilia, Calabria'. Turra's herbarium was in the Museo civico, Vicenza, but was destroyed during the second World War (Stafleu & Cowan, 1986).

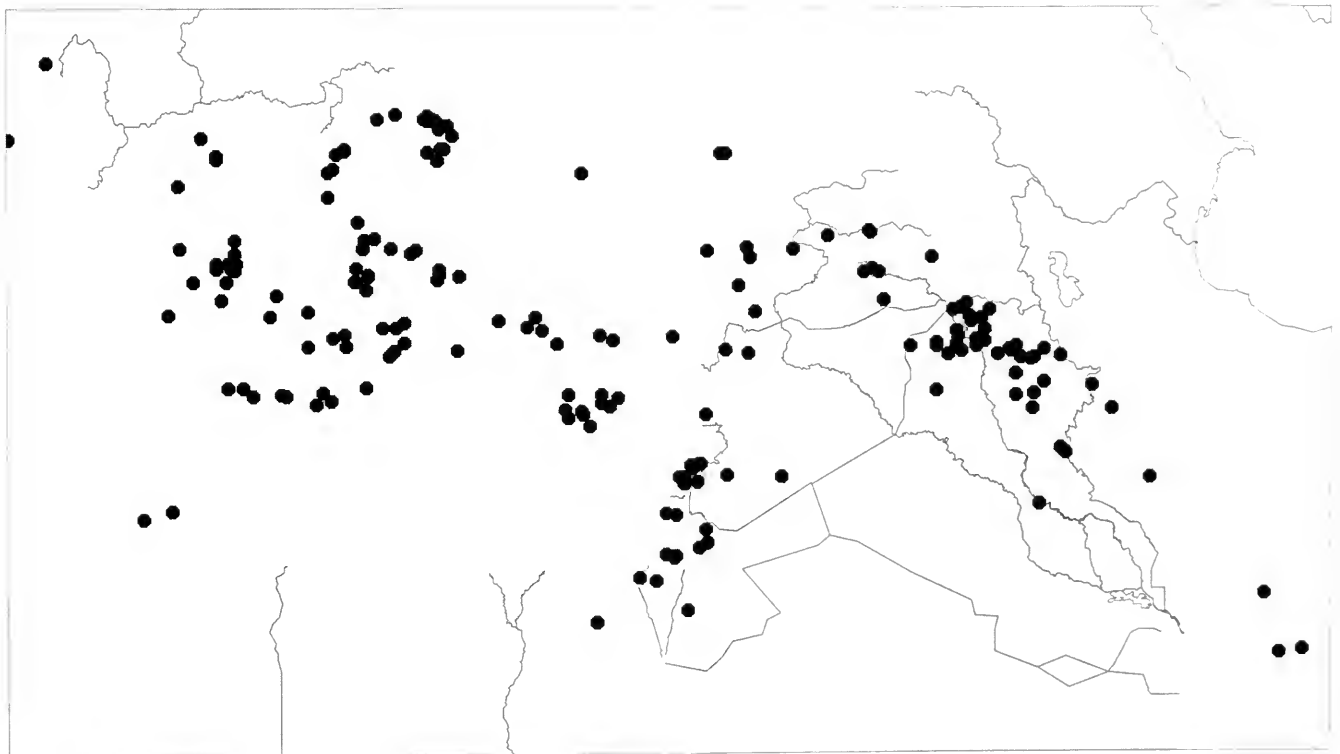
Fig. 7, Map 5a, b.

*H. crispum* L., *Mant. pl.:* 106 (1767); Choisy, *Prodr. monogr. fam. Hypéric.:* 49 (1821), in DC., *Prodr.* **1:** 549 (1824); Sibth. & Sm.,





Map 5a 4. *H. triquetrifolium*, west area ●, other records ○.



Map 5b 4. *H. triquetrifolium*, east area ●.

*Fl. Graeca* 8: 55, t. 776 (1833); Spach, *Hist. nat. vég.*, Phan. 5: 385 (1836), in *Ann. Sci. nat.*, Bot. 5: 357 (1836); Unger & Kotschy, *Ins. Cypern*: 353 (1865); Boiss., *Fl. orient.* 1: 806 (1867); Rouy in Rouy & Fouc., *Fl. France* 3: 350 (1896); Halácsy, *Consp. fl. graecae* 1: 283 (1900); Woron. in Kuzn., Busch & Fomin, *Fl. Cauc. Crit.* 3(9): 45 (1906); Hand.-Mazz. in *Ann. Naturhist. Mus. Wien* 27: 60 (1913); Holmboe, *Veg. Cypr*: 127 (1914); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.*, 2nd ed. 21: 179 (1925); Nabelek in *Spisy Pří. Fak. Sci. Masarykova Univ.* 35: 53 (1932); Stefanoff in *God. Agr.-les. Fak. Univ. Sofiya* 10: t. 4 f. 28 (1932), 11: 176 (1933), 12: 88 (1934), in *Pflanzenareale* 4: karte 6a (1933); Rech. f., *Fl. Aegaea*: 263 (1943); H. Lindb. in *Acta Soc. Sci. Fenn.*, Ser. B. 2 (no.7): 23 (1946); Gorskova in Shishkin & Bobrov, *Fl. URSS* 15: 244 (1949); Täckholm, *Students' Fl. Egypt*: 223 (1956); Edgecombe, *Weeds of Lebanon*, 3rd ed.: 252 + t. (1970); nom. illegit. Type as for *H. triquetrifolium* Turra.

Icones: Zohary, *Flora Palaestina* 1: t. 328 (1966); N. Robson in Meikle, *Fl. Cyprus* 1: t. 16 (1977); Cadete in Valdés, Talavera & Galiano, *Fl. Andalusia Occid.* 1: 315 (1987).

*Perennial herb* 0.15–0.55(–0.77) m tall, erect to decumbent, rooting at the base, the roots bearing shoots, with stems solitary or few, widely branched along most of length, usually forming pyramid. *Stems* 2-lined, with black glands on the lines and sometimes elsewhere; internodes 10–30 mm, longer than leaves. *Leaves* sessile; lamina 3–20 × 1–9 mm, triangular-lanceolate or rarely narrowly ovate to linear-oblong, concolorous, sometimes glaucous, chartaceous; apex acute, margin crisped-undulate, base cordate-amplexicaul; venation: 2–3(–4) pairs of main laterals from base or near base of midrib, tertiary reticulation usually obsolete; laminar glands pale, ± dense, very small; intramarginal glands black, spaced. *Inflorescence* 1–7(–11)-flowered, from 1–2 nodes, with flowering branches ± horizontally spreading from all other nodes, sometimes excepting 1–6 immediately beneath apical one, the whole broadly pyramidal; pedicels 1–5 mm; bracts and bracteoles 1.5–2.5 mm long, lanceolate, entire or rarely apically denticulate. *Flowers* 8–12(–14) mm in diam., stellate; buds broadly ellipsoid to globose, rounded. *Sepals* 5, subequal to unequal, 1–2.2(–3) × 0.5–1 mm, oblong to ovate-oblong or lanceolate, acute to rounded-apiculate or rounded, entire or eroded-denticulate, erect in bud and fruit; veins 3, unbranched; laminar glands pale, 2, linear, distally interrupted; intramarginal glands absent. *Petals* 5, bright? yellow, not red-tinged dorsally, 4.5–7 × 1–1.5 mm, c. 3.5–5 × sepals, linear-oblong, entire; laminar glands pale, striiform and punctiform, and occasionally black, solitary; marginal glands absent or rarely black, few. *Stamens* 15–40, '3'-fascicled, longest 2.5–5 mm, c. 0.6–0.8 × petals; anther gland black. *Ovary* 3-locular, 1.5–2 × 0.5–1 mm, ellipsoid to broadly ovoid; styles 3, free, 2.5–3 mm, 1.7–3 × ovary, spreading; stigmas narrow. *Capsule* 3–5 × 2–3.5 mm, 2.5–3 × sepals, ovoid; valves with longitudinal linear vittae and occasionally a few lateral vesicles. *Seeds* darkish brown, 1.5–1.8 mm, subcylindric, not carinate or appendiculate; testa finely foveolate to scalariform-foveolate. 2n=16 (Reynaud, 1973, 1975).

In dry open stony ground and cultivated fields; 0–1350 m (Israel), -c. 2100 m (Iraq).

S. Spain (Málaga, Andalusia), Gibraltar, Balearic Is., S. France, S. Italy, Sicily, Malta, Tunisia, Algeria, Libya (Cyrenaica), Montenegro, Albania, Greece (mainland and islands), Crete, Cyprus, Turkey, Levant south to Egypt (Sinai) and Jordan, Iraq, NW Iran. Probably not native west of Sicily and Cyrenaica or in Montenegro.

**SPAIN.** Málaga: Málaga, cerca del aerodromo, May 1965 (fl), *Borja* s.n.

(BM); San Julian, 18 May 1952 (fl), *Roivainen* s.n. (H). **Andalusia:** Andevalo, *fide* Ramos (1987).

**GIBRALTAR.** Near First River Ferry, 26 June 1912 (fl), *Wolley-Dod* 1478 (BM).

**BALEARIC IS. Minorca:** Alayor, naturalized (*fide* Knoche, 1922: 188).

**FRANCE. Bouches du Rhône:** Les Camoins, between Neoules and Marseilles, 10 July 1968 (fl), *Blaize* s.n. (H); Aix-en-Provence, July 1891, *Bruyas* s.n. (JE). **Hérault:** Montpellier, Port Juvenal, July 1932 (fl), *Auersmitz*? s.n. (BM).

**ITALY. Puglia:** Apulia, circa Manfredonia, 3–15 m, 28 June 1875 (fl), *Porta & Rigo* 241 (BM, FR, JE, K); Taranto, Leucaspide, 30 June 1908 (fl), *Lacaita* 291/08 (BM). **Calabria:** Reggio, Pellaro, 13 July 1898 (fl & e. fr), *Rigo* 472 (H). **Campania:** Naples, n.d. (fl), *Lindley* s.n. (K).

**SICILY. Messina:** 10 km NE of Taormina, Capo San Alessio, 100 m, 17 July 1983 (fl), *Akeroyd, Jury & Rumsey* 3572 (RNG). **Catania:** Catania, June 1885, *Ross* s.n. (JE). **Siracusa:** Siracusa, Roman amphitheatre, 100 m, 17 July 1983 (fl & fr), *Akeroyd, Jury & Rumsey* 3564 (RNG). **Caltanissetta:** Caltanissetta, August 1898, *Ross* 220 (JE). **Agrigento?** Palermo a Camastra, June (fl & fr), *Todaro* 1240 (BM, JE, K). **Enna:** ad Simethi prope Regalbuto, 28 June 1840 (fl), *Heldreich* s.n. (BM).

**MALTA.** No precise locality, 1926 (fl), *Bankart* s.n. (BM).

**TUNISIA. Kroumerie:** Ghardimaou, 22 April 1938 (fl), *Simpson* 38,360 (BM). **Dorsale:** Zaghuan, 250 m, 19 July 1969 (fl), *Tomkinson* 37 (BM). **Kairouane:** Bou-Arada, September 1898 (fl & fr), *Le Testu* s.n. (BM). **Centrale:** Dougga, 300 m, 16 June 1969 (fl), *Tomkinson* 29 (BM).

**ALGERIA. Constantine:** Oued Zenati (*fide* Quézel & Santa, 1963: 683).

**LIBYA. Cyrenaica:** Gibel Akhdar, between Al-Marj and Beida, 25 April 1968 (fl), *Boulos* 3070 (BM).

**MONTENEGRO.** S. end of Petrovak (between Budva and Bar), Cona Gora, 12 July 1976 (fl), *Halliday* 88/76 (LANC).

**ALBANIA.** Present (*fide* Demiri, 1983: 315).

**GREECE. Makedhonia (Khalkidhiki):** 8 km NE of Néa Moudania (ancient Olynthos), 100 m, 9 September 1981 (fl & fr), *Hussein, Jury & Rutherford* 78 (BM, RNG\*); Néa Potidaia, 6 August 1971 (fl), *Westfield Coll. Exped.* 315 (BM). **Thessalia:** inter Larissa [Lárisa] et Thyraios, 31 July 1885, *Haussknecht* s.n. (JE). **Sterea Ellás:** S. of Athens on coastal road to Cape Sounion, 24 September 1962 (fr), *Bourden* 117 (BM); prope Athenas, Skaramanga, 28 May 1939 (fl), *Lindberg* s.n. (H). **Argolis:** in ruinis arcis Mykénai [Mycenae], 250 m, 26 June 1971 (fl), *Černoch* 22070 (BM); excavations of ancient Epidaurus, 19 October 1975 (fl), *Kramer* 5521 (H). **Messinia:** near Kalamata, 100 m, 10 July 1975 (fl), *Nydegger* s.n. (BM, H). **W. Aegean Is.:** Ídhra, Kamisi, 2 June 1968 (fl), *N. Post* 3260 (BM). **Kikladhes:** Naxos, inter Naxos et Chalki, 28 June 1932 (fl), *Rechinger f.* 2289 (BM). **E. Aegean Is.:** Khíos, Campos, 17 July 1939 (fl), *Platt* 362 (K); Kálimnos, ad Myrthies, c. 200 m, 3 June 1035 (st), *Rechinger f.* 7843 (BM); Samos, Vathy, 16–23 June 1932 (fl), *Rechinger f.* 1915 (BM). **Dhodhekánisos:** Ródhos, près Salakos, 16 June 1870 (fl), *Bourgeau* 16 (BM, E, G, K); Ródhos, N. of Charakion, near ruins of Fernkios, 3 May 1952 (st), *Fagerstén* s.n. (H). **Karpathos:** Avlona, 300 m, 24 July 1950, *Davis* 18024 (K).

**KRÍTI. Khania:** La Cannée, 2 July 1883 (fl), 3 August 1883 (fr), *Reverchon* 17 (BM, FR, H, JE, K); Kissamos [Kisámou], 20 July 1938 (fl & fr), *Davis* 290 (BM). **Rethímnos:** Kesantopelta, 19 July 1976 (fl & fr), *Raihalme* s.n. (H). **Iraklïon:** Knossos, ruins of Knossos Palace, 18 July 1079 (fl), *Lassig* 7914 (H). **Lasíthi:** between Gournia and Tolotti, facing Psira I., 31 May 1966 (fl), *Whitefoord* 11 (BM).

**CYPRUS. Paphos:** Yeroskipos, 20 June 1939 (fl), *Lindberg* s.n. (H, K). **Limassol:** Prodhromos, 1350 m, 9 September 1955 (fl), *Atherton* 588 (K). **Larnaca:** prope Athienou [Athienou], 26 May 1862 (fl), *Kotschy* 972 (JE, K). **Nicosia:** Nicosia, English School, 150 m, 5 October 1958 (fr), *Oswald* 13 (K). **Kyrenia:** Kythraea, June 1880 (fl), *Sintenis & Rigo* 581 (BM, K).

**TURKEY. Europe – Tekirdağ:** Gallipoli, Kilia, n.d. (fl), *Ingoldby* 585 (K). **Istanbul:** Kuçukçekmece to Büyükçekmece, 50–100 m, 12 August 1962 (fl), *Davis (& Coode)* 39246 (BM, E, K). **Asia – Çanakkale:** Umurbey, Umurbey Çayı, 22 July 1981 (fl), *Kurtto* 3306 (H). **Kocaeli:** Karamürsel to Yalova, above Gemlik, 70 m, 8 July 1978 (fl), *Uotila* 27133 (H). **Amasia:** ad pagum Sana, 350–500 m, 10 July 1889 (fl), *Bormüller* 1489 (BM, JE, K). **Tokat:** Tokat, n.d. (fl), *Wiedermann* 35 (JE, K). **Izmir:** Zeytinadağ civari, 18 September 1954 (fr), *Baytop* 2654 (BM, ISTE\*). **Ankara:** Ankara, 575 m, 10 July 1939 (fl), *Frödin* 199 (U). **Maraş:** Elbistan distr., Kapidere, 31 July 1952 (fl), *Davis (Dodds & Çetik)* 20419 (BM, E, K). **Elazığ:** 60 km E. of Elazığ, 1



September 1954 (fl), *Davis* (& *Polunin*) 24813 (BM, E, K). **Bitlis**: Bitlis Gorge S. of Kambos Dağ, 1250 m, 16 August 1956 (fl), *McNeill* 598 (E, K). **Muğla**: Datça to Marmaris, 4 km, 10 m, *Dudley* in *Davis* 35439 (E, K). **Denizli**: Pamukkale, 400 m, 28 June 1967 (fl), *Sorger* 67-40-18 (BM, WU\*). **Antalya**: Manavgat to Alanya arasi, 24 July 1957 (fl), *Baytop* 5043 (BM, ISTE\*). **İçel**: Silifke-Mut main road, 19 June 1971 (fl), *Ayanoğlu, Sezile & Çubukçu* 1111 (BM). **Gaziantep**: Aintab [Gaziantep], 600 m, 16 June 1865 (fl), *Hausknecht* 812 (BM, E, JE, K). **Mardin**: Kischemill, 23 July 1888 (fl), *Stapf* in *Sintenis* 1343 (JE, K).

**SYRIA**. **North**: prope Aleppo [Halep], 1771? (fl), *Russell* s.n. (BM); 30 km due W. of Balad Sinjar, 7 June 1934 (fl), *Field & Lazar* 685 (K) (or in Iraq?). **South**: Mt Hermon [Jebel esh Sheikh], 1855 (fl), *Kotschy* 706 (H-M).

**LEBANON**. **Coast**: bei Ghazir [Jdaidet Ghazir], c. 400 m, 19 June 1934 (fl), *Busujan* 220 (H-M, JE); Saïda, près de Darbesine, 28 June 1853 (fl), *Blanche* 950, 950a (JE, K). **Lower mountains**: Ain Zhalta and higher, 1950 m, 28 August 1954 (fl), *Trott* 2041 (K).

**ISRAEL**. **Samaria**: 1.6 km outside Nazareth on Tiberias road, 15 August 1962 (fl), *Curle* 61 (K); Jabal Qulayb [Mt Carmel?], 1350 m, 12 June 1937 (fl), *Myers & Dinsmore* 12090 (H). **Judaea**: Jerusalem, Mt Scopus, 13 August 1933 (fl & fr), *Amdursky* 262 (H-M); Sheikh Nuran, May 1918 (fl), *White* s.n. (K); Ghaza, Abasan, 11 November 1964 (fl & fr), *Boulos* s.n. (K).

**JORDAN**. near Amman, Al-Jubaiha, University Campus, 22 July 1974 (fl), *Boulos* 7300 (BM); 5 km S. of Shaubak, 29 June 1974 (fl), *Jallad, Lahham & Hanania* 609 (H); Khanazareh [Khanasira?], 800 m, 6 October 1950 (fl & fr), *Chapman* 51 (K).

**EGYPT**. **Sinai**: Rajah, 4 June 1945 (fl), *Davis* 10426 (K).

**IRAQ**. **Amadiyah**: Zawitah, 900 m, 27 July 1933 (e. fr), *Guest* in *Rustam* 3754 (K). **Rawanduz**: just below Chaklawa, Erbil liwa, 28 August 1962 (fl), *Barkley & Asker* 3413 (K). **Sulaimaniyah**: Kirkuk liwa, Jarmo, 750 m, 22 May 1955 (fl), *Haines* W.226 (K). **Mosul**: N. of Mosul, October 1929 (fl & fr), *Dimmock* in *Rogers* 0418 (BM, K). **Nineveh**: 50 km from Mosul to Dohuk, 410 m, 11 June 1958 (fl), *Chapman* in *NHI* 26253 (K). **Arbil**: 5 km N. of Erbil, 25 August 1962 (fr), *Barkley* 3355 (K). **Kirkuk**: Kor Mor, 30 km N. of Tuz, 9 June 1929 (fl), *Rogers* 0310A (BM, K). **Diwala**: Naft Khana [Naft Khaneh], June 1929 (fl), *Rogers* 0320 (K).

**IRAN**. **Kurdistan**: Palangan, 1800–2100 m, 9 August 1962 (fl), *Transhalr & Termé* 12298E (W). **Kermanshah**: Ridjab, 24 July 1962 (fl), *Transhalr & Termé* 12300E (W). **Fars**: Kotal Pirjan, June 1960 (fl), *Borounand* 5820E (EVIN\*, W). Lorestan: Kouhdasht, Synareh?, 850 m, 13 August 1973 (fl), *Moussari* 34325E (BM, EVIN\*).

*Hypericum triquetrifolium* is the eastern Mediterranean counterpart of the Atlantic 2. *H. undulatum*; but it has quite a different habitat. The habit, however, although very different at first glance, is approached by some widely branching forms of *H. undulatum*; and some of these (e.g. *Valorado* s.n. from Portugal, *sine loc.* (BM)) have rather similar but larger leaves. Hagemann & Meusel (1984) describe it as a derived xerophilous species

5. ***Hypericum perforatum* L.**, *Sp. Pl.*: 785 (1753), *Syst. Nat.* 12th ed.: 170 (1767); Choisy, *Prodr. monogr. Hypéric.*: 50 (1821), in DC., *Prodr.* 1: 549 (1824); Ledeb., *Fl. altaic.* 3: 364 (1831), *Fl. ross.* 1: 447 (1842); Spach, *Hist. nat. vég.*, Phan. 5: 388 (1836), in *Ann. Sci. nat. Bot.* 5: 357 (1836); Rehb.,  *Ic. fl. germ. helv.* 6: t. 343, f. 5177 (1844); Boiss., *Fl. orient.* 1: 809 (1867); Maxim. in *Bull. Acad. Imp. Sci. Saint-Petersbourg* 27: 432 (1882), *Mélanges Biol. Bull. Acad. Imp. Sci. Saint-Petersbourg* 11: 166 (1882); S. Watson in *Proc. Amer. Acad. Arts* 17: 329 (1882); Coulter in *Bot. Gaz.* 11: 107 (1886), in A. Gray, *Syn. fl. N. Amer.* 1: 288 (1897); Hemsley in *J. Linn. Soc., Bot.* 23: 74 (1886); Rouy in Rouy & Fouc., *Fl. France* 3: 332 (1896); Reiche in *Anales Univ. Chile* 93: 561 (1896), *Fl. Chile* 1: 269 (1896); Diels in *Bot. Jahrb. Syst.* 29: 476 (1900); R. Keller in *Bot. Jahrb. Syst.* 33: 554 (1904); Schinz in *Vierteljahrsschr. Naturf. Ges. Zürich* 49: 241 (1905); Woron. in Kuzn., Busch & Fomin, *Fl. Cauc. Crit.* 3(9): 49 (1906); H.

Léveillé in *Bull. Soc. Bot. France* 54: 595 (1908); Pampanini in *Nuovo Giorn. Bot. Ital.* 17: 672 (1910); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 520 (1911), in *Mitt. Naturwiss. Vereins. Steiermark* 51: 240 (1915); Thellung in *Allg. Bot. Z.* 1912: 19 (1912); Rehder in Sargent, *Pl. wilson.* 3: 452 (1917); Urban, *Symb. antill.* 9: 406 (1925); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.* 2nd ed. 21: 180 (1925); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 526 (1925); Hayek, *Prodr. Fl. Pen. balc.* 1: 533 (1925); Fedtch. & Shishkin, *Fl. Yugo-vost* 3: 711 (1930); Hand.-Mazz., *Symbol. sin.* 7: 404 (1931); Stefanoff in *God. Agr.-les. Fak. Univ. Sofiya* 10: t. 4 f. 32 (1932), 11: 176 (1933), 12: 88 (1934), in *Pflanzenareale* 4: Karte 7 (1933); Grossg., *Fl. Kavk.* 3: 68 (1932), 2nd ed. 6: 175, karta 194 (1962); Gorschkova in Shishkin & Bobrov, *Fl. URSS* 15: 248, t. 12 f. 1 (1949); Y. Kimura in Nakai & Honda, *Nova Fl. Jap.* 10: 131 (1951); Ross-Craig, *Draw. Brit. Pl.* 6: t. 7 (1952); Guşul. & Nyár. in Savul., *Fl. R. P. Roman.* 4: 29 (1956); Gleason & Cronquist, *Man. Vasc. Pls NE. U.S. & Canada*: 469 (1963); O. Schwarz in *Drudea* 5: 60 (1965); Lauener in *Notes Roy. Bot. Gard. Edinburgh* 27: 63 (1966); N. Robson in Davis, *Fl. Turkey* 2: 400, tt. 12 f. 4, 13 f. 20 (1967), in Tutin et al., *Fl. Europaea* 2: 269 (1968), in Rechinger f., *Fl. Iranica* 49 (Guttif.): 17 (1968), in Nasir & Ali, *Fl. W. Pakistan* 32 (Guttif.): 8, f. 2G-K (1973), in Cullen et al., *Eur. gard. fl.* 4: 60 (1995), in Wisskirchen & Haeupler, *Standardliste Farn- u. Blütenpfl. Deutschl.*: 270 (1998); Fosberg in *Occas. Pap. Berenice Pauahi Bishop Mus.* 24: 22 (1969); Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* 4: 260, t. 49 ff. 3, 4 (1970) & Stjep.-Vesel. in Josifović, *Fl. Srbije* 3: 118 (1972); Anon., *Iconogr. Cormoph. Sinicae* 2: 879, f. 3488 (1972); Scoggan, *Fl. Canada* 3: 1097 (1978); Hagemann in *Flora* 183: 99, tt. 1–8 excl. 5B (1983); Ramos in *Trab. Dept. Bot. Univ. Complut. Madrid* 12: 49, t. 3 f. 2 (1983), in *Acta Bot. Malac.* 11: 167, f. 6a (1986), in Castroviejo et al., *Fl. Iberica* 3: 163, t. 45 (1993); Valdés, Talavera & Galiano, *Fl. Andalus. Occ.* 1: 314 + map & fig. (1987); Li Xiwen in *Fl. R.P. Sinicae* 50(2): 67, t. 15 ff. 1–4 (1990); Biswas in Sharma & Sanjappa, *Fl. India*, 3: 73, f. 27 (1993); Benson & McDougall in *Cunninghamia* 4: 301 (1995); Azadi in *Fl. Iran*, 27: 11 + map (1999). Type: 'Habitat in Europae pratis' (probably Sweden), *Herb. Linn.* 943/34 (sphalm. 94) (LINN!-lectotype, Robson, 1968).

Fig. 8 (for icones and maps see under subspecies).

*Perennial herb* 0.2–0.6(–1) m tall, erect or rarely decumbent to procumbent from creeping and rooting base, budding on roots late in season,<sup>3</sup> with stems numerous to few, much branched especially distally. *Stems* 2-lined, with few black glands on lines; internodes 5–25 mm, shorter than leaves. *Leaves* sessile to 1 mm petiolate; lamina (5–)10–25(–30) × (1–)3–10(–15) mm, oblong or elliptic to linear or rarely orbicular or triangular-lanceolate, paler beneath, chartaceous; apex obtuse or apiculate to rarely acute, margin plane or ± recurved to revolute, base subcordate (or rarely cordate)-amplexicaul to rather narrowly cuneate; venation: c. 2 pairs of main laterals from lower quarter to eighth of midrib, tertiary reticulation lax or scarcely visible; laminar glands pale, scattered and sometimes black, few, punctiform; intramarginal glands black, spaced, interspersed with small dense pale ones. *Inflorescence* 3- to numerous-flowered, from 1–3 nodes, with flowering branches curved-ascending from up to 15 or sometimes more nodes below, the whole cylindrical to broadly pyramidal or subcorymbiform; pedicels c. 0.5–2 mm; bracts and bracteoles up to 4(–7) mm long, narrowly lanceolate to linear, entire. *Flowers* 15–25(–35) mm in diam., stellate; buds narrowly ovoid,

<sup>3</sup>See Salisbury (1942: 106), Hagemann (1983: 106, f. 3 and refs.).

acute. *Sepals* 5, equal, 3–7 × 0.7–1.5 mm, narrowly oblong or lanceolate to linear, acute to finely acuminate with acumen sometimes glandular, entire, erect in bud, recurved in fruit; veins 3(5), unbranched; laminar glands pale and often a few black, in 2(4) rows, striiform (basally) to punctiform; intramarginal glands few, black or absent. *Petals* 5, golden yellow, not tinged red in bud, (8–)12–15 × 5–6 mm, 3–4 × sepals, oblong to oblong-elliptic, asymmetric, distally ± crenate; laminar glands all pale to mostly black or rarely absent (subsp. *chinense* pro parte), linear or partly striiform to punctiform; intramarginal glands black, distal, in sinuses when present. *Stamens* 40–60, '3'-fascicled, longest 6–8 mm, c. 0.5–0.7 × petals; anther gland black. *Ovary* 3-locular, 3–5 × 1.3–1.8 mm, narrowly ovoid to ovoid-ellipsoid; styles 3, free, 4–6 mm, c. 1.5–2 × ovary, broadly to rather narrowly spreading; stigmas narrow. *Capsule* 3–10 × 3–6 mm, 0.7–1.5 × sepals, narrowly to broadly ovoid or narrowly ovoid-conic; valves with dorsal vittae and lateral vittae or yellowish, striiform to punctiform vesicles. *Seeds* dark brown, c. 1 mm, cylindrical, not carinate or appendiculate; testa finely linear-foveolate.  $2n=32$  (Noack, 1939, Mulligan, 1957 et auct. plur.;  $n=16$ , Nielsen, 1924, Hoar & Haertl, 1932, Noack, 1939 et auct. plur.), 48 (Noack, 1939, Robson, 1981, Ciccarelli, Garbari & Mártonfi, 2001),  $2n=16$  (Schwarz, 1965, as *H. veronense*; Strid & Franzén, 1981, as var. *angustifolium*; Papanicolaou, 1984, Ciccarelli, Garbari & Mártonfi, 2001, as *H. perforatum*).

Open woodland, meadows, grassland and steppes, riverbanks, stony and grassy slopes, roadsides, in dry or well-drained habitats; 10–c. 2750 m (China), –2780 m (Tajikistan), –3150 m (Afghanistan).

General distribution of the species: Europe (except extreme north), north-west Africa, Canary Is., Madeira, Azores; Turkey, Cyprus, the Levant and western Saudi Arabia to north-west India (Uttar Pradesh), Transcaucasia, Turkmenistan to Altai, Angara-Sayan and NW Mongolia; China (W. Xinjiang and from Gansu east to Hebei, south to Jiangxi and west to Yunnan). Introduced into many other parts of the world, viz. Canada, U.S.A., Mexico, Cuba, Haiti, Brazil (Paraná), Uruguay, Argentina, Chile, Juan Fernandez, Sudan Rep. (Jebel Marra), S. Africa, Réunion, Australia, New Zealand, Japan.

*Hypericum perforatum* is apparently an allotetraploid ( $2n=32$ ) (Gustafsson, 1947; Robson, 1958a, 1975), which, for reasons of morphology and geography, would appear to have arisen from a cross between two diploid taxa ( $2n=16$ ), viz. 1a. *H. maculatum* subsp. *immaculatum* (Balkans) and 6. *H. attenuatum* (western Siberia to China). Morphologically it (or, rather, typical broad-leaved var. *perforatum*) is close to *H. maculatum*, but it differs in the 2-lined stem internodes, the more oblong leaves with lax reticulate venation and rather dense pale laminar gland dots, the lanceolate acute sepals, and the petals with black marginal glands, characters that all tend towards *H. attenuatum*. It differs from both presumed parents in its capsule valves with oblique vittae or vesicles, a glandular pattern that is unique in sect. *Hypericum* (of which it is the type species). The presence of linear laminar glands in the petals and pale laminar leaf glands suggests that the *maculatum* parent was var. *immaculatum* rather than var. *maculatum*, with its punctiform to striiform petal glands and usual lack of pale laminar leaf glands. If, as seems probable, the ancient hybridization occurred in Central Asia (the Altai region?), then (i) the current restricted distribution of var. *immaculatum* in the Balkans is a relict of a much wider one, and (ii) the extension of the current distribution of var. *maculatum* into Central Asia is relatively recent.

Cytologically, *H. perforatum* behaves as a hybrid (Noack, 1939;

Gustafsson, 1946–47; Mártonfi et al., 1996a). The pollen undergoes normal reduction division; but meiotic abnormalities (lagging chromosomes) lead to sterility that is usually about 30% but can be up to 70% (Nielsen, 1924; Hoar & Haertl, 1932). Only c. 3% of the embryo sacs are produced by normal meiosis ( $n=16$ ), the remaining (unreduced) ones being produced parthenogenetically ( $n=32$ ). The latter, however, are pseudogamous, i.e. they require pollination for seed development. Fertilization is therefore possible, though not necessary. Occasionally the  $n=32$  embryo sacs are fertilized, resulting in hexaploid ( $2n=48$ ) plants. The records of *H. perforatum* with  $2n=16$  chromosomes (see p. 63) would appear to be from dihaploids, i.e. from plants that have resulted from the development of reduced but unfertilized embryo sacs. Since in allotetraploids (i) each chromosome is duplicated and (ii) the more different the parents are, the less is the likelihood that there will be multiple chromosome associations, it seems reasonable to expect dihaploids to occur in *H. perforatum*. Two of these occurrences have been reported in the more reduced forms of the species (var. *angustifolium* and var. *microphyllum*), and two (Papanicolaou, 1984; Ciccarelli, Garbari & Mártonfi, 2001) were in *H. perforatum* without qualification. Gagnieu & Wilhelm's report (1965) of  $n=12$  for var. *angustifolium* is no doubt either a miscount for  $n=16$  or, just possibly, from fertilization by a triploid pollen grain. This cytological variation is accompanied by wide morphological variation, which is complicated in the wild by 'back-crosses' to at least two of the subspecies of *H. maculatum* (Robson, 1981: 168, f. 55) (see p. 104).

The morphological variation in *H. perforatum*, though great, appears to be continuous and therefore theoretically indivisible. For reasons of practicality, however, it is convenient to recognize some previously described variants as subspecies<sup>4</sup>, a rank that reflects their geographical basis better than the hitherto more usual varieties. For one well-known taxon, however, even this is impossible. The southern European plants with narrow leaves and vesicular capsule vittae ('var. *angustifolium* DC.') cannot be separated from those with small (narrow to broad) leaves and similar capsule vittae ('var. *microphyllum* DC.'). Indeed, the latter are probably polyphyletically derived from the former, and some may be merely the result of habitat-induced variation. Bearing in mind these reservations, the overall variation in *H. perforatum* can be described and classified in four intergrading subspecies.

- (a) From its presumed origin in western Siberia into northern and central Europe and eastward into NW Mongolia the initially sessile leaves become gradually shortly petiolate (although remaining sessile in northern Russia (always?) and sometimes in Scandinavia), and the base changes from rounded to broadly cuneate, the capsule vittae remaining continuous and almost always narrow. This is the type form (subsp. a. *perforatum*). In dry habitats the leaves become narrow with revolute margins, thus superficially resembling a form of subsp. *veronense* (see c. below); but the leaves are petiolate and the capsule glands are different. Such plants have frequently been recorded as 'var. *angustifolium* DC.', but the vesiculate capsule vittae differ from those of similar forms of subsp. *veronense*. Where the capsule is vesiculate (as it is, for example, in southern England on chalk, sand, wall-tops, etc.), such capsules are derived from *continuous* lateral vittae, as is shown by the occurrence of intermediate states. True 'var. *angustifolium*' would appear to have been derived from forms in which the lateral vittae have been interrupted before becoming enlarged and vesiculate. Another development of vesiculate capsules of this type in subsp.

<sup>4</sup>For *H. perforatum* var. *latifolium* Gaudin and synonyms, see under 17xb. *H. × desetangii* nothosubsp. *carinthiacum* nothoforma *perforatiforme*.

- perforatum* has occurred in the southern Balkans. In the mountains of Bulgaria and northern Greece there are erect to procumbent plants with small, obovate to orbicular leaves and capsules with lines of flattish vesicles ('var. *humile* Stranski'). These are interpreted here as an extreme montane development of subsp. *perforatum*, there being continuous variation from (i) typical subsp. *perforatum* to (ii) a smaller-leaved form with rather dense inflorescences and small fruits, then to (iii) a similar, decumbent form with capsule valves having two lines of flattish 'vesicles', and finally to (iv) a dwarf form with small narrower leaves.
- (b) Both presumed parents have sessile leaves, with the base rounded in *H. maculatum* and subcordate to cuneate in *H. attenuatum*. Therefore the one variant of *H. perforatum* with sessile cordate-amplexicaul leaves would also appear to have a good claim to at least approach the primitive form. This is subsp. b. *songaricum* (var. *songaricum* (Ledeb. ex Rchb.) K. Koch), of which the tallest plants with the largest leaves and most luxuriant growth (approaching those of the presumed parental species) occur in eastern Kazakhstan and probably also in NW Xinjiang. The leaves become gradually smaller southward (Kyrgyzstan – '*H. komarovii*') and westward (W. Kazakhstan, S. Russia and the southern Ukraine – var. '*gracile* ') and in dry regions develop a glaucous lower surface and recurved margins.
- (c) From the Caucasus region into eastern Turkey and northern Iran narrower-leaved plants become frequent ('var. *collinum*' Woron.), and the capsules, which are still relatively large, have interrupted and often somewhat swollen oblique vittae. The leaves then become first narrower and then smaller (often with revolute margins) eastward into central Asia (Tadjikistan) and India (east along the Himalaya to Uttar Pradesh) and westward into the Mediterranean region, where the typical narrow-leaved and small-leaved plants of subsp. *veronense* (= respectively var. *angustifolium* DC. and var. *microphyllum* DC.) occur and extend into Macaronesia, NW Africa, SW Saudi Arabia (Asir) and the Sudan Republic (Jebel Marra), although whether its occurrence in Jebel Marra is natural is doubtful (Wickens, 1976b: 76, 99, map 59). It has been introduced into various other countries and continents. Where its distribution meets that of subsp. *perforatum* in southern and central Europe, the intermediate forms that occur are presumably hybrid in origin, unless subsp. *veronense* has arisen polyphyletically in southern Europe, the Caucasus region and (possibly) Central Asia. In the trends in this subspecies the leaves first become narrow (vars *collinum*, *angustifolium*) and then small (var. *microphyllum*=subsp. *veronense*); but in relatively mesophytic areas these small leaves may become broad again (e.g. var. *ellipticum* Freyn non Durand & Pittier in mountain Turkmenistan).
- (d) In China, after a gap in distribution from NW Mongolia to Gansu and adjacent Qinghai (where some specimens closely approach subsp. *perforatum* in form), there is a southward trend to Yunnan and Guizhou in which the leaves and flowers become smaller, the latter being crowded in small (terminal and lateral) inflorescences at the end of elongated branches (subsp. d. *chinense*). This subspecies has been introduced into Japan ('*H. foliosissimum* Koidz.').
- 5a. ***Hypericum perforatum*** subsp. ***perforatum*** Stjep.-Vesel. in Josifović, *Fl. Srbije* 3: 118 (1972); Ramos in Castroviejo et al., *Fl. Iberica* 3: 165, t. 45 ff. f–j (1993).  
Fig. 8, Maps 6–8.
- H. officinarum* Crantz, *Stirp. austr.* 2: 66 (1763), 2nd ed.: 99 (1769); Moench, *Methodus*: 129 (1794), nom. illegit. Crantz cites the *Sp. pl.* phrase name (except '*Floribus trigynis*') and number. Type as for *H. perforatum* L.
- H. vulgare* Lam., *Fl. France* 3: 151 (1778); Rupr. in *Mém. Acad. Imp. Sci. Saint-Petersbourg* 7, Sér. 15, no. 2: 248 (1869), nom. illegit. Type as for *H. perforatum* L.
- H. officinale* Gaterau, *Descr. pl. Montauban*: 135 (1789); Steud., *Nomencl. Bot.*: 421 (1821) qua syn.; Raynal in *Taxon* 17: 516 (1968), nom. illegit. Type as for *H. perforatum* L.
- H. perforatum* var. [β] sensu Choisy, *Prodr. monogr. fam. Hypéric.*: 50 (1821).
- ? *H. perforatum* var. [ζ] *albiflorum* Choisy in DC., *Prodr.* 1: 550 (1824). Type: not found (1974).
- H. perforatum* var. *vulgare* Schimp. & Spenn. in Spenn., *Fl. friburg* 3: 888 (1829); Neilr., *Fl. Nied.-Oesterr.* 2: 826 (1859); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 528 (1925); Briquet, *Prodr. fl. Corse* 2(2): 150 (1936); Guşul & Nyár. in Şavul., *Fl. R. P. Roman.* 4: 29 (1956); Grossg., *Fl. Kavk.* 2nd ed. 6: 175 (1962). Type as for *H. perforatum* L.
- H. marylandicum* Birol. ex Colla, *Herb. pedem.* 1: 467 (1833), 7: 97, t. 50 f. 2 (1837). Type: no locality cited, *Herb. Birol.* (TO-holotype, photograph!).
- H. perforatum* var. [γ] *latifolium* sensu W. Koch in Rohling, *Deutsch Fl.* 3rd ed. 5: 349 (1839), *Syn. fl. germ. helv.* 2nd ed. 1: 146 (1843), *Syn. deut. schweiz. Fl.* 2nd ed. 1: 155 (1846) pro parte omnes excl. typum. The type of Koch's var. *latifolium* is that of var. *latifolium* Gaudin (1829), which he cites; his specimens (L) are typical *H. perforatum* subsp. *perforatum*. See 5xbb. *H. × desetangsii* nothosubsp. *carinthiacum* nothoforma *perforatiforme* for Gaudin's plant.
- H. assurgens* Peterm., *Anal. Pfl.-Schlüssel*: 67 (1846), in synonym.; Rouy in Rouy & Fouc., *Fl. France* 3: 337 (1896). Type: Germany, Leipzig, bei Roumaritz, *Petermann* s.n. (W!-holotype). The 'type specimen' appears to be pure *H. perforatum*, not *H. humifusum* × *perforatum* as reported by Rouy & Foucaud; and the name does not appear on Petermann's *Fl. Lips.*: 563 (1838) as cited by them.
- H. perforatum* var. *petiolatum* Peterm., *Anal. Pfl.-Schlüssel*: 67 (1846). Type: Germany, Leipzig, Konnevitze, *Petermann* s.n. (LZ+)
- H. lineolatum* Jord. in F.W. Schultz, *Arch. fl. France Allem.* 1: 343 (1854). Type: France, Ain, 'montagnes du Bugey à Junnimont', *Jordan* s.n. (LY-lectotype, selected here; BM!-isolectotype).
- ? *H. deidesheimense* Sch. Bip. ex Trev., *Hyper. sp. animadv.*: 10 (1861). Type: Germany, Rheinhessen-Pfalz, Deidesheim, *Schultz-Bip.* s.n. (P?-holotype).
- H. perforatum* var. *alpinum* Parl., *Fl. Ital.* 5: 512 (1872); Fiori & Paol., *Fl. Italia* 1: 388 (1898); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 524 (1911). Type: Italy, Piemonte, sopra i Bagni di Valdieri al Vallasco nella regione superiore del Faggio, 1300 m, *Parlatore* s.n. (FI-lectotype, Ciccarelli, Garbari & Robson, 2002); come pure nella regione superiore dell'Abeto del Monte Cramont', *Parlatore* s.n. (FI-syntype). Fröhlich (1911: 524) compares (synonymizes?) this with his forma *lineolatum* of subsp. *vulgare*.
- H. perforatum* var. *anomalum* Frid. in Lange, *Haandb. Danske fl.* 4th ed.: 700 (1887). Type: Denmark, Slesvig [Sønderjylland], Haderslev, 1886 (fl), *Haspelmath* s.n. (C!-holotype).
- H. perforatum* var. [α] *typicum* Beck, *Fl. Nieder-Österr.* 2: 530 (1892); Fiori & Paol., *Fl. Italia* 1: 388 (1898). Type as for *H. perforatum*.
- H. perforatum* var. *vulgare* subvar. *lineolatum* (Jord.) Rouy in Rouy & Fouc., *Fl. France* 3: 333 (1896). Type as for *H. lineolatum* Jord.
- H. perforatum* var. *ellipticum* Durand & Pittier in *Bull. Soc. Roy.*

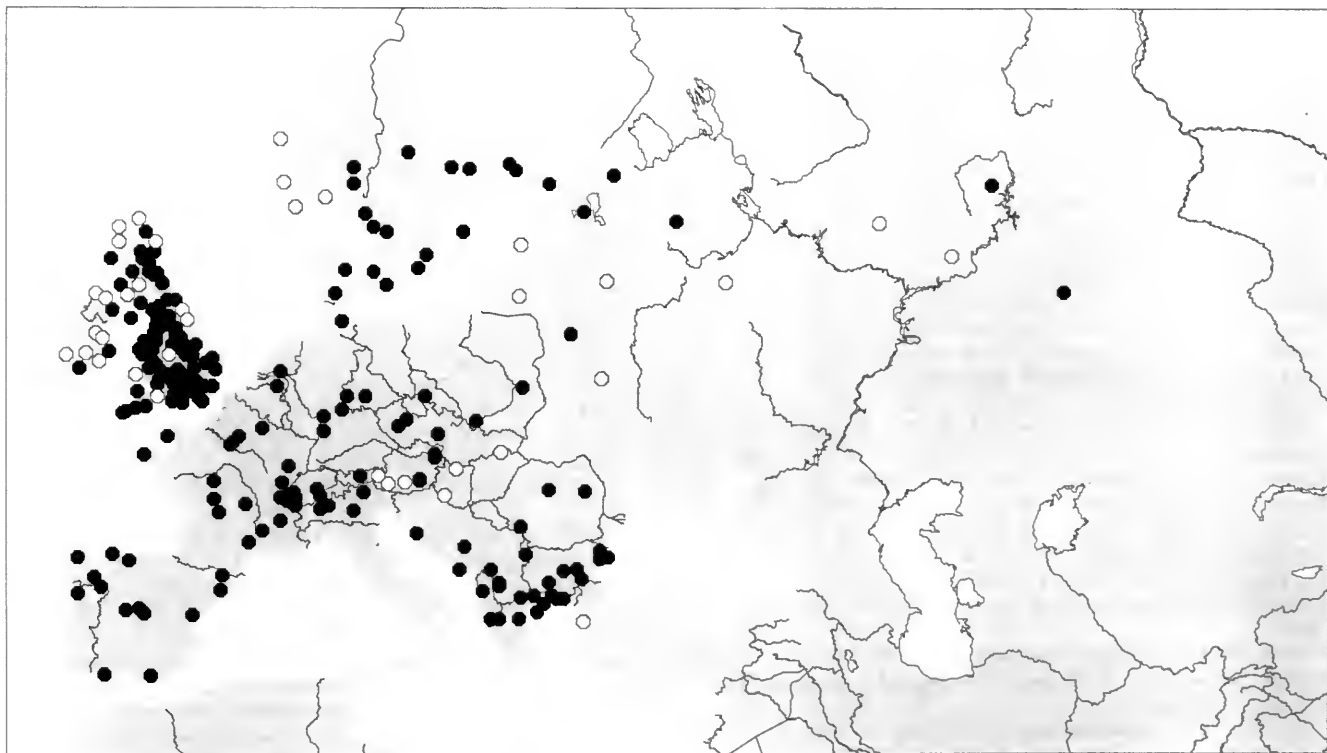


**Fig. 8** *H. perforatum*. A. subsp. *perforatum*: (a) habit; (b) sepal; (c) petal, omitting laminar glands; (d) capsule. B. subsp. *songaricum*: (e) branch; (f) capsule. C. subsp. *veronense*: (g) branch; (h) sepal; (i) petal, omitting laminar glands; (j) capsule. D. subsp. *chinense*: (k) stem and branch; (l) leaves (depauperate); (m) capsule (a, e, g, k, l  $\times 2/3$ ; rest  $\times 6$ ). A. (a–c) *Martinez* s.n.; (d) *Seemen* s.n. B. (e, f) *Becker* s.n. C. (g–i) *Riera* et al. 17197; (j) *Lacaña* 28. D. (k) *Wilson* 2425; (l) *Bullock* s.n.; (m) *Father Hugh* s.n.

- Bot. Belgique* **20**: 80 (1881). Type: Switzerland, Vaud, bois près de Rolle, *vide* '*H. perforatum* [var.] a' sensu Rapin, *Cat. fl. vaud.*, 2nd ed.: 123 (1862) (G?-holotype). Hegi (1925: 528) reduced this to a form of var. *vulgare*.
- H. vulgare* Bubani, *Fl. pyren.* **3**: 345 (1901), non Lam. (1778). Bubani ascribed this name to pre-Linnaean authors.
- H. perforatum* var. *normale* Woron. in Kuzn., Busch & Fomin, *Fl. Cauc. Crit.* **3**(9): 56 (1906). Type as for *H. perforatum* L.
- H. perforatum* subsp. *vulgare* (Schimp. & Spenn.) A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 522, f. 2 (1911), in *Mitt. Naturwiss. Vereins Steiermark* **51**: 240 (1915); Hayek, *Prodr. Fl. Pen. balc.* **1**: 533 (1925).
- H. perforatum* subsp. *vulgare* forma *brevisepalum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 524 (1911). Type: Austria, Styria, Gösting bei Graz, 11 July 1909 (fl), *Fröhlich* GZU16368 (GZU!-lectotype, selected here).
- H. perforatum* subsp. *vulgare* forma *lineolatum* (Jord.) A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 524 (1911), in *Mitt. Naturwiss. Vereins Steiermark* **51**: 240 (1915). Type as for *H. lineolatum* Jord. Fröhlich also describes this taxon in *adnot.* as 'subvar. *lineolatum*', a later homonym than that of Rouy (1896).
- H. perforatum* subsp. *vulgare* forma *lucidum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl., I.* **120**(1): 524 (1911), in *Mitt. Naturwiss. Vereins Steiermark* **51**: 240 (1915). Type: Austria, Styria, Stiftingtal bei Graz, 26 July 1910 (fl), *Fröhlich* GZU16378 (GZU!-lectotype, selected here).
- H. perforatum* var. *humile* Stranski (date?) [description not found]; Stoj. & Stef., *Fl. Bulg.*: 774 (1948); Stoj., Stef. & Kitan., *Fl. Bulg.* **2**: 720 (1967). Type: Bulgaria (SO).
- H. perforatum* var. *vulgare* forma *brevisepalum* (A. Fröhl.) Hegi, *Ill. Fl. Mitt.-Eur.* **5**(1): 528 (1925).

- H. perforatum* var. *vulgare* forma *anomalum* (Frid.) Hegi, *Ill. Fl. Mitt.-Eur.* **5**(1): 528 (1925).
- H. perforatum* var. *vulgare* forma *lineolatum* (Jord.) Hegi, *Ill. Fl. Mitt.-Eur.* **5**(1): 528 (1925), sphalm. '*lanceolatum*'.
- H. perforatum* var. *vulgare* forma *lucidum* (A. Fröhl.) Hegi, *Ill. Fl. Mitt.-Eur.* **5**(1): 528 (1925).
- H. perforatum* subsp. *vulgare* var. *lineolatum* (Jord.) Hayek, *Prodr. Fl. Pen. balc.* **1**: 533 (1925).
- H. perforatum* var. *cereticum* Sennen, ined.? 'Type': Spain, Lérida, La Cerdaña, Targassonne, 1600 m, 15 September 1916 (fr), Sennen s.n. (BC, BM!).
- H. perforatum* var. *decompositum* Nyár. in *Bul. Grád. Bot. Univ. Cluj* **19**: 85 (1939); Guşul. & Nyár. in *Savul., Fl. R. P. Roman.* **4**: 29 (1956). Type: Romania, Transsilvania, distr. Treiscaune, ad balneas Şugaş, supra opp. Sf. Gheorghe, 7 September 1928 (fr), Nyárády s.n. (CL-holotype, photocopy!).
- H. perforatum* var. *semihumifusum* Nyár. in *Bul. Şti. Acad. Republ. Populare romîne, Sect. Şti. Biol. etc.* **7**: 226, t. 2 f. 3 (1955); Guşul. & Nyár. in *Savul., Fl. R. P. Roman.* **4**: 29 (1956). Syntypes: Romania, Walachia, Piteşti, Mt. Cozia, 1200–1400 m, 17 May, 20 June & 19 August 1950 (fl & fr?), Nyárády s.n. (CL).
- H. perforatum* subsp. *perforatum* var. *pellucidum* O. Schwarz in *Drudea* **5**: 61 (1965), nom. illegit. (Art. 37.1). Type: none cited.
- H. perforatum* var. *perforatum* – N. Robson in *Wisskirchen & Haeupler, Standardliste Farn- u. Blütenpfl. Deutschl.*: 270 (1998).
- Icones: Rchb., Ic. fl. germ. helv.* **6**: t. 343, f. 5177 (1844); Ross-Craig, *Draw. Brit. Pl.* **6**: t. 7 (1952); Ramos in Castroviejo et al., *Fl. Iberica* **3**: t. 45 ff. f–j (1993).

*Leaves* usually petiolate; lamina (5–)12–25(–30) × (2–)5–10 mm, broadly to narrowly oblong or ovate to rarely elliptic or orbicular or obovate (l:b=(1–)2–3(–5)), base rounded to broadly cuneate, not



**Map 6** 5a. *H. perforatum* subsp. *perforatum*, Eurasia ●, other records ○. The north European plain, Bavaria and the upper Danube region under-represented.

glaucous beneath. *Inflorescence* not usually congested, with branches relatively short, straight. *Petals* with laminar glands all pale to mostly black. *Capsule* valves with lateral vittae linear, narrow or rarely swollen distally but not interrupted, the vesicles forming a regular row, not scattered irregularly.

Distribution of the species excluding (i) the Mediterranean region, Macaronesia, Jebel Marra, SW Saudi Arabia (Asir), nearly all Asiatic Turkey, Transcaucasia and Iraq to NW India; (ii) Kazakhstan and adjacent southern Russia; (iii) China. Introduced into North America, Mexico, Cuba, Haiti, Brazil (Paraná), Uruguay, Argentina, Chile, Juan Fernandez, Hawaiian Islands and possibly New Zealand and Australia (no confirmed records).

**SCOTLAND.** **Sutherland:** Kildonan, 1882 (Anthony, 1976: 64). **Easter Ross:** Strathpeffer, 1967 (Duncan, 1980: 40). **Inverness:** Beauly, 1954 (McCallum Webster, 1978: 115). **Moray:** Forbes, near Greshop House, 12 August 1961 (fl), *McCallum Webster* 5864 (K). **S. Aberdeen:** Ballater, mouth of R. Muick, 30 July 1955 (fl), *Robson* s.n. (BM). **Forfar:** Clova, Birkhill, n.d. (fl), *Gardiner* s.n. (BM). **Mid Perth:** Aberfeldy, July 1929 (fl), *Meinertzhagen* s.n. (BM). **Stirling:** Loch Lomond, Balmaha, 30 July 1962 (fl), *Kenneth* s.n. (BM). **Mid Ebudes:** Mull, Achnadriish, July 1968 (e. fl), *Kingston* s.n. (BM). **Midlothian:** Inveresk, 1851 (fl), *Syme* s.n. (BM). **Berwick:** Nenthorn parish, near Newton Don, 3 August 1960 (fl), *Bangerter* 948 (BM). **Kirkcudbright:** Tongland, July 1883 (fl), *Coles* s.n. (BM).

**ISLE OF MAN.** Peel, 5 September 1944 (fl), *Paton* s.n. (BM).

**ENGLAND.** **Cumbria:** Seascale, September 1903 (fl), *N. Simpson* 3025 (BM). **Northumberland:** Middleton Hall, Wooler Water, 4 July 1958 (bud), *Bangerter* 645 (BM). **NE Yorks.:** near Hill Ghyll, 4 August 1926 (fl), *Foggitt* s.n. (BM). **Mid-W. Yorks.:** Arncliffe village, 18 July 1959 (fl), *Gerrans* 717 (BM). **E. Yorks.:** Wauldley, 2 August 1951 (fl), *Radford* s.n. (BM). **S. Lancs.:** Liverpool, Oglet, 13 July 1972 (fl), *Greenwood* s.n. (LIV). **Notts.:** Budby, Fanny's Grove, 20 July 1963 (fl), *Bowden & Hillman* 37 (BM). **S. Lincs.:** Grantham, Sattersford, 19 July 1913 (fl), *Fishers* s.n. (BM). **Shropshire:** Ferny Dingle, 10 July 1961 (fl), *Butler & Milward* 415 (BM). **W. Gloucs.:** Tidenham, 16 July 1909 (fl), *Riddelsdell* s.n. (BM). **Bucks.:** 1.6 km SE of Ellesborough, Coombe Hill, 28 July 1954 (fl), *Melderis* 681 (BM). **E. Norfolk:** Lopham Middle Fen, 3 July 1973 (fl), *Jones & Vickery* 29 (BM). **N. Essex:** Berechurch, 2 July 1954 (fl), *Jermyn* 226 (BM). **E. Kent:** Isle of Sheppey, near Warden Point, 20 September 1953 (fr), *Bangerter* 205 (BM). **Surrey:** near Croydon, Riddlesdown, 17 July 1954 (fl), *J. & M. Cannon* 2761 (BM). **N. Hants.:** near Alton, Selborne Hanger, 22 July 1974 (fl), *Gerrans* 1817 (BM). **Dorset:** Parkstone, 23 October 1927 (fr), *Salmon* s.n. (BM). **N. Somerset:** Clevedon, 11 July 1934 (fl), *Waterfall* s.n. (BM). **S. Devon:** Buckfastleigh, 4 July 1973 (fl), *Chicken* 524 (BM). **W. Cornwall:** N. of Camborne, near Godevry and Gwithian, 27 June 1953 (fl), *Murphy* s.n. (BM).

**WALES.** **Glamorgan:** Parkmill, July 1903 (fl), *Riddelsdell* s.n. (BM). **Radnor:** near Llangunlo Stn, 5 August 1956 (fl), *P.C. & J. Hall* 52/56 (BM). **Merioneth:** Penmanpool, 7 July 1961 (fl), *Raven [ & Benoit]* 16308 (BM). **Caernarvon:** Llandudno junction, Conway estuary opposite Conway, August 1962 (fr), *Brummitt* 62.224 (LIV). **Denbigh:** S. of Llangollen, Pengwern, 28 August 1877 (fl), *Bailey* s.n. (BM).

**IRELAND.** **E. Cork:** near Fernroy, 1849 (fl), *Chandlee* s.n. (BM). **Mayo:** Mulranny, 16 August 1947 (fl & e. fr), *Ross-Craig & Sealy* 1520 (K). **Carlow:** Staplestown, n.d. (fl), *Collector?* (BM). **Wexford:** W. of Bunclody, Drumerry quarry, 5 September 1962 (fl & fr), *McCallum Webster* 8048 (K). **Wicklow:** Ovoca, July 1882 (fl), *Fawcett* s.n. (BM). **Down:** near Newcastle, Sliddyford, 6 September 1952 (fr), *Turrill* s.n. (K). **Antrim:** Logan Canal, 1.6–5 km from Belfast, n.d. (e. fr), *A.G. More* s.n. (BM).

**CHANNEL ISLES.** **Jersey:** St. Helier, 14 July 1883 (fl), *Fawcett* s.n. (BM).

**THE NETHERLANDS.** **Gelderland:** Bennekom, b/d Vijrus, 20 July 1927 (fl), *Vermeulen* s.n. (K). **Brabant:** Valkenswaard, 4 August 1979 (fl), *P. van Royen* 11833 (K, L\*).

**BELGIUM.** **W. Vlieland:** near Proven, 1 July 1918 (fl), *G.C. Brown* s.n. (BM). **Brabant:** Opwijk, vallei van de Brabantse beek, 18 August 1981 (fl), *Robrecht* 1533 (BM, BR\*). **Hainault:** Obourg, 8 August 1862 (fr), *Martinis* in van Huerck 142 (BM, K). **Namur:** Wavreille, June 1914 (fl), *G.A.B.* s.n. (BM).

**FRANCE.** **Ardennes:** Rethel, 1 August 1897 (fr), *Gérard* in Soc. Rochel. 4049 (BM). **Oise:** Paris, forêt de Chantilly, 15 June 1912 (fl), *Ronniger* s.n. (W). **Hts de Seine:** Bois de Meudon près Paris, October 1875 (fl), *Bonnet* s.n. (K). **Finistère:** Brittany, Haelgost, 22 July 1913 (fl), *Perrycoste* 3639 (BM). **Loire atl.:** Mauves, July 1860 (fl), *Gadeceau* s.n. (BM). **Maine-et-Loire:** la route à Montfaucon s. Moine, 10 July 1888 (fl), *Gadeceau* s.n. (BM). **Hte Vienne:** Le Dorat, 21 July 1929 (fl), *Jalicon* s.n. (BM). **Cher:** Noirlac, 22 June 1864 (fl), *Déséglise* s.n. (BM). **Hte Saône:** entre le Loritellet et le mont près Conflans, 2 August 1856 (fl), *Perrier* 277 (BM). **Jura:** Salins les Bains, 425 m, 15 August 1892 (fl), *Deschamps* (BM, BR\*). **Hte Savoie:** Mont Salève, 29 July 1922, *Lacaita* 29/22 (BM). **Savoie:** Belleville, 300 m, 2 September 1861 (fr), *Perrier* in *Billot* 3349bis (BM). **Puy de Dôme:** Auvergne, Mont Dore, August 1920 (fl), *Norman* s.n. (BM).

**ANDORRA.** Vallée du Valira, July 1933 (fl), *Font* in *Sennen* s.n. (BM).

**SPAIN.** **La Coruña:** near Coruña, August 1888 (e. fr), *Guardia* s.n. (BM). **Orense:** c. 50 km E. of Orense, Monte Manzaneda, 1410 m, 22 August 1982 (fl), *Goyder & Jury* 606 (BM, RNG). **Santander:** Picos de Europa, between Fuente Be and Espinama, 877–1200 m, 5 August 1969 (e. fr), *Grimes* 319 (BM, RNG). **Viscaya:** Monasterio de Nuestra Señora de Guadalupe, Cáceres, 24 June 1958 (fl), *Guinea* 2789 (RNG). **Lérida(?):** Cerdagne, Estavar, 1230 m, 8 September 1929 (fr), *Sennen* s.n. (BM). **Madrid:** Madrid, Real Casa de Campo, June 1930 (fl), *Martinez* s.n. (BM, MA\*). **Avila:** Hoyacasero, Río Alberche at Venta del Obispo, 1250 m, 14 July 1983 (fl), *M. & S. Gardner* 2002 (BM, RNG).

**PORTUGAL.** **Minho:** [Braga] juxta Guimaraeus [Guimarães] in Durminia [Minho?], n.d. (fl), *Baron Paiva* s.n. (K).

**ITALY.** **Novara:** Alpi Lepontine, Valle Formazzo, Altillone, 1300 m, 4 August 1912 (fl), *Roggiani* s.n. (BM).

**SWITZERLAND.** **Ticino:** Monte Generoso, 6 July 1856 (fl), *Murray* s.n. (BM). **Valais:** Brieg [Brig] to Viesch, 22 July 1881 (fl), *Linton* s.n. (BM). **Vaud:** near Vevey, 30 June 1856 (fl), *Murray* s.n. (BM).

**AUSTRIA.** **Niederösterreich:** Weinverteil, Hagenbrunn, zwischen Kronawettberg und Tradenberg, 23 June 1993 (bud), *Vitek* s.n. (BM). **Steiermark:** ad pagum Gösting prope urbem Graz, 460 m, September 1909 (fl & fr), *Reiter* in *Hayek*, Fl. Stir. Exsicc. 1016 (BM). **Tirol:** Seefeld, 1200 m, 23 August 1936 (fl), *Wyatt* 77 (K).

**GERMANY.** **Baden-Württemberg:** Schwarzwald, Heselbach, 4 August 1931 (fl), *Williams* s.n. (BM). **Hessen:** Milseberg, 13 September 1913 (fl), *Arnold* s.n. (FR). **Thuringen:** Strasse Wilhelmstal-Etterwinden, 7 August 1948 (fl), *Launert* 166 (BM). **Schleswig-Holstein:** Forst Neumünster, 17 July 1969 (fl), *Holm-Nielsen* et al. in *Fl. Germ. Exsicc.* 16 (BM, TAI).

**DENMARK.** **Jylland:** Ajstrup, S. of Aarhus, 23 July 1965 (fl), *Pedersen* in *Fl. Jul. Exsicc* 140 (BM, TAI). **Sjælland:** Nordsjælland, Tisvilde Hegn., 1913 (fl), *Dahl* D. 45b (BM).

**NORWAY.** **Vestfold:** Jahlsberg, Oslo Fjord, Aasgaardstrand, 10 September 1934 (fl), *Williams* s.n. (BM).

**SWEDEN.** **Blekinge:** Kellovik, Injauley, 191– (fl), *F.G. Johansson* s.n. (BM). **Malmöhus:** Malmö, July 1886 (fl), *G. Johansson* s.n. (BM). **Göteborg:** Ringon, 23 July 1957 (l. fl), *Blom* s.n. (BM). **Småland:** Madesjö, 29 July 1909 (fr), *Medelius* s.n. (BM). **Gotland:** Visby, July 1912 (fl), *E. Th. Fries* s.n. (BM). **Södermanland:** Millsten, 8 August 1929 (fr), *Asplund* s.n. (BM). **Uppsala:** Söderby Karl, Brölunde, 12 July 1956 (fl), *H. Smith* 2037 (BM). **Värmland?:** par. Hilared, ad Tarsered, 12 July 1916 (fl), *Ohlson* s.n. (BM).

**FINLAND.** **Uusimaa:** Varsinais-Suomi, Korppoo, Jurmo, Huwudskär, 23 July 1965, *Kause & Seikkula* s.n. (JE).

**ESTONIA.** **Tartu:** Dorpat bei Ropkoi, 25 July 1860 (e. fr), *Gruner* s.n. (BM).

**BELORUS.** Distr. Nowogródek [Novogrudsk], ad Niankow, 1893 (fl), *Dybowski* in *Rehman & Wolszczak*, Fl. polon. exsicc. 148 (BM).

**RUSSIA.** **St Petersburg?:** Ingria, June–August 1860 (fl), *Herb. Fl. Ingricae* 134 (BM, K). The species is recorded by Gorschkova (1949: 249) from all regions, except Karelia-Lapland and the Arctic, east to Angara-Sayan (Chuna Angara watershed). The precise areas of overlap between the distributions of subsp. *perforatum* and subsp. *songaricum* are uncertain but appear to be in the central Ukraine and the southern Altai (see Maps 6 and 9). The species (no doubt subsp. *perforatum*) has also been recorded from the Mongolian side of the Altai mountains (Gubanov, 1996: 76).

**POLAND.** **Lublin:** Lublin distr., 1 July 1884, *Królestwa* s.n. (JE). **Bielsko-Biala:** Wadowice, Wiepoz k. Andrychowa (pr. Andrychów), 18 July 1938 (fl), *Łańcucka* in Pl. Pol. exsicc. 328 (BM, JE, K). **Jelenia Góra:** Sudetia,



Hirschberg, Perle des Westens, 1 August 1958, *Köhler & Zippold* s.n. (JE). **Walbrzych?**: Reichenstein [Złoty Stok], Dörndorf, 20 August 1899 (fl), *Troedel* s.n. (FR); Schweidnitz [Świdnica], Költtschenberg, September 1882 (l. fl), *Peck* s.n. (FR).

**CZECH REPUBLIC. Bohemia**: prope vicum Průhonice haud procul Pragam, c. 300 m, 22 August 1958 (l. fl & fr), *Nitka* in Fl. Czech. Exsicc. 148 (BM).

**SLOVAKIA. Bratislavsky Kr.**: N. Bratislava, 1803, *Collector?* s.n. (JE).

**HUNGARY.** [Province?]: Gau Mayn?, August 1873 (fl), *Leichtermis?* s.n. (BM).

**ROMANIA. Transylvania**: [Carus Severin] Banat, N. of Turnu Severin, 24 km above Băile Herculane up Cerna valley, 27 July 1971 (fl), *Frazer Jenkins* 3499 (BM). **Moldavia**: Mun. Bacău, prope pagum Măgum, c. 400 m, 25 August 1971 (fl), *D. Mititelu, Barabaş & L. Mititelu* in Fl. Exsicc. Distr. Bacov. 351 (BM). **Walachia**: Oltenia, distr. Gorj, Cimpul Experimental Ciocirlău, 29 June 1965 (fl), *Cirtu & Zaharia* in Fl. Olten. Exsicc. 960 (BM).

**BULGARIA. Tolbukhin**: Süddobrukscha, Kap Kaliskra, 16 August 1958 (fr), *Meyer* 645 (JE). **Varna**: Süddobrukscha, Varna, Weg vom Strande zum Aladsha Monastir, 11 August 1958 (fl & fr), *Meyer* 414 (JE). **Sliven**: prope Sliven, in monte Sini Kamil, 20 June 1907 (fl), *Schneider* lt. balc. 583 (BM). **Yambol?**: Strandsha-Planina, zwischen Blgari und Kostı, c. 300 m, 14 October 1958 (fr), *Meyer* 2088 (JE). **Stara Zagora**: Stara Planina, Krstec, zwischen Stara Zagora und Trnovo [Veliko Turnovo], 28 October 1958 (fl), *Meyer* 2234 (JE). **Smolyan?**: in Rhodope Centralis ad Selča-Djorlen, 12 July 1924 (fl), *Stefanoff* s.n. (BM) ['var. *humile*'].

**SLOVENIA.** Carniola, September 1854 (fl), *Ball* s.n. (K).

**CROATIA. Dalmacija**: Velebit Mts, 840 m, 2 July 1962 (fl), *Mathew & Pycraft* 212 (BM).

**SERBIA. Srbija**: Vranja [Vranje], 1919 (fl), *Tindal Lucas* 104 (BM) [hybrid?]; circa urbem Gevlegi supra pagum Sermenin, Mt Rožin, 17 July 1937 (fl), *Grebenschikoff* s.n. (K). **Kosovo**: Bertiscus (Alpes boreales albanicae) in fauce rivuli Sušica prope oppidum Peč (Ipek), 750–950 m, (fl), *K.H. Rechinger & Scheffer* Iter balc. 1933 782 (K).

**BOSNIA.** Sarajevo, 750 m, 12 July 1960 (fl), *McCallum Webster* 4036 (K).

**MONTENEGRO.** Distr. Vasojačići, Korpice, 30 August 1903 (fl & e. fr),

*Hannibal* in *Baldacci* Alb. X 44 (BM). Distr. Kuči, Poprat (Trijapsi), 4 July 1900 (fl), *Baldacci* Alb. VII 56 (BM, K).

**ALBANIA.** Patok, Mamuras, 6 m, 15 May 1936 (fl), *Pennington* 206 (K).

**MAKEDONIJA.** Šar Planina, 900–1200 m, 9 September 1968 (fl), *Roper* 9 (BM). Gostiver to Navrovo, 3 km NE of top of pass, 1100 m, 19 July 1970 (fl), *Edmondson* 227 (BM).

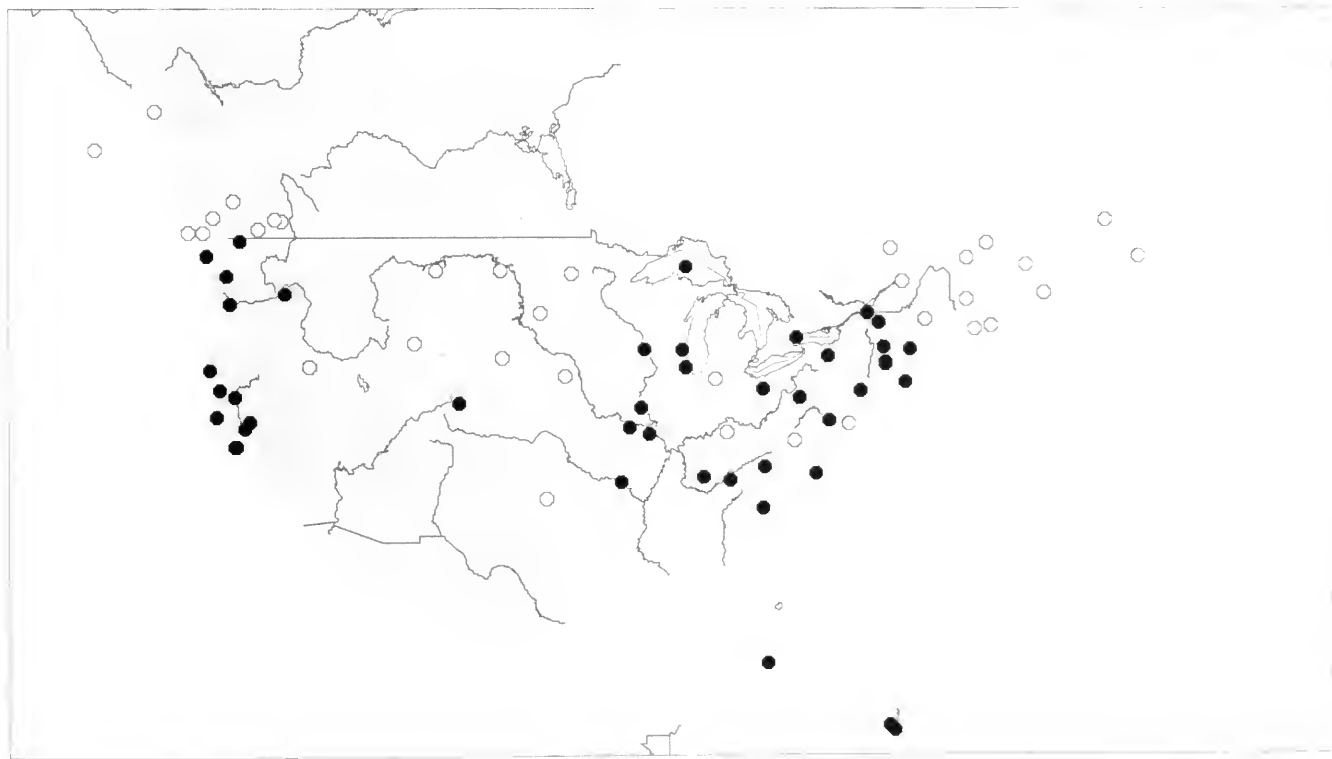
**GREECE. Thraki**: Thracia occid., in monte Karlik-Dagh prope Komotini (Gümülschina), 1200 m, 2 July 1936 (fl), *K.H. & F. Rechinger* Iter Graecum IV 10478 (BM). **Makedonia**: N. Khalkidiki, Oros Cholomon, c. 8 km WSW of Arnaea, 1100 m, 10 September 1981 (fl & fr), *Husain, Jury & Rutherford* 99 (BM, RNG\*) ['var. *humile*'].

**TURKEY. Balikesir**: Mt. Ida, prope Kareikos, 3 July 1883 (fl), *Ascherson* in *Sintenis* 474 (BM).

#### INTRODUCTIONS

**CANADA. Newfoundland**: *vide* Scoggan (1978: 1097). **Prince Edward Island**: Royalty Road, 9 August 1888 (fl), *Macoun* s.n. (BM). **Nova Scotia**: Bridgetown, 5 July 1872 (fl), *Fowler* s.n. (P). **New Brunswick**: Rothesay, 1 September 1875 (fl), *Mathew* s.n. (P). **Quebec**: Quebec, foot of Heights of Abraham, 13 August 1959 (fr), *Stearn* 2403 (BM); Co. Sherbrooke, Jouvence, 17 September 1976, *Bourassa* 43 (H). **Ontario**: Stanford Township, 10 August 1943 (fl), *K.O. Wood* s.n. (BM); Ottawa (West), Nurminutly, 15 July 1927, *Pesola* s.n. (H). **Br. Columbia**: W. Vancouver, corner 17th Street and Duchess Ave., 9 August 1963 (fl), *Bird* 9061 (BM); Vancouver I., Cowichan Lake Road, 171 m, 28 June 1967, *Turner* et al. 552 (H).

**U.S.A. Maine**: Marion Co., Marion, 28 August 1956 (fl), *Rees* 403 (BM). **Vermont**: Windham Co., Townshend, 10 July 1937 (fl), *E. & H. Moldenke* 9893 (BM). **New Hampshire**: Rockingham Co., just S. of Portsmouth on US Rt. 1, 22 August 1967 (fr), *Ahles* 69436 (BM). **Massachusetts**: Hampshire Co., Northampton, off Daymon Rd., 19 July 1979 (fl & fr), *Ahles* 87101 (BM). **Rhode I.**: Newport Co., Tiverton, Four Corners, 2 July 1979 (fl), *Ahles* 83182 (H). **New York**: Tompkins Co., Connecticut Hill, 7 September 1983 (fl), *Kearney* 39 (BM). **New Jersey**: Somerset Co., Watchung, 4 July 1934 (fl), *Moldenke* 8066 (BM, TAI). **Pennsylvania**: Westmoreland Co., c. 2.5 km S. of Ligonier on PA hwy 711, 400 m, 1 July 1979 (fl), *Utech* 79–327 (BM, W). **Maryland**: Prince Georges Co., Beltsville, 8 July 1950 (fl), *Petrak* 314 (W).



Map 7 5a. *H. perforatum* subsp. *perforatum*, North America (introduced) ●, other records ○.



Map 8 5a. *H. perforatum* subsp. *perforatum*, South America (introduced) ●.

**Virginia:** Giles Co., just off Va. 700, entrance to Mountain Lake Biol. Stn., 1146 m, 28 July 1968 (fl & fr), *Culwell* s.n. (BM). **N. Carolina:** Avery Co., E. side of Grandfather Mountain, below summit, 1560 m, 21 July 1968 (fl), *Culwell* s.n. (BM). **Tennessee:** McMinn Co., Etowah, 20 July 1969 (fr), *Rogers* 43984 (H). **Arkansas:** Pope Co., US 64 at Happy Bend Rd., 6.7 km E. of junction with Ark. 105 in Atkins, 120 m, 12 June 1968 (fl), *Culwell* s.n. (BM). **Missouri:** Marion Co., near Hannibal, 13 July 1918 (fl), *Davis* 8969 (H). **Illinois:** Cork Co., E. from Des Plaines R., S. of Irving Park Rd., 4 July 1956 (fl), *Bennett* s.n. (W). **Indiana:** Lake Co., Roby, 12 July 1906 (fl), *Lansing* 2551 (W). **Ohio:** Trumbull Co., Vienna Twp., 25 July 1965 (fl & fr), *Sturm* 160 (W). **Michigan:** Barago Co., Ford Forestry Center, 13 July 1974 (fl), *Bourdo* 28729 (W). **Wisconsin:** Waukesha Co., Bishop's Woods, 22 June 1970 (fl), *Klopatek* s.n. (H). **Colorado:** Boulder Co., S. Boulder Creek 9.6 km S. of Boulder, 27 June 1967 (fl), *Weber* 13190 (H). **Washington:** Olympic Peninsula, Deer Park, 390 m, 17 July 1965 (fl), *Fisk & Chapman* 97 (H). **Oregon:** Jackson Co., P.O. Prospect, Rogue R. bottoms, Farewell Forestry Camp, 780 m, 28 July 1959 (l. fl), *Demaree* 41365 (BM). **California:** Trinity Co., New River, Up Grade Mine, 10 August 1950, *Wheeler* 6774 (BM, RSA\*). Also recorded from Connecticut, Delaware, D.C., S. Carolina, W. Virginia, Kentucky, Texas, Oklahoma, Kansas, Nebraska, Iowa, Minnesota, N. & S. Dakota, Wyoming, Montana and Idaho (Robson, ined.).

**MEXICO.** Kbg., 1865 (fl), *Bilimeck* s.n. (MEXU). No precise locality, n.d. (fl), *McMinn* s.n. (P).

**CUBA.** **Matanzas:** Matanzas, December 1822 (fl & fr), *Poeppig* s.n. (BM, P, W). **Oriente:** Sierra de Nipe, Woodfred, c. 500 m, 24 September 1922 (st), *Ekman* H.9313 (S).

**HAITI.** Massif de la Selle, Pétionville, c. 1400 m, 31 July 1924 (fr), *Ekman* H.1217 (S, US); above Port au Prince, 1600 m, 1947 (fl), *Heldring-Talma* s.n. (U).

**BRAZIL.** **Rio de Janeiro:** Serra do Itatiaia, Retiro, 17 May 1902 (fl & fr), *Dusén* 258 (S).

**URUGUAY.** **Montevideo:** Sayago, 15 February 1936 (fr), *Rosengurt* B 2049 (GH).

**ARGENTINA.** **Buenos Aires:** Bella Vista, October 1915 (st), *Hicken* 444 (GH). **Chubut:** Lago Puelo, 10 February 1955 (fr), *Burkhart* 19915 (US).

**CHILE.** **Talca:** Empedrado, 11 March 1972 (fr), *Mahu* 8710 (H).

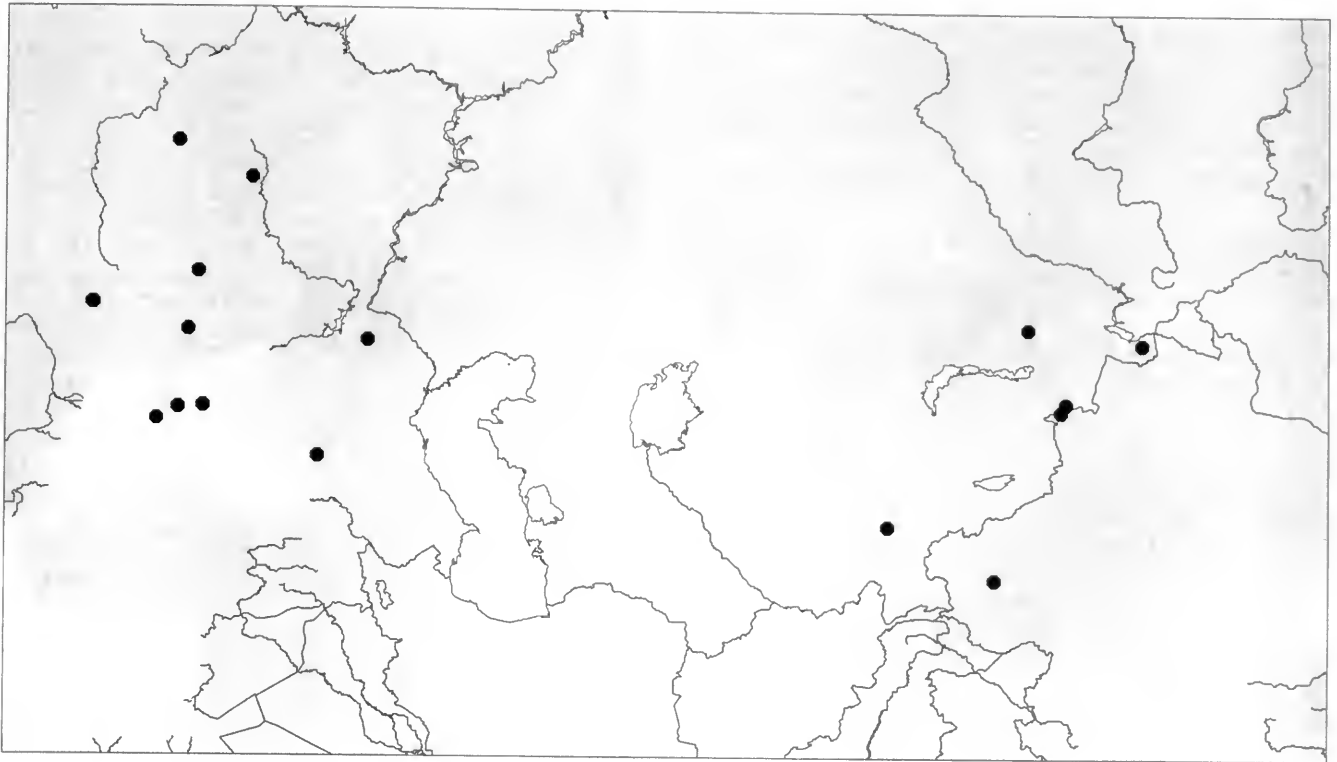
**Concepción:** Saltos del Laja, 5 January 1971 (fl), *Lourteig* 2518 (S). **Nuble:** Termas-Chillan, 8–10 km de las Termas, 2000 m, 7 January 1971 (fl), *Lourteig* 2535 (P, S). **Bio Bio:** Parlahueque, December 1929 (fl), *Piria* 197 (GH). **Malleco:** Manzanar, 13 January 1986 (e. fr), *Pedersen* 14214 (BM). **Cautin:** Dpto Victoria, around Termas de Tolhuaca and 16 km towards Curacuatín, 950–1180 m, 12 March 1939 (fr), *Morrison & Wagenknecht* 17488 (GH, K, MO). **Valdivia:** La Unión Reserva Forestal, January 1969 (fl), *Mahu* 9739 (H). **Llanquihue:** Alerce, 14 February 1936 (fr), *Cabrera* 3691 (F, S).

**JUAN FERNANDEZ.** **Masafuera:** Papal, 23 January 1955 (fl), *Kuschel* 147 (S).

**HAWAIIAN ISLANDS.** **Hawaii:** North Kona, road up Hualalāni, Kaupulehu, 1500 m, 9 September 1961 (fl & fr), *Fosberg* 42087 (BISH); Hualalāi [Puu Hualalei], 1 July 1964 (fl), *Carlson* s.n. (BISH).

Subsp. *perforatum* typically has broad, relatively large leaves and large flowers and fruits with narrow linear oblique vittae. In dry habitats (e.g. chalk soils, walls), however, narrow-leaved smaller-flowered plants superficially resembling subsp. *veronense* are often seen; but these have lateral capsule vittae typical of subsp. *perforatum* or with the distal ends forming a line of vesicles, not irregular like those of Mediterranean forms of subsp. *veronense*. Such plants occur in England (and probably elsewhere in NW Europe) as well as in the U.S.A. and Canada, the true subsp. *veronense* being absent from these areas. Where the distributions of subsp. *perforatum* and subsp. *veronense* overlap (in southern France, southern Germany, Austria and northern Italy), forms intermediate between the subspecies occur. These are similar to the northern dry-habitat forms in having narrow petiolate leaves, but the capsule glands are also intermediate in form, i.e.  $\pm$  irregularly vesiculate but with several dorsal linear vittae. Examples of such intermediate specimens from Austria (Styria) were cited by Fröhlich (1911) as subsp. *angustifolium*, e.g. Fölling bei Maria Trost, 23 July 1910 (fr), *Fröhlich* GZU16326 (GZU). There is evidence that such populations show cytological irregularities (Garbari, in litt.)





Map 9 5b. *H. perforatum* subsp. *songaricum* ●.

It seems likely that subsp. *perforatum* was introduced into North America independently in the east and the west.

A low, erect to procumbent southern Balkan plant with small, rather broad leaves ( $l : b = 1-2.5$ ) and capsule valves bearing lines of vesicles has been named *H. perforatum* var. *humile* Stranski, but no valid description has been traced. On account of intermediate forms that link it with typical subsp. *perforatum*, it apparently belongs to that subspecies. Specimens have been seen from Albania, Bulgaria and Greece.

5b. *Hypericum perforatum* subsp. *songaricum* (Ledeb. ex Rchb.)  
N. Robson, *stat. nov.*

Fig. 8, Map 9.

*H. perforatum* var. [β] *latiglandulosum* Choisy in DC., *Prodr.* 1: 550 (1824). Type: Ukraine, Tanais [R. Don], 1819 (fl), *Goldbach* s.n. (G-DC!-holotype).

*H. songaricum* Ledeb. ex Rchb., *Icon. bot. pl. crit.* 3: 72, t. 283 f. 446 (1825); Spreng., *Syst. veg.* 4(2): 297 (1827). Type: Kazakhstan, 'ad lacum Noor-Saisan dictum', fl., *Ledebour* s.n. (LE-holotype).

*H. perforatum* var. *songaricum* (Ledeb. ex Rchb.) K. Koch in *Linnaea* 15: 714 (1841); Woron. in Kuzn., Woron. & Fomin, *Fl. Cauc. crit.* 3(9): 56 (1906).

*H. perforatum* var. *gracile* Gruner in *Bull. Soc. Imp. Naturalistes Moscou* 41(3): 132 (, 869). Type: Ukraine, Zaporozh'ye, 'Gubern. Catherinoslav, in demissis ad Borysthenem infra urbem Alexandrowsk' [Zaporozh'ye], 20 June 1865 (fl), *Gruner* s.n. (BM!-holotype?).

*H. komarovii* Gorschk. in *Bot. Žurn. SSSR* 24: 428, f. 1 (1939). Type: Kirghizstan [Kirghizia], in monte Arslanbob supra Namas-tasch, 23 August 1925 (fl), *Massagetov* 335 (LE-holotype).

Icon: Rchb., *Icon. bot. pl. crit.* 3: t. 283 f. 446 (1824).

Leaves sessile (at least on main stems); lamina 6–15 × 2–10 mm,

oblong to oblong-ovate ( $l : b = 2.5-4$ ), base ± shallowly cordate-amplexicaul, often glaucous beneath. *Inflorescence* not congested, with branches relatively short, straight. *Petals* with laminar glands all pale. *Capsule* valves with lateral vittae linear, narrow or slightly swollen but rarely interrupted.

Northern Kazakhstan and adjacent Kyrgyzstan and China (NW Xinjiang), south-eastern Russia and the Ukraine (including Krym).

**CHINA.** Xinjiang: Altay Xian, 1100 m, 18 August 1956 (fl & fr). *Ching* 2434 (CDBI, IBSC); Huocheng [Suiding] Xian, 1500 m, 22 June 1965 (fl), *Cheo* et al. 650862 (IBSC, KUN, NAS).

**KAZAKHSTAN.** Almatinskaya Obl.: Songaria, in dumetis montium Alatau, n.d. (fl), *Schrenk* s.n. (K, LE\*); Semiryechensk prov., Vyernyi distr., Zaylinskiy (Trans-Ilian) Alatau, 14 July 1907 (fl), *Sokalsky* 118 (BM). Zapadnyy-Kazakhstan Obl.: Chingirlauskiy rayon, Kara-Alag, 16 July 1935 (e. fr), *Akastovy*(?) s.n. (A\*, BM, LE).

**KYRGYZSTAN.** \*Osh: in monte Arslanbob [Pik Skobeleva] supra Namas-tasch, 23 August 1925 (fl), *Massagetov* 335 (LE).

**RUSSIA.** Astrakhanskaya Obl.: Sarepta, 16 June 1879 (fl), *Becker* s.n. (BM). Stavropolskiy Krai: S. of Karachayevsk, near Gora Dembay Ul'gen, 11 July 1971 (fl), *Fraser Jenkins* 3219 (BM).

**UKRAINE.** Orlovskaya Obl.: Prov. Orel, circuit. Felitz, inter Polna et pag. Morskaja, 20 June 1868 (bud), *Gruner* s.n. (BM). Dnipropetrovskaya Obl.: Gubern. Catherinoslav [Dnipropetrovs'k], in demissis ad Borysthenem [Dnieper] infra urbem Alexandrowsk [Zaporozhye], 20 June 1865 (fl), *Gruner* s.n. (BM). Krym: prope Karasubazar [Belogorsk, Bilohirs'k], 23 June 1900 (fl), *Callier* 564 (BM, FR, JE, K); in aprices Tauriae montosae, n.d. (fl), *Pallas* s.n. (BM).

Some Crimean specimens lack the cordate leaf base of this subspecies but are otherwise clearly a reduced form of it. The following specimens are intermediate between subsp. *songaricum* and subsp. *perforatum* in having the leaves on the main stem sessile but those on branches petiolulate:

**UKRAINE.** Cherkasky Obl.: Uman, Farco, June 1867 (fl), *Golde* s.n. (BM, K). ? Obl.: Valka, zwischen Veselaya und Zingalni (?), 5 May 1865 (fl),

*Gruner* s.n. (BM); an Ackerrändran (?) bei Condo-dorf, 18 July 1859 (fl), *Gruner* s.n. (BM).

The following specimen is intermediate between subsp. *songaricum* and subsp. *veronense* in having narrow leaves with those on the main stem cordate at the base.

**CHINA, Xinjiang:** [Kashi Xian] Yarkand Expedition, 1870 (fl), *Henderson* s.n. (K).

The Fraser-Jenkins specimen from the Russian Caucasus listed above also shows some characters intermediate between those of subspecies *songaricum* and *veronense*.

5c. ***Hypericum perforatum* subsp. *veronense*** (Schrank) H. Lindb. in *Öfvers. Förh. Finska Vetensk.-Soc.* **48**: 73 (1906); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 530, f. 5 (1911), in *Mitt. Naturwiss. Vereins Steiermark* **51**: 241 (1915); Hayek, *Prodr. Fl. Pen. balc.* **1**: 533 (1925); Stjep.-Vesel. in Josifović, *Fl. Srbije* **3**: 119 (1972); Robson in *Bull. Soc. Ech. Vasc. Eur. Bass. Médit.* **27**: 20 (1998), Ciccarelli, Garbari & Robson, (2002). Type: as for *H. veronense* Schrank. Note: Lindberg's '*H. perforatum* L. \**Veronense* (Schrank)' is to be regarded as a new combination at subspecies rank. He indicated new combinations at varietal rank in this paper by an initial small letter.

Fig. 8, Maps 10–12.

?*Hypericum perforatum* [var.] *angustifolium* Borkh. in *Neues Mag. Bot.* **1**: 26 (1794); N. Robson in Wisskirchen & Haeupler, *Standardliste Farn- u. Blütenpfl. Deutschl.*: 270 (1998). Type: Germany, not stated. The varietal epithet *angustifolium* has previously always been attributed to De Candolle, but Borkhausen's *H. perforatum angustifolium* has priority. By the date of his publication, a trinomial is assumed to be a variety. Borkhausen's type, however, is unknown (Stafleu & Mennega, 1993: 340); and so whether his plant belongs to the narrow-leaved Mediterranean form with vesicular capsule glands (var. *angustifolium* DC.) or a narrow-leaved form of var. *perforatum* (with vittate, not vesicular capsule valves) cannot be ascertained. In either case De Candolle's var. *angustifolium* is a later homonym. However, as the variation between narrow-leaved plants with large and small leaves in the Mediterranean region is continuous, allowing the recognition of no more than one taxon, De Candolle's epithet *microphyllum* is available for it as a variety.

*H. veronense* Schrank in *Neues Bot. Taschenb. Anfänger Wiss. Apothekekunst* **22**: 95 (1811); Link, *Enum. hort. berol. alt.* **2**: 276 (1821); Jord. in Schultz & Billot, *Annots Fl. France & Allemagne*: 49 (1855); Engl. in *Verh. bot. Vereins Brandenburg* **12**: 49 (1870); O. Schwarz in *Drudea* **5**: 61 (1965). Type: Italy, Verona, an den ehemaligen Sitzen des Amphiteaters zu Verona, October 1808 (fr), *Schrank* (not found). Neither Professor Garbari (Univ. of Pisa; in litt.) nor I have been able to locate type material of this 'species', which, according to Prof. Garbari, does not grow now at the type locality. (Schrank himself refers to strenuous efforts to extirpate it, even at that time.) There is no doubt, however, that Schrank's plants belonged to the narrow-leaved Mediterranean subspecies, even though the plants that he grew from their seeds were somewhat larger with leaves (some or all?) shortly petiolate. In the absence of type material, a neotype is therefore required: Italy, Verona, Anfiteatro di Verona, August 1874, *Cesati* s.n. (RO!-neotype, Ciccarelli, Garbari & Robson, 2002, ined.).

*H. perforatum* var. [δ] *angustifolium* DC. in Lam. & DC., *Fl. France*, 3rd ed. **5**: 630 (1815); Gaudin, *Fl. helv.* **4**: 628 (1829); W. Koch, *Syn. fl. germ. helv.*: 134 (1835), in Röhl. *Deutschl. Fl.*, 3rd ed. **5**: 349 (1839); Beck, *Fl. Nieder-Österreich*: 530 (1892);

Rouy in Rouy & Fouc., *Fl. France* **3**: 333 (1896); Zelen., *Prodr. fl. Taur.*: 233 (1906); Hegi, *Ill. Fl. Mitt.-Eur.* **5**(1): 528 (1925); Briquet, *Prodr. fl. Corse* **2**(2): 151 (1936); Guşul. & Nyár. in Sävul., *Fl. R. P. Roman.* **4**: 29, t. 2 f. 2 (1956); N. Robson in Tutin et al., *Fl. Europaea* **2**: 269 (1968), in Cullen et al., *Eur. gard. fl.* **4**: 60 (1995); Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* **4**: 261 (1970). Type: France, Pyrenées Orientales, Roussillon, Prades, 1814 (fl), *Coder* s.n. (G-DC-holotype, microfiche!).

*H. perforatum* var. [ε] *microphyllum* DC. in Lam. & DC., *Fl. France*, 3rd ed. **5**: 630 (1815); Choisy, *Prodr. monogr. fam. Hypéric.*: 51 (1821), in DC., *Prodr.* **1**: 550 (1824); Guss., *Fl. sicil. syn.* **2**(1): 378 (1843); Rouy in Rouy & Fouc., *Fl. France* **3**: 333 (1896); Fiori, *Nuov. Fl. Italia* **1**: 522 (1924); Briquet, *Prodr. fl. Corse* **2**(2): 151 (1936); Guşul. & Nyár. in Sävul., *Fl. R. P. Roman.* **4**: 30 (1956); N. Robson in Tutin et al., *Fl. Europaea* **2**: 269 (1968), in Cullen et al., *Eur. gard. fl.* **4**: 60 (1995), in Wisskirchen & Haeupler, *Standardliste Farn- u. Blütenpfl. Deutschl.*: 270 (1998); Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* **4**: 261, t. 49 f. 3 (1970). Type: France, Lozère, aux environs de Mende, 1810 (fl), *Prost* s.n. (G-DC-holotype, microfiche!).

*H. perforatum* var. [γ] sensu Choisy, *Prodr. monogr. fam. Hypéric.*: 50 (1821).

*H. perforatum* var. [γ] *elatum* Choisy in DC., *Prodr.* **1**: 550 (1824), in Zoll., *Syst. Verz.* **1–2**: 151 (1854). Type: Italy, Florence, 10 August 1808 (fl), *De Candolle* s.n. (G-DC!-lectotype, selected here).

*H. stenophyllum* Opiz, *Naturalientausch* no. 9: 158 (1825). Syntypes: Czech Republic, 'in Böheim', *Opiz* s.n. (PR-syntype); Austria, 'in Oberösterreich', *Brittinger* s.n. (PR-syntype). A specimen from the Czech Republic, Hodkoviccka [Prague], 25 July 1850 (fr), *Opiz* (PR!), labelled '*Hypericum stenophyllum* Opiz' by Opiz himself, is subsp. *veronense* and, in the apparent absence of the syntypes, can be taken as a representative specimen of his species.

*H. perforatum* var. *nanum* Gaudin, *Fl. helv.* **4**: 627 (1829). Type: not stated. 'An *H. perforatum* β *microphyllum* Dec. Fl. Fr. Suppl. p. 630?' (LAU-holotype).

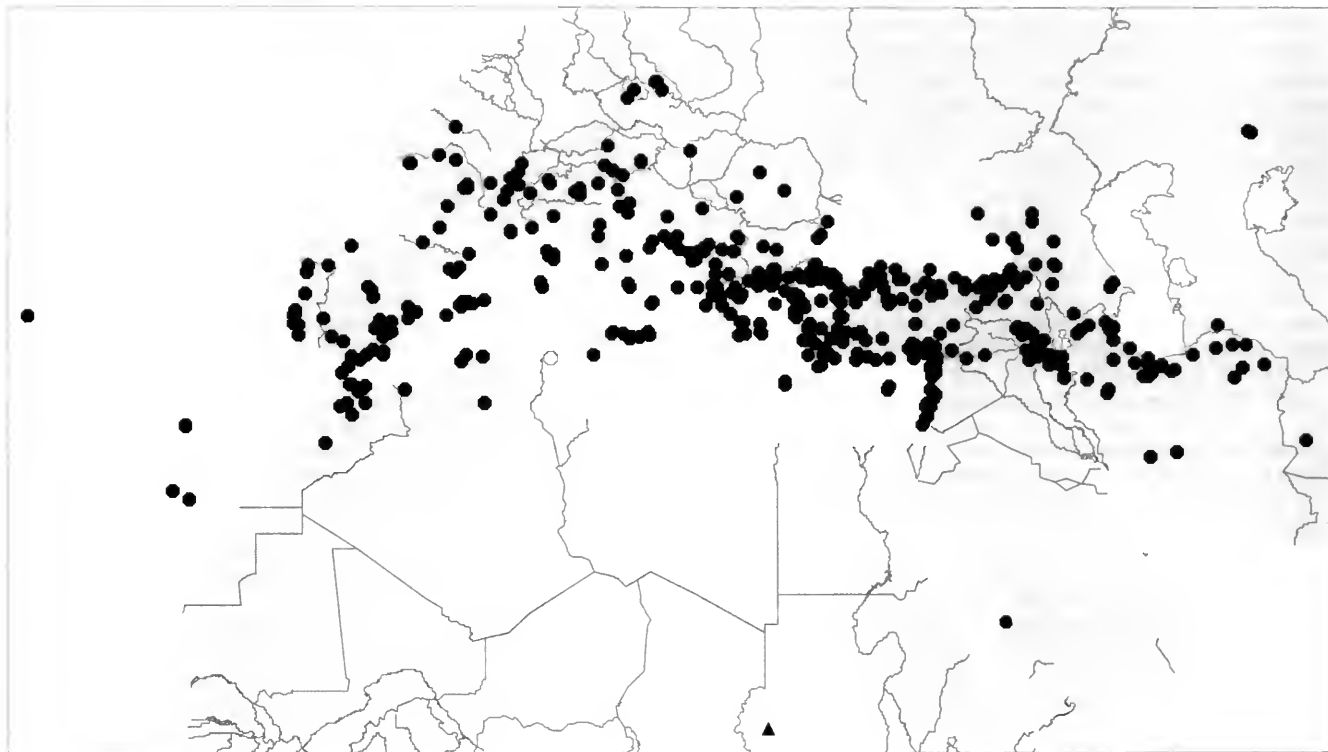
*H. perforatum* var. *veronense* (Schrank) Ces. in Cattaneo, *Not. Nat. Civ. Lombardia*: 291 (1844); Beck, *Fl. Nieder-Österreich* **2**: 530 (1892); R. Keller ex Albov in *Trudy Tiflissk. Bot. Sada* **1**: 4 (1895); Béguinot in Fiori, Béguinot & Pampini, *Flora Italica Exsiccata*, no. 817 (1904); Woron. in Kuzn., Busch & Fomin, *Fl. Cauc. Crit.* **3**(9): 56 (1906); Hegi, *Ill. Fl. Mitt.-Eur.* **5**(1): 528 (1925); Grossg., *Fl. Kavk.*, 2nd ed. **6**: 54, 175 (1962). Soldano (1991: 248) claimed that Cesati made a *comb. nov.* at the rank of subspecies; but there would seem to be no justification for interpreting '*Hypericum perforatum* L. β *veronense* Schrnk.' as other than a variety. He certainly did not make the combination *H. perforatum* subsp. *angustifolium* (DC.) Cesati attributed to him by Gamisans & Jeanmonod (1993: 183). See Robson & Lambinon (2000). Béguinot's combination was made independently.

*H. perforatum* var. *stenophyllum* (Opiz) Wimm. & Grab., *Fl. Siles.* **2**(2): 82 (1829); Neilr., *Fl. Nieder-Oesterr.*: 826 (1859).

*H. schlosseri* Heuff. in *Flora* **36**: 626 (1853); Schlosser & Vokut., *Fl. croat.*: 381 (1869); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 537 (1911) in adnot. Type: Croatia, in rupibus Zagoniaae, *Schlosser* s.n. (W?).

*H. microphyllum* Jord. in F. Schulz, *Arch. fl. France Allem.*: 341 (1854). Type: France, Rhône, environs de Lyon, *Jordan* s.n. (LY-holotype; BM!-isotype).

*H. chrysostictum* Webb, *Fragm. fl. aethiop.-aegypt.*: 54 (1854). Type: [Saudi Arabia?; not recorded from Ethiopia] 'Occurrit in herb. Figariano sine loci natalis indicatione.' (FI!-holotype).



**Map 10** *Sc. H. perforatum* subsp. *veronense*, Mediterranean and S. Europe ●, other records ○, introductions ▲. Reported from south Germany.

*H. aetnaeum* Tornab., *Fl. sicul.*: 171 (1887), *Fl. aetnea* 1: 213 (1889). Type: Sicily, Mt. Etna, 'in elatis arenosis et ad nemora', Nicolosi s.n. (CAT-holotype).

*H. noëanum* Boiss., *Fl. orient.*, Suppl.: 130 (1888). Type: Bulgaria, Rumelia, 'Hab. in monte Haemo minore Thraciae' [Iztochni Rodopi], Noë s.n. (G!-holotype).

*H. perforatum* var. [γ] *angustifolium* subvar. *lineolatum* Rouy in Rouy & Fouc., *Fl. France* 3: 333 (1896). Type: France, Cher, Mehun, Sables de Beauvoir, 3 July 1840 (fl), *Déséglise* in *Billot* exsicc. no. 3349 (P?-holotype; BM!, JE!-isotypes).

*H. perforatum* var. [δ] *mediterraneanum* Rouy in Rouy & Fouc., *Fl. France* 3: 333 (1896). Type: France?, not stated.

*H. perforatum* var. *typicum* forma *microphyllum* (DC.) Fiori in Fiori & Paol., *Fl. Italia* 1: 388 (1898).

*H. perforatum* var. *ellipticum* Freyn in *Bull. Herb. Boissier* II, 3: 1064 (1903), non Durand & Pittier (1881). Type: Turkmenistan, Ashabad, in monte Ak-tepe, 17 June 1900 (l. fl), *Sintenis* 564a (G-lectotype, selected here; BM!, K!-isolectotypes); prope Suluklu ad fines Persiae, 4 September 1900 (l. fl), *Sintenis* 564b (G-syntype; JE!).

*H. perforatum* var. *moesicum* Velen. in *Sitzungsber. Königl. Böhm. Ges. Wiss. Prag* 1903(28): 2 (1904), op. cit. 1910(8): 3 (1911); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 538 (1911) in synonym. Type: Bulgaria, in Sredna Gora ad Adžar [Svezhen], 1902 (fl), *Stříbrny* s.n. (W?).

*H. perforatum* var. *collinum* Woron. in Kuzn., Busch & Fomin, *Fl. Cauc. Crit.* 3(9): 55 (1906); Grossg., *Fl. Kavk.* 2nd ed. 6: 55, 175 (1982). Type: Georgia, Sukhumi, 'no sklonam' gori Cherniyavskago, June 1904, *Woronow* s.n. (LE-lectotype, selected here).

*H. perforatum* var. *corioides* Vokut., nomen in scheda (WU); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 538 (1911), in synonym.

*H. perforatum* subsp. *angustifolium* (DC.) A. Fröhl. in *Sitzungsber.*

*Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 534, f. 6 (1911), in *Mitt. Naturwiss. Vereins Steiermark* 51: 241 (1915); Hayek, *Prodr. Fl. Pen. balc.* 1: 533 (1925); Stjep.-Vesel. in *Fl. Srbije* 3: 119 (1972); A. Ramos in Castroviejo et al., *Fl. Iberica* 3: 165, t. 45 ff. a-e (1989).

*H. perforatum* var. *floribundum* Sennen, ined.? 'Type': Spain, Barcelona, S. Celloni, 20 July 1922 (fl), *Sennen* 4864 (BC, BM!).

*H. nachitschevanicum* Grossh. in *Izv. Azerbajdzansk. Fil.*, no. 1: 46 (1941), *Fl. Kavk.*, 2nd ed. 6: 171, karta 195 (1962). Type: Azerbaijan, Nakhitchevan, inter pp. Urmys et Pazmara, 21 August 1933 (fl & fr), *Karjagin & Isaev* s.n. (BAK-holotype; LE!-isotype; BM!, K!-photographs).

*H. perforatum* var. *longicapsulum* Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* 4: 261, 709, t. 49 f. 4 (1970) '*longicapsula*'. Type: Bulgaria, Mt. Vitoša [Cherni Vrūkh], in pratis prope refugium 'Pogledec', loco dicto 'Karkama', 1600 m, 18 September 1967 (fr), *N. Vihodčevsky* (SO-holotype).

Icons: Valdés, Talavera & Galiano, *Fl. Andalucía Occid.* 1: 315 (1987); Castroviejo et al., *Fl. Iberica* 3: t. 45, ff. a-e (1993).

Leaves usually sessile (at least on main stems); lamina 9–20 × 1–4 mm, usually linear (l:b=5–9) but sometimes narrowly triangular-lanceolate or linear-oblong (l:b=2.5–4), or occasionally broadly ovate to elliptic or obovate, but then small (c. 5–10 × 4–5 mm), base cuneate, paler but not glaucous beneath. Inflorescence occasionally congested, with branches relatively short, straight or curved-ascending. Petals with laminar glands all pale or rarely mostly black. Capsule valves with lateral vittae swollen at base (but not forming a regular distal row) or ± interrupted to punctiform and wholly swollen (vesicular).

Southern Russia, the Ukraine (Krym) and the Caucasus region east to Kazakhstan and N. India (Uttar Pradesh) and west to the Mediter-

ranean region and southern Europe (N. to central France, southern Germany and southern Poland) and extending to Macaronesia, north-west Africa, Sudan Republic (Jebel Marra) and Saudi Arabia (Asir). Introduced into Hawaii, New Zealand, Australia and South Africa. Records of var. *angustifolium* from Canada and the U.S.A. would appear to refer to the narrow-leaved form of subsp. *perforatum* found in dry habitats in England (see p. 94). The record of *H. perforatum* from Karpathos (Turland, Chilton & Press, 1993: 94) is an error for *H. tetrapterum*.

**RUSSIA. Ciscaucasia:** Stavropolskiy Kray, N. of Pyatigorsk, Mt Mashuk, 18 November 1975 (fl & fr). *O. & J. Degener* 33,789 (NY); Karachayevo-Cherkesskaya ASSR, südlich Teberda, c. 1350 m, 11 August 1957 (fr), *Meyer, Lippold & Kohler* 257 (JE); Severo-Osetinskaya ASSR, Vladikavkas [Orzhonikidze], August 1981 (fl & fr), *A. & V. Brotherus* 192 (BM, H).

**UKRAINE. Krym:** Yalta, Massandra, 22 June 1969 (fl), *Rintanen* s.n. (H).

**GEORGIA. Abkhazskaya ASSR:** Pizunda [Pitsunda], 19 July 1966 (fr), *F.K. & J. Meyer* 8560 (JE). **Gruziya:** prope Tiflis [Tbilisi], June 1981 (fl), *A.H. & V.F. Brotherus* 192a (BM, H); Batumi, östlich Machindžauri, 25 July 1978 (fr), *H. & R. Manitz* s.n. (JE).

**AZERBAJDZHAN.** Nachrespublica, inter Urmys et Paxmara, 21 August 1933 (fr), *Karjagin & Isaev* s.n. (BM and K photographs, LE); Chizy distr. (olim Kuba), prope p. Alty-agatsh, 21 June 1935 (fl), *Gurvitsh* s.n. (K); Nakhichevan – see type of *H. nachitschevanicum* Grossh. in synonymy.

**ARMENIA.** In montes 'Bazumski khrebet' in vicinitate oppidi Kirovakan (Karalkisa), 1600–1800 m, 22 July 1975 (fl), *Vašák* s.n. (W); Sevanskiy raion, Goranrotuv n.–o. Sevan, 6 July 1926 (fr), *Savur* s.n. (LE); Kafanskiy raion, gor. Kadzharan, Tandzasar, 1850–2150 m, 16 September 1966 (fr), *Manakian* s.n. (BM).

**TURKEY. Kars:** Ardahan, Gürçayir village, 31 July 1976 (fl), *Sanda* 1196 (BM). **Bitlis:** Corgih to Bitlis, 2250 m, 31 July 1976, *Tong* 207 (E). **Hakkari:** Cilo Dağ, in Diz deresi above Kursi, 1890 m, 7 August 1954 (fr), *Davis & Polunin* D. 23962 (BM, E, K). **Çoruh:** Borça to Hopa, 300 m, 22 June 1957 (fl), *Davis & Hedge* D. 29882 (BM, E, K). **Erzurum:** Palandöke Dağ, 25 km from Çat to Erzurum, 2350 m, 27 July 1966 (fl), *Davis* 47385 (E). **Trabzon:** Höhe südlich Trabzon, 250 m, 26 June 1931 *Görz* 654 (BM). **Amasya:** Erbaa to Kozlu, 550 m, 5 June 1967 (fl), *Tobey* 2190 (E). **Malatya:** 5 km NW Darendé, 1200 m, 8 September 1977 (FL), *Sorger* 77–105–22 (WU). **Hatay:** Hassa, Tüyek village, 9 July 1974 (fl), *E. Sezik* 680 (BM). **Nevşehir:** Göreme, c. 10 km W. of Urgüp, c. 1000 m, 3 August 1956 (fl), *McNeill* 399 (E, K). **İçel:** Bulgar Dagħ, 'Gullek Boghas', 1140 m, 23 August 1853 (fl & fr), *Kotschy* 282a (G). **Kastamonu:** Daday to Azdavay, 30 km, 1100 m, 30 July 1962 (fl & fr), *Coođe & Yaltirik* D. 38658 (E, K). **Ankara:** Elma Dagħ bei Ankara, c. 1600 m, 25 June 1932 (fl), *Kotte* 317 (K). **Antalya:** Manavgat, 4 June 1973 (fl), *Himmetoğlu* H17 (BM, BAS\*). **Bolu:** Ala Dağ distr., Kartal Kaya (Mt.), 2000 m, 11 August 1960 (fl), *Khan, Prance & Ratcliffe* 490 (E). **Eskişehir:** Eskişehir, 500 m, 27 May 1971 (fl), *Price* 638 (K). **İsparta:** Egridir distr., Barla Dağ foothills, 1200 m, 1 August 1960 (fl), *Khan, Prance & Ratcliffe* 4219 (E, K). **İstanbul:** Alaton, 28 July 1967 (fl), *Baytop & Atila* 11585 (E, ISTE\*). **Kütahya:** Gediz, 850 m, 7 July 1962 (fl), *Davis & Coođe* D. 36969 (E, K). **Burdur:** Yeşilova to Denizli, c. 6.5 km, by Salda Golu, 1100 m, 1 June 1962 (fl), *Dudley* D. 35303 (E, K). **Kırklareli:** Demirköy, 19 July 1959 (fl), *Baytop* 5488 (BM). **İzmir:** Selçuk, Ephesus, 31 May 1972 (fl), *E. & G. Sezik* 260 (BM, HUB\*). **Muğla:** Marmaris, c. 4 km E. of Marmaris, s.l., 18 May 1983 (fl), *Murto* 1376 (H).

**GREECE. Thasos:** Glifada, 18 May 1986 (fl), *Raitraluna?* s.n. (C). **Thraci:** Nom. Xanthi, NE of village Dimarion, c. 26 km N. of Xanthi, 550 m, 28 July 1977 (fr), *Strid & Georgiadhou* 13485 (C). **Makedhonia (E):** [Nom. Kavala] c. 4 km W. of Kavalla, 11–12 July 1970 (fr), *K.H. Rechinger* 38260 (W). **Makedhonia (W):** Nom. & Ep. Grevenon, Mt. Smolikas, 2–3 km S. of Samarina towards Armata, 1275–1350 m, 27 August 1975 (fl), *Hartwig & Seberg* 4814 (C). **Epirus:** Distr. Janina, ad Paleochori Syrakou, 2 August 1895 (e. fr), *Baldacci* III 304 (BM). **Ionian Is.:** Korfu, S. of Korfu town, Kanoni, 20 May 1978 (bud), *A. Hansen* 441 (C). **Thessalia:** prov. Trikala, distr. Kalambaka, Meteora, between Ajia Triada and St. Roussanis, 600 m, 17 June 1977 (fl), *Stearn* A.64 (BM). **Stereia Ellás:** Graviá, 480 m, 20 June 1937 (fl), *Balls & Gourlay* B. 3352 (BM). **Peloponnisos:** Prov. Achaia, Distr. Kalavrita, Mt. Helmos, lower SE slopes, 3 km W. of village Feneos, 1000–1200 m, 30 July 1980 (fr), *Baden & Francén* 684 (C). **Evvoia:** Mt. Dirphys,

c. 1930 (fl), *Guiol* s.n. (BM). **Sporadhes:** Rhodos, S. of Kremasti, 9 May 1966 (fl), *A. Hansen* s.n. (C).

**KRITI.** Distr. Kissamos, Enneachoria, inter Myli et Elos, c. 100 m, 30 May 1942 (fl), *K.H. Rechinger* Iter Graecum VI 13437 (BM, K).

**ALBANIA.** Nordalbanische Alpen (Prokletija), Tethi, Shtegu i Dhenve, c. 1400–1600 m, 26 September 1961 (fl & fr), *Meyer* 6427 (BM, JE); Korca, Mali i Moravës, bei Drenova, 1100–1200 m, 12 September 1962 (fr), *Meyer* 6141 (BM, JE); Viossa-Tal, an der Landstrasse nördlich Perati, c. 300 m, 10 July 1959 (fr), *Meyer* 3835 (JE).

**MAKEDONIJA.** Gorge of Crni Drim near Lukovo, N. of Struga, 650 m, 12 June 1971 (fl), *Chater* 432 (BM).

**MONTENEGRO.** Distr. Vasojačići, Murino, 1 September 1903 (fl & e. fr), *Baldacci* Iter Alb. X 46 (BM); 10 km S. of Titograd [Podgorića], 50 m, 20 June 1965 (fl & e. fr), *Wrigley* 65/1360 (K).

**BOSNIA & HERZOGOVINA.** Velež planina, 1500 m, 6 July 1912 (fl), *Sagorski* s.n. (BM); Jajce, 1925 (fl), *Leathes* s.n. (BM); Sarajevo, 750 m, 12 July 1960 (fl), *McCallum Webster* 4036 (K).

**SERBIA.** Kosovo, c. 10 km S. of Priština towards Uroševac, 600 m, 9 September 1972 (fr), *Kukkonen* 8565 (H); Šavac-Pomoravlje, Damin, 13 September 1979 (fl), *Cvetković* 15 (BM); Vranja, 1919 (fl & fr), *Tindall Lucas* 104 (BM).

**CROATIA.** Velebit Mts, pass above Karlobag, 690 m, 17 July 1962 (fl), *Mathew & Pycraft* 339 (BM); Insel Krk, Omišaly, 17 July 1931 (fl & fr), *Hotel?* s.n. (BM).

**SLOVENIA.** Istrien, zwischen Tulisevica und Draga di Lovrana, 23 June 1935 (fl), *Ronniger* s.n. (W); within 9.5 km of Bled, Mt. Triglav, 300–1200 m, 1923 (fl), *Leathes* s.n. (BM).

**BULGARIA. Mihailovgrad:** Predbalkan, Ostabhang des Midshur [Midžor], 4 September 1958 (fr), *Meyer* 1171 (JE). **Sofiya:** Mt. Vitosha, c. 1400 m, 26 July 1952, *Vihodčevsky* s.n. (JE). Blagoevgrad: Struma-Tal, bei Marikostinovo, 23 September 1958 (fr), *Meyer* 1500 (JE). Plovdiv: in valle Akdere [Tundzha] prope Kalofer, 11 August 1893 (fr), *Wagner* 26 (BM, W\*). **ROMANIA. Transylvania:** Cluj, Turda Gorge, 23 July 1963 (fl), *Dandy* 1425 (BM). **Dobrogea:** Constanța, Tekirg Cirol [Techirghiol], n.d. (fl), *Cretzoiu* s.n. (K).

**HUNGARY. Pest:** Pass between Doroy and Pilisovorosvar on Budapest road, 7 July 1962 (fl), *Curle* 44 (BM). **SLOVAKIA.** Vrchol Sitna, c. 1000 m, 1957, *Hostička & Zelený* (PRC\*), only locality (*vide* Zelený, Jasičková & Zahradníková, 1982: 310).

**CZECH REPUBLIC.** Possibly occurs (*vide* Čelakovský, 1875: 521).

**POLAND. Wałbrzych:** Silesia, Schweidnitz [Swidnica], Költschenberg, September 1882 (l. fr), *Peck* s.n. (FR).

**GERMANY. Thüringen:** Gera, Jena, Lichtenhain am Bahndamm, 20 June 1950 (fl), *Launert* 269 (BM) (verg. ad subsp. *perforatum?*). **Baden-Württemberg:** Istein in Baden, July 1919 (fl & fr), *Meebold* s.n. (K).

**AUSTRIA. Salzburg:** Leopoldskroner-Moor, 490 m, June 1877 (fl?), *Eysn* s.n. (JE). **Steiermark:** bei Kelsdorf (Graz), 2 August 1910 (fl & fr), *Fröhlich* GZU16323 (GZU). **Kärnten:** Carinthia, fluv. Gail, July 1864? (fl), *Pichlers* s.n. (JE, K). **Tirol (E.):** prope Lienz, July 1863 (fl & fr), *Ausserdorfer* s.n. (BM, K).

**SWITZERLAND. Zürich:** Albis, 3 August 1854 (fl), *Hort* s.n. (BM). **Vaud:** Des Pierrettes, près Lausanne, 7 September 1877, *Ferrat* s.n. (JE). **Genève:** Compesières, August 1855 (fl), *Chavin & Perrier* 55 (BM). **Ticino:** [Monte] Generoso, Bela Vista, 10 August 1899, *Gyoperzer* s.n. (JE).

**ITALY. Piemonte:** Liguria, Portofino Peninsula, 10 September 1963 (fr), *Robson* 1813 (BM). **Lombardia:** Brescia, Lago d'Isèo between Vello and Toline, 195 m, 2 June 1983 (fl), *Hind* 165 (BM, RNG\*). **Venezia:** Verona, Torri del Benaco, 100–200 m, 15 July 1904 (fl), *Rigo* in Fl. Ital. Exsicc. 817 (BM). **Campania:** Ravello, above Sta Cattarina, 2 October 1879 (st), *Lacaita* s.n. (BM). **Puglia:** Brindisi, 8 km W. of town, 31 May 1960 (fl), *Brummitt* 60. E. 802 (K, LIV\*). **Calabria:** Aspromonte, c. 50 km SW of Reggio di Calabria, below Bova, c. 750 m, 10 June 1979 (fl), *Davis & Sutton* D. 64779 (BM).

**SICILY. Palermo:** c. 5 km W. of Cefalù, 30 m, 25 May 1979 (fl), *Davis & Sutton* D. 63726 (BM). **Monreale:** Weg nach San Martino, 27 May 1927 (fl), *Ronniger* s.n. (W). **Messina:** Taormina, 28 May 1964 (fl), *Brummitt* 4567 (K). **Pantellaria:** P. Spadillo, 27 May 1960 (fl), *Davies* s.n. (K).

**MALTA. Malta:** Kordin (Haslam, Sell & Wolseley, 1977); occurrence doubtful or plant extinct (Lanfranco, 1982).

**SARDINIA.** Sassari: near Stintino, La Salina, 5 June 1971 (fl), *Dunford & Moyes* 143 (BM).

**CORSICA. Haute-Corse:** Bastia, oberhalb der Stadt, 1 June 1914 (fl), *Ronniger* s.n. (W); Cirque de Bonifato, près de la Maison forestière, c. 530 m, 8 July 1999 (fl), *Lambinon* 99/Co.276 (BM, LG\*). **Corse-du-Sud:** Zouya to Porto Vecchio, 21 April 1933 (fl), A.C. & E. *Godman* 127 (BM).

**FRANCE. Vendée:** Mortagne, 24 June 1869 (fl), *Genevier* s.n. (BM). **Deux Sèvres:** Puy St. Bonnet, 26 June 1861 (fl), *Genevier* s.n. (BM). **Charante-mar:** Autran, July 1884, *Giraudias* s.n. (JE). **Cher:** Allogny, 12 July 1878 (fl & fr), A.Z.P. s.n. (BM). **Saône-et-Loire:** Rougers, 4 August 1891 (fl & fr), *Gillot* s.n. (BM). **Hte-Saône:** Goren, près Conflans, 14 September 1858 (fr), *Perrier* s.n. (BM). **Rhône:** Arnas, August 1897 (fr), *Gandoger* s.n. (H). **Isère:** Viray, vallée du Vézy, August 1910 (fl & e. fr), *Giraudias* s.n. (BM). **Puy-de-Dôme:** Volvic, 750 m, 18 September 1893 (fr), *Héribaud* in Soc. Rochel. 3438 (BM). **Cantal:** Anglard de Salers, July 1928 (fl), *Chanar* s.n. (BM). **Hte Savoie:** Passy, coteaux au Reyard, 11 July 18— (fl), *Depierre* s.n. (BM). **Savoie:** Vérel-Pragondran, près de Chambéry, 19 August 1852 (fl), *Chabert* in *Billot* 1847 (BM, JE). **Htes-Alpes:** environs de Gap, July 1854 (fl), *Blanc* in *Billot* 1846 (BM). **Alpes-mar:** Cipières village, 700 m, 29 June 1992 (fl), *Hepper* 9431 (BM, K\*). **Drôme:** Donzère, barrage between Canal and R. Rhône, 17 June 1969 (fl), *Verdcourt* 2682 (K). **Var:** c. 2 km NW of Cotignac, 350 m, 5 August 1981 (fl), *Longton* 4443 (BM). **Vaucluse:** Entrechaux à Faucon, 23 June 1981 (fl), *Bamps* 6960 (BM, BR\*). **Bouches-du-Rhône:** Camargue, Canal de Fumemort, 2 km from Tour du Valat, 10 June 1968 (fl), *Kendrick & Moyes* 206 (BM). **Gard:** Saint-Christolles-Alès (S. d'Alès), c. 170 m, 13 July 2000 (fr), *Lambinon* 0/F/246 (BM, LG\*). **Ardèche:** St. Jean de Pourcharesse, 600 m, 3 September 1984 (fl & e. fr), *Dechamps* 10013 (BM, BR\*). **Aveyron:** Chérondeles, 15 July 1905 (fl), *Carbonel* s.n. (BM). **Lot:** Causse d'Alvignac, July 1868 (fr), *Mah—* s.n. (BM). **Landes:** near Dax, June 1924 (fl), *Heard* s.n. (BM). **Aude:** Moussan, 28 May 1903 (fl), *Septimin-Donat* s.n. (BM). **Pyrenées-or:** Lorède, 21 June 1906 (fl), *Conill* s.n. (FR).

**BALEARIC ISLANDS. Mallorca:** Alcudia, Mal Pas beach, 9 August 1967 (fr), J. & M. *Cannon* 3366 (BM). **Menorca:** San Luis, E. of Punta Prima, c. 10 m, 14 April 1967 (o. fr), *Bowden & Sims* 1180 (BM). **Ibiza:** San Juan Bautista, between Puerto de San Miguel and San Miguel, c. 30 m, 16 January 1971 (st), *Ferguson* 2773 (BM).

**SPAIN. Gerona:** N. of Puerto de la Salva, c. 20 m, 17 June 1959 (fl),

*Chamberlain* 815 (BM). **Barcelona:** San Celoni, 20 July 1922 (fl), *Secondaire* in *Sennen*, Pls d'Espagne 4864 (BM, RNG). **Huesca:** Sierra de Guara, between Casa de Fabara and Fabara Gorge, 15 August 1970 (fr), J. & F. *Richardson* 21 (RNG). **Viscaya:** Orduña, emirna del Balneariode la Nueva, 10 July 1947 (fl), *Guinea* 1555 (RNG). **León:** near Cistierna, 6 July 1927 (fl), *Wilmott* s.n. (BM). **Madrid:** Guadalupe, 14 June 1958 (fl), *Guinea* s.n. (RNG). **Ciudad Real:** 3 km SW of Alhambra, Sierra de Alhambra, 950 m, 29 June 1974 (l. fl), *Leadley & Petty* 172 (BM, RNG). **Albacete:** Almansa, W. end of Sierra de El Mugerón, 1150 m, 22 June 1979 (fl), *Reading Univ. Bot. Dept. Exped.* 150 (BM, RNG). **Valencia:** Utiel, Utiel to Pantano de Generalissimo, 21 km N. of town, 641 m, 20 June 1979 (bud), *Reading Univ. Bot. Dept. Exped.* 55 (BM, RNG). **Almería:** Laujar de Andarax, Nacimiento, c. 900 m, 8 July 1978 (fl), *Roivainen* s.n. (H\*, RNG). **Jaen:** Sierra de Cazorla, near Cueva de la Magdalena, 900 m, 7 July 1951 (fl), *Heywood* 1058 (BM, RNG). **Cordoba:** Sierra Morena, Cjo N. S. of Fuente Sagra, 7 km W. of Cordoba, 10 June 1927 (fl), *Wilmott* s.n. (BM). **Granada:** Puerto de la Ragua, crossroads with road to Alpujana, 1400 m, 19 June 1988 (fl), *Valdès et al.* 1011 (RNG). **Málaga:** Marbella, 500 m, N. de Puerto Cabopino, 30 m, 10 August 1984 (fl), *Michel* 7029 (BM, BR\*). **Sevilla:** entre Cantillana y Alcolea del Río, Km 9.0–9.1, 11 May 1986 (bud), *López & Molina* CL 791/86 (RNG, SEV\*). **Huelva:** c. 5 km S. of Aracena on road N433, 600 m, 3 July 1974 (fl & fr), *Leadley & Petty* 205 (BM, RNG).

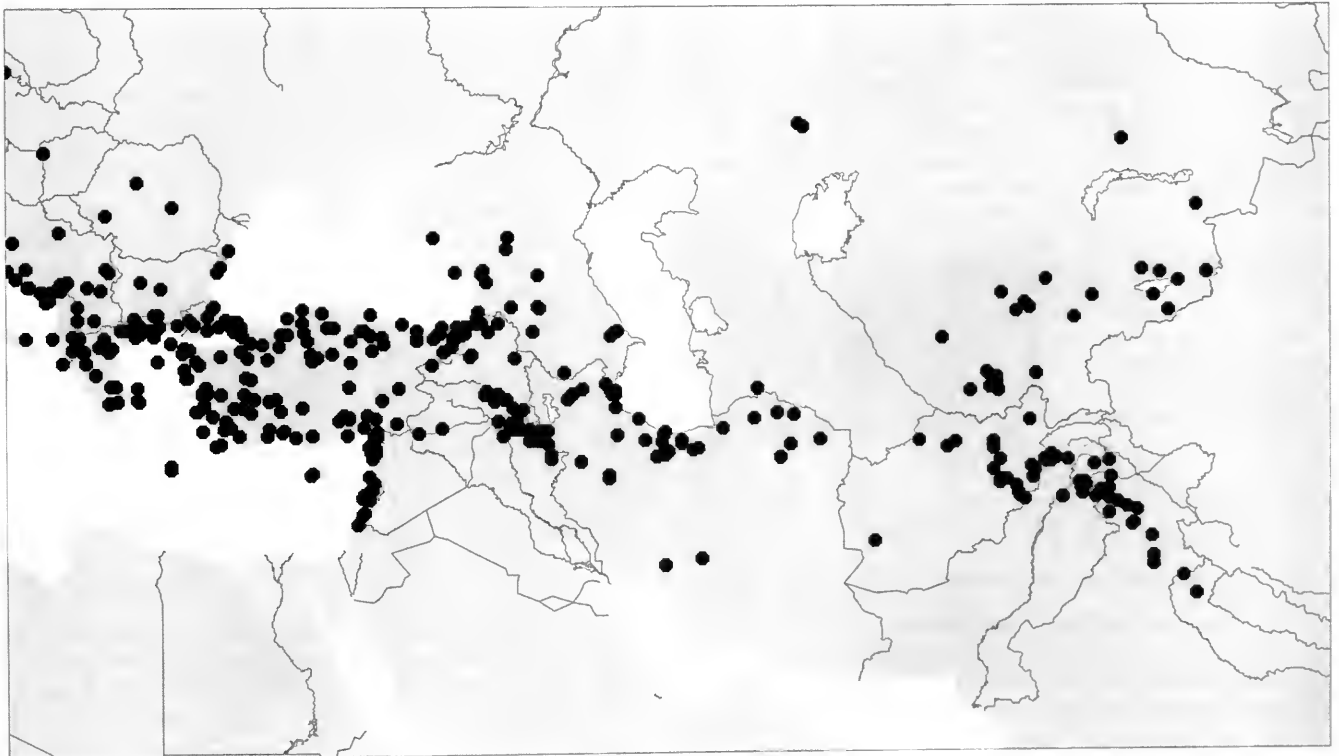
**GIBRALTAR.** Guadacarte, 23 May 1927 (fl & fr), *Croffen* s.n. (BM).

**PORTUGAL. Minho:** Caldas do Gerês, June 1887 (fl), *Murray* s.n. (BM). **Trás-os-Montes:** 6.4 km N. of Bragança, 450 m, 9 August 1957 (fl), *Epsom College* 325 (BM). **Beira littoral:** Coimbra, prope Carreira do Tiro, 50 m, 8 June 1936 (fl), *Rothmaler* s.n. (JE). **Estremadura:** Torres Vedras, arredores de Runa, July 1881 (fr), *Barros & Cunha* s.n. (BM). **Ribatejo:** Serra Monte Junto, 2 km from Cercal, above São Salvador, 300 m, 6 July 1974 (fl), *Leadley & Petty* 259 (BM, RNG). **Baixo Alentejo:** Sines, proximo do Monte de Chaminé, 13 June 1981 (fl), *Barbosa, Gomes & Morena* 13889 (RNG).

**AZORES. Graciosa:** Monte d'Ajuda, 30 m, 7 July 1971 (fl), *Gonçalves* 3003 (BM).

**MADEIRA.** Monte, 550 m, 19 October 1984 (fl & fr), *Short* 13 (BM). Ponta do Clerigo, 480 m, 11 June 1985 (fl), *Press* 896 (BM).

**CANARY ISLANDS. Santa Cruz:** Calderata, 1 June 1913 (fl), *Sprague*



Map 11 5c. *H. perforatum* subsp. *veronense*, Orient and Central Asia ●.

& Hutchinson 189 (K). **Tenerife:** Teneriffe, 1845 (fr), *Bourgeau* 246 (BM). **Las Palmas:** near S. Cruz, June 1892 (fl), *Murray* s.n. (BM).

**MOROCCO. Tanger:** Tangier, July, *Schousboe* s.n. (JE). **Rif:** Targuist, Targuist to Al Hoceima, 3 km W. of Beni-Hadifa, 960 m, 29 June 1993 (fl), *Jury* 11278 (BM, RNG). **Centre nord:** Zerhouan, ruins of Roman city of Volubilis, 390 m, 4 June 1994 (fl), *Jury* 14865 (BM, RNG). **Moyen Atlas:** Taza, c. 42 km from Taza to Sidi Abdallah, around Jbel Tazzeka, 1200 m, 15 June 1992 (fl), *Optima Iter V* 996 (RNG). **Haut Atlas:** Demnat, Djebel Tihlatin, tribu de Ait Maala [Mahala], 25 July 1879 (fr), *Ibrahim* s.n. (BM).

**ALGERIA. Oran:** Tlemcen, 15 June 1917 (fl), *Faure* s.n. (BM). **Alger:** Gorge de Chiffa (Blida-Medea), 500 m, 11 June 1971 (fl), *Davis* 53451 (BM). **Kabylie:** between Tizi Ouzou and Makouda, Oued Sebaou, 50–100 m, 17 June 1975 (fl), *Davis* 59146 (BM).

**TUNISIA.** NW mountains (regions Kroumirie, Mogods, Dorsale Tunisienne), *fide* Pottier-Alapetite (1979: 508).

**SUDAN REPUBLIC. Darfur:** Jebel Marra, Wadi Saria, 2300 m, 8 March 1983 (fr), *S. Miehe* 958 (BM); Jebel Marra, S. of Jebel Abau, c. 2600 m, 7 December 1954 (l. fl), *Jackson* 3335 (K).

**SAUDI ARABIA. Asir:** Taif-Al Baha-Jabal Ibrahim road, 15 km N. of Al Mindak, 2040 m, 17 March 1987 (fl & e. fr), *Collette* 6079 (BM, E\*, K).

**ISRAEL. Upper Galilee:** near Dafneh [Dafna?], 27 May 1945 (fl), *Norris* s.n. (BM).

**LEBANON. Coast:** environs de Brumana, July to September 1979?, *Cramer* s.n. (G); Baynu, 13 June 1943 (fl), *Davis* 6412 (BM, K). **Lebanon:** Cedars, 20 July 1865 (fl), *G. Post* s.n. (K); Zahleh [Zahlé], 7 May 1875 (fl), *Post* 809 (K).

**SYRIA. North:** Monts Nusairy, Ain Halakim, 750–900 m, June 1910 (fl), *Haradjian* 3537 (K); 20 km S. of Ordu [Ordu], 800–900 m, 8 June 1938 (fl), *Dinsmore* 20360 (K).

**CYPRUS. Kyrenia:** environs du Monastère Armenien, 600–900 m, 26–30 May 1912 (fl), *Haradjian* 348 (K). **Paphos:** Lisso [Lyso], c. 600 m, 10–16 June 1913 (fl), *Haradjian* 851 (K). **Troödos:** distr. Limassol, between Vasa and Agios Amvrosios, 21 May 1941 (fl), *Davis* 3538 (BM, K).

**IRAQ. Amadiyah:** Rowandiz [Rowanduz] Gorge, 24 June 1934 (e. fr), *Field & Lazar* 856 (BASBG, K, W); 35 km NE of Zakho, Daimka village, 820 m, 5 July 1976 (fl), *Al-Kaisi & Hamid* 45365 (K). **Rowanduz:** Bekarl,

2200 m, 2 August 1956 (fl), *Haley* 17 (BM); Erbil distr., Montes Qandil, Pushtashan, c. 1100 m, 28 July–1 August 1957 (fl), *K.H. Reehinger* 11035 (W). **Sulimaniyah:** Sulimanieh, in mont., June 1867 (fl), *Hausknecht* s.n. (BM, K); Sulaimaniya liwa, A'hmidau swamp, 28 July 1964 (fl), *Makki* 551 (W).

**IRAN. Azarbaijan:** Tabriz to Marand, 1500 m, 27 July 1971 (l. fl), *Termé* EVIN 34352E (BM, EVIN\*). **Kordestan:** 64 km SW of Mahabad, 1500 m, 29 July 1962 (fl), *Furse* 3494 (K, W). **Lorestan:** Bicheh, 1100 m, 29 May 1937 (fl), *Köie* 1506 (C\*, W). **Kohkiluyeh va Buyer Ahmadi:** Tale' Khosravi to Sissakht, 29 July 1949 (fl), *Beh houdi* 975E (W). **Zanjan:** pass between Zandjan and Rudbar, 36 km from Zandjan, 2100 m, 9 July 1972 (fl), *Goldblatt* 776 (BM). **Hamadan:** Hamadan, 2100 m, 7 September 1929 (fl), *Rogers* 9507 (BM, K). **Gilan:** Astara to Resht, 16 km S. of Astara, 30 m (by Caspian shore), 7 June 1962 (fl), *Furse* 2846 (K, W). **Mazandaran:** Elburz Mts, above Allamul, between Chalus and Karadz, c. 1980 m, 23 June 1966 (fl), *Archibald* 2403 (E, K). **Teheran:** prope urbem Teheran, 1843 (fl), *Kotschy* 756 (BM, K); Haft Hartz Valley, N. of Teheran, 2100 m, June 1934 (fl), *Trott* 181 (K). **Khorasan:** in montibus inter Budjnurd [Bujnurd] et Morawe Tappeh, c. 1300 m, 25–27 July 1937 (fl & fr), *K.H. & F. Reehinger* 1875 (W).

**AFGHANISTAN. Farah?:** Khash-Dt., 2400 m, 8 August 1937 (fr), *Koelz* 12913 (W). **Fariab:** c. 6.5 km N. of Darrah Zang village, c. 1320 m, 30 June 1971 (fl), *Grey-Wilson & Hewer* 1312 (K). **Jozjan:** Tuzkar, 1200 m, 15 September 1939 (fr), *Koelz* 13977 (W). **Baghlan:** Salang Pass, N. side, 1800 m, 24 June 1966 (fl), *Furse* 8056 (K). **Parwan:** montée sud vers Col de Salang, 2500 m, August 1964 (fr), *Haysu* 487 (W). **Kabul:** Paghman, 25.6 km W. of Kabul, 2400–2700 m, 23 June 1939 (fl), *Chaworth-Musters* s.n. (BM). **Logar:** Ghorband, 1700 m, 14 August 1938 (fr), *Köie* 2789 (W). **Konar:** 17.6 km NW of Kamdesh towards Barg-i-Matal, c. 1567 m, 3 July 1969 (fl), *Hewer* 1378 (K). **Nangarhar:** Mama Kheyli, 1200 m, 23 May 1937 (fl), *Koelz* 11576 (W).

**PAKISTAN. Kurram:** Kurram Valley, Ziran, Imam Bagh, 30 August 1972 (fr), *Kazmi* 3749 (H). **Dir:** Lowari, 6 July 1968 (fl), *Nasir* 5108 (RAW). **Swat:** Khawazakiela to Shangla, c. 1300 m, 2 June 1965 (fl), *Lamond* 1691 (E, KUH). **Hazara:** Jabri, 10 km from Shogran, 15 April 1978 (fl), *Muq. Shah & Dil. Khan* 2403 (BM, ISL\*). **Chitral:** Kesu, 1290 m, 24 May 1958 (e. fr), *Bowes Lyon* 714 (BM, RAW, W). **Gilgit:** Buni, 2100 m, 1876? (fr), *Giles* 392



Map 12 5c. *H. perforatum* subsp. *veronense*, Australia and New Zealand (introduced) ▲. Also in W. Australia (see records).



(K). **Baltistan:** Balti, 2400 m, June 1915, *Schlich* 56 (BM).

**INDIA. Kashmir:** Manasbal, 1560 m, 5 June 1940 (fl), *Ludlow & Sherriff* 8120 (BM). **Himachal Pradesh:** Pangi, Chenab R., N. bank between Darwas and Ishtwari, c. 2400 m, 12 June 1981 (fl), *Sayers* 3713 (BM). **Uttar Pradesh:** Tihri-Garhwal, Ganges valley near Jāngla, 2400–2700 m, 12 July 1883 (st), *Duthie* 977 (BM).

**TURKMENISTAN. Aschabad:** ad montem Aktepe [Kopet-Dag], 17 June 1900 (fl), *Sintenis* 564a (BM, K); Kasil Arwat, Karakala, m. Sundsodagh, 31 May 1901 (fl), *Sintenis* 1862 (JE).

**UZBEKISTAN.** Taschkent, bei Tschimgan, westlich Ausläufer des Tian Shan, 1700 m, 14 July 1975 (fl), *Breckle* 3632 (K); Denauskiy raion, Akhunbabeva, 1 July 1938 (fl), *Parabskaya* s.n. (LE).

**TAJIKISTAN.** Pamiro-Alai, Zalekhsi, N. slope of Aatni, R. Gulibysta 4–5 km N. of Stalinabada [Dushanbe], 7 June 1942 (fl), *Grigoriev* 225 (LE); Kondor Gorge, 30 km N. of Dushanbe, W. side of R. Varzob, 1100 m, 13 July 1975 (fl & e. fr), *Pankhurst & James* 93 (BM).

**KYRGYZSTAN.** Tian-schan occid., in valle fl. Talos, prope pagum Pokrovka, 14 June 1919 (fl & fr), *Kushelev* in HTU 077243 (TAI); Ferganskiy khrebet, Arslanbobskiy nut farm, R. Yasky-chu, 11 October 1933 (fr), *Sokolov* s.n. (LE).

**KAZAKHSTAN.** Semirychensk prov., Vyernyy [Almaty] distr., Zayliyskiy (Trans-Ilian) Alatau, 14 July 1907 (fl), *Sokalsky* 118 (BM); Ketmenskiy khrebet, Ushchelye, R. Ketmen, 20 September 1931 (fr), *Rodin* 1508 (LE).

#### INTRODUCTIONS

**SOUTH AFRICA. Cape Province:** Stellenbosch, College of Agriculture, 23 November 1948 (fl), *Hulme* s.n. (BM, K); Cape Town, slopes of Papegaaiberg, c. 105 m, 15 January 1969 (l. fl), *Taylor* 7376 (K, PRE\*).

**RÉUNION.** See Robson & Stevens, *Flore des Mascareignes* 49. Guttifères: 6 (1980). These populations probably belong to subsp. *veronense*, but the specimens have not been re-studied.

**AUSTRALIA. New South Wales:** Faulconbridge, 435 m, 17 November 1982 (fl), *Coveny* 11405 (K, NSW\*). **A.C.T.:** Canberra, Jarrabomberra Avenue, just S. of junction with Narrabundah Lane, 580 m, 5 December 1980 (fl), *Canning* 5031 (BM, CBG\*). **Victoria:** Far NE, Corryong, near Anzac Drive, 25 November 1972 (fl), *R.V. Smith* 72/57 (K, MEL\*). **South Australia:** Mt Lofty Ranges, Blackwood, 251 m, [comm. April 1929] (l. fl), *Pritchard* s.n. (BM, K, GH). **Western Australia:** approx. 8 km NE of York on York-Meckering road, 7 November 1979 (bud), *Dixon* s.n. (K).

**NEW ZEALAND. North Island:** South Auckland, Taumarunui, 20 April 1928 (fl), *Allan* s.n. (K); Wellington, Masterton, 10 January 1929 (fl), *Allan* s.n. (K). **South Island:** Nelson, near Nelson City, 23 January 1929 (fr), *Allan* s.n. (K); Otago, Oamaru, 9 January 1929 (fl), *Allan* s.n. (K).

**HAWAIIAN ISLANDS. Hawai'i:** North Kona, Huallai, 1961, *Fosberg* 42087 (BISH\*) (*fide* Wagner, Herbst & Sohmer, 1999: 526).

*Hypericum perforatum* var. *collinum* Woron. (from Georgia) and records of *H. veronense* and *H. perforatum* var. *veronense* from the Crimea (Vul'f, 1953: 110) and the Caucasus region both apparently refer to a narrow-leaved form of subsp. *veronense* with interrupted rather than vesicular lateral capsule vittae.

5d. *Hypericum perforatum* subsp. *chinense* N. Robson, **subsp. nov.**<sup>5</sup> A subsp. *perforatum* inflorescentiis vel inflorescentiis partialibus vel inflorescentiis totis et partialibus congestis, ramulis pro ratione longis curvato-ascendentibus, petalis glandulis in lamina insertis nigris vel carentibus, differt. Type: China, Sichuan, Wa-shan, 2100–2400 m, July 1908 (fl), *Wilson* 2425 (BM!-holotype; A-isotype).

Fig. 8, Map 13.

*H. perforatum* var. *microphyllum* H. Léveillé in *Bull. Soc. Bot. France* 54: 595 (1908); Lauener in *Notes Roy. Bot. Gard. Edinburgh* 27: 5 (1966) qua syn.; non DC. (1815). Type: China, Guizhou, Kouy-yang, pied de la montagne, 28 June 1897 (fl),

*Bodinier* 1665 (E-holotype; BM!-isotype).

*H. foliosissimum* Koidz. in *Acta Phytotax. Geobot.* 3: 215 (1934); Nemoto, *Fl. Japan, Suppl.*: 483 (1936). Type: Japan, Honshu, Prov. Sima, Kamomura, Arasima, 27 July 1934, *T. Ito* s.n. (? -holotype). See note on next entry.

*H. perforatum* var. *angustifolium* sensu Ohwi, *Fl. Japan*: 781 (1936); Y. Kimura in *Bot. Mag. (Tokyo)* 52: 406, f. 9 (1938), in Nakai & Honda, *Nova fl. jap.* 10: 133, ff. 47, 48 (1951); Momiyama in Satake et al., *Wild Fls Japan* 2: 118, t. 114 f. 3 (1982). Momiyama states that the Japanese plant was originally introduced from Europe; but examination of Japanese specimens indicates that they match subsp. *chinense* rather than the south European subsp. *veronense*.

Icon: Li Xiwen in *Fl. R. P. Sin.* 50(2): 68, t. 15, ff. 1–4 (1990).

*Leaves* petiolate; lamina (7–)10–25 × 3–7(–15) mm, ± narrowly elliptic to narrowly oblong or linear (l:b=2.5–3.5), base rather narrowly cuneate to subcordate-amplexicaul, ?glaucous beneath. *Inflorescence* and/or partial inflorescences congested, branches relatively long, curved-ascending. *Petals* with laminar glands black, linear to punctiform, or often absent. *Capsule* valves with lateral vittae linear, narrow or somewhat interrupted or shortened but not swollen.

China (eastern Qinghai and Gansu east to Shandong and south to Yunnan and Guizhou). The northern populations tend to have larger and relatively broader leaves.

**CHINA. Hebei:** *fide* Li Xiwen (1990). **Shanxi:** *fide* Li Xiwen (1990). **Shaanxi:** Zhouzhi Xian, Chenhe Xiang, 1400 m, 14 August 1958 (fl & fr), *Zhang* 44 (IBSC, KUN, NAS); Chungmanshan, Hsingpaochuan, 20 August 1934 (fl & fr), *Pai* 1071 (PE); Tai-pei Shan, 1910 (fr), *Purdum* s.n. (K). **Gansu:** Yanchang Xian, Gongjiagou, 2150 m, 1 July 1989 (fl & fr), *Yuan* 1008 (A, BM, CAS, PE\*); Tianshui, 1350 m, 20 July 1951 (fl & fr), *Zhang* 46 (KUN, PE). **Henan:** Lushi Xian, 1660 m, 2 October 1958 (fr), *Fu* 1640 (IBSC); Xichuan Xian, Lugou Sandaohu, 220 m, October 1956 (fr), *Henan For. Dept.* 1445 (PE). **Shandong:** Fei Hsien, Mong Shan, 12 July 1936 (fl), *Cheo & Yen* 38 (BM, W). **Jiangsu:** *fide* Li Xiwen (1990). **Jiangxi:** Kew Kiang [Jiujiang], 1873 (fl), *Shearer* s.n. (BM). **Hunan:** Wugang Xian, Yunshan, Qishucuo, 1150 m, 17 October 1963 (fr), *Liu & He* 16288 (IBSC); Changsha, Xiaonamen, 9 May 1964 (fl), *Chen & Yue* 1498 (NAS). **Hubei:** Wuchang, Luojia Shan, May 1932 (fl), *Chung* 9034 (A, NY, W); Badong Xian, 15 July 1957 (fl), *Fu & Zhang* 776 (IBSC, KUN); Shennongjia For. Distr., along Qiadonggou Canyon, 1900 m, 27 August 1980 (fl & fr), *Sino-Amer. Exped.* 396 (A, NY). **Sichuan:** Wenchuan Xian, 23 July 1928 (fl), *Fang* 1492 (GH, K, NY, PE, US); Fengjie Xian, Zhuyuan, 600 m, 24 July 1958 (fl & fr), *Chang* 25617 (IBSC, KUN, PE); Dujiandyan Municipality, Longxi For. Farm, 800 m, 2 September 1988 (fr), *Boufford et al.* 14433 (A, BM, CAS, NY, PE\*). **Guizhou:** Pin-fa, Kweiting, 400–550 m, 27 June 1930 (fl), *Tsiang* 5341 (IBSC, NAS, NY, PE); Yinjiang Xian, Huguosi, W. side of Fanjing Shan, 22 September 1986 (fl), *Sino-Amer. Guizhou Exped.* 1453 (BM, NY). **Yunnan:** vicinity of Yunnan-sen [Kunming], 1906 (fl), *Maire* 1505 (K); no precise locality, July 1936 (fl & fr), *McLaren* U.109 (A); [also *Cavalerie* 3125 (K)].

#### INTRODUCTIONS

**JAPAN. Hokkaidō:** Furano city, Yamabe, Tokyo University Forest, 13–15 July 1979 (fl), *Sohma & Takahashi* 478 (H).

#### Key to hybrids of *Hypericum perforatum*

This key should be used bearing in mind (a) the variability of the parental taxa, (b) the continuity of variation between parents and hybrids of *H. × desetangii* nothosubsp. *desetangii* and (c) that subsidiary lines present in younger stems may disappear in old ones

<sup>5</sup>Some specimens of subsp. *chinense* have been labelled 'subsp. *confertiflorum* (Debeaux) N. Robson', but the type of *H. perforatum* var. *confertiflorum* has proved to belong to *H. attenuatum*.





Map 13 5d. *H. perforatum* subsp. *chinense* ●, introduced ○.

- 1 Stem internodes 2-lined (from leaf bases) or with weaker and usually incomplete subsidiary lines (from between leaves); leaves relatively laxly reticulate-veined ..... 2  
 Stem internodes  $\pm$  completely 4-lined; leaves relatively densely reticulate-veined ..... 5
- 2(1) Stem internodes 2-lined only; sepals usually narrow, more rarely broad, always acute with a hair point; capsule valves with not very numerous vittae to punctiform vesicles ..... 3  
 Stem internodes also with weakly developed subsidiary lines; sepals narrow or quite broad, acute; capsule valves with relatively numerous narrow longitudinal vittae ..... 4
- 3(2) Sepals entire, lanceolate; capsule with lateral vittae linear and shortened; leaves spreading, venation sometimes densely reticulate ..... 5xx.  $\times$  **medium**  
 Sepals eroded-denticulate to glandular-ciliate, elliptic to lanceolate; capsule with lateral vittae linear or absent, not shortened; leaves often deflexed, venation laxly reticulate .....  
 ... 5xbb.  $\times$  **desetangsii** nsubsp. **carinthiacum** nf. **perforatiforme**
- 4(2) Sepals narrowly oblong to linear-lanceolate, finely acuminate or apiculate, eroded-denticulate to entire; leaves usually rather densely pale-gland-dotted ..... 5xa.  $\times$  **desetangsii** nsubsp. **desetangsii**  
 Sepals broadly elliptic to linear-lanceolate, acute to acuminate,  $\pm$  eroded-denticulate to subfimbriate or entire; leaves sparsely pale-gland-dotted .....  
 ... 5xbb.  $\times$  **desetangsii** nsubsp. **carinthiacum** nf. **perforatiforme**
- 5(1) Leaves usually rather densely pale-gland-dotted, venation very laxly to rather densely translucent-reticulate; sepal apex usually very acute or eroded-denticulate with fine hair-point; sepals and petals with sparse dark glands ..... 5xa.  $\times$  **desetangsii** nsubsp. **desetangsii**  
 Leaves without or almost without pale gland dots, venation rather densely translucent-reticulate; sepal apex obtuse or subacute, entire or finely denticulate, without distinct hair-point; sepals and petals without or with relatively numerous dark glands ..... 6
- 6(5) Petal laminar glands all or some black; leaf apex obtuse, not acute, base cuneate to rounded .....  
 ... 5xba.  $\times$  **desetangsii** nsubsp. **carinthiacum** nf. **maculatiforme**  
 Petal laminar glands all pale; leaf apex obtuse or sometimes sometimes acute, base cuneate to cordate-amplexicaul .....  
 ..... 5xc.  $\times$  **desetangsii** nsubsp. **balcanicum**
- 5x. **Hypericum**  $\times$  **desetangsii** Lamotte in *Bull. Soc. Bot. France* **21**: 121 (1874); Bonnet in *Bull. Soc. Bot. France* **25**: 277 (1878); Schinz in *Bull. Herb. Boissier* II, **3**: 11, 13 (1902), in *Vierteljahrsschr Naturf. Ges. Zürich* **49**: 241 (1905); Tourlet in *Bull. Soc. Bot. France* **50**: 307 (1903); Thellung in *Allg. Bot. Z.* **1912**: 19 (1912); Salmon in *J. Bot. (Lond.)* **51**: 317, t. 528 (1913); R. Keller in *Engl. & Prantl, Nat. Pflanzenfam.*, 2nd ed. **21**: 179 (1925); N. Robson in *Bot. Soc. Brit. Isles Proc.* **3**: 99 (1958), in *Bull. Br. Mus. (Nat. Hist.)*, Bot. **8**: 168, f. 55 (1981), in *Wisskirchen & Haeupler, Standardliste Farn- u. Blütenpfl. Deutschl.*: 268 (1998); A. Fröhl. in *Preslia* **32**: 97–99, f. 2 (1960); O. Schwarz in *Drudea* **5**: 64 (1965). Type: France, Aube, Chapelle-St.-Luc près Troyes, 11 July 1841 (l. fl), *Des Étangs* s.n. (CLF!-lectotype, selected here); Garenne de Villechétif près Troyes, 5 August 1840 (e. fr), *Des Étangs* s.n. (K!-syntype). But see note under 1x. *H. x laschii* (p. 76) regarding the identity of these Des Étangs specimens.

Fig. 9, Maps 14, 15.

*H. maculatum* Crantz  $\times$  *H. perforatum* L.; A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **120**(1): 557 (1911).

*Stems* almost completely 4-lined to 2-lined. *Leaves* broadly ovate or



**Fig. 9** *H. × desetangii*: A. n. subsp. *desetangii*: (1): (a) branch; (b) stem section; (c) leaf; (d) sepal; (e) petal. B. n. subsp. *desetangii*: (2): (f) branch; (g) stem section; (h) leaf; (i) sepal; (j) petal; (k) capsule. C. n. subsp. *carinthiacum* n. forma *perforatiforme*: (l) stem section; (m) leaf; (n) sepal; (o) petal. D. n. subsp. *carinthiacum* n. forma *maculatiforme*: (p) stem section; (q) leaf; (r) sepal; (s) petal. E. n. subsp. *balcanicum*: (t) stem section; (u) leaf; (v) sepal; (w) petal (a, f  $\times 2/3$ ; b, c, g, h, l, m, p, q, t, u  $\times 2$ ; rest  $\times 4$ ). A. *Anou*. s.n. (France, Puy de Dôme). B. *Salmon* s.n. (England, Sussex). C. *Kerner* 3649. D. *Lillefosse* s.n. E. *Rechinger* 782.

broadly elliptic or ovate-oblong to linear; tertiary reticulate venation dense to lax; pale laminar glands dense (especially in upper leaves) to very few. *Sepals* broadly elliptic to linear-lanceolate, obtuse to acuminate, entire or ± eroded-denticulate to subfimbriate. *Petals* with black laminar glands rather numerous to few, mostly linear to mostly punctiform, or absent; black marginal glands present. *Capsule* with vittae all linear and vertical or some lateral, oblique and irregular to elongate-vesicular.

Intermediate between the parents, but back-crossing to both at the tetraploid level of *H. maculatum* (subsp. *obtusiusculum*) has resulted in a complete series of intermediate forms of *H. × desetangii* nothosubsp. *desetangii* (cf. Crackles, 1990). At the diploid level (subsp. *maculatum*), two distinct forms of nothosubsp. *carinthiacum* occur, one triploid (2n=24) (*H. maculatum* (n=8) × *H. perforatum* (n=16) or, probably rarely but conceivably, *H. perforatum* (n=16, i.e. reduced) × *H. maculatum* (n=8)), the other pentaploid (2n=40) (*H. perforatum* (n=32, i.e. unreduced) × *H. maculatum* (n=8)). In the cross with subsp. *maculatum* (nothosubsp. *carinthiacum*), these forms are at least sometimes distinguishable (respectively nothoforma *maculatiforme* and nothoforma *perforatiforme*); but in the cross with the presumed diploid subsp. *immaculatum* (nothosubsp. *balcanicum*), no distinct morphological forms are apparent and no chromosome counts have yet been made. As the specimens with this alleged parentage are intermediate between the parents, however, they are likely to be triploid. See Noack (1939) for a discussion of the cytology, but not the nomenclature.

Although records are scattered, distribution of the hybrids would appear to be confined to the areas of distribution overlap of the parents; but vegetative propagation and (in nothosubsp. *desetangii*) partial fertility of the hybrids have sometimes resulted in their occurrence in the absence of one or both parents.

5xa. **Hypericum × desetangii** Lamotte nothosubsp. **desetangii** – N. Robson in Wisskirchen & Haeupler, *Standardliste Farn- u. Blütenpfl. Deutschl.*: 268 (1998).

Map 14.

5. *H. perforatum* L. × 1c. *H. maculatum* subsp. *obtusiusculum* (Tourlet) Hayek

*H. perforato-quadrangulum* Lasch in *Linnaea* 4: 415 (1829).

*H. linnaeanum* Callay & Gren. in Gren., *Fl. jurass.* 1: 154 (1863), nomen.

?*H. × mixtum* Du Moulin in *Oesterr. bot. Z.* 17: 390 (1867); A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. I*, 120(1): 568 (1911), in *Mitt. Naturwiss. Vereins Steiermark* 51: 227 (1915). Type: Germany, Bavaria, bei Neuburg, Bertolzheim, Du Moulin s.n. (W?- holotype). It is not certain from the description whether this is an earlier synonym of *H. × desetangii* or a later synonym of *H. maculatum* Crantz (cf. Mártonfi, Repčák & Mihoková, 1996b). Fröhlich (1911: 568) was unable to find the type specimen in W; so, unless or until it is discovered and proves to be *H. × desetangii*, it seems best to maintain the well known name.

*H. desetangii* var. *genuinum* Bonnet in *Bull. Soc. Bot. France* 25: 277 (1878); Burnat, *Fl. Alpes marit.* 2: 27 (1896); Schinz in *Bull. Herb. Boissier II*, 1: 14, 21 (1902), in *Vierteljahrsschr. Naturf. Ges. Zürich* 49: 241 (1905). Type as for *H. × desetangii* Lamotte.

*H. acutum* subsp. *desetangii* (Lamotte) Rouy in Rouy & Fouc., *Fl. France* 3: 336 (1896), comb. illegit. (Art. 52).

*H. acutum* subsp. *desetangii* var. *genuinum* (Bonnet) Rouy in Rouy & Fouc., *Fl. France* 3: 336 (1896), comb. illegit. (Art. 52).

*H. quadrangulum* subsp. *desetangii* (Lamotte) Tourlet in *Bull. Soc. Bot. France* 50: 307 (1903); A. Fröhl. in *Oesterr. Bot. Z.* 63: 18

(1913), in *Mitt. Naturwiss. Vereines Steiermark* 51: 220 (1915); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 518 (1925).

*H. maculatum* subsp. *erosum* (Schinz) A. Fröhl. × *H. perforatum* L. sensu A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 559 (1911).

*H. maculatum* subsp. *obtusiusculum* (Tourlet) Hayek × *H. perforatum* L., A. Fröhl. in *Oesterr. Bot. Z.* 63: 15 (1913).

*H. × desetangii* nothovar. *desetangii* qua nothomorph sensu N. Robson in Tutin et al., *Fl. Europaea* 2: 269 (1968), in Cullen et al., *Eur. gard. fl.* 4: 60 (1995).

*H. erosum* (Schinz) O. Schwarz in *Drudea* 5: 63 (1965) pro parte quoad typum. Type as for *H. quadrangulum* var. *erosum* Schinz.

Icon: Salmon in *J. Bot. (Lond.)* 51: t. 528 (1913).

*Stems* usually partially 4-lined. *Leaves* ovate or broadly elliptic to narrowly oblong or linear; tertiary reticulate venation dense to lax; pale laminar glands usually present, sometimes dense, especially in upper leaves. *Sepals* narrowly oblong to lanceolate or linear-lanceolate, eroded-apiculate to acuminate and entire or denticulate. *Petals* with black laminar glands usually few, linear to elongate-punctiform, and some marginal. *Capsule* with vittae all linear and vertical or some lateral, oblique and linear to elongate-vesicular. 2n=32, 40 & 48 (Robson, 1956, 1975, 1981; Robson & Adams, 1968; Mártonfi et al., 1996a). For record of 2n=24, see p. 105.

Habitat range of the parents excluding extremes of humidity.

Distribution of *H. maculatum* subsp. *obtusiusculum*, i.e. NW Europe south to central France and Switzerland and east to western Germany and Austria.

**SCOTLAND. S. Aberdeen:** Drum, bank of R. Dee, 15 August 1956 (fr), Robson s.n. (BM). **W. Perth:** Perth, R. Tay, Moncrieffe I., 17 July 1938 (fl), Mackechnie & Wallace s.n. (BM, K). **Argyll:** Dunoon, 23 July 1888 (fl), King s.n. (BM). **Ayr:** West Kilbride, 24 July 1973 (fl), B. Simpson s.n. (BM). **Renfrew:** Mr Hutcheson's School playing fields, 12 September 1987, Dickson s.n. (GL). **Lanark:** Rotten Calder at Redlees Quarry, 13 September 1987 (fl), Dickson s.n. (GL). **Berwick:** Earlston, 1926 (e. fr), Hayward s.n. (BM).

**ENGLAND. Cumberland:** between Little Skelton and Ellaby, 19 June 1969 (fl), Halliday s.n. (LANC). **Durham:** near Nunstanton Carr, 82 m, 18 July 1975 (fl), Graham 8714 (BM). **NW Yorks.:** Swaledale, Langton, 23 August 1967 (l. fl), Gillingham s.n. (BM). **SE Yorks.:** Harswell old station, 20 July 1988 (fl), Duncan s.n. (BM). **S. Lancs.:** Wigan, Gathurst, 1947 (fl), Edmondson LIV1975.560.7 (LIV). **Cheshire:** Castle Mill, 1 August 1867 (fl), Bailey s.n. (BM). **Shropshire:** Craig Llwyn, 28 September 1971 (fr), Benoit s.n. (BM). **Oxford:** Hailey, Syngue Wood, 13 September 1946 (l. fl), N. Simpson 46302 (BM). **Bucks.:** between Cadmore End and Fingest, 11 August 1946 (fl), Sandwith 3139 (BM). **S. Essex:** Woodhatch near Theydon Boys, 19 July 1914 (fl), C.E. Britton 1247 (K). **W. Kent:** S. of Ightham Court, 8 September 1957 (e. fr), McClintock s.n. (BM). **Surrey:** Burgh Heath, Perrott's Farm, 15 August 1929 (l. fl), Wallace s.n. (BM). **E. Sussex:** Lewes, Seaford Road, 11 July 1936 (fl), N. Simpson 36868 (BM). **Dorset:** near Wimborne, 22 August 1928 (fl), L.B. Hall in N. Simpson 45808 (BM). **S. Devon:** A 373 between Honiton and Awliscombe, 19 July 1989 (fl), Margetts s.n. (BM).

**WALES. Glamorgan:** near Lisvane, Cefn On Halt, 3 July 1968 (fl), Pinkard s.n. (H). **Radnor:** near Builth Beacon, 18 August 1940 (fl), Pugsley s.n. (BM). **Merioneth:** near Barmouth Junction (Morfa Mawddach) station, 5 October 1971 (fr), Benoit s.n. (BM). **Caernarvon:** Bangor, Talybont, Penbryn, 27 August 1972 (fl), Roberts (BM). **Denbigh:** Llangollen, 15 August 1953 (fl), Herb. Liverpool Mus. 1973.305.356 (LIV).

**IRELAND.** Recorded from West Kerry only (Scannell & Synnott, 1987), but likely to be more widespread.

**FRANCE. Aisne:** Villers-Cotterets, 17 August 1879 (l. fl & e. fr), Bonnet in Soc. Dauph. 2409 (BM, FR). **Oise:** Aulmont près Senlis, 25 September 1835 (fr), Gay s.n. (K). **Seine-et-Marne:** Nemours, 17 July 1892 (fl), Jaupert 631 (BM). **Aube:** Villechétif [loc. class.], 29 July 1989, Guyot s.n. (H); see p. 102. **Côte-d'Or:** Magny-la-Ville, June 1887 (fl), Wilmott s.n. (K).



**Map 14** 5xa. *H. × desetangsii* subsp. *desetangsii* ●. Recorded in Ireland only from the south-west (Co. Kerry), but possibly more widespread.

**Saône-et-Loire:** Curgy, près Autun, 6 August 1889 (fl), *Gillot* 435 (BM). **Allier:** Sussat, la Veauce, July 1873 (fl), *Déséglise* s.n. (BM). **Hte-Vienne:** le Dorat, 5 July 1929 (fl), *Elias* in *Héribaut-Joseph* 441 (BM). **Hte-Savoie:** Constans, 2 August 1896 (fl), *Boreau* s.n. (BM). **Savoie:** Forêt d'Apremont [près Chambéry], 30 July 1906 (l. fl), *Chabert* s.n. (BM).

**BELGIUM. Namur:** entre Doisches et Petit-Doisches contre la frontière française, au SW du Baquet, 16 July 1977 (fl), *Duvigneaud* 77B642 (H).

**GERMANY. Rheinland Pfalz:** Zweibrücken, n.d., *Herb. Ekart/Irmisch* s.n. (JE). **Baden-Württemberg:** [Schwabischen Alpen] Donstetten, August 1875 (fl & fr), *Kemmler* s.n. (FR).

**SWITZERLAND. Valais:** Champéry, 4 September 1881 (fl), *Lacaïta* s.n. (BM). **Zürich:** Affoltern, July 1902 (fl), *Schinz* s.n. (FR). **St. Gallen:** zwischen Litzibach und Vilters, c. 500 m, 8 July 1951 *Büel* s.n. (BM, ZT\*).

**AUSTRIA. Salzburg:** bei Hellbrun, 26 August 1913 (fl), *Fröhlich* s.n. (BM). **Steiermark:** ad vicum Maria-Trost prope urbem Graz, inter parentes, c. 430 m, July 1911 (fl), *Fröhlich* in *Hayek*, Fl. stir. exs. 1199 (BM, GZU, H).

The above description covers the range of variation in this hybrid, which becomes increasingly difficult to recognize as it approaches each parent in form. The typical ( $f_1$ ) form has incomplete subsidiary stem lines, rather broadly oblong leaves with intermediately dense venation and laminar glands, oblong sepals with eroded-apiculate apex, and capsule vittae (both dorsal and lateral) linear. The chromosome counts of 48 and 40 were, presumably, the results respectively of the fertilization of an unreduced embryo sac and a back-cross from that to another unreduced embryo sac.

5xb. *Hypericum × desetangsii* nothosubsp. *carinthiacum* (A. Fröhl.) N. Robson [in *B.S.B.I. News*, no. 49: 50 (1988) in adnot.] in Wisskirchen & Haeupler, *Standardliste Farn- u. Blütenpfl. Deutschl.:* 268 (1998); Lihová, Mártonfi & Mártonfióvá in *Caryologia* 53: 127 (2000). Type as for *H. × carinthiacum* A. Fröhl.

Fig. 9, Map 15.

5. *H. perforatum* L. × 1b. *H. maculatum* Crantz subsp. *maculatum*

*H. maculatum* subsp. *typicum* A. Fröhl. × *perforatum* L., A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 557 (1911); in *Österr. Bot. Z.* 63: 14 (1913).

*H. × carinthiacum* A. Fröhl. in *Mitt. Naturwiss. Vereins Steiermark* 51: 228 (1915). Fröhlich (1913) listed a series of localities in Carinthia where this hybrid was found, but did not designate a type either there or in his 1915 paper. See 5xba. *H. × desetangsii* nothosubsp. *carinthiacum* nothoforma *maculatifforme* for lectotype.

*H. × desetangsii* nothomorph. *carinthiacum* (A. Fröhl.) N. Robson in *Repert. Spec. Nov. Regni Veg.* 74: 23 (1967), in Tutin et al., *Fl. Europaea* 2: 269 (1968); in *Watsonia* 9: 203 (1972).

*Stems* almost completely 4-lined to 2-lined. *Leaves* broadly ovate or broadly elliptic to ovate-oblong; tertiary venation dense to lax; pale laminar glands very few. *Sepals* broadly elliptic to linear-lanceolate, acute to acuminate, entire or ± eroded-denticulate to (glandular-) subfimbriate. *Petals* with black laminar glands rather numerous to few, mostly linear to mostly punctiform, or absent, black marginal glands present. *Capsule* with vittae all linear, dorsal and lateral, oblique, the latter regular or sometimes irregular.  $2n=24, 40$  [48, 56 experimentally] (see below).

Habitat range of the parents?

The above description covers both triploid and pentaploid hybrids with both varieties of subsp. *maculatum*. As regards these hybrids, Noack (1939) found the triploid to be intermediate between the parents, but could not distinguish the pentaploid from pure *H. perforatum*. Mártonfi et al. (1996b), on the other hand, were able to distinguish the pentaploid, and thus indirectly confirmed Fröhlich's (1913, 1915, 1960) recognition of two distinct forms of this hybrid. Seeds obtained from a wild-collected pentaploid plant yielded  $5 \times 2n=40$ ,  $5 \times 2n=48$  and  $3 \times 2n=56$  plants (Lihová, Mártonfi & Mártonfióvá, 2000).

5xba. *Hypericum* × *desetangsii* nothosubsp. *carinthiacum* nothoforma *maculatiforme* (A. Fröhl.) N. Robson in Wisskirchen & Haeupler, *Standardliste Farn-u. Blütenpfl. Deutschl.*: 269 (1998). Type as for *H.* × *carinthiacum* forma *maculatiforme* A. Fröhl.

Map 15.

*H. quadrangulum* var. *erosum* Schinz in *Bull. Herb. Boissier* II, 3: 21, 22 (1902). Type: Switzerland, Zürich, Dreiländer Stein an der Hohe Rone, 31 July 1902 (fl), *Schinz* s.n. (Z)!-lectotype, selected here – see also Mártonfi et al., 1999: 340). Fröhlich (1911) raised Schinz's taxon to subspecific rank in *H. maculatum* and later (1913, 1915) reduced the combination to a synonym of *H. maculatum* subsp. *obtusiusculum* (Tourlet) Hayek. All the specimens cited by Schinz, however, have proved to be hybrids belonging to the above nothoforma.

*H. quadrangulum* subsp. *erosum* (Schinz) Schinz in *Vierteljahrsschr. Naturf. Ges. Zürich* 49: 240, 241 (1905). Type as for *H. quadrangulum* var. *erosum* Schinz.

*H. maculatum* Crantz × *perforatum* L. forma *sub-maculatum* in *Oesterr. Bot. Z.* 63: 14 (1913).

*H.* × *carinthiacum* forma *maculatiforme* A. Fröhl. in *Mitt. Naturwiss. Vereins Steiermark* 51: 229 (1915); Guşul. & Nyár. in *Sävul., Fl. R. P. Roman.* 4: 46 (1956). Type: Austria, Carinthia, Nordhänge der Golitza südlich Rosenbach, c. 800 m, 16 August 1911 (fl), *Fröhlich* GZU 16301 (GZU)!-lectotype, selected here).

*H. perforatum* subsp. *latifolium* var. *obscurum* O. Schwarz in *Drudea* 5: 61 (1965), nom. illegit. (Art. 37).

Stems with subsidiary lines almost complete though much less prominent than principal lines, i.e. 4-lined. Leaves ovate to ± broadly elliptic or elliptic-oblong, with tertiary reticulation dense, quite visible. Sepals ovate to lanceolate or linear-oblong, rounded or obtuse to finely apiculate or acute, entire or finely denticulate,

usually black-glandular-punctate.  $2n=24$  (Noack, 1939).

**SCOTLAND.** Moray: Boat-of-Garten, station yard, 4 August 1978 (fl), *McCallum Webster* 19460 (BM). Argyll: head of Loch Feochan, 11 July 1994 (fl), *B.H. Thompson* s.n. (BM); Kintyre, Skipness, 31 July 1899 (fl), *Somerville* s.n. (BM). Lanark: Bothwell Castle, 26 July 1987 (fl), *Dickson* s.n. (GL).

**NORWAY.** Hordaland: Hardanger, Strandebarm, 10 July 1940 (fl), *Lillefosse* s.n. (BM, K, O\*).

**FRANCE.** Loire: St. Miedard, July 1895 (fl), *Anthelme* s.n. (H). Hte-Savoie: near Chambéry, above St. Jean Arvey, c. 600 m, 18 July 1954 (fl), *De Wit* 5368 (WAG).

**GERMANY.** Hessen: Grossherz, Vilbeler Wald, 12 July 1973 (fl), *Dürer* s.n. (FR); Kr. Alsfeld, Schnellhausen, Hahnberg, 8 July 1950 (fl), *Hupke* s.n. (JE). Thüringen: Erfurt, Chaussee, July 1931, *Reinecke* s.n. (JE).

**SWITZERLAND.** Jura: La Dôle, 1864 (fl), *Favrat & Barbey* 77 pp. (K). Zug: Geissboden, c. 950 m, 19 July 1902 (fl), *Schinz* s.n. (Z). Schwyz: Aufsteig zum Rikliklosterli von Goldau aus, 8 September 1902 (fr), *Schinz & Brunies* s.n. (Z). Zürich: Limmatal bei Herdern-Altstetten, c. 400 m, 3 August 1925, *W. Koch* s.n. (H).

**AUSTRIA.** Steiermark: bei Strassgang bis Graz, n.d. (fl & fr), *Fröhlich* s.n. (BM, GZU); bei M.[aria] Trost, 10 August 1911 (fl), *Fröhlich* s.n. (BM, GZU). Niederösterreich: Berchtoldsdorf, July 1919 (fl), *Fens?* s.n. (K).

**ROMANIA.** Transylvania: in monte Transsilv., July, *Schur* s.n. (JE).

On the basis of specimens seen, nothoforma *maculatiforme* seems to be rarer than nothoforma *perforatiforme*.

5xbb. *Hypericum* × *desetangsii* nothosubsp. *carinthiacum* nothoforma *perforatiforme* (A. Fröhl.) N. Robson in Wisskirchen & Haeupler, *Standardliste Farn- u. Blütenpfl. Deutschl.*: 269 (1998).

Map 15.

*Hypericum perforatum* [var.] β *latifolium* Gaudin, *Fl. helv.* 4: 627 (1829); *W. Koch* in *Röhling, Deutschl. Fl.* 3rd ed. 5: 349 (1839), *Syn. fl. germ. helv.*, 2nd ed.: 146 (1843), *Syn. deut. schweiz. Fl.*



Map 15 5xb. *H.* × *desetangsii* nsubsp. *carinthiacum*. a. nforma *maculatiforme* ●; b. nforma *perforatiforme* ○. 5xc. nsubsp. *balcanicum* ▲.

- 2nd ed: 155 (1846), pro parte omnes quoad typum; Neilr., *Fl. Nieder-Oesterr.*: 826 (1859); Rouy in Rouy & Fouc., *Fl. France* 3: 333 (1896); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 528 (1925); Guşul. & Nyár. in Savul., *Fl. R. P. Roman.* 4: 29 (1956); Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* 4: 261 (1970); N. Robson in Cullen et al., *Eur. gard. fl.* 4: 60 (1995), in Wisskirchen & Haeupler, *Standardliste Farn-u. Blütenpfl. Deutschl.*: 270 (1998). Type: Switzerland, no precise locality, Gaudin s.n. (LAU-holotype). The specimens labelled var. or subsp. *latifolium* that I have seen all have partly developed subsidiary stem lines and otherwise also agree with Fröhlich's description of *H. carinthiacum* f. *perforatiforme* and specimens identified by him as such. Other than Koch himself, all the above authors cited this taxon as *H. perforatum* var. *latifolium* Koch; but Koch cited Gaudin, to whom this name should be credited. I have not seen Gaudin's type; but never having seen an undoubted *H. perforatum* with broad sepals, I assume that it belongs here.
- H. perforatum* var. *platycalyx* Čelak., *Prodr. fl. Böhmen*: 520 (1875). Type: Czech Rep., Středočeský, Jungbunzlau [Mladá Boleslav], Čelakovský (PR?). Čelakovský cited 'γ *latifolium* Koch' after his 'γ *platycalyx*'; the type must therefore be that of var. *latifolium* Koch, i.e. var. *latifolium* Gaudin (see above). Čelakovský's 'type' is not in PR (Dr B. Skočdoplová, in litt. 2001). The only Hippelli specimens from Jungbunzlau in that herbarium are of subsp. *veronense*, whilst the only one labelled 'var. *platycalyx*' (15 July 1910) by Čelakovský is subsp. *perforatum*.
- H. perforatum* [var.] β *latifolium* subvar. *lineolatum* Rouy in Rouy & Fouc., *Fl. France* 3: 333 (1896). Type as for '*H. lineolatum* Jord. pro parte'. Rouy 'split' Jordan's type of *H. lineolatum* between his subvar. *lineolatum* of var. *vulgare* and subvar. *lineolatum* of var. *latifolium*. As Jordan's specimen is the type of var. *vulgare*, the subvar. of var. *latifolium* becomes typeless.
- H. perforatum* subsp. *latifolium* (Gaudin) A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 525, f. 3a (1911), in *Mitt. Naturwiss. Vereins Steiermark* 51: 240 (1915); Hegi, *Ill. Fl. Mitt.-Eur.* 5(1): 528 (1925); Hayek, *Prodr. Fl. Pen. balc.* 1: 533 (1925); Stjep.-Vesel. in Josifovć, *Fl. Srbije* 3: 119 (1972).
- H. perforatum* subsp. *latifolium* forma *dentatum* A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 527, f. 3b, c (1911). Type: Austria, Steiermark, Plesch bei Gratwein, 5 September 1909 (fl & fr), *Fröhlich* GZU 16341 (GZU!-lectotype, selected here).
- H. perforatum* subsp. *latifolium* forma *fimbriatum* A. Fröhl. in *Sitzungsber. K. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 529, f. 4 (1911). Type: Austria, Steiermark, Mühlbachkogel bei Gratwein, c. 1000 m, 18 July 1909 (fl), *Fröhlich* GZU 16345 (GZU!-lectotype, selected here).
- H. maculatum* Crantz × *perforatum* L. forma *sub-perforatum* A. Fröhl. in *Oesterr. Bot. Z.* 63: 14 (1913).
- H. × carinthiacum* forma *perforatiforme* A. Fröhl. in *Mitt. Naturwiss. Vereins Steiermark* 51: 229 (1915); Guşul. & Nyár. in Savul., *Fl. R. P. Roman.* 4: 46 (1956). Type: Austria, Kärnten, Drauwiesen bei M.[aria] Elend, 16 July 1911 (fl), *Fröhlich* GZU 16300 (GZU!-lectotype, selected here).
- H. maculatum* subsp. *desetangsiiforme* A. Fröhl. in *Mitteil. Naturw. Ver. Steierm.* 51: 219 (1915); Hegi, *Ill. Fl. Mitteleuropa* 5(1): 518 (1925). Type: Austria, Steiermark, bei Graz, Jüdenndorf, July 1913 (fl), *Fröhlich* GZU 16155 (GZU!-lectotype, selected here).
- H. maculatum* subsp. *desetangsiiforme* var. *aporosum* A. Fröhl. in *Mitteil. Naturw. Ver. Steierm.* 51: 220 (1915). Type: Austria, Steiermark, bei Maria Trost, July 1913 (fl), *Fröhlich* GZU 16171 (GZU!-lectotype, selected here).
- H. × desetangsiiforme* nothomorph *perforatiforme* (A. Fröhl.) N. Robson in *Bull. Br. Mus. (Nat. Hist.), Bot.* 8: 168 (1981); Mártonfi, Repčák & Mihoková (1996b).
- H. carpaticum* Mártonfi in *Folia Geobot.* 36: 374 (2001). Type: Slovakia (E.), [Volovské vrchy Mts] village of Pracovce, path near dextral feeder of Hrelíkov potok brook, 27 July 1995 (fl), Mártonfi 2012 (BRA-holotype). Mártonfi (2001: 378) describes this pentaploid population as 'most likely of hybridogenous origin, with *H. perforatum* and *H. maculatum* [i.e. subsp. *maculatum*] as parents.' He claims, however, that it 'was stabilized and sufficiently reproductively isolated from its parents due to inherited apomixis' to allow it to be treated as a species. On the basis of his description and illustrations, however, it seems to be no more distinct from the rest of nothoforma *perforatiforme* than are parts of that taxon (e.g. 'subsp. *desetangsiiforme*'). It seems most appropriate, therefore, to include it in nothoforma *perforatiforme*.
- Stems with incomplete and scarcely prominent subsidiary lines or 2-lined. Leaves elliptic to rather narrowly oblong, with tertiary reticulation denser than in *H. perforatum* but obscure. Sepals elliptic to lanceolate and acute to finely acuminate or oblanceolate and apiculate, sometimes eroded-denticulate, usually black-glandular-striate to -punctate, those on main stems sometimes becoming markedly depressed ('*desetangsiiforme*'). 2n=40 (Noack, 1939, as *H. perforatum* × *quadrangulum*; Mártonfi et al., 1996a, b; Lihová, Mártonfi & Mártonfi, 2000 [also 2n=48, 56 experimentally]).
- SWEDEN.** Göteborg: Ringön, 23 July 1957 (l. fl), *Blom* s.n. (BM, GB\*).
- FINLAND.** Uusimaa: Nylandia, par. Kyrkslätt, Tero in pago Österby, 8 August 1907 (fl), *H. Lindberg* Pl. Fin. Exsicc. 806 (K).
- FRANCE.** Hautes Pyrénées: between Gèdre and Gavarnie, 900 m, 21 July 1922 (fl), *Hutchinson, Matthews & Riley* 14 (K).
- GERMANY.** Mecklenburg-Pommern: Dalwitz, 1864 (fl), *Kokeil* s.n. (K)
- CZECH REPUBLIC.** Bohemia, Jihočeský Kraj: \*in silvis Novosedlecký revír prope opp. Písek, August 1941, *M. Deyl* PR 164950 (PR). Moravia, Severomoravský Kraj: Hohenstadt [Zabreh], bei Unterheinzendorf, July 1933 (fl), *Hruby* s.n. (H).
- SLOVAKIA.** Košický Kraj: Prakovce, 3 August 1993 (fl), *Mártonfi* 1452 (BM); \*Žylinský Kraj: Kysuce, near Nová Bystrica, c. 600 m, 7 July 1959, *Futák* s.n. (SAV).
- AUSTRIA.** Steiermark: Mühlbachkogel, bei Gratwein, 25 July 1910 (fl), *Fröhlich* GZU 16338 (GZU). Kärnten: [Cult. ex] Karawanken, nördlich der Goliza, n.d. (fl), *Fröhlich* GZU 215 (GZU). Niederösterreich: in hort. bot. Vindobon., n.d. (fl), *Kerner* in Fl. Exs. Austro-Hung. 3649 (BM, K).
- SWITZERLAND.** ? : Pont d'Of, 16 July 1856 (fl), *Depierre* s.n. (BM).
- ITALY.** Bolzen [Bolzano]: Ritten, n.d. (fl), *Hausmann* s.n. (BM, IBF\*).
- HUNGARY.** \*Comit. Vas: 'Tótszgyörgy', 12 July 1882, *Borbás* BP 261470 (BP).
- ROMANIA.** Transylvania: Adamsdorf [Adamos], bei Bruñes, 15 June 1873 (fl), *Schur* 12138 (BM).
- BOSNIA.** Igman planina, am Veliko Palje, 14 June 1908 (fl), *Ualy* s.n. (K).
- Specimens apparently correctly identified as *H. perforatum* var. *latifolium* K. Koch are indistinguishable from those keying out to *H. × carinthiacum* var. *perforatiforme*; and the distribution of the *H. perforatum* variety does not exceed that of *H. maculatum* subsp. *maculatum*. I have therefore concluded that it, too, is a manifestation of this hybrid, not a form of *H. perforatum* itself. In addition, the voucher specimen for the count of 2n=40 by Mártonfi et al. (see p. 105) agrees with the description and authentic specimens of *H. maculatum* subsp. *desetangsiiforme* A. Fröhl., which I have therefore also included in the synonymy of nothoforma *perforatiforme*.
- 5xc. *Hypericum × desetangsiiforme* nothosubsp. *balcanicum* N. Robson, *nothosubsp. nov.* Type: Greece, E. Makedhonia, Nom. Serron,



Mt Vrondous, near the EOS ski centre, 1700–1800 m, 26 July 1981 (fl), *Farsakoglou, Franzén & Strid* 19521 (C!-holotype). Map 15.

*H. maculatum* Crantz subsp. *immaculatum* (Murb.) A. Fröhl. × *perforatum* L.

A nothosubsp. *carinthiacum* foliis sessilibus plerumque latioribus apice interdum acutis basin interdum cordatis, glandulis laminaribus petalorum pellucidis haud nigris, differt.

*Leaves* sessile; lamina broadly ovate to elliptic-oblong, apex rounded to acute, base cuneate to cordate-amplexicaul. *Petals* without black laminar glands.

**SERBIA. Kosovo:** Bertiscus, riv. Sušica prope Pré (Ipek) [Peč], c. 800 m, 12 July 1933 (fl), *Rechinger f. & Scheffer* 782 (BM).

**BULGARIA. Samokov:** Vakarel, c. 750 m, 16 July 1945, *Kitanov* 370 (JE). **Predbalkan:** Ostabhang des Midshur [Midžor], 4 September 1958 (fr), *Meyer* 1171 (JE). **Dobruja:** Süddobrudsha, Varna, Weg vom Strand zum Aladsha Monastir, 11 August 1958 (fl & e. fr), *Meyer* 414 (JE).

**GREECE. Makedhonia (E.):** Nom. Kavalas, Mt Pangaion, summit area, Tsekour Madra, 1550–1750 m, 26 July 1977 (fl & e. fr), *Papanicolaou* 411 (C).

These specimens are intermediate in form between *H. perforatum* and *H. maculatum* subsp. *immaculatum* and would therefore appear to be hybrids. Nevertheless, the Bulgarian specimens (with the possible exception of *Kitanov* 370, which I have not seen recently) and one of the Greek ones have apparently ripe or immature fruit, which, if they are triploids, would be unlikely. The type and the Kosovo specimen, however, are convincingly intermediate and would seem to be true hybrids.

5xx. **Hypericum × medium** Peterm., *Fl. lips. excurs.*: 563 (1838); Rchb., *Icon. fl. germ. helv.* 6: f. 5178 (1842–1844); Rouy in Rouy & Fouc., *Fl. France* 3: 337 (1896); N. Robson in Stace, *Hybridization and the flora of the Br. Isles*: 166 (1975). Syntypes: Germany, Leipzig, ad pagum Leutsch, July–August (fl), *Petermann* s.n. (LZ).

5. *H. perforatum* L. × 4. *H. tetrapterum* Fr.

*H. × sparsiflorum* Schur in *Verh. Naturf. Vereins Brünn* 15(2): 158 (1877). Type: Moravia, bei Bisterz auf der Mnischihora, im Punkwathale nächst Brünn, July–August 187-, *Schur* s.n. (BRNU? or LW?).

*H. perforato-acutum* sec. O. Kuntze & Focke *vide* Rouy & Foucaud, *Fl. France* 3: 337 (1896).

*H. acutum* × *perforatum*; A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 592 (1911).

*H. × dubioides* Druce in *Bot. Soc. Exch. Cl. Br. Isles* 8(5): 868 (1929), nomen. Only the formula *H. perforatum* × *quadrangulum* was cited.

Icon: Rchb., *Icon. fl. germ. helv.* 6: f. 5178 (1842–1844).

Intermediate between the parents *Stems* without or with partial subsidiary lines. *Leaves* oblong to elliptic-lanceolate with dense to lax, rather obscure reticulate venation; pale laminar glands relatively few, varying in size. *Sepals* oblong to lanceolate, acuminate, without black glands. *Petals* without or with linear to striiform black laminar glands. *Capsule* with shortened lateral vittae.

This hybrid is rare, on account of the differing habitats of its parents, but could occur anywhere where their distributions overlap. Fröhlich (1911: 593) cites three German localities, but I have seen only the two French specimens, the third (Romanian) one having been determined by Dr Mártonfi.

**FRANCE. Jura:** Beauvoisin près Chaussin, 6 July 1853 (fl), *Michalet* s.n. (K); Chaussin, September 1873 (fr), *Michalet* s.n. (CLF).

**GERMANY. Leipzig.** See type.

**CZECH REP. Moravia.** See type of *H. × sparsiflorum* Schur.

**ROMANIA. Transylvania:** \*Comit. Hunyad., Pareng mts, in Bordi, 21 June 1906, *Jávorka* BP 11535 (BP).

5xxx. (**Hypericum perforatum** L. × **H. maculatum** Crantz) × **H. tetrapterum** Fr.

5x. *H. × desetangsii* Lamotte × 3. *H. tetrapterum* Fr.

(*H. maculatum* Crantz × *H. perforatum* L.) × *H. acutum* Moench sensu A. Fröhl. in *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* 120(1): 591, f. 13 (1911).

Approaching *H. tetrapterum* in habit. *Stems* with wider subsidiary lines than *H. perforatum* × *maculatum*. *Leaves* broadly ovate, almost semi-amplexicaul, with laxer reticulation venation and quite densely and finely pale-gland-dotted. *Inflorescence* more compactly flowered. *Flowers* smaller than in the hybrid parent, c. 20 mm in diam. *Sepals* relatively broadly ovate, acuminate; laminar glands all or mostly pale, striiform to punctiform. *Petals* darker yellow than in *H. tetrapterum*, like those of the hybrid parent, with pale glands only. *Stamens* c. 2/3 × petals. *Ovary* broadly ovate (no fruit seen).

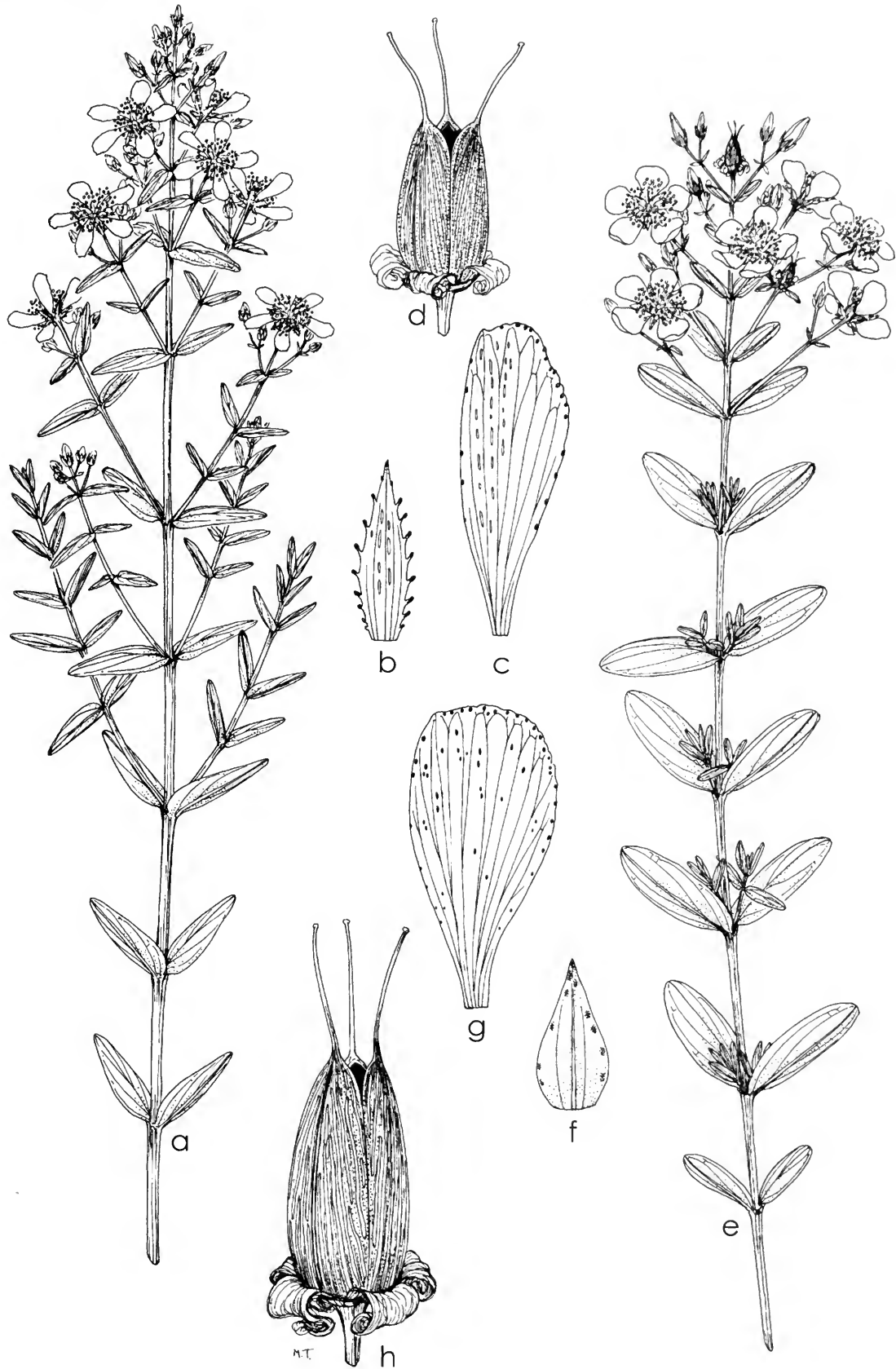
Switzerland (Schwyz, St. Gallen).

**SWITZERLAND. Schwyz:** Roblosen, near Einsiedeln, 900 m. *Thellung* s.n. (Z\*). **St. Gallen:** Fürstenland, in den Senke östlich von Gründenwald bei Winkeln, 640 m, 2 August 1946 (fl), *Koch* 46/421 1 (H).

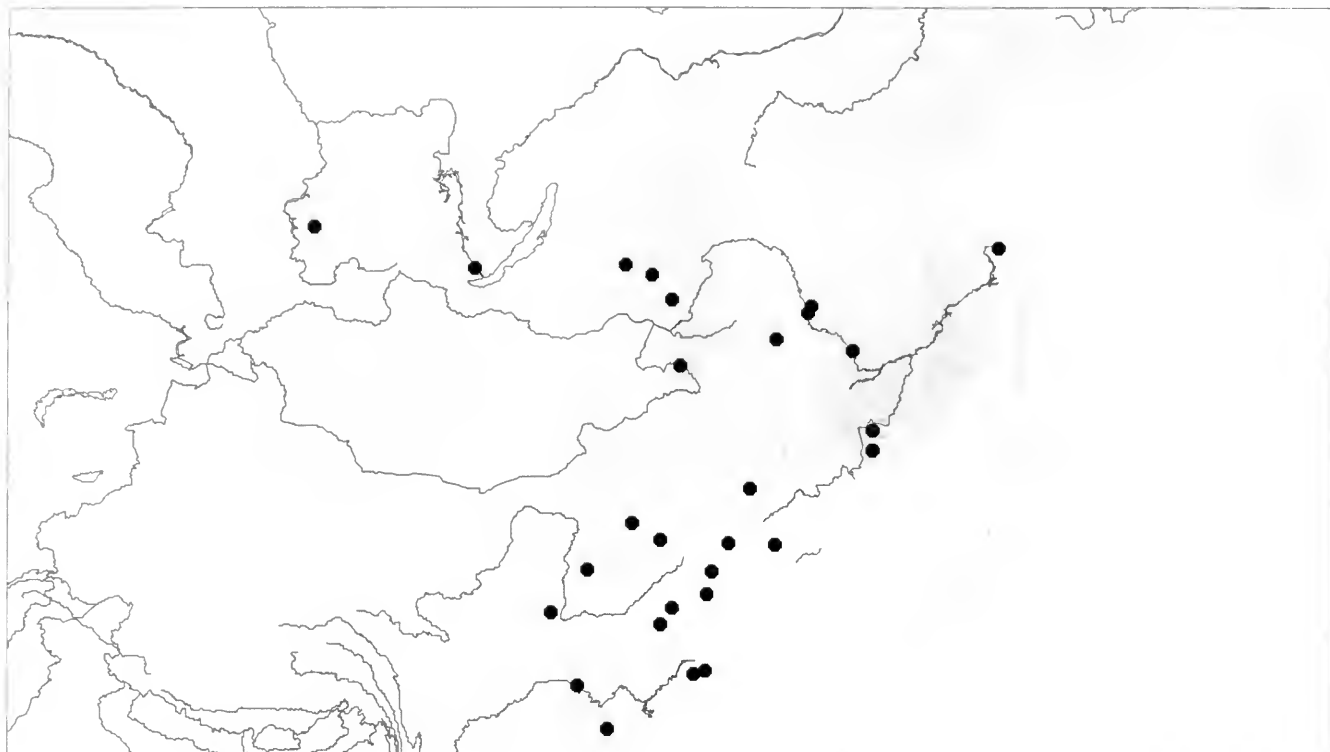
Like *H. × medium*, this hybrid has parents with widely differing habitat requirements and must therefore be rare. The above data have been extracted mainly from Fröhlich's account (1911: 591).

*Hypericum assurgens* Peterm., *Anal. Pflanzenschl. bot. Excurs. Leipzig*: 67 (1846), which Petermann himself published as a synonym of his *H. perforatum* var. *petiolatum* (described on the same page), was claimed by Otto Kuntze (*Flora* 63: 293, 1880) to be the unlikely hybrid *H. humifusum* × *perforatum*. On the basis of the Petermann specimen named *H. assurgens* in W!, I regard this plant as a rather long-petioled form of *H. perforatum* subsp. *perforatum* (see p. 89).

6. **Hypericum attenuatum** Fisch. ex Choisy, *Prodr. monogr. Hypéric.*: 47, t. 6 (1821), in DC., *Prodr.* 1: 548 (1824); Turcz., *Fl. Baical.-Dahur.* 1: 251 (1842); Ledeb., *Fl. ross.* 1: 448 (1842); Maxim., *Primit. fl. amur.*: 65 (1859), in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* 27: 433 (1882), *Mél. Biol. Bull. Acad. Imp. Sci. Saint-Pétersbourg* 11: 166 (1882); Regel, *Tent. fl. ussuri*: 33 (1861); Hance in *J. Bot.* 12: 259 (1874), op. cit. 16: 104 (1878); Franchet, *Pl. david.* 1: 56 (1884); Forbes & Hemsley in *J. Linn. Soc. Bot.* 23: 72 (1886); Diels in *Bot. Jahrb. Syst.* 29: 476 (1901); Freyn in *Oesterr. Bot. Z.* 52: 17 (1902); Komarov, *Fl. Manshur.* 3: 43 (1905); H. Léveillé in *Bull. Soc. Bot. France* 54: 594 (1908); Nakai, *Fl. kor.* 1: 95 (1909), 2: 453 (1911); Komarov & Klob.-Alis., *Opred r. Dal'nevost. kr.* 2: 747, t. 232 f. 2 (1932); Kitagawa, *Lineament. Fl. Mandshur.*: 317 (1939); Gorschkova in Shishkin & Bobrov, *Fl. URSS* 15: 236 (1949); Komarov, *Fl. Manchzh.* 5: 48 (1950); Y. Kimura in Nakai & Honda, *Nova fl. jap.* 10: 213 (1951), in *J. jap. Bot.* 34: 323 (1959); Kitamura & Murati in *Acta Phytotax. Geobot.* 20: 197 (1962); Noda, *Fl. N. E. Prov. (Manch.) China*: 794 (1971); Anon., *Iconogr. Cormoph. Sinicae* 2: 875, f. 3480 (1972); Wu C.-J. in *Fl. Intramangol.* 4: 91, t. 42 ff. 1–3 (1979); Lee, T. B. *Ill. Fl. Korea*: 545 cum f. (1989);



**Fig. 10** A. *H. elegans*: (a) habit; (b) sepal; (c) petal; (d) capsule. B. *H. attenuatum*: (e) habit; (f) sepal; (g) petal; (h) capsule (a, e  $\times 2/3$ ; c, g, h  $\times 4$ ; rest  $\times 8$ ). A. (a-c) Bločky s.n.; (d) Lauert s.n. B. (e) Kang 57; (f, g) Campbell s.n.; (h) Kang 68.



Map 16 6. *H. attenuatum* ●.

Li Xiwen in *Fl. R. P. Sinicae* 50(2): 69, t. 15 ff. 5–8 (1990); N. Robson in Cullen et al., *Eur. gard. fl.* 4: 60 (1995); non *H. attenuatum* Link (1822) (= *H. canariense* L.). Type: Russia, Irkutsk, Dauria prope Macarova in valle granitica et alibi, n.d. (fl), Fischer s.n. (G-DC-holotype, microfiche!; P!-isotype).

Fig. 10, Map 16.

*H. perforatum* var. *confertiflorum* Debeaux in *Actes Soc. Linn. Bordeaux* 31: 130 (1876), *Florule du Tché-foû*: 35 (1877) ['*confertiflora*']; Maxim. in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* 27: 432 (1882), *Mél. Biol. Bull. Acad. Imp. Sci. Saint-Pétersbourg* 11: 166 (1882). Type: China, Shandong, Tchéfou [Chefoo=Yantai], 12 July 1860 (fl & e. fr), Debeaux Exp. de Chine 60. (P!-lectotype, selected here). Although this name was adopted by me as the provisional basionym of the Chinese subspecies of *H. perforatum*, and I determined some specimens of it as *H. perforatum* subsp. *confertiflorum*, a syntype borrowed from P clearly belongs to *H. attenuatum*, a species for which the epithet *confertiflorum* is appropriate.

?*H. kamtschaticum* var. *senanense* sensu Y.N. Lee, *Fl. kor.* 3rd ed.: 232, f. 685 (1998).

Icones: Wu C.-J. in *Fl. Intramongolica* 4: 92, t. 42 ff. 1–3 (1979); Li Xiwen in *Fl. R. P. Sinicae* 50(2): 68, t. 15 ff. 5–8 (1990).

Perennial herb 0.1–0.45(–0.7) m tall, erect from rootstock or creeping rhizomatous base, with stems numerous to few, caespitose, much branched. Stems 2-lined, with black punctiform and striiform glands on lines and often sparsely (reddish or black) elsewhere; internodes (10–)15–40 mm, usually exceeding leaves. Leaves sessile; lamina (8–)15–31(–38) × (3–)5–12(–15) mm, elliptic or elliptic-oblong to oblanceolate or rarely ovate, paler beneath, chartaceous; apex obtuse to rounded, margin entire, plane, base subcordate to cuneate; venation: 2 pairs of main

laterals from lower sixth of midrib, tertiary reticulation dense but often rather obscure and apparently lax; laminar glands punctiform, small, pale and black, few or scattered, mainly distal; intramarginal glands black, spaced. Inflorescence many- to few- (rarely 1-) flowered from 1–4 nodes, sometimes with flowering branches from up to 4 nodes below, the whole cylindrical to pyramidal; pedicels (1.5–)3–4 mm; bracts and bracteoles 3.5–6.5 mm long, oblong-elliptic, entire. Flowers 13–20(–25) mm in diam., stellate; buds ovoid, subacute to acute. Sepals 5, unequal to subequal, (3.5–)5–10 × 1–4 mm, erect in bud and fruit, triangular-ovate to lanceolate, acute to subacuminate, entire; veins 5–7, distally branched; laminar glands pale, striiform to punctiform and black, punctiform, scattered, rather sparse or rarely absent; intramarginal and marginal glands black, punctiform, sparse, distal. Petals 5, golden? yellow, tinged red in bud, 8–12 × 4–7 mm, 2.4–3 × sepals, oblong-obovate, asymmetric, entire, laminar glands black, punctiform to striiform, scattered, marginal glands black, distally dense. Stamens c. 90, '3'-fascicled, longest 8–10 mm, c. 0.7–0.8 × petals; anther gland black. Ovary 3-locular, 2.5–3.5 × 2–3 mm, narrowly ovoid; styles 3, free, 4–4.5 mm, 1.3–1.6 × ovary, widely spreading; stigmas narrowly capitate. Capsule (4–)6–10 × 2–6 mm, 2–3 × sepals, broadly ovoid or oblong-ovoid to narrowly conic; valves densely longitudinally vittate, occasionally with a few black longitudinal glandular streaks. Seeds dark? brown, c. 0.7 mm, cylindrical, slightly carinate and apiculate, not appendiculate; testa finely linear-foveolate. 2n=16 (Probatova & Sokolovskaya, 1986).

Fields, pastures, steppes, grassy and dry stony slopes, pebble shores, forest margins and clearings; China: s.l. (Liaoning)–2000 m (Guizhou); Russia.

Russia (E. Siberia: Angara-Sayan, Dauria, Lena-Kolyma; Far East:

Zeya-Bureya, Uda, Ussuri, Sakhalin<sup>96</sup>), Mongolia, China (Nei Mongol, Heilongjiang and Jilin south to Guizhou, N. Guangxi and Guangdong), Korea.

**RUSSIA. Angara-Sayan:** Inter Irkutsk et Jenisseisk, ad fl. Angara (Tunguska super.) pro pagum Padun, 1867 (fl), *Czekanowski* s.n. (BM); Prov. Irkutsk, distr. Balagansk, prope Bashejewskoje, 11 July 1904 (fl), *Malzew* 1919 (BD, H). **Dauria:** Chita distr., Priiskovaya stn, valley of R. Nercha, NE slope of Mt Krasnyy mys, 28 June 1952 (fl), *Sergievskaya & Obolentsev* s.n. (H); Nertschinsk, 1899 (fl), *Karo* 143 (BD, BM, H, JE, K). **Lena-Kolyma:** see type. **Zeya-Bureya:** Zejskaja Pristan am Zeaflusse, July 1899 (fl), *Karo* 359 (BM, H, JE, K); Blagowjestschensk in Amurgebeite, 1898 (fl), *Karo* 224 (BM, JE). **Uda:** present (*fide* Gorschkova, 1949: 237). **Ussuri:** Prov. Amurensis, fluvium Amur circa stationem Radde, 25 June 1895 (fl), *Komarov* Fl. Man. 1092 (BM, K). **Sakhalin?** (see footnote 6).

**MONGOLIA.** Khalka Gol, 26 July 1902 (fl & e. fr), *Campbell* s.n. (BM); Ourato, Oulachan occid., August 1882? (fl), *David* 1944 (K).

**CHINA. Nei Mongol:** Solon Qi, Honggolj, 17 August 1956 (fr), *Liou T.N.* et al. 8250 (NAS, PE); Ergun Qi, 720–850 m, 9 July 1951 (fl & fr), *Wang Z.* et al. 1197 (PE). **Heilongjiang:** Ning'an Xian, Jingpo Hu, 20 July 1975 (fl), *Fu P.Y.* et al. 3327A (IFP); Yilan Xian, Weiken R., 7 August 1959 (fl), *Chang, Yu Liang* et al. 1971 (IBSC). **Jilin:** Jilin Shi, Longtan Shan, 8 September 1956 (fr), *Chang Y.L.* et al. 911 (KUN, PE); Jiutai Xian, Tumenling Village, 300 m, 28 August 1950 (fr), *Fu P.Y.* et al. 2027 (IBSC, PE); Mukden to Kirin, Tangho-ko, Sungari R. to Hui-fa R., 1886 (fl), *James* s.n. (K). **Liaoning:** Chikuanshan, Tiehling, 250 m, 18 July 1930 (fl), *Kung H.W.* 648 (PE); near Mukden, Lao-yeh Ling and other hills, May–August 1886 (fl), *James* s.n. (K). **Hebei:** Neiqiu Xian, Xiaolingdi Village, 1600–1700 m, 21 July 1950 (fl & fr), *Liu Y.* 13150 (NAS); Hsiao-wutai Shan, 1500 m, 29 August 1913 (fr), *Meyer* 1376 (GH, K). **Shanxi:** Wutai Xian, Gengzhen Xiang, 2000 m, 19 July 1959 (fl & fr), *Kuan & Chen* 2433 (PE); Xiangning Xian, Guanwang Temple, 17 July 1960 (fl), *Liu X.Y.* 20863 (HNWP); Wenshui, S. of Hechiata, 14 August 1925 (fl), *Keng* 68 (BMP, GH). **Shaanxi:** Schansi, 1500 m, 18 August 1935 (fl), *Licent* 12519 (GH); Shang Xian, 1060 m, 6 August 1952 (fl & fr), *Wang T.P.* 16043 (PE); Mt Lao-y-san, Sciuz-scien, June 1897 (fr), *Fr Hugh* s.n. (BM). **Gansu:** *fide* Li Xiwen (1990). **Shandong:** Fei Xian, Meng Shan, 350 m, 12 July 1936 (fl & fr), *Cheo & Yen* 38 (GH); *ibid.*, 20 July 1936 (fl & fr), *Cheo & Yen* 122 (BM); Wulian Xian, Wulian Shan, 20 July 1959 (fr), *Cheo T.Y.* et al. 5128 (NAS). **Henan:** Lushi Xian, Laochun Shan, 555 m, 4 August 1935 (fl), *Liou K.M.* 4892 (PE); Xinyang Xian, Youhe Gongshe, 500 m, 18 July 1965 (fl), *Chen & Ming* 14 (PE). **Jiangsu:** Wuxi, Hui Shan, 11 July 1956 (fl), *Ting & Wang* 925 (NAS); Zhenze, Dong Shan, Huachuan Ling, 29 July 1958 (fr), *Wu W.X.* 3782 (IBSC). **Anhui:** Wuhu, 20 June 1941 (fl), *Migo* s.n. (NAS); Chu Xian, Langyashan, 2 August 1951 (fr), *Huadong Working Sm* 3148 (PE). **Zhejiang:** Jinhua Xian, 24 July 1927 (fl), *Keng Y.L.* 873 (NAS, PE). **Fujian:** Wuyi Shan, peak of Huanggang Shan, 2130 m, 20 July 1980 (fl), *Wuyishan Exped.* 80-0147 (IBSC). **Jiangxi:** Suichuan Xian, 1100 m, 22 September 1963 (fr), *Yue J.S.* et al. 4159 (IBSC); Julian Shan, n.d. (fl & fr), *Julianshan Forestry Farm* 781088 (IBSC). **Guangdong, Guangxi:** *fide* Li Xiwen (1990). **Hunan:** Sangzhi Xian, Bamaoxi Gongshe, 1500 m, 3 July 1975 (fl), *Li & Shao* 750126 (IBSC); Fenghuang Xian, Liantouyang Xiang, 600 m, 17 September 1988 (fl & fr), *Wuling Exped.* 1209 (IBSC). **Hubei:** Ichang and immediate neighbourhood, 1885–1888 (fr), *Henry* 4157 (BM, GH, K); Wuchang, Luojishan, July 1932 (fr), *Chung H.H.* 9078 (A). **Sichuan:** Sintsin Hsien [Xinjin Xian], 600 m, 23 July 1938 (fr), *Wang T.P.* 8309 (PE). **Guizhou:** Hsing Shan, 2000 m, 11 October 1931 (fr), *Steward* et al. 536 (PE).

**KOREA (N).** Namp'o-Si: in herbidis Chinnampo [Namp'o], August 1906 (e. fr), *Faurie* 618 (BM).

*Hypericum attenuatum*, is most closely related to 1. *H. maculatum* and 11. *H. scouleri* (respectively from western Eurasia and western North America), differing from both *inter alia* by the constantly 2-lined stem, from *H. maculatum* by the acute sepals, and from *H. scouleri* by the gland-dotted petals. It would seem to be one diploid parent (with *H. maculatum* subsp. *maculatum*) of the amphidiploid *H. perforatum*.

Kitamura & Murati (1962) sank the Japanese *H. tosaense* Makino (1903), with its f. *insulare* Y. Kimura (1951) and var. *atumense* (Y. Kimura) Y. Kimura (1959), and *H. momoseanum* Makino (1931) into *H. attenuatum*, but these taxa appear to be distinct from that species (see key, p. 67). See also Y. Kimura (1959), who included them all in an '*H. attenuatum* Superspecies'.

7. **Hypericum elegans** Stephan ex Willd., *Sp. Pl.* 3: 1469 (1802); M. Bieb., *Fl. taur.-caucas.* 2: 230 (1808), 3: 519 (1819); Poiret, *Encycl. Suppl.* 3: 701 (1814); Choisy, *Prodr. monogr. Hypéric.*: 55 (1821) 'non Steph.' (which is said to = *perforatum*), in DC., *Prodr.* 1: 551 (1824); Ledeb., *Fl. altaic.* 3: 368 (1831), *Fl. ross.* 1: 450 (1842); Spach, *Hist. nat. vég.*, Phan. 5: 389 (1836), in *Ann. Sci. Nat. Bot.* 5: 357 (1836); Boissier, *Fl. orient.* 1: 805 (1867); Kerner in *Oesterr. Bot. Z.* 24: 165 (1874); Krylov, *Fl. Altaya* 1: 190 (1901); Woronow in Kuzn., Busch & Fomin, *Fl. Cauc. Crit.* 3, No. 9: 45 (1906); Hayek, *Prodr. Fl. Pen. Balc.* 1: 537 (1925); Stefanoff in *God. Agr.-les. Fak. Univ. Sofia* 10: t. 4 f. 24 (1932), 11: 175 (1933), 12: 87 (1934), in *Pflanzenareale* 4: karte 7 (1933); Krylov, *Fl. Zap. Sib.* 8: 1907 (1935); Fedtchenko & Shishkin, *Fl. Yugo-Vost. Evrop. časti SSSR* 5: 711 (1938); Stoyanov & Stefanov, *Fl. bulg.*: 774 (1948); Gorschkova in Shishkin & Bobrov, *Fl. URSS* 15: 243 (1949); E. Wulf, *Fl. Kryma* 2(3): 109 (1953); Karnaukh in Klokov & Visjulina, *Fl. URSR* 7: 307 (1955); Kornás in Szafera & PawBowski, *Fl. Polska* 7: 28 (1955); Rzazade in Karjagin et al. (Eds), *Fl. Azerbaidžana* 6: 257 (1955); Goşul. & Nyár. in Sävul., *Fl. R. P. Romana* 4: 33, t. 3 f. 1 (1956); Janchen in Höfler & Knoll, *Cat. Fl. Austr.* 1: 257 (1957); Zelený in *Sborník Klubu Přírod. v Brně* 32: 69 (1960); Grossg., *Fl. Kavk.*, 2nd ed. 6: 175, karta 191 (1962); Vasyléva in Pavlov, *Fl. Kazakhstana* 6: 163 (1963); Robson in Davis, *Fl. Turkey* 2: 401, f. 12.25 (1967), in Tutin et al. (Eds), *Fl. Europaea* 2: 269 (1968), in Huxley & Griffiths (Eds), *R.H.S. Dict. Gardng* 2: 629 (1992), in Cullen et al. (Eds), *Eur. Gard. Fl.* 4: 60 (1995); Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* 4: 261, t. 49 f. 1 (1970); Stjep.-Veseli. in Josifović, *Fl. Srbje* 3: 119, t. 23 ff. 5, 5a (1972); Hegi, *Ill. Fl. Mitt.-Eur.*, 2nd ed. 5(1): 522, ff. 1998 (map), 2007 (1975); Meusel, *Vergl. Chor. Zentraleurop. Fl.* 2: 288, Karte 285c (1978); Zelený, Jasičová & Zahradníková in Futák & Bertová, *Fl. Slovenska* 3: 311, t. 38 f. 2, map 57 (1982); Hagemann in *Flora* 173: 109, tt. 9–11, 39 (1983); Dostál, *Nová Květena ČSSR* 1: 584 (1989). Type: Russia, 'Habitat in Sibiria', n.d. (fl), *Stephan* in Herb. Willd. 14473 (B-WILLD-holotype, micro!).

Fig. 10, Map 17.

*H. kohlianum* Spreng., *Fl. hal. tent. nov.*: 214, t. 9 (1806); Baumg., *Enum. stirp. Transsilv.* 2: 392 (1816); Schur, *Enum. pl. Transsilv.*: 132 (1866). Type: Germany, Halle, 'in vineis ad Bennstadt rarius', July (fl), *Sprengel* s.n. (JE!-holotype).

*H. pulchrum* Pallas ex M. Bieb., *Fl. taur.-cauc.* 2: 230 (1808), in synon.

*H. hyssopifolium* [var.]  $\gamma$  sensu Choisy, *Prodr. monogr. Hypéric.*: 56 (1821). Choisy cited 'Bieb. cauc. 2. p. 231'. 'Type' as for var. *pauciglandulosum* Choisy (1824).

*H. hyssopifolium* var. *pauciglandulosum* Choisy in DC., *Prodr.* 1: 552 (1824). Type: Ukraine?, Tanais [R. Don], 1819, *Goldbach* s.n. (G-DC!-holotype).

*H. elegans* var. *pectinatum* Čelak. in *Oesterr. Bot. Z.* 24: 140 (1874). Type: Russia, Ciscaucasus, 'in pratis ad rivum Kuma prope pagum Maslow, July 1843 (fl), *Hohenacker* s.n. (W-holotype; K!-isotype).

<sup>96</sup>Maximowicz (1882) attributed *H. attenuatum* sensu F. Schmidt, Fl. Sachal. no. 87, to *H. erectum*, but Gorschkova (1949) included Sakhalin in the distribution of *H. attenuatum*. Vorobiev et al. (1974) did not include this species in their key to vascular plants of Sakhalin and the Kurile Islands. Maximowicz would seem to have been correct.

*H. elegans* var. *stepposum* Sävil. & Rayss, *Mat. fl. Basarab.* 3: 175 (1934); Guşul. & Nyár. in Sävil., *Fl. R. P. Roman.* 4: 34, t. 5 f.1 (1956); Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* 4: 262 (1970). Type: Romania, Reg. Constanţa, intra Valea Nucaliler şi Mahmudia (r. Tulcea), *Sävulescu* ? s.n. (BUCA).

*H. elegans* var. *genuinum* Guşul. in Sävil., *Fl. R. P. Roman.* 4: 34 (roman.), 385 (latin) (1956). Type as for *H. elegans* Stephan ex Willd.

*H. elegans* var. *elegans* Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* 4: 262 (1970).

*H. elegans* var. *pedunculatum* Jordanov & Kož. in Jordanov, *Fl. R. P. Bulg.* 4: 262, 709 (1970) ('pedunculata') in clav., nom. invalid. sine descr. lat. (Art. 36).

Icones: Rchb., *Iconogr. bot. pl. crit.* 3: 68, t. 280 f. 443 (1825); *Icon. fl. germ. helv.* 6: t. 350 (1842–1844); Fedchenko & Shishkin, *Fl. Yugo-Vost. Evrop. časti SSSR* 3: 712, f. 487 (1938).

Perennial herb 0.18–0.45(0.55) m tall, erect or occasionally shortly ascending and rooting from rootstock, with stems solitary or few, usually branched at most nodes. Stems incompletely 2-lined (nodes terete near base), with ± dense black punctiform glands on or near lines and occasionally elsewhere; internodes 8–40 mm, shorter than to usually exceeding leaves. Leaves sessile; lamina 15–25(–33) × 3–9(–12) mm, oblong-lanceolate or ovate-lanceolate to triangular-lanceolate, paler beneath, chartaceous; apex subobtuse, margin entire, revolute, base subcordate, subplexicaul; venation: 3 pairs of main laterals from near base of midrib, tertiary reticulation obscure; laminar glands all pale, dense, or with a few black, scattered, punctiform; intramarginal glands black, rather dense. Inflorescence (1–)5–c. 65-flowered, from 1–4 nodes, with flowering branches from up to 5 nodes below, the whole corymbiform to ± narrowly pyramidal or narrowly cylindrical; pedicels 1–2 mm; bracts and bracteoles 3.5–5 mm long, lanceolate, sparsely black-glandular-denticulate. Flowers (15–)20–25 mm in diam., stellate; buds narrowly ovoid, (sub)acute. Sepals 5, free, 4–6 × 1–2 mm, erect in bud and fruit, lanceolate to ovate-lanceolate, acute, with ± irregular prominent glands to long-glandular-ciliate; veins 3(5), unbranched; laminar glands pale, linear to distally punctiform; marginal glands black, ± elongate, sessile or on cilia. Petals golden? yellow, not tinged red in bud, (8–)10–12 × (3–)5–6 mm, 2.4–4 × sepals, oblong-obovate, asymmetric, entire to subentire, laminar glands pale, ± punctiform, distal, marginal glands black, immersed or rarely ± prominent, distally dense. Stamens 40–50, '3'-fascicled, longest 7–10 mm, 0.8–0.9 × petals; anther gland black. Ovary 3-locular, 2–2.5(–3) × 1–1.5 mm, cylindrical-ovoid; styles 3, free, 4–6 mm, 1.7–3 × ovary, widely spreading; stigmas narrowly capitate. Capsule (6)–7–8 × 4–5 mm, c. 1.5–2 × sepals, cylindrical-ovoid to conic; valves rather densely longitudinally and obliquely vittate. Seeds yellowish-brown, 0.8–1 mm, cylindrical, not carinate; testa finely linear-foveolate. 2n=32 (n=16, Chattaway, 1926).

Well-drained habitats: meadows, stony and scrub steppes and stony slopes on chalk and limestone, *Betula* and *Pinus-Betula* woods on sand, shores of rivers and lakes; 0–500 m.

Russia (E. Siberia: Angara-Sayan; W. Siberia: Ob (S.), Upper Tobolsk, Irtysh, Altai; European Russia: Volga-Kama, Transvolga, Lower Don, Ciscaucasia, Daghestan, Volga-Don, Upper Volga), Ukraine (Upper Dnieper [near Kremenets], Middle Dnieper, Upper Dniester, Black Sea, Crimea) [apparently absent from Transcaucasia, despite area records in Gorschkova (1949)]; Germany (Saxony, Rhineland), Czech Republic, Slovakia, Poland, Hungary, Romania, Moldova, Serbia, Bulgaria, Turkey (European) (?)

**RUSSIA.** Angara-Sayan, Ob, Upper Tobolsk, Irtysh: all *fide*

Gorschkova (1949). Altai: Chemal distr., Gora Biryutka, 29 June 1927 (fl), *Shishkin* s.n. (H). Volga-Kama, Transvolga: both *fide* Gorschkova (1949). Lower Don: Novotscherkassk, 9 June 1911 (fl), *Jakushev* s.n. (BM, FR). Ciscaucasia: ad rivum Kuma prope pagum Maslow, July 1843 (fl), *Hohenacker* s.n. (BM, K); am Terek bei Galjugajer, August (fl & fr), *Herb. Steven* s.n. (H). Daghestan: *fide* Grossgeim (1962: map 191). Volga-Don: Prov. Kursk, prope urbem Koroczka, 1 July 1900 (fl), *Schirjewsky* 1604 (H). Upper Volga: *fide* Gorschkova (1949).

**UKRAINE.** Upper Dnieper: *fide* Gorschkova (1949). Middle Dnieper: Poltava, n.d. (fl), *Rogouris* s.n. (H). Upper Dniester: Probabin prope Horodenka [Gorodenka], n.d. (fl), *Bločky* s.n. (BM). Black Sea: Crimea, Simferopol, prope pagum Massanka, 5 July 1900 (fl), *Callier* 901 (JE, K); Tarkhankutskiy peninsula, balka Onsina near Otlesh, 4 June 1935 (fr), *Dzens-Litovskaya* s.n. (LE).

**AZERBAIJAN?** E. Transcaucasia, *fide* Gorschkova (1949), but not Grossgeim (1962: map 191).

**GEORGIA?** W. Transcaucasia, *fide* Gorschkova (1949), but not Grossgeim (1962: map 191).

**GERMANY.** Upper Saxony: Erfurt, Schwellenburg, 23 July 1852 (fl), *Launert* s.n. (BM); Erfurt, Mühlhausen, Weinberg, 1951, *Meyer* s.n. (JE); Halle, Sachsenburg, 1906 (fl), *Kappel* s.n. (BM); Halle, Rossleben, Bottendorf, 1931, *Rothmaler* s.n. (JE). Rheinhessen-Pfalz: Alzeyer Hügelland, Wissberg bei Spredlingen, W-Seite des Gipfelplateaus, 260 m, 9 July 1978 (fl), *Kalheber* 78-477 (H).

**CZECH REPUBLIC.** Moravia: Jímoravský Kraj, Hodonin distr., inter pagos Čejč et Čejkovice, c. 220 m, 13 July 1971 (l. fl & fr), *Vicherek* 1539 (H); Severomoravský Kraj, Vyškov, prope Větrmky, June 1936 (fl), *Weber* s.n. (H).

**SLOVAKIA.** Two records – see Zelený et al. (1982: map 57).

**POLAND.** Wałbrzych: Dolny Ślaska, 35–40 km W. of Nysa (*fide* Kornaś, 1955: 28).

**HUNGARY.** Pest: Comit. Pest, in monte Csiki-hagy prope Török-Bábut, 3 June 1926 (fl), *Degen* s.n. (BM).

**ROMANIA.** Transylvania [Alba]: Langenthal [Valea Lungă], 18 June 1871 (fl), *Barth* 515 (BD, BM, H, JE); distr. Alba, inter pagos Ciumbud et Băgău, c. 300–350 m, 14 June 1930 (fl), *Nyárády* s.n. (H). Moldavia: distr. Iaşi, in foenatis montis 'Ciocăllău' prope pagum Rediu-Tatar, c. 150 m, 21 June 1938 (fl), *Răvărut* in *Fl. Rom. Exsicc.* 2003a (BD). Wallachia: Dobrogea, Radu-Negru [by wellau Constanţa o Burarqu], 11 July 1931 (fl), *Häyrén* s.n. (H).

**MOLDOVA.** Bessarabia: a Aktherman en Bessarabie, 1822, *Tardent* s.n. (G-DC).

**SERBIA.** Vojvodina: *fide* Stjep.-Vesel. (1972: 120).

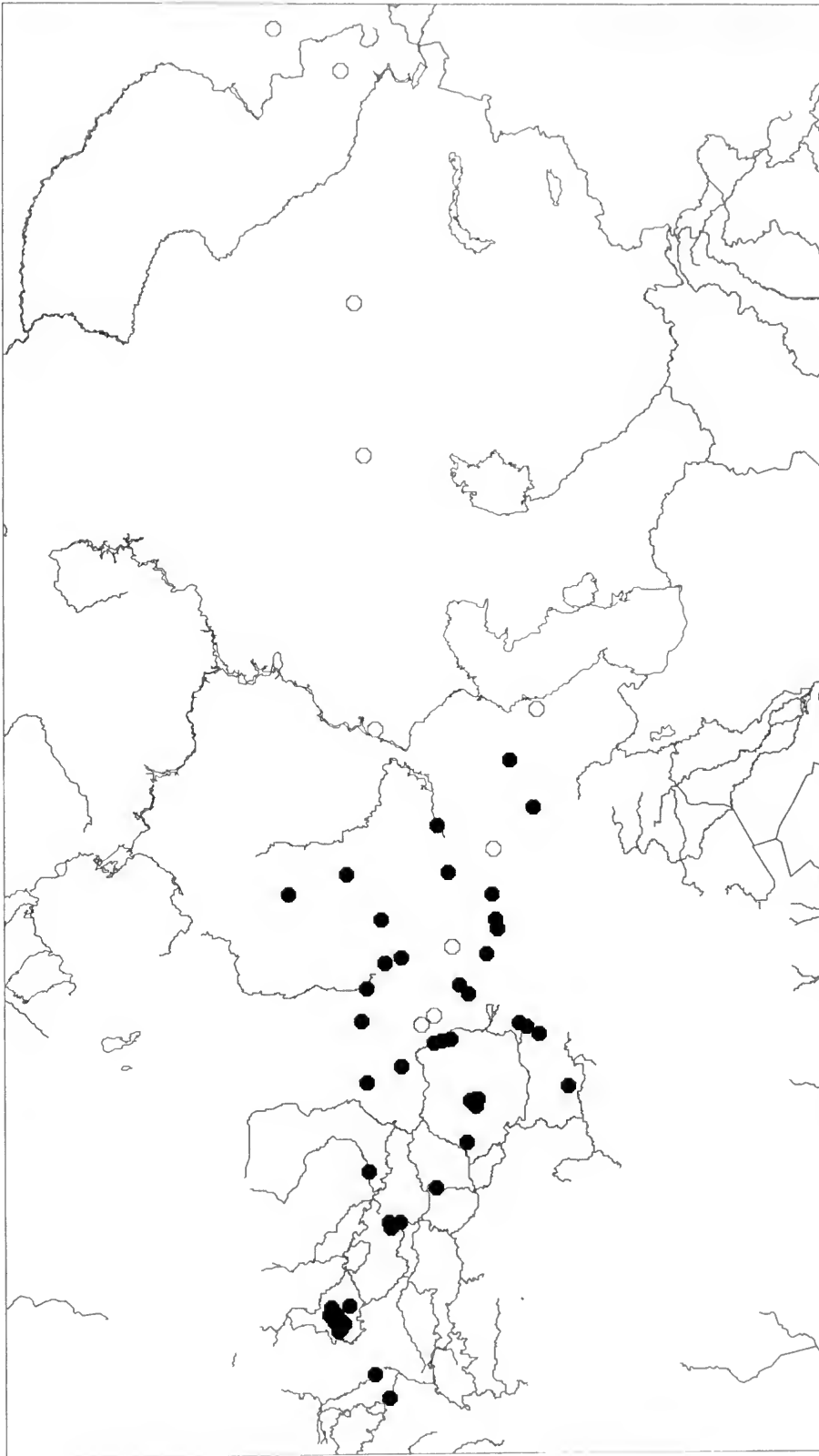
**BULGARIA.** Varna: Baltschik, Schiblak, oberhalb des Strandes, 15 June 1961 (fl), *Bisse* & *Schneider* 166 (JE). Plovdiv: M. Rhodope centr. supra Stanimak [Azenovgrad], 10 June 1892, *Wagner* in *Degen* s.n. (JE); Rhodope in collibus ad Alvan Dere, June 1901 (fl), *Stříbrný* s.n. (BM).

**TURKEY.** Istanbul: Büyük Han, c. 100 m, *Davidov* s.n. See Davis, *Fl. Turkey* 2: 401 (1967).

7x. *Hypericum elegans* Stephan ex Willd. × *H. perforatum* L.? *Raciborski* s.n. (June 1904), from Ukraine, Podolia, colles Miodobory, Okno [Okna?] (BM) seems to be this hybrid, which has not hitherto been recorded. It is morphologically intermediate between the two suggested parents.

8. *Hypericum tosaense* Makino in *Bot. Mag. (Tokyo)* 17: 79 (1903); H. Léveillé in *Bull. Soc. bot. France* 53: 502 (1906); Makino & Nemoto, *Fl. Japan*: 545 (1925), 2nd ed.: 753 (1931); Y. Kimura in Nakai & Honda, *Nova fl. jap.* 10: 221, ff. 73.4, 74 (1951), *Enum. Sperm. jap.* 3: 184 (1954); Ohwi, *Fl. Japan* (Engl. transl.): 632 (1965); Horikawa, *Atlas of jap. fl.* 2: 681 (1976); Momiyama in Satake et al. (Eds), *Wild fls Japan* 2: 118, t. 114 f. 2 (1982). Type: Japan, Shikoku, Prov. Tosa [Kōchi], Ikku-mura, 27 September 1892 (fl & fr), *T. Makino* s.n. (MAK!-holotype). Map 18; also Kimura (1959: 324, f.1) and Horikawa (see above).

*H. tosaense* f. *tosaense* Y. Kimura in Nakai & Honda, *Nova fl. jap.* 10: 222 (1951).



Map 17 *H. elegans* ●, other records ○. A record from the Altai region is insufficiently localized.





Map 18 a. 8. *H. tosaense* ●; b. 9. *H. iwatelittorale* ■; c. 10. *H. momoseanum* ○; d. 11. *H. yezoense* ▲, other records △.

*H. tosaense* f. *insulare* Y. Kimura in Nakai & Honda, *Nova fl. jap.* **10**: 222 (1951), *Enum. Sperm. jap.* **3**: 184 (1954); Momiyama in Satake et al. (Eds), *Wild Fls of Japan* **2**: 118 (1982). Type: Japan, Shikōku, [Kagawa] Ins. Syodo [Shōdo], Ikedamura, 30 August 1910 (fl), *R. Hirama* s.n. (TI!-holotype).

*H. attenuatum* pro parte sensu Kitamura & Murati in *Acta Phytotax. Geobot.* **20**: 197 (1962).

*Perennial herb* (0.15–)0.25–0.57(–0.75) m tall, erect from creeping and rooting base, with stems solitary, branched above. *Stems* 2-lined, with black punctiform glands on and near lines; internodes 10–20 mm, mostly exceeding leaves. *Leaves* sessile; lamina 5–20 × 2–8 mm, elliptic or ovate-oblong to narrowly oblong or obovate-oblong, paler beneath, chartaceous; apex obtuse to rounded, margin entire, base rounded to broadly cuneate; venation: 2(3) pairs of main laterals from lower quarter of midrib; laminar glands pale, punctiform, dense; intramarginal glands black, dense. *Inflorescence* 3-c. 30-flowered from up to 3 nodes, with flowering branches from up to 4 nodes below, corymbiform to cylindrical and then dense; pedicels 2–3 mm; bracts and bracteoles small, linear-lanceolate to linear, entire. *Flowers* 15–18 mm in diam, stellate; buds ellipsoid, obtuse. *Sepals* 5, unequal, 2.5–3 × 1–1.5 mm, triangular-ovate to lanceolate, gradually to abruptly acuminate, entire; veins 5, outer pair(s) branched; laminar glands pale, punctiform to linear-striiform; intramarginal glands black, punctiform, spaced. *Petals* 5, bright yellow, veined red in bud, 9–15 × c. 5–8 mm, 3.5–5 × sepals, oblong-elliptic, somewhat asymmetric, distally ± markedly crenate; laminar glands pale, linear to punctiform, scattered; marginal glands black, distally dense. *Stamens* 60–70, '3'-fascicled, longest 7–11 mm, 0.65–0.8 × petals; anther gland black. *Ovary* 3-locular, 2.5–4.8 × c. 1.5 mm, ovoid; styles 3, free, 3.5–4.5(–5) mm, 1–1.6 × ovary, spreading-outcurved; stigmas narrow *Capsule* 7–9 × 3.5–5 mm, c. 3 × sepals, ovoid-conic to ovoid; valves longitudinally vittate. *Seeds*

dark brown, c. 1 mm long, cylindrical; testa linear-foveolate.  $2n=16$  (Kogi, 1984).

'Sunny places on hills'.

Japan (Shikōku (Tosa area) and Shōdo I.).

**JAPAN. Shikōku:** Kagawa: Ins. Syoda, Ikeda-mura, 30 August 1910 (fl), *R. Hirama* s.n. (TI). **Kōchi:** Prov. Tosa, Ikku-mura, 27 September 1892 (fl & fr), *T. Makino* s.n. (MAK).

*Hypericum tosaense* occurs in two restricted area of southern Japan (south coast of Shikōku and Shōdo Island between Shikōku and Honshū) and would appear to be a relict species linking the mainland *H. attenuatum* with the equally relict 9. *H. iwatelittorale* from northern Honshū, both morphologically and geographically. *Forma insulare* (from Shōdo I.) differs from the type form in having narrower leaves, more flowers per inflorescence and longer styles (2 × rather than 1.2 × ovary), characters that, in this group, do not seem to warrant separate taxonomic recognition at more than the *forma* level, if at all.

9. ***H. iwatelittorale*** H. Koidz. in *J. Pl. Iwateken* **II**, **2**: 89 (1937) ('*iwate-littorale*'). Type: Japan, Honshū, Prov. Rikūti [Iwate], Shimohei-gun, Todogasaki, 12 August 1934 (fl & fr), *Y. Fukuda* 569 in Herb. H. Koidz. 95611 (TNS!-holotype); loc. cit., 12 August 1934 (fl & fr), *Y. Fukuda* 569 in Herb. H. Koidz. 95612–95613 (TNS!-isotypes).

Map 18.

*Perennial herb* 0.25–0.32 m tall, erect, with stems solitary or few and caespitose, branched above. *Stems* 2-lined, with black punctiform glands on lines; internodes exceeding to equalling leaves. *Leaves* sessile (main stem) to c. 0.5 mm petiolate (laterals); lamina (8–)12–14 × 5–8 mm, ovate to elliptic-oblong (main stem) or elliptic to oblanceolate (laterals), paler beneath, chartaceous; apex rounded

to rounded-obtuse, margin entire, base cuneate to rounded-amplexicaul (upper); venation: 3–(4) pairs of laterals from lower quarter to fifth of midrib; laminar glands pale, punctiform, dense; intramarginal glands all black or some reddish, dense to spaced. *Inflorescence* (1)3-c. 30-flowered from up to 3 nodes, with flowering branches from up to 4 nodes below, corymbiform to cylindrical and then dense; pedicels 0.8–1 mm; bracts small, lanceolate, entire. *Flowers* 9–10 mm in diam., stellate?; buds ellipsoid, subacute. *Sepals* 5, subequal, 3–4 × 1–2 mm, ovate-oblong to lanceolate, acute to subacuminate, entire; veins 5, outer pair(s) branched; laminar glands pale, linear-striiform to punctiform; intramarginal glands black, few or absent. *Petals* 5, bright yellow, not tinged red in bud, 6–9 × c. 2–3 mm, obovate-oblong, distally subrenate; laminar glands pale, linear to punctiform, and sometimes 1–2 black, distal, striiform-punctiform; marginal glands black, very few or absent. *Stamens* c. 50?, '3'-fascicled, longest c. 7 mm, c. 0.8 × petals; anther gland black. *Ovary* 3-locular; styles 3, free, 3.5–4 mm, ? × ovary, spreading-outcurved; stigmas narrow. *Capsule* 5–8 × 4–5 mm, c. 2 × sepals, ovoid-conic to ovoid; valves longitudinally vittate. *Seeds* dark brown, 1.2 mm long, cylindrical; testa linear-foveolate. 2n=?

Coastal.

Japan (Honshū-Iwate).

**JAPAN. Honshū. Iwate:** Shimohei-gun, Todogasaki, 12 August 1934 (fl & fr), Y. Fukuda 569 in Herb. H. Koidzumi 95611 (TNS).

*Hypericum iwatelittorale* was included doubtfully by Kimura (1951) in *H. pseudopetiolatum* (subsect. 2. *Erecta*), but the gland-dotted raised stem lines reveal that its true position is in subsect. 1. *Hypericum*. It is morphologically very close to *H. tosaense* but considerably distanced geographically. Taken together, the small morphological differences (see key, p. 68) and the wide spatial separation warrant its recognition as a species.

10. ***Hypericum momoseanum*** Makino in *J. Jap. Bot.* 7: 12 (1931); Nemoto, *Fl. Japan, Suppl.*: 485 (1936); Y. Kimura in Nakai & Honda, *Nova fl. jap.* 10: 218, f. 73.3 (1951), in *J. Jap. Bot.* 34: 323, f.1 (1959); Momiyama in Satake et al. (Eds), *Wild Fls of Japan* 2: 118 (1982). Type: Japan, Honshū, Prov. Sinano [Nagano], Mt. Hachibuse, 18 July 1930 (fl), *Momose* s.n. (TI!-holotype).

Map 18.

*H. momoseanum* var. *momoseanum* Y. Kimura in Nakai & Honda, *Nova fl. jap.* 10: 219 (1951).

*H. momoseanum* var. *atumense* Y. Kimura in Nakai & Honda, *Nova fl. jap.* 10: 219 (1951); in Satake et al. (Eds), *Wild fls Japan* 2: 118 (1982). Type: Japan, Honshū [Aichi], Prov. Mikawa, Atumi-gun, Fukue, Kantekiyama, 3 August 1939 (fl), *Yamamoto* s.n. (TI!-holotype).

*H. tosaense* var. *atumense* (Y. Kimura) Y. Kimura in *J. Jap. Bot.* 34: 326 (1959).

*H. attenuatum* pro parte sensu Kitamura & Murati in *Acta Phytotax. Geobot.* 20: 197 (1962).

*H. yezoëense* var. *momoseanum* (Makino) Ohwi in *Fl. Japan* (Engl. transl.): 632 (1965). The original (Japanese) edition (Ohwi, 1953: 782) mentions *H. momoseanum* under *H. yezoëense* but makes no formal combination.

*Perennial herb* 0.25–0.65 m tall, ascending from woody base, with stems single, unbranched or with short sterile branches throughout. *Stems* 2-lined, with black punctiform glands on and near lines; internodes 15–30 mm, equalling leaves. *Leaves* sessile, amplexicaul; lamina 15–30 × 5–11 mm, oblong to elliptic or oblanceolate, paler

beneath, thickly chartaceous; apex rounded-obtuse, margin plane, base rounded; venation: 3–4 pairs of main laterals from base and lower quarter of midrib, tertiary reticulation lax; laminar glands punctiform, pale (minute) and black, submarginal and distal; intramarginal glands black, dense. *Inflorescence* 7–11-flowered, from 2–3 nodes, with flowering branches from up to 4 nodes below, the whole subcorymbiform to condensed-cylindric; pedicels 0.7–3 mm (apical to 5 mm); bracts and bracteoles linear, entire. *Flowers* 15–20 mm in diam., stellate; buds elliptic, obtuse. *Sepals* 5, subequal, 3–5 × 0.7–2 mm, oblong-ovate to lanceolate or narrowly elliptic, acute to gradually acuminate, entire; veins 5, occasionally branched; laminar glands pale, linear to striiform, sometimes also a few punctiform and occasionally a few black, distal, punctiform; intramarginal and submarginal glands black, spaced. *Petals* 5, 'yellow', 8.5–12 × 2.5–3.5 mm, 2.5–3 × sepals, obovate to oblanceolate, subsymmetric, distally not or scarcely crenate; laminar glands pale, linear to punctiform and sometimes a few black, distal, punctiform. *Stamens* c. 40, '3'-fascicled, longest 7–8 mm, 0.7–0.85 × petals; anther gland black. *Ovary* 3-locular, c. 3.5 × 2 mm; styles 3, free, 4–5 mm, 1.2–1.4 × ovary, 'erecto-patent'; stigmas narrowly capitate. *Capsule* and *Seeds* not seen. 2n=?

Habitat not recorded.

Japan (central Honshū – two localities).

**JAPAN. Honshū. Nagano:** Mt. Hachibuse, 18 July 1930 (fl), *S. Momose* s.n. (TI). **Aichi:** Atsumi-gun, Fukue, Kantekiyama, 3 August 1939 (fl), *S. Yamamoto* s.n. (TI).

In habit and distribution *H. momoseanum* is intermediate between the southern *H. tosaense* and the northern *H. yezoëense*. Like the former species it has a very restricted distribution, being confined to two stations in central Honshu (Nagano and Aichi Prefectures). Kimura (1959) described var. *atumense* as having stems unbranched or almost so and larger flowers than var. *momoseanum*, in which the stems are branched (as in *H. yezoëense*). The differences do not seem to warrant taxonomic recognition.

11. ***Hypericum yezoëense*** Maxim. in *Bull. Acad. Imp. Sci. Saint-Petersbourg* 31: 16 (1886), *Mél. Biol. Bull. Acad. Imp. Sci. Saint-Petersbourg* 12: 420 (1886); Matsumura, *Index pl. jap.* II-2: 370 (1912); Miyabe & Miyake, *FL. Saghalin*: 79 (1915); Y. Kimura in *Bot. Mag. (Tokyo)* 51: 701, ff. 20–21 (1937), in Nakai & Honda, *Nova fl. jap.* 10: 216, f. 73.1 (1951), *Enum. Sperm. jap.* 3: 186 (1954), in *J. Jap. Bot.* 34: 323, ff. 1, 2 (1959), in *Asahi ... shokobutsu*, no. 64: 1508 (1977); Sugawara, *Ill. fl. Saghalien* 3: t. 600 (1940); Gorschkova in Shishkin & Bobrov, *Fl. URSS* 15: 238 (1949); Ohwi, *Fl. Japan* (Engl. trans.): 632 (1965); Lauener in *Notes Roy. Bot. Gard. Edinburgh* 27: 5 (1966); Kitamura & Murati, *Clrd Ills Herb. Pls Japan* 2: 66 (1972). Type: Japan, Yezo [Hokkaidō, S. Oshima], circa Hakodate, 20 July 1878 (fl), *R. Yatabe* s.n. (LE-holotype; TI!-isotypes).

Fig. 11, Map 18; also Kimura (1959: 324, f. 1).

*H. attenuatum* [var.] *β fruticosum* F. Schmidt in *Mém. Imp. Acad. Sci. Saint-Petersbourg*, 7e sér., 12(2): 119 (1868) [*'fruticulosa'*]. Types: Russia, Sachalin, Sachkotau, 18 July 1860 (fl), *Friedr. Schmidt* s.n. (LE-syntype); loc. cit., late August 1860 (fr), *Friedr. Schmidt* s.n. (LE-syntype).

*H. procumbens* R. Keller in *Bull. Herb. Boissier* 5: 639 (1897); H. Léveillé in *Bull. Soc. Bot. France* 53: 502 (1906); Matsumura, *Index pl. jap.* II-2: 370 (1912); Miyabe & Miyake, *Fl. Saghalin*: 79 (1915); Makino & Nemoto, *Fl. Japan*: 546 (1925); non Desf. ex Willd. (1802) nec Michx. (1803). Type: Japan, Hokkaidō, 'in

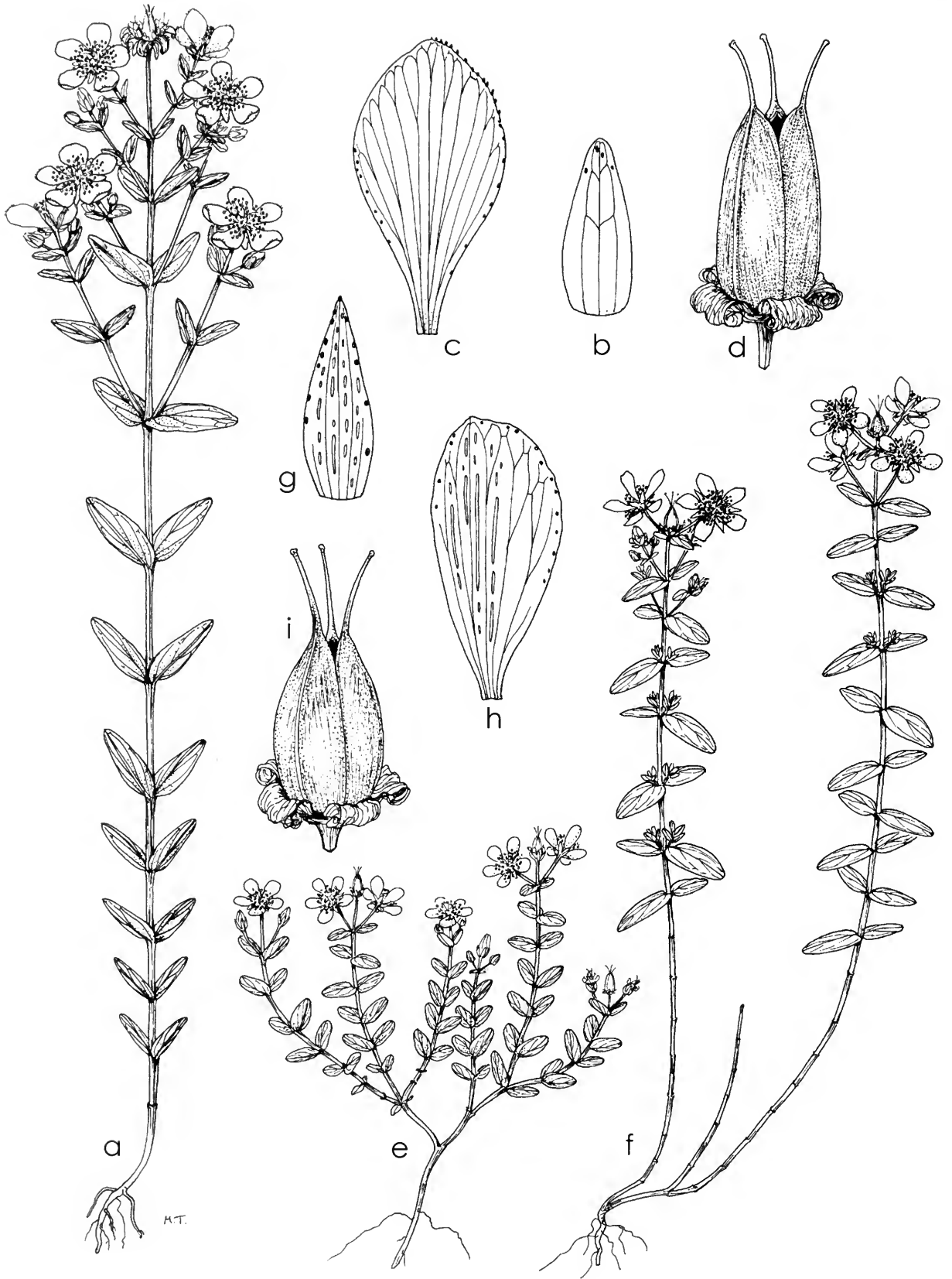


Fig. 11 A. *H. scouleri*: (a) habit; (b) sepal; (c) petal; (d) capsule. B. *H. scouleri* 'nortoniae': (e) habit. C. *H. yezoënsis*: (f) habit; (g) sepal; (h) petal; (i) capsule (a, e, f  $\times 2/3$ ; c, d, h, i  $\times 4$ ; b, g  $\times 8$ ). A. (a) Copeland 426; (b, c) Kellogg & Harford 102; (d) Jones 5682. B. (e) Moore & Steyermark 3711. C. (f, g, h) Furuse 940; (i) Faurie 6905.

- promontorio Gangenzaki', 7 June 1894 (fl), *Faurie* 13325 (G-holotype?; FI!, K!).
- H. mororanense* R. Keller in *Bull. Herb. Boiss.* **5**: 640 (1897), in *Bot. Jahrb. Syst.* **33**: 553 (1904), op. cit. **44**: 49 (1909), op. cit. **58**: 194 (1923) in obs. ['morarense']; H. Léveillé in *Bull. Soc. Bot. France* **53**: 502 (1906), op. cit. **54**: 595 (1908); Matsumura, *Index pl. jap.* **II-2**: 367 (1912); Makino & Nemoto, *Fl. Japan*: 543 (1925), 2nd ed. **2**: 753 (1931). Type: Japan, Hokkaidō, Iburi, Mororan [Muroran], *Faurie* 10304 (Z?-lectotype, selected here); Hokkaidō [Shiribeshi], Promontorium Asushi, *Faurie* 5061 (Z?-syntype; K!).
- H. oliganthemum* R. Keller in *Bot. Jahrb. Syst.* **33**: 553 (1904); H. Léveillé in *Bull. Soc. Bot. France* **53**: 502 (1906) ['iloganthum']; Matsumura, *Index pl. jap.* **II-2**: 367 (1912); Makino & Nemoto, *Fl. Japan*: 544 (1925), 2nd ed.: 751 (1931). Type: Japan, precise locality not cited, *Rein* s.n. (B†-holotype).
- H. mororanense* forma *tetragynum* H. Léveillé in *Bull. Soc. Bot. France* **53**: 502 (1906); Matsumura, *Index pl. jap.*: 367 (1912). Type: Japan, Hokkaidō [Soya], in rupibus maritimis Rebusshiri, 1 August 1889, *Faurie* 3086 (P?-holotype). Kimura (1937: 702) pointed out that flowers with abnormal numbers of parts, such as occur in the type of this variety, are not uncommon in northern or alpine regions of Japan.
- H. porphyrandrum* H. Léveillé & Vaniot in *Repert. Spec. Nov. Regni Veg.* **6**: 330 (1909); Matsumura, *Index pl. jap.* **II-2**: 368 (1912); Makino & Nemoto, *Fl. Japan*: 544 (1925), 2nd ed.: 751 (1931); Gorskova in Shishkin & Bobrov, *Fl. URSS* **15**: 257 (1949). Type: Russia: Sakhalin I., in rupibus Tonaichan, 18 September 1908 (fl), *Faurie* 521 (P?-holotype; KYO!-isotype).
- ?*H. pseudo-nikkoense* H. Koidz. in *J. Pl. Iwateken* **2**(2): 87 (1937). Type: Japan, Honshū, Prov. Rikutiu [Iwate], Geibikei, *G. Toba* in Herb. H. Koidz. 95578 (TSN?-holotype).
- ?*H. yoiitense* H. Koidz. in *J. Pl. Iwateken* **2**(2): 101 (1937). Type: Russia, Kurile Is., Kunashir, Yoito, *I. Yamamoto* in Herb. H. Koidz. 102121 (TNS?-holotype).
- Icones: S. Sugawara, *Illustr. fl. Saghalien* **3**: t. 600 (1940); Y. Kimura in *J. jap. Bot.* **34**: 325, f. 2 (1959).

*Perennial herb* 0.1–0.3(–0.35) m tall or long, erect to ascending or more rarely procumbent from creeping and rooting base, with stems numerous to few and caespitose or rarely solitary, branched or not. *Stems* 2-lined (if slender almost 4-angled), with black punctiform glands on lines only; internodes (4–)12–28 mm, usually exceeding leaves. *Leaves* sessile; lamina 8–20(–25) × 3–9 mm, ovate (uppermost) to elliptic-lanceolate or ± narrowly oblong to oblanceolate, slightly paler beneath, chartaceous; apex obtuse to rounded, margin plane, base broadly cuneate to subamplexicaul; venation: 2–3 pairs of main laterals from lower quarter of midrib; laminar glands pale, punctiform, dense and black, punctiform, few, towards margin, or absent; intramarginal glands black, dense. *Inflorescence* 3–9-flowered from 1–2 nodes, without or with one pair of flowering branches from node below, corymbiform to subpyramidal; pedicels 0–1 mm (that of terminal flower to 4 mm in fruit); bracts reduced-foliar, bracteoles 4–5 mm long, linear-lanceolate, entire. *Flowers* 15–20 mm in diam., stellate; buds narrowly ovoid, subacute. *Sepals* 5, unequal, 4–6 × 1.2–2 mm, erect in bud and fruit, lanceolate to oblong-lanceolate, acute, entire; veins 3–5, unbranched; laminar glands pale, punctiform and sometimes a few black, punctiform, distal; intramarginal glands black, punctiform, rather sparse, distal. *Petals* 5, pale yellow, not? tinged red in bud, 8–12 × 3.5–5 mm, 2 × sepals, obovate-oblong, asymmetric, subtentire; laminar glands pale, linear to punctiform, scattered; marginal and intramarginal glands black, irregular, locally dense. *Stamens* c. 30–50, '3'-fascicled,

longest c. 8–10 mm, c. 0.9 × petals; anther gland black. *Ovary* 3-locular, 3–3.2 × 1.5–2 mm; styles 3, free; stigmas narrowly capitate. *Capsule* 5–8 × 3?–4 mm, c. 1.3 × sepals, broadly to narrowly ovoid; valves longitudinally vittate. *Seeds* dark brown, 1–1.3 mm, cylindrical; testa linear-foveolate. 2n=?

Habitat not recorded.

Japan (extreme northern Honshū, Hokkaidō), Russia (southern Sakhalin; Kuriles – Kunashiri and Shikotan Is.).

**JAPAN, Honshū.** **Iwate:** Motomura, Akka-mura, Shimohei-gun, 400 m, 13 June 1957 (bud), *Shimizu* 2052 (K). **Aomori, Akita:** see Kimura (1959: 324, f. 1). **Hokkaidō.** **Ōshima:** Eramachi, 22 July 1890 (l. fl), *Miyabe & Tokubuchi* s.n. (K); \*Esan Isoya, 26 July 1926, *Tatewaki* 6110 (SAPS?). **Shiribeshi:** in Shiribeshi, August 1905 (fl), *Faurie* 6905 (BM); \*Isoya, 18 July 1888, *Y. Tokubuchi* s.n. (TI?). **Ishikari:** Hassabu, August 1916 (fl), *Kudo* in HTU 77274 (TAI); \*Mt. Tengu, 15 August 1931, *Yamamoto* s.n. (SAPS?). **Iburi:** \*Mororan, *Faurie* 10304 (P?). **Hidaka:** \*Iwayama, Samani, 18 June 1884, *K. Miyabe* s.n. (TI?). **Rumoi, Abashiri:** see Kimura (1959: 324, f. 1). **Soya:** Rebun I., Funado-mari-choo, 13 August 1975 (l. fl), *Furuse* 9407 (K). **Nemuro:** Hanasaki, prope urbem Nemuro, 7 July 1909 (l. fl), *Takeda* s.n. (K). **RUSSIA, Sakhalin:** \*Toyouhara [Yuzhno-Sakhalinsk], Takinosawa, 2 August 1928, *N. Hiratsuka* s.n. (TI?); \*Makunkotan circa Motodomari [Tomari?], 15 September 1906, *T. Miyake* (TI?). **Kurile Is.:** \*Kunashiri, 26–27 July 1935, *Y. Takahashi* s.n. (TI?); Shikotan, Notoro, 2 August 1931, *Ohwi* s.n. (KYO?).

*Hypericum yezoense* is a reduced 'form' of the central Honshū 10. *H. momoseanum*, differing from it in habit and inflorescence size. Kimura (1937: 703) notes that the Korean record for this species is erroneous, as is Maximowicz's description of the ovary as one-celled.

12. *Hypericum scouleri* Hook., *Fl. bor.-amer.* **1**: 111 (1831), *Pl. Hartweg.*: 301 (1848); Torrey & Gray, *Fl. N. Amer.* **1**: 160 (1838); Torrey in Emory, *Rep. U. S. Mex. bound.* **2**(1): 36 (1858); Greene, *Fl. francisc.* **1**: 112 (1891), *Man. bot. San Franc. Bay*: 63 (1894); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.*, 2nd ed., **21**: 179 (1925); Peck, *Man. pls Oregon*: 481 (1941); Gillett & Robson in *Publs. Bot. Natl. Mus. Nat. Sci. Canada* no. 11: 28, t. 12, map 9 (1981); Scott, *Alpine Fl. Rocky Mts* **1**: 458 + f. + map (1996). Type: U.S.A., [Oregon] 'Nw. coast of America, near the Columbia', n.d. [1825] (fl), *Scouler* s.n. (K!-lectotype, selected here; NY-isolectotype); [Washington?] grassy plains of the Columbia, 1825 (fl), *Douglas* s.n. (BM!-syntype); ex eodem loco, 1826 (fl), *Douglas* s.n. (BM!-syntype). Fig. 11, Map 19.

- H. skouleri* sensu Walp., *Rep. bot. syst.* **1**: 387 (1842), sphalm.
- H. formosum* sensu A. Gray, *Pl. wright.* **2**: 17 (1853); Torrey in Emory, *Rep. U. S. Mexico bound.* **2**(1): 36 (1858); Kearney & Peebles, *Arizona fl.*: 556 (1951); Clark, *Wild fls Pac. Northwest*: 312, 322 (1976); Dorn, *Man. Vasc. Pls Wyoming* (2): 818 (1977), *Vasc. Pls Wyoming*: 184 (1988); Scoggan, *Fl. Canada* **3**: 1096 (1978); Martin & Hutchins, *Fl. New Mexico* (2): 1280 + f., map 758 (1981); Welsh et al., *Utah Fl.*, rev. ed.: 353 (1993); non Kunth (1822).
- H. formosum* var. *scouleri* (Hook.) Coult. in *Bot. Gaz.* **11**: 108 (1886); Abrams, *Ill. Fl. Pac. States* **3**: 116, f. 3233 (1951); Munz, *Calif. Fl.*: 192 (1959); Scoggan, *Fl. Canada* **3**: 1096 (1978).
- H. simulans* Rose in *Contr. U. S. Natl. Herb.* **10**: 124 (1906); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.* 2nd ed., **21**: 179 (1925). Type: Mexico, Hidalgo, Canales Station, 1800 m, 8 August 1904 (fl), *Pringle* 8993 (US!-holotype; BM!, C!, F!, G!, GH!, K!, MEXU!, NY!, P!, W!-isotypes).
- H. collinum* var. *schmitzii* R. Keller in *Bull. Herb. Boissier* **II**, **8**: 187

- (1908). Type: Mexico, Chihuahua, Potrero pasada la Piedat, 1856? (fl), *Schmitz* s.n. (W!-holotype, F!, US!-photographs).
- H. nortoniae* M.E. Jones in *Bull. Univ. Montana* no. 61, Biol. Ser. no. 15: 39, t. 5 (1910) [*'Nortoniae'*]. Type: U.S.A., Montana, McDonald Peak, 2190 m, 2 September 1908 (fl), *M.E. Jones* s.n. (POM!-lectotype, selected here).
- H. formosum* subsp. *scouleri* (Hook.) C.L. Hitchc., *Vasc. Pls Pac. N.-W.* 3: 434 + f. (1961); Taylor & Macbryde, *Vasc. Pls Br. Columbia*: 203 (1977); Thorne in *Aliso* 9: 193 (1978), independent comb.; E. Murray in *Kalmia* 12: 21 (1982), independent comb.; Moss, *Fl. Alberta*, 2nd ed. rev. Packer: 404, map 765 (1983).
- H. formosum* var. *nortoniae* (M.E. Jones) C.L. Hitchc., *Vasc. Pls Pac. N.-W.* 3: 434 + f. (1961) [*'nortoniae'*]; Scoggan, *Fl. Canada* 3: 1096 (1978).
- H. formosum* subsp. *formosum* sensu C.L. Hitchc., *Vasc. Pls Pac. N.-W.* 3: 434 (1961); McVaugh, *Fl. Novo-Galicia* 3: 51 (2001), pro parte quoad loc. s. w. US; non *H. formosum* Kunth (1822).
- H. formosum* var. *formosum* sensu Dorn, *Man. Vasc. Pls Wyoming* (2): 818 (1977), *Vasc. Pls Wyoming*: 184 (1988); Scoggan, *Fl. Canada* 3: 1096 (1978); non *H. formosum* Kunth (1822).
- H. scouleri* subsp. *nortoniae* (M.E. Jones) J.M. Gillett in *Canad. J. Bot.* 57: 185 (1979); Gillett & Robson in *Publs. Bot. Natl. Mus. Nat. Sci. Canada* no. 11: 30, map 9 (1981). Type as for *H. nortoniae* M.E. Jones.
- H. scouleri* subsp. *scouleri* Gillett & Robson in *Publs. Bot. Natl. Mus. nat. Sci. Can.* no. 11: 30 (1981).

Icons: Gillett & Robson in *Publs. Bot. Natl. Mus. Nat. Sci. Canada* no. 11: 29, t. 12 (1981); C.L. Hitchc., *Vasc. Pls Pac. N.-W.* 3: 434 (1961).

*Perennial herb* 0.05–0.6(–0.8) m tall, erect or ascending from creeping and branching rhizomatous and often stoloniferous base, with stems solitary or up to *c.* 10, not caespitose, sometimes with short ascending stem branches. *Stems* shallowly 2-lined or often partially 4-lined (with evident complete or incomplete subsidiary lines) or rarely almost terete, eglandular or sometimes with a few reddish punctiform glands usually on or near lines; internodes 15–50 mm, usually exceeding leaves. *Leaves* all sessile or lower subpetiolate, spreading or rarely erect; lamina 12–28(–32) × 6–15(–18) mm, oblong-elliptic or elliptic to triangular-ovate or suborbicular or (lower) obovate, paler beneath, chartaceous; apex obtuse to rounded, margin plane, base rounded to subcordate or (lower) cuneate; venation: 4–5 pairs of basal and lateral main veins from lower third of midrib; tertiary reticulation rather dense but obscure to lax; laminar glands pale, punctiform, small to large and sometimes 1–2 or more (rarely all) black, distal and submarginal; intramarginal glands black, dense. *Inflorescence* (1–)8–20-flowered from 1–3(4) nodes, sometimes with flowering branches from 1–2(3) nodes below, the whole narrowly cylindrical to pyramidal; pedicels 2–6 mm; bracts and bracteoles 3–6 mm long, ovate-lanceolate to ovate, entire. *Flowers* 6–15(–25) mm in diam., stellate; buds broadly ellipsoid to subglobose, obtuse to rounded. *Sepals* 5, unequal to subequal, 2.5–5.5 × 1–2 mm, erect in bud and fruit, *c.* 0.25 united, ovate to lanceolate or narrowly oblong, acute to rounded, entire or sometimes with a few sessile glands or regularly or irregularly shortly glandular-ciliate to -denticulate; veins 5, distally branched; laminar glands pale, striiform and sometimes black, punctiform to striiform or linear; intramarginal and marginal glands black, irregular or distally regular. *Petals* 5, golden yellow, sometimes tinged red in bud, 7–12 × 3–7 mm, ± narrowly obovate, asymmetric, distally subrenate to entire; laminar glands pale, linear to striiform, occasionally a few black, punctiform to striiform;

marginal glands black, distally dense. *Stamens* *c.* 50–90(–103), '3'-fascicled, longest 6–10 mm, *c.* 0.7–0.9 × petals; anther gland black. *Ovary* 3(4)-locular, 3–5 × 2–2.5 mm, ovoid; styles 3, free, (2–)3–6(–8) mm, *c.* 1–1.7 × ovary, widely spreading; stigmas narrowly capitate. *Capsule* 6–10 × 3.5–6 mm, ovoid to narrowly ovoid-pyramidal; valves densely longitudinally vittate. *Seeds* brown, (0.5–)0.7–0.8 mm, cylindrical, not carinate or appendiculate, sometimes? apiculate; testa linear-reticulate. 2n=16, n=8 (Kyhos, 1967; Ward & Spellberg, 1983).

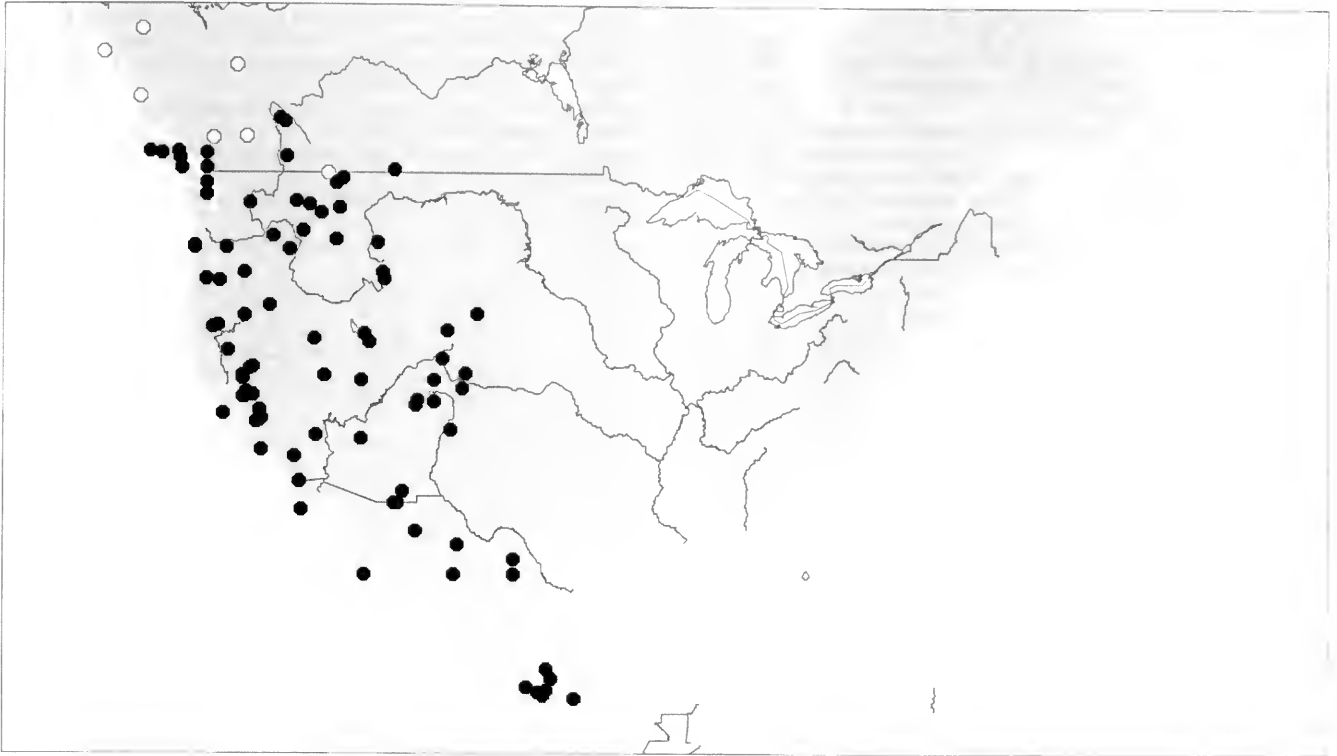
Wet meadows, bogs and grassy or rocky banks, stream and lake margins, thickets, coniferous forest, screes; Canada: *c.* 50–1800 m; U.S.A.: 400–2700 m; Mexico: 1800–3000 m.

Canada (British Columbia (N. to *c.* 55°), extreme SW Alberta), western U.S.A. (E. to Montana, Wyoming, Colorado, New Mexico), Mexico (Baja California Norte and Sierra Madre Occidental from Sonora, Chihuahua and Coahuila to Michoacán, México and Vera Cruz [Orizaba]).

**CANADA. British Columbia:** Kokanee Glacier Park, 1800 m, 15 August 1938 (fl), *Moir* 276 (K); Selkirk and Rocky Mts, near 51° 30' N, Spillamasheen Valley, 1800 m, 30 July 1904 (fl), *Heacock* 411 (BM, JE, K, Z); Vancouver Island, Cameron Lake, near Port Alberni, 181 m, 5 August 1965, *Ashlee* 215 (H). **Alberta:** *vide* Gillett & Robson (1981: map 9).

**U.S.A. Washington:** Douglas Co., near Egbert Spring, 390 m, 2 July 1993 (fl), *Sandberg & Leiber* 361 (BM, K, US\*). **Oregon:** Klamath Co., summit of Cascade Mts, Crescent Lake, 1251 m, 17 August 1934 (fl), *Constance* 977 (K); Harney Co., Shirk, 1500 m, 19 July 1996 (fl & e. fr), *Leiber* 2598 (BM, US\*). **Montana:** Gallatin Co., Bozeman, Middle Creek, 14 July 1905 (fl), *Blankinship* 98 (BM, H); Mineral Co., Fish Creek, near mouth of Cache Creek, 1050 m, 11 July 1923 (fl), *Hitchcock* 1696 (K). **Idaho:** Latah Co., 6.4 km E. of Farmington, 28 June 1892 (fl), *Sandberg, MacDougal & Heller* 512 (BM, K, Z); Shoshone Co., 6.4 km E. of Burke, *c.* 1620 m, 12 August 1949 (fl), *Cronquist* 6069 (G). **Wyoming:** Teton Co., Grand Teton National Park, cirque above Indian Paint Brush Canyon, 2750 m, 220 August 1931 (fl & fr), *Moore & Steyermark* 3711 (BM, W); Park Co., Lewis R., Yellowstone National Park, 9 August 1899 (fl), *A. & E. Nelson* 63881 (BM, K). **Colorado:** Montezuma Co., Mancos, 9 July 1898 (fl), *Baker, Earle & Tracy* 889 (BM, K, W); El Paso Co., Colorado Springs, 1650 m, June 1879 (fl), 6.4 km NW of Brighton, 2220 m, 4 August 1964 (fl), *Bennett* 8440 (W). **Utah:** Pluto Co., Marysvale, Tate Mine, 2700 m, 2 August 1894 (fr), *M.E. Jones* 5862 (BM); Salt Lake Co., Big Cottonwood Creek canyon, Wasatch Mts, 6.5 km NW of Brighton, 2220 m, 4 August 1964 (fl), *Bennett* 8440 (W). **Nevada:** White Pine Co., southern Schell Creek Range, E. of Mt Grafton, 2250 m, 11 August 1969 (fl), *Holmgren* 3869 (W); Douglas? Co., L. Tahoe, 1866 m, 29 July 1931 (fl), *L.S. Rose* s.n. (JE). **California:** Butte Co., Jonesville, 1550 m, 18 July 1930 (fl), *Copeland* 426 (BM, H, K, TAL, W, Z); El Dorado Co., Sierra Nevada Mts, Placerville-Tahoe road, 0.8 km W. of Lover's Leap, 13 July 1935 (fl), *Belshaw* 1158 (K); San Bernardino Co., Lythe Creek canyon, 14 July 1902 (fl), *Abrams* 2727 (K, Z). **Arizona:** Coconino Co., Bill Williams Mtn, 2100 m, 22 July 1898 (fl), *MacDougal* 319 (G); Cochise Co., Chiricahua Mts, Barfoot Park, 2400–2475 m, 26 September 1906 (fr), *Blumer* 1426 (K, W, Z). **New Mexico:** Caltron Co., Gila National Forest, Mogollon, Willow Creek Rec. Area, 2640 m, 26 July 1963 (fl), *Demaree* 48702 (BM); Santa Fe Co., Santa Fe, Creekbottom, 1847 (fl), *Fendler* 53 (BM, K, W).

**MEXICO. Baja California Norte:** Sierra San Pedro Mártir, 2100 m, 21 August 1967 (e. fr), *Moran & Thorne* 14453 (CAS, DS). **Sonora:** San Jose Mts, 8 km S. of Naco, 1800 m, 6 July 1928 (fl), *Wolf* 2516 (GH). **Chihuahua:** Sierra Madre near Colonia Garcia, 2250 m, 5 August 1899 (fl), *Townsend & Barber* 224 (BM, F, G, GH, K, MEXU, MICH, MO, NY, P). **Coahuila:** Múzquiz, Hacienda Mariposa, foot of E. slope of Sierra de Puerto Santa Ana, 23 June 1936 (fr), *Wynd & Mueller* 245 (K). **Durango:** Metates, N. of Cueva, 2650–2700 m, 29–30 August 1934 (fl), *Pennell* 18384 (US). **Zacatecas:** Sierra Madre, August 1897 (fl), *Rosen* 2382 (NY, US). **Hidalgo:** Sierra de Pachuca, 2850 m, 4 August 1898 (fl), *Pringle* 6941 (BM, C, F, G, GH, K, MEXU, MICH, MO, NY, US, W). **México:** Lagunas de Zempoala Nat. Park, 3 August 1949 (fl), *McAdams* 88 (MICH). **Distr. Fed.:** Desierto de los Leones, 23 September 1938 (fl), *Lyonnet* 2586 (US). **Michoacán:** 6.4 km W.



Map 19 12. *H. scouleri* ●, other records ○.

of Hidalgo, c. 2000 m, 17 July 1940 (fl), *Hitchcock & Stanford* 7194 (F, GH, NY). **Vera Cruz:** Orizaba, 1846 (fl), *Heller* 143 (W).

Many authors have included *H. scouleri* in the central Mexican *H. formosum* Kunth as a synonym, subspecies or variety, but the similarities in sepal form and glandularity of these species are due to convergence. *Hypericum formosum* is related to an undescribed subspecies of the Mexican *H. oaxacanum* R. Keller (sect. 9b. *Graveolentia*), whereas the affinities of *H. scouleri* are with the eastern Asian 6. *H. attenuatum*.

Gillett (1979) and Gillett & Robson (1981) treated the dwarf, small-flowered alpine form of *H. scouleri* as a distinct subspecies, subsp. *nortoniae* (M.E. Jones) J.M. Gillett. Further work, however, has revealed a range of intermediate forms between the two 'subspecies' that prevents their recognition. Likewise, the differentiation of a southern U.S. population ('*H. formosum* subsp. *formosum*' sensu C.L. Hitchc.) from a northern one ('*H. formosum* subsp. *scouleri* (Hook.) C.L. Hitchc. '), based on the 'broader, blunter and less glandular sepals' of the latter, does not appear to be warranted. The glandular, often acute sepals of this New Mexican form are an extreme development in *H. scouleri*, not an indication of affinity with *H. formosum*. In Mexico the sepals become more black-glandular south-eastwards, so that, in the plants known as *H. simulans*, they have black linear laminar glands; but the margin is always entire.

**ACKNOWLEDGEMENTS.** Once again, as for Part 4(1), I am especially indebted to Dr Peter Raven and Dr Ihsan Al-Shebaz (MO) for help with loans and for hospitality during my studies of Chinese *Hypericum* in St. Louis, to Yang Chiang (NAS) for label translation and for compiling a database for me, and to Prof. Li Xiwen (KUN) for his publications on Chinese *Hypericum*. I am also very grateful to Prof. Hideaki Ohba (TI) for facilitating loans of

Japanese specimens. My studies of western Eurasian species have been helped particularly by Dr Pavol Mártonfi (KO), whose work on hybridity in the *H. perforatum* group has thrown considerable light on aspects of this difficult complex; and Prof. Jacques Lambinon (LG), Prof. Fabio Garbari and Dr Daniela Ciccarelli (both PI) have all helped me to clarify the variation in *H. perforatum* itself. As before, I have obtained assistance from many colleagues at the BM, particularly from Mike Gilbert (computing matters, nomenclature and general discussion) and Prof. Chris. Humphries and Josephine Camus (mapping); and Malcolm Beasley and his colleagues in the Botanical Library have, as usual, been very helpful. My thanks are also due to the directors of the following herbaria for loans and/or study facilities: A, ANG, ANK, BASBG, BAV, BC, BD, BISH, BP, BRNM, C, CAS, CL, CLF, DS, E, EVIN, F, FI, FR, G, GH, GL, GRM, GZU, H, HNWP, IBSC, JE, K, KO, KUH, KUN, KYO, L, LANC, LD, LE, LINN, LIV, MAK, MARS, MEXU, MICH, MO, NAS, NY, P, PE, POM, PR, RAW, RNG, S, SEV, SZ, TAI, TI, TNS, TO, U, UBC, UPS, US, W, WAG, WIS, WU, Z. I am again deeply indebted to Margaret Tebbs for the drawings. My wife Eve has, as always, been a help and support in many ways. Finally, I must thank the Keeper of Botany, Prof. Richard Bateman, and his immediate predecessors for study facilities in the Botany Department, and the Stanley Smith Trust for a grant towards illustration costs.

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- Sect. *Euhypericum* Godr. 67  
 Subsect. *Heterotaenium* R. Keller 67  
 Series *Perforata* Gorschk. 67  
 Subsect. *Homotaenium* R. Keller 67  
 Series *Acuta* Gorschk. 67  
 Series *Attenuata* Gorschk. 67  
 Series *Crispa* Gorschk. 67  
 Series *Elegantia* Gorschk. 67  
 Series *Kamtschatica* Gorschk. pro parte 67  
 Series *Quadrangula* Gorschk. 67
- Sect. *Graveolentia* N. Robson 61  
 Sect. *Homotaenium* Y. Kimura 67  
 Series *Bilineata* Y. Kimura 67  
 Series *Crispa* Y. Kimura 67  
 Series *Quadrangula* Y. Kimura 67
- Sect. *Hypericum* 61, 62, 65, 66, 67  
 Subsect. *Erecta* N. Robson 61, 62, 66, 115  
 Subsect. *Hypericum* 61, 62, 65, 66  
 Series *Hypericum* 61–66, 67  
 Series *Senanensia* 61, 62, 65, 66, 68
- Sect. *Roscyna* (Spach) R. Keller 61, 62, 63, 65  
*acutum* Moench (=3) 80, 81  
 subsp. *boeticum* (Boiss.) Cout. (=2b) 80  
 subsp. *corsicum* (Steud.) Rouy (=3b) 84  
 var. *rotundifolium* sensu Briq. (=3b) 84  
 subsp. *desetangii* (Lamotte) Rouy (=5xa) 104  
 var. *genuinum* (Bonnet) Rouy (=5xa) 104  
 var. *imperfatum* (Bonnet) Rouy (=1c) 73  
 subsp. *eu-acutum* Hayek (=3a) 81  
 subsp. *tetrapterum* (Fr.) Maire (=3a) 81  
 subsp. *undulatum* (Schousb. ex Willd.) Rouy (=2) 78  
 var. *anagallidifolium* (Boiss.) Post (=3c) 84  
 var. *anagallidioides* (Jaub. & Spach) Zohary (=3c) 84  
 var. *corsicum* (Steud.) Halácsy (=3b) 84  
 var. *insulare* (Foucaud & Mandon) Briquet (=3b) 84  
 var. *rotundifolium* (Willk.) Schinz (=2b) 80  
 var. *typicum* Guşul. (=3) 81  
 var. *undulatum* (Schousb. ex Willd.) Pau (=2) 78  
 forma *humile* (Boenn.) Hegi (=3) 81  
 forma *patulum* (Boenn.) Hegi (=3) 81  
*acutum* × *perforatum* (=5x) 108  
*aetnaeum* Tornab. (= 5c) 97  
*alatum* Retz. (= 3?) 80  
*anagallidifolium* Boiss. (= 3c) 84  
*anagallidioides* Jaub. & Spach (= 3c) 84  
*ascyron* L. 61, 62  
 subsp. *ascyron* 62  
 subsp. *gebleri* (Ledeb.) N. Robson 62  
 subsp. *pyramidatum* (Aiton) N. Robson 62  
*assurgens* Peterm. (=5a) 89, 118  
*attenuatum* Fisch. ex Choisy (6) 62, 63, 65–67, 88, 89, 108, 109\*, 111, 114, 119  
 var. *fruticosum* F. Schmidt (=11) 115  
*attenuatum* sensu Kitamura & Murati (=6+8+10) 114, 115  
*baeticum* sensu auct. plur. (=2b) 78  
*boeticum* Boiss. (=2b) 79, 80  
 sensu Syme (=2) 78  
*borbasii* Formáneek (=3) 81  
 × *carinthiacum* A. Fröhl. (=5xb) 105  
 forma *maculatiforme* A. Fröhl. (=5xba) 65, 106  
 forma *perforatiforme* A. Fröhl. (=5xbb) 65, 107  
*carpathicum* Mártonfi (=5xbb) 107  
*chrysostictum* Webb (=5c) 96  
*collinum* var. *schmitzii* R. Keller (=12) 117  
*commutatum* Nolte (=1b) 71, 76  
*confertum* (Choisy) G. Don (=3) 81  
*corsicum* Steud. (=3b) 84  
*crispum* L. (=4) 67, 84  
*deciens* H. Watson (=2) 78  
*deidesheimense* Sch. Bip. ex Trev. (?=5a) 89  
*delphinense* Vill. (=1b) 71, 73  
 × *desetangii* Lamotte (5x) 63, 64, 76, 78, 102, 103\*  
 nothomorph *carinthiacum* (A. Fröhl.) N. Robson (=5xb) 105  
 nothomorph *desetangii* sensu N. Robson (=5xa) 104  
 nothomorph *perforatiforme* (A. Fröhl.) N. Robson (=5xbb) 88, 107  
 nothosubsp. *balkanicum* N. Robson (5xc) 64, 103\*, 104, 107  
 nothosubsp. *carinthiacum* (A. Fröhl.) N. Robson (5xb) 64, 65, 104, 105  
 nothomorph *maculatiforme* (A. Fröhl.) N. Robson (5xba) 65, 103\*, 106  
 nothomorph *perforatiforme* (A. Fröhl.) N. Robson (5xbb) 65, 103\*, 106, 107

## SYSTEMATIC INDEX

Accepted names are in roman and synonyms in *italics*; new names and principal references are in **bold**. An asterisk denotes a figure.

*Holosepalum* (Spach) Fourr. 73, 81  
*dubium* (Leers) Fourr. (=1c) 73  
*quadrangulum* (L.) Fourr. (=3) 81  
*Hypericum* L. 61  
 Sect. *Concinna* N. Robson 61

- nothosubsp. *desetangsii* (5xa) 64, 103\*, **104**  
nothovar. *desetangsii* sensu N. Robson (=5xa) 104  
var. *genuinum* Bonnet (=5xa) 104  
var. *imperfatum* Bonnet (=1c) 73, 74  
*desetangsii* sensu Lloyd (=2) 78  
× *desetangsii* × *tetrapterum* (5x × 3) 108  
× *dubioides* Druce (=5xx) 108  
*dubium* Leers (=1c) 65, 68, 71, 73, 74, 75  
var. *genuinum* Syme (=1c) 73  
var. *maculatum* sensu Bab. (=1c) 73  
var. *perforatum* (Tourlet) Pugsley (=1c) 74  
*dubium* sensu Bab. (=1c) 73  
*dubium* sensu Mauri (=1b) 71  
*elegans* Stephan ex Willd. (7) 62, 63, 65, 109\*, **111**  
var. *elegans* Jordanov & Kož. (=7) 112  
var. *genuinum* Guşul. (=7) 112  
var. *pectinatum* Čelak. (=7) 111  
var. *pedunculatum* Jordanov & Kož. (=7) 112  
var. *stepposum* SÍvul. & Rayss (=7) 112  
*elegans* × *perforatum* (7x) 112  
*erectum* Thunb. 62, 111  
*erosum* (Schinz) O. Schwarz (=5xba) 104  
*erosum* sensu O. Schwarz p. p. excl. *typum* (=1c) 74, 75  
*fallax* Grimm (=1b) 71  
subsp. *fallax* 71  
var. *fallax* 71  
forma *punctatum* O. Schwarz (=1b) 71  
var. *quadrangulare* (L.) O. Schwarz (=3) 81  
var. *quadrangulare* sensu O. Schwarz p. p. (=1b) 71  
subsp. *immaculatum* (Murb.) O. Schwarz (=1a) 70  
*foliosissimum* Koidz. (=5d) 101  
*formosum* Kunth 119  
subsp. *formosum* sensu C.L. Hitchc. (=12) 118, 119  
subsp. *scouleri* (Hook.) C.L.Hitchc. (=12) 118, 119  
var. *formosum* sensu Dorn (=12) 118  
var. *nortoniae* (M.E. Jones) C.L. Hitchc. (=12) 118  
var. *scouleri* (Hook.) Coult. (=12) 117  
*formosum* sensu A. Gray (=12) 117  
*hyssopifolium* Vill.  
var.  $\gamma$  sensu Choisy (=7) 111  
var. *pauciglandulosum* Choisy (=7) 111  
*immaculatum* (Murb.) Vierh. (=1a) 70  
*insulare* Foucaud & Mandon (=3b) 84  
*intermedium* Bellync (=1xb) 76  
*iwatellitorale* H. Koidz. (9) 65, **114**, 115  
*kamtschaticum* Ledeb.  
var. *pibairense* Miyabe & Y. Kimura 65, 66, 68  
var. *senanense* sensu Y.N. Lee (=6?) 110  
*kohlianum* Spreng. (=7) 111  
*komarovii* Gorschk. (=5b) 89, 95  
× *laschii* A. Fröhl. (1x) **75**, 76, 102  
nothoforma *froelichii* N. Robson (1xb) 76  
nothoforma *laschii* (1xa) 76  
*leersii* C.C. Gmel. (=1c) 73  
*lineolatum* Jord. (=5a) 89  
*linnaeanum* Callay & Gren. (=5xa) 104  
*maculatum* Crantz (1) 62, 76, 88, 106, 111  
subsp. *desetangsii*forme A. Fröhl. (=5xbb) 107  
var. *aporosum* A. Fröhl. (=5xbb) 107  
subsp. *erosum* sensu Schinz & Keller (=1c) 74  
var. *imperfatum* (Bonnet) A. Fröhl. (=1c) 74  
forma *latisepalum* A. Fröhl. (=1c) 74  
[sub]forma *lucidum* A. Fröhl. (=1c) 74  
[sub]forma *nigrum* A. Fröhl. (=1c) 74  
var. *perforatum* (Tourlet) A. Fröhl. 74  
subsp. *erosum* × *acutum* (=1xb) 76  
subsp. *erosum* × *perforatum* (=5xa) 104  
subsp. *eu-maculatum* Schinz & Thell. (=1b) 71  
subsp. *immaculatum* (Murb.) A. Fröhl. (1a) 62, 63, 65, 66, **68**, 69\*, 71, 75, 108  
var. *epunctatum* A. Fröhl. (=1a) 70  
var. *punctatum* A. Fröhl. (=1a) 70  
subsp. *immaculatum* × *attenuatum* (1a × 6) 63  
subsp. *immaculatum* × *perforatum* (=5xc) 108  
subsp. *maculatum* (1b) 62–65, 68, 69\*, 71, 75, 76, 107, 111  
forma *punctatum* (Schinz) Stjep.-Vesel. (=1b) 71  
subsp. *maculatum* × *perforatum* (1b × 5) 64, 102  
subsp. *maculatum* × *tetrapterum* (1b × 3) 64, 75  
subsp. *obtusiusculum* (Tourlet) Hayek (1c) 63–65, 68, 69\*, **73**, 75, 104, 106  
var. *imperfatum* (Bonnet) A. Fröhl. (=1c) 74  
var. *perforatum* (Tourlet) A. Fröhl. (=1c) 74  
subsp. *obtusiusculum* × *perforatum* (=5xa) 64, 104  
subsp. *obtusiusculum* × *tetrapterum* (1c × 3) 76  
subsp. *quadrangulum* (L.) Hayek (=3) 81  
subsp. *quadrangulum* sensu Hayek (=1b) 71  
subsp. *styriacum* A. Fröhl. (=1c) 74  
subsp. *styriacum* × *acutum* (=1c × 3) 76  
subsp. *typicum* A. Fröhl. (=1b) 71  
var. *genuinum* (Schinz) A. Fröhl. (=1b) 71  
var. *punctatum* (Schinz) A. Fröhl. (=1b) 71  
forma *luteum* A. Fröhl. (=1b) 71  
subsp. *typicum* × *acutum* (=1b × 3) 76  
subsp. *typicum* × *perforatum* (=1b × 5) 105  
subsp. *undulatum* (Schousb. ex Willd.) P. Fourn. (=2) 78  
var. *babingtonii* H. & J. Groves (=1c) 74  
var. *immaculatum* (Murb.) Guşul. & Nyár. (=1a) 70  
*maculatum* × *acutum* (=1 × 3) 75  
*maculatum* × *perforatum* (1 × 5) 64, **76**, 102, 108  
*maculatum* × *perforatum* forma *sub-maculatum* (= 5xba) 106  
*maculatum* × *perforatum* forma *sub-perforatum* (=5xbb) 107  
(*maculatum* × *perforatum*) × *acutum* (=5xxx) 108  
*maculatum* × *tetrapterum* (1x) 64, 75  
*marylandicum* Biroli ex Colla (=5a) 89  
× *medium* Peterm. (5xx) 64, **108**  
*microphyllum* Jord. (=5c) 96  
× *mixtum* Du Moulin (=5xa?) 76, 104  
*momoseanum* Makino (10) 65, 111, **115**, 117  
var. *atumense* Y. Kimura (=10) 115  
var. *momoseanum* (=10) 115  
*mororanense* R. Keller (=11) 117  
forma *tetragynum* H. Léveillé (=11) 117  
*nachtschevanicum* Grossh. (=5c) 97, 98  
*neapolitanum* Ten. (=3) 78, 81, 82  
var. *confertum* (Choisy) Guss. (=3) 81  
*noëanum* Boiss. (=5c) 97  
*nortoniae* M.E. Jones (=12) 118  
*oaxacanum* R. Keller 119  
*obtusum* Moench (=1c) 73  
*officinale* Gaterau (=5a) 89  
*officinarum* Crantz (= 5a) 89  
*oliganthemum* R. Keller (=11) 117  
*ovalifolium* Koidz. 62  
*perforato-acutum* O. Kuntze & Focke (=5xx) 108  
*perforato-quadrangulum* Lasch (=5xa) 104  
*perforatum* L. (5) 62–66, 71, 75, **87**, 88, 89, 90\*, 98, 101, 104–107, 110, 111  
subsp. *angustifolium* (DC.) A. Fröhl. (=5c) 96, 97  
subsp. *chinense* N. Robson (5d) 66, 89, 90, **101**  
subsp. *latifolium* (Gaudin) A. Fröhl. (=5xbb) 107  
forma *dentatum* A. Fröhl. (=5xbb) 107  
forma *fimbriatum* A. Fröhl. (=5xbb) 107  
var. *obscurum* O. Schwarz (=5xba) 106  
subsp. *perforatum* (5a) 65, 88, **89**, 90\*, 92, 94, 95, 96, 98  
var. *pellucidum* O. Schwarz (=5a) 91  
subsp. *songaricum* (Ledeb. ex Rchb.) N. Robson (5b) 65, 66, 89, 90\*, **95**, 96  
subsp. *veronense* (Schränk) H. Lindb. (5c) 66, 88, 89, 90\*, 94, **96**, 101  
subsp. *vulgare* (Schimp. & Spenn.) A. Fröhl. (=5a) 91  
forma *brevisepalum* A. Fröhl. (=5a) 91  
forma *lineolatum* (Jord.) A. Fröhl. (=5a) 91  
forma *lucidum* A. Fröhl. (=5a) 91  
var.  $\beta$  sensu Choisy (=5a) 89  
var.  $\gamma$  sensu Choisy (=5c) 96  
var. *albiflorum* Choisy (=5a?) 89  
var. *alpinum* Parl. (=5a) 89  
var. *angustifolium* Borkh. (=5c?) 96  
var. *angustifolium* DC. (=5c) 88, 89, 96  
subvar. *lineolatum* Rouy (=5c) 97  
var. *angustifolium* sensu Ohwi (=5d) 101  
var. *anomalum* Frid. (=5a) 89  
var. *cereticum* Sennen (=5a) 91  
var. *collinum* Woron. (=5c) 89, 97, 101  
var. *confertiflorum* Debeaux (=6) 101, 110  
var. *corioides* Vokut (=5c) 97  
var. *decompositum* Nyár. (=5a) 91  
var. *elatum* Choisy (=5c) 96  
var. *ellipticum* Durand & Pittier (=5a) 89  
var. *ellipticum* Freyn (=5c) 97

- var. *floribundum* Sennen (=5c) 97  
 var. *gracile* Gruner (=5b) 89, 95  
 var. *humile* Stranski (=5a) 89, 91, 93  
 var. *latifolium* Gaudin (=5xbb) 88, 106  
   subvar. *lineolatum* Rouy (=5xbb) 107  
 var. *latifolium* sensu W. Koch (=5a) 89  
 var. *latiglandulosum* Choisy (=5b) 95  
 var. *lineolatum* (Jord.) Hayek (=5a) 91  
 var. *longicapsulum* Jordanov & Kož. (=5c) 97  
 var. *mediterraneanum* Rouy (=5c) 97  
 var. *microphyllum* DC. (=5c) 96  
 var. *microphyllum* H. Léveillé (=5d) 101  
 var. *moesicum* Velen. (=5c) 97  
 var. *nanum* Gaudin (=5c) 96  
 var. *normale* Woron. (=5a) 91  
 var. *perforatum*, N. Robson (=5a) 91  
 var. *petiolatum* Peterm. (=5a) 89  
 var. *platycalyx* Čelak. (=5xbb) 107  
 var. *semihumifusum* Nyár. (=5a) 91  
 var. *songaricum* (Ledeb. ex Rchb.) K. Koch (=5b) 89, 95  
 var. *stenophyllum* (Opiz) Wimm. & Grab. (=5c) 96  
 var. *typicum* Beck (=5a) 89  
   forma *microphyllum* (DC.) Fiori (=5c) 97  
 var. *veronense* (Schrank) Ces. (=5c) 96  
 var. *vulgare* Schimp. & Spann. (=5a) 89  
   forma *anomalum* (Frid.) Hegi (=5a) 91  
   forma *brevisepalum* (A. Fröhl.) Hegi (=5a) 91  
   forma *lineolatum* (Jord.) Hegi (=5a) 91  
   forma *lucidum* (A. Fröhl.) Hegi (=5a) 91  
   subvar. *lineolatum* (Jord.) Rouy (=5a) 89  
 perforatum × *elegans* (5×7) 64  
 perforatum × *maculatum* subsp. *maculatum* (5×1b) 105  
 perforatum × *maculatum* subsp. *obtusiusculum* (5 × 1c) 104  
 (perforatum × *maculatum*) × *tetrapterum* (5x × 3) 108  
 perforatum × *tetrapterum* (5 × 3) 108  
*perforatum* group 119  
*porphyrandrum* H. Léveillé & Vaniot (=11) 117  
*procumbens* R. Keller (=11) 115  
*przewalskii* Maxim. 61  
*pseudo-nikkoense* H. Koidz. (=11?) 117  
*pseudopetiolatum* R. Keller 115  
*pulchrum* Pallas ex M. Bieb. (=7) 111  
*quadrangulare* sensu L. et auct. (=3) 71, 80  
   var. *alatum* (Retz.) Boenn. (=3) 81  
   var. *humile* Boenn. (=3) 81  
   var. *patulum* Boenn. (=3) 81  
*quadrangulum* L. (=3) 67, 71, 80, 81  
   subsp. *acutum* (Moench) Goday & Carbonell (=3) 81  
   subsp. *corsicum* (Steud.) Fiori & Fiori (=3b) 84  
   subsp. *desetangii* (Lamotte) Tourlet (=5xa) 104  
   subsp. *erosum* (Schinz) Schinz (=5xba) 106  
     var. *epunctatum* Schinz (=1c) 74  
   subsp. *immaculatum* (Murb.) Wettst. (=1a) 70  
   subsp. *maculatum* (Crantz) Goday & Carbonell (=1b) 71  
   subsp. *obtusiusculum* Tourlet (=1c) 73  
     var. *imperforatum* (Bonnet) Tourlet (=1c) 73  
     var. *perforatum* Tourlet (=1c) 73  
   subsp. *quadrangulum* sensu Tourlet (=1b) 71  
   subsp. *undulatum* (Schousb. ex Willd.) Goday & Carbonell (=2) 78  
   var. β sensu Choisy (=1c) 73  
   var. γ sensu Choisy (=1b) 71  
   var. δ sensu Choisy (=3) 80  
   var. *acutum* (Moench) Fiori (=3) 81  
   var. *ambiguum* Schur (=1c?) 73  
   var. *confertum* Choisy (=3) 80, 81  
   var. *dubium* (Leers) Choisy (=1c) 73  
   var. *erosum* Schinz (=5xba) 106  
   var. *genuinum* Schinz (=1b) 71  
   var. *immaculatum* Murb. (=1a) 70  
   var. *macrophyllum* Schur (=1b) 71  
   var. *maculatum* (Crantz) Choisy (=1b) 71  
   var. *occidentale* Franch. (=1c) 73  
   var. *punctatum* Schinz (=1b) 71  
   var. *subcorymbosum* Schur (=1b) 71  
   var. *tetrapterum* (Fr.) Borg (=3) 81  
     forma *undulatum* (Schousb. ex Willd.) Borg (=2) 78  
   var. *undulatum* (Schousb. ex Willd.) Choisy (=2) 76  
*quadrangulum* sensu Colm. (=2) 78  
*quadrangulum* sensu Des Étangs (=1xb) 76  
*quadrangulum* sensu Fr. et auct. (=1b) 71  
*quadratum* Stokes (=3) 80  
*quadrialatum* Wahlenb. (=3) 81  
*repens* Duby ex Nyman (=3b) 84  
*rotundatum* Schur (=3) 81  
*schlosseri* Heuffl. (=5c) 96  
*scouleri* Hook. (12) 62, 65, 66, 111, 116\*, 117  
   subsp. *nortoniae* (M.E. Jones) J.M. Gillett (=12) 118  
   subsp. *scouleri* (=12) 118  
*simulans* Rose (=12) 117  
*skouleri* Walp. (=12) 117  
*songaricum* Ledeb. ex Rchb. (=5b) 95  
   × *sparsiflorum* Schur (=5xx) 108  
*stenophyllum* Opiz (=5c) 96  
*tenellum* Tausch (=3b) 84  
*tetragonum* Fr. (=1b) 71  
*tetraptero-quadrangulum* Lasch (=1x) 75  
*tetrapterum* Fr. (3) 61, 64, 65, 67, 71, 76, 77\*, 78, 80, 81, 98  
   subsp. *corsicum* (Steud.) Zangh. (=3b) 84  
   subsp. *tetrapterum*, Zangh. (=3a) 82  
   subsp. *undulatum* (Schousb. ex Willd.) P. Silva (=2a) 78  
   var. *anagallidifolium* Boiss. (3c) 84  
   var. *boeticum* (Boiss.) Cout. (=2b) 78, 79, 80  
   var. *corsicum* (Steud.) Boiss. (3b) 84  
   var. *intermedium* Coss. & Germ. (=1xb?) 76  
   var. *neapolitanum* (Ten.) N. Terracc. (=3) 81  
   var. *rotundifolium* Willk. (=2b) 79, 80  
   var. *tenellum* (Tausch) Parl. (=3b) 84  
   var. *tetrapterum* (3a) 77\*, 80, 82  
   var. *undulatum* (Schousb. ex Willd.) Cout. (=2a) 78  
   forma *stigmaphyllum* Woron. (=3) 81  
*tetrapterum* group 71  
   *tosaense* Makino (8) 62, 65, 111, 112, 114, 115  
     var. *atumense* (Y. Kimura) Y. Kimura (=10) 111, 115  
     forma *insulare* Y. Kimura (=8) 114  
     forma *tosaense* Y. Kimura (=8) 112  
   *triquetrifolium* Turra (4) 62, 63, 65, 67, 77\*, 84, 87  
   *umbellatum* Miel. ex Wohlf. (=1b) 71  
   *undulatum* Schousb. ex Willd. (2) 61, 64, 65, 76, 78, 87  
     var. *boeticum* (Boiss.) Lange (2b) 65, 79, 80  
     var. *undulatum* (2a) 65, 77\*, 78, 80, 81  
   *undulatum* × *tetrapterum* (2 × 3) 80  
   *veronense* Schrank (=5c) 96  
   *vulgare* Bubani (=5a) 91  
   *vulgare* Lam. (=5a) 89  
*yamamotoi* group 62  
   *yamamotoi* var. *riparium* Y. Kimura 62  
   *yezoëense* Maxim. (11) 65, 115, 116\*, 117  
     var. *momoseanum* (Makino) Ohwi (=10) 115  
*yezoëense* group 62  
   *yoiitense* H. Koidz. (=11?) 117



# The natural history of reproduction in *Solanum* and *Lycianthes* (Solanaceae) in a subtropical moist forest

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## CONTENTS

|                                   |     |
|-----------------------------------|-----|
| Introduction .....                | 125 |
| Methods .....                     | 127 |
| Study site .....                  | 127 |
| Taxa studied .....                | 127 |
| Floral phenology .....            | 127 |
| Flower and fruit production ..... | 129 |
| Flower visitors .....             | 129 |
| Pollen load analysis .....        | 129 |
| Results .....                     | 129 |
| Floral phenology .....            | 129 |
| Flower production .....           | 131 |
| Fruit production .....            | 131 |
| Flower visitors .....             | 131 |
| Pollen load analysis .....        | 133 |
| Discussion .....                  | 133 |
| Floral phenology .....            | 133 |
| Flower production .....           | 133 |
| Fruit production .....            | 135 |
| Flower visitors .....             | 135 |
| References .....                  | 136 |

**SYNOPSIS.** The phenology and pollination of seven understory species of buzz-pollinated Solanaceae (*Solanum erythrorichum*, *S. lanceifolium*, *S. rudepannum*, *S. cordovense*, *S. nudum*, *Lycianthes hypoleuca* and *L. gorgonea*) were investigated at the end of the dry season in the subtropical moist forest at the Las Cuevas Research Station, Chiquibul Forest Reserve, Cayo District, western Belize. Three phenological phenomena were tracked: the opening and closing of flowers, flower production and fruit production. The large short-lived white flowers of *S. lanceifolium*, *S. rudepannum*, *Lycianthes hypoleuca* and *L. gorgonea* opened around sunrise and closed at sunset. The purple flowers of *S. erythrorichum* and the small white flowers of *S. nudum* and *S. cordovense* opened more or less randomly. All seven study species flowered at least once during the months of May, June and July; there was substantial overlap in the flowering of some species. Four species, *S. rudepannum*, *S. cordovense*, *S. lanceifolium* and *S. erythrorichum*, developed mature fruit during the monitoring period while the remaining species possessed immature fruit at the termination of the study. Thus, it appeared that these seven solanaceous species would provide a fairly constant supply of mature fruit during the rainy season. During observations of pollinators, 17 different bees in the families Colletidae, Halictidae and Apidae were found to visit the buzz-pollinated flowers of *Solanum* and *Lycianthes*. Analysis of the pollen loads revealed that bees were highly constant to Solanaceae although it was not possible to determine their constancy to particular species. Very few visits were observed to *S. cordovense* and *L. gorgonea*.

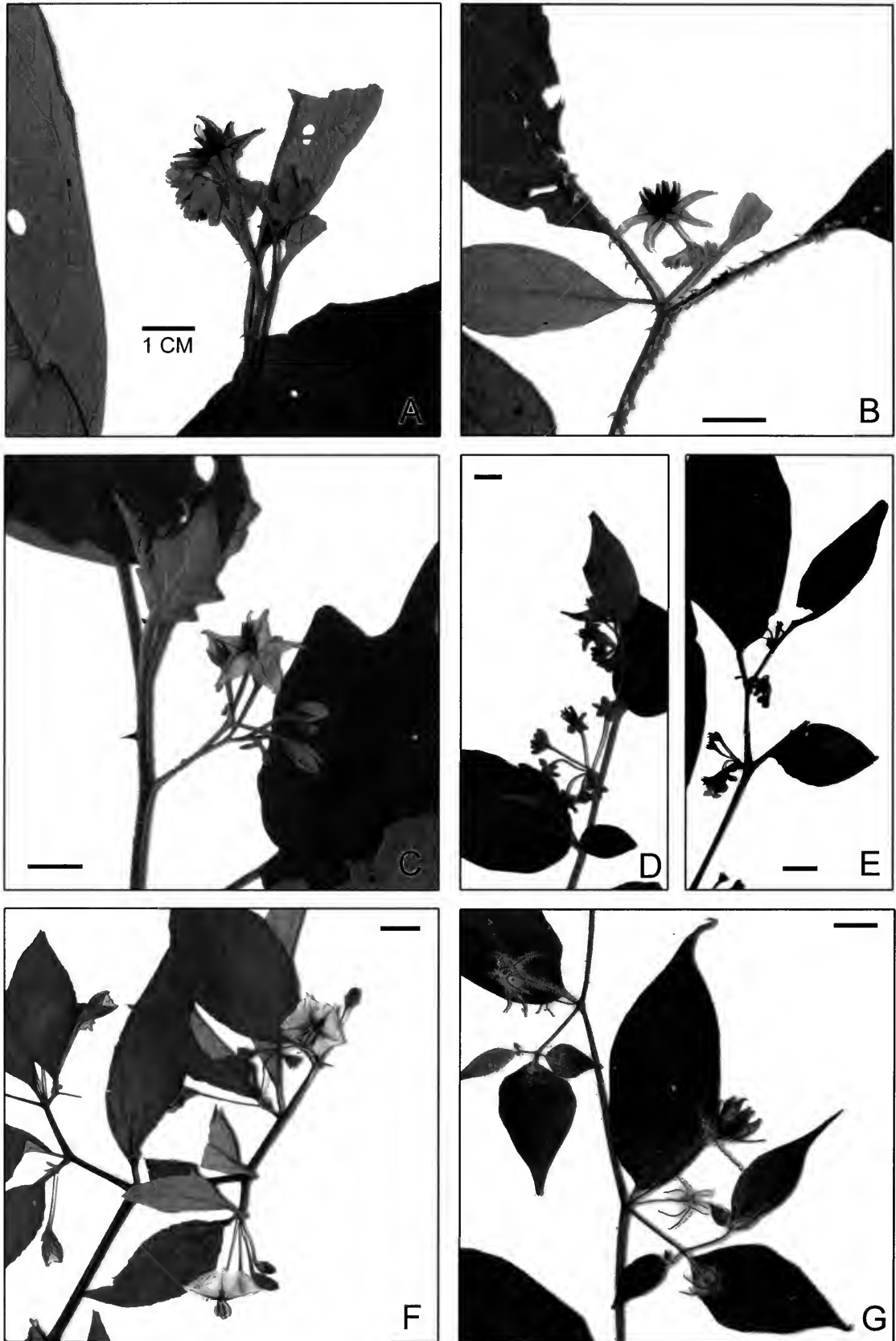
## INTRODUCTION

The Solanaceae is an economically important, cosmopolitan family with over 2500 species in some 90 genera. The family has members occurring in all habitats, and their habit ranges from canopy trees to minute ephemeral herbs. Flowers in the family Solanaceae exhibit a wide array of forms (Knapp, 2002), and are pollinated by a similarly

wide variety of organisms, including bees, hummingbirds and bats (Cocucci, 1999). In Mesoamerica, the family is an important component of the forest understory in a variety of habitats, and in Belize, it is the eleventh most diverse vascular plant family overall (Balick et al., 2000).

*Solanum* L. and *Lycianthes* (Dunal) Hassl. are the two largest genera in the family (D'Arcy, 1991). *Solanum* comprises 1500 or more species, 800–900 of which occur in the New World (D'Arcy,





**Fig. 1** Study species of Solanaceae at LCRS. Photographs taken from vouchers cited in the text. A. *Solanum erythrotrichum*, B. *S. lanceifolium*, C. *S. rudepannum*, D. *S. cordovense*, E. *S. nudum*, F. *Lycianthes hypoleuca*, G. *L. gorgonea*. Scale bar = 1 cm.

1991; Nee, 1999). *Lycianthes* contains approximately 200 species distributed in both tropical America and Asia (D'Arcy, 1973, 1979; Symon, 1985), and despite being superficially similar to *Solanum* (see below), it is closely related to the genus *Capsicum* L. (Olmstead et al., 1999). Approximately ten species of *Lycianthes* and 30 species of *Solanum* occur in Belize (Balick et al., 2000; Knapp et al., in press).

Although phylogenetically distant, members of *Solanum* and *Lycianthes* share similar, convergent, floral morphology. The flowers possess a five-parted gamopetalous corolla. The five equal stamens are fused to the corolla tube, and the bright yellow tubular anthers form a cone around the style (typical 'solanoïd' flowers, Endress, 1994; Fig. 1). The flowers of *Solanum* and *Lycianthes* are buzz-pollinated (Buchmann, 1983; Nevers, 1986; Lester et al., 1999). When buzzing a flower, an insect grasps the cone of tubular anthers with the front pairs of legs, wraps the abdomen around the apical pores of the anthers, and vibrates the anthers by rapidly contracting the indirect flight muscles (Michener, 1962; Buchmann & Hurley, 1978). This audible action causes pollen to burst out of the anther and land onto the venter of the insect. As the flowers of these *Solanum* and *Lycianthes* species offer no nectar and little scent, pollen is the only reward available to their pollinators (Symon, 1979; D'Arcy et al., 1990; pers. obs.). Although the mechanism of buzz pollination in Solanaceae has been well characterized (Michener, 1962; Buchmann, 1983), detailed studies which identify both the buzz-pollinated plant species and their pollinators are few (but see Linsley & Cazier, 1963; Anderson & Symon, 1988).

Here we examine the phenological patterns and pollination biology of seven sympatric buzz-pollinated species of *Solanum* and *Lycianthes* in the Chiquibul forest of western Belize. In studying their phenology, we tracked the daily opening and closing of flowers as well as the seasonal timing of flower and fruit production. Characterizing these daily and seasonal floral events in turn set the stage for investigations of pollination biology. In undertaking this study, we seek to expand our knowledge of Solanaceae in Belize, their natural history and range of pollinators.

## METHODS

### Study site

The Chiquibul Forest Reserve, Cayo District, western Belize, is nested completely within the Chiquibul National Park (Fig. 2). The vegetation comprises deciduous semi-evergreen and deciduous seasonal forest with stands of Caribbean pine to the north (Wright et al., 1959). The Macal River roughly divides the Caribbean pine forest to the north from the broad-leaved tropical forest of the Chiquibul to the south. Las Cuevas belongs to the subtropical moist life zone (Holdridge et al., 1971). While largely protected, some selective logging of commercial species such as mahogany (*Swietenia macrophylla*) and cedar (*Cedrela odorata*) is carried out in the Chiquibul on a >40 year rotational basis. The area has also suffered hurricane damage in the past (most recently from Hurricane Hattie in 1961), and the forest is a mosaic of different successional stages.

Our field studies were carried out at the Las Cuevas Research Station (LCRS) (16°44' N, 88°59' E; altitude 550–600 m; Fig. 2) operated jointly by the Forest Department of the Government of Belize and The Natural History Museum, London. Las Cuevas is situated in the centre of the Chiquibul Forest Reserve on the north-western side of the Maya Mountains, and has an annual rainfall of c. 1500 mm. The dry season at Las Cuevas runs from December to May, while the rainy season begins in mid to late June and ends in

January. This study began on 27 May 2000 and continued until 23 July 2000, thus covering the transition from the dry season to the wet season. The flowering of understory herbs including *Solanum* is known to peak during this transition period in Costa Rica and in Panama (Croat, 1969, 1975; Opler et al., 1980; Knapp, 1986), and in cerrado habitats in Brazil (Oliviera & Gibbs, 2000). Therefore, June and July were expected to be ideal months in which to study the reproductive biology of the understory Solanaceae in Belize. Though the study was conducted primarily along a trail to Monkey Tail River, pollinator behaviour was also studied at an observation tower located 1 km northwest of the station.

### Taxa studied

The habit, flowers and fruit of the seven species studied at Las Cuevas are briefly described below. The *Solanum* species are listed in their respective infrageneric taxon (sensu Nee, 1999). The infrageneric classification of *Lycianthes* is not well understood, so this information was not included in the descriptions below.

- *Solanum erythrotrichum* Fernald (Subgenus *Leptostemonum*) – An erect spiny shrub, with purple flowers (2 cm in diameter), tapering anthers and globose, slightly hairy green hard fruit, around 1.5 cm in diameter. It is commonly found in partly shaded disturbed areas and tree falls. (Voucher: S.D. Smith 008, BRH, BM). Fig. 1A
- *S. lanceifolium* Jacq. (Subgenus *Leptostemonum*) – A herbaceous weedy vine with short recurved spines. Its flowers are white, up to 2 cm in diameter with tapering anthers, and the small round fruit are 1 cm in diameter and bright red at maturity. It is found in thickets and in the canopies of small to medium trees. (Voucher: S.D. Smith 034, BRH, BM). Fig. 1B
- *S. rudepannum* Dunal (Subgenus *Leptostemonum*) – An erect spiny shrub, which produces large white flowers up to 2.75 cm in diameter and hard round berries which are about 2 cm in diameter and green at maturity. It prefers clearings such as road verges and fields. (Voucher: S.D. Smith 013, 037, BRH, BM). Fig. 1C
- *S. cordovense* Sessé & Moç. (Subgenus *Solanum*) – A clambering woody shrub with small white flowers (1 cm in diameter). The fruit is a globose juicy black berry, 1–1.25 cm in diameter. It is common along partly shady trails or in thickets. (Voucher: S.D. Smith 002, BRH, BM). Fig. 1D
- *S. nudum* Dunal (Subgenus *Solanum*) – A ubiquitous, entirely glabrous shrub with small white flowers similar to those of *S. cordovense*. Its fruit are yellowish-green berries of 1 cm in diameter. It is abundant in sunny areas along trails and roads. (Voucher: S.D. Smith 038, BRH, BM). Fig. 1E
- *Lycianthes hypoleuca* Standl. – A vigorous climbing shrub with large rotate white flowers (1.8–2 cm in diameter) and round red fruits just under 1 cm in diameter. It is found occasionally in small forest gaps or on hillsides, either in part-shade or full sun. (Voucher: S.D. Smith 026, BRH, BM). Fig. 1F
- *L. gorgonea* Bitter – A delicate scandent shrub with flowers similar to those of *L. hypoleuca*. Its fruit are slightly ovate, red berries of about 1 cm in diameter. It is quite infrequent, occurring only in the shady understory. (Voucher: S.D. Smith 012, BRH, BM). Fig. 1G

### Floral phenology

Information was systematically collected on the time of opening, the time of closing and the extent to which the corollas were open (e.g., partly open to fully open with petals reflexed). These data were used to characterize the movements of the corolla and the longevity of the

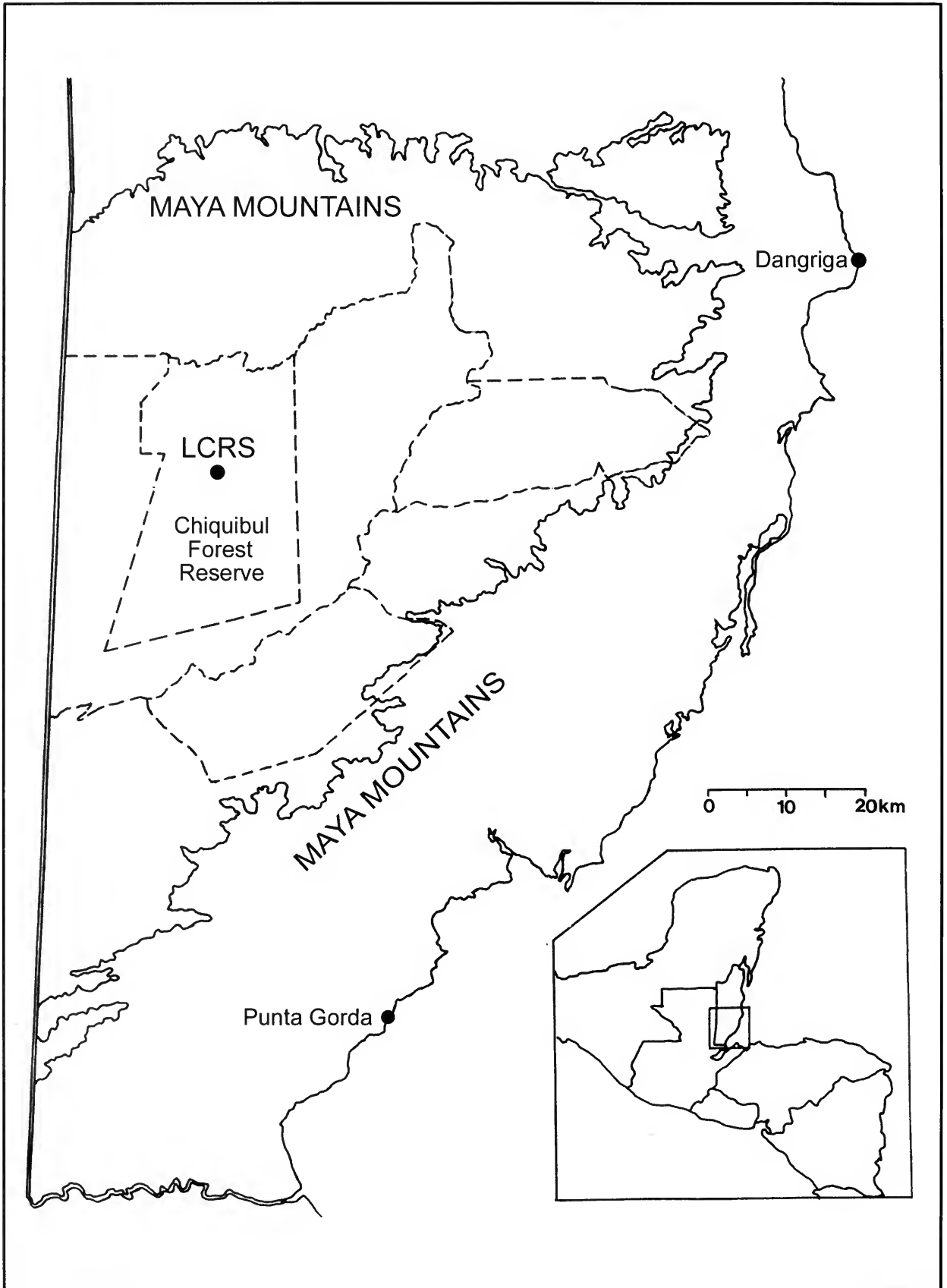


Fig. 2 Map of southern Belize (Belize shown in inset) showing position of Chiquibul Forest Reserve and the Las Cuevas Research Station (filled circle).

flowers. One mature individual was selected from each of the study species, and up to 25 flowers per individual were tagged and monitored for their entire lifespan. At the beginning of the study, the flowers were checked every four hours. Once it was determined whether the flowers of a given species close at night or not, flowers were checked only from 0500 hours to 2100 hours for the remainder of the study. The position at 0100 hours was interpolated from observations at 2100 hours and 0500 hours. For example, if the corolla was 50% open at 2100 hours and was 100% open at 0500 hours, its position at 0100 hours was recorded as 75% open. At Las Cuevas, the sun rises around 0500 hours and sets at 1845 hours. The position of the petals was recorded as follows: 0 = unopened bud (beginning) or flower dead (end); 0.1=closed but petals not appressed as in the bud; 0.25=flower 25% open; 0.50=flower half-open; 0.75=flower 75% open; 1.0=flower open with petals perpendicular to the pedicel; 1.25=flowers with petals reflexed. After the flower bloomed, 0.1 indicated that the flower had closed but remained attached whereas 0 indicated that the flower had fallen off. A flower was considered open to visitors when it was 40% open; below that level the aperture was too small for the bees to access the reproductive organs (pers. obs.).

### Flower and fruit production

All mature individuals (up to a maximum of 25) of the seven study species present in the first two kilometers of the trail to Monkey Tail River were tagged, and (starting June 1) every three days, the number of inflorescences, flowers and fruit was recorded. An inflorescence was counted from the moment it was visible at the tip of the branch to the abscission of its last flower. *Lycianthes gorgonea* and *L. hypoleuca* were not included in the counts of inflorescences because the flowers occurred singly. A flower was counted if its petals were open sufficiently so that the cone of anthers could be easily seen. Fruit were only counted when the ovary had doubled in size, i.e., once they were so large that it was clear that they would not be aborted. Approximate canopy cover was also recorded for each individual in the study in order to make a preliminary assessment of its effect on these species. The percent canopy cover above each individual was estimated visually and recorded in one of the following five categories: 0% cover, 25% cover, 50% cover, 75% cover and 100% cover.

### Flower visitors

Observations were taken from 0400 hours to 1900 hours and sporadically throughout the night. Flower visitor activity was most intense between sunrise and noon, so most observations took place between 0500 hours and 1200 hours. Observations included time of visit, number of flowers visited, length of visit and activities on the flowers. Each study species was observed for 18 to 20 hours or more. Every different visitor was collected using a sweep net and transferred directly into an eppendorf tube containing 1 ml isopropanol. Bees too large to fit into a tube were immediately washed in isopropanol to remove pollen, and this pollen sample was kept for pollen analysis (see below). When possible, several specimens of each visiting species were captured, so that later pollen load analysis could give some indication of the overall constancy of the species. Chris O'Toole (Oxford University) identified each bee to genus level and to species when possible.

### Pollen load analysis

To remove pollen, each bee was transferred from its eppendorf tube to a 12 ml glass tube. The eppendorf tube was rinsed out with an additional one ml of isopropanol, which was added to the glass tube.

Each bee was then shaken vigorously for 30 seconds to free the pollen from the body. The body was visually checked afterwards to assure that the pollen had been removed, and washed further if necessary. The tubes containing the pollen suspended in isopropanol were centrifuged at 5000 × g for five minutes to pellet the pollen. The isopropanol was poured off and the tubes inverted on a paper towel to drain. Then, 0.3 ml melted glycerol jelly was added to the pellet and stirred. One drop of this mixture was poured onto a glass slide and topped with a slide cover. Three hundred pollen grains were counted on each slide, and the percentage of solanaceous pollen calculated from this count. Solanaceous pollen was distinguishable from other pollen grains because it is small, smooth and tricolporate. It was not possible to distinguish between the study species with the light microscope. Density of pollen grains was estimated at 40x magnification and was coded as follows: 1=one pollen grain per view or less; 2=1 to 5 pollen grains per view; 3=5 to 10 pollen grains per view; 4=10 to 20 pollen grains per view; 5=greater than 20 pollen grains per view.

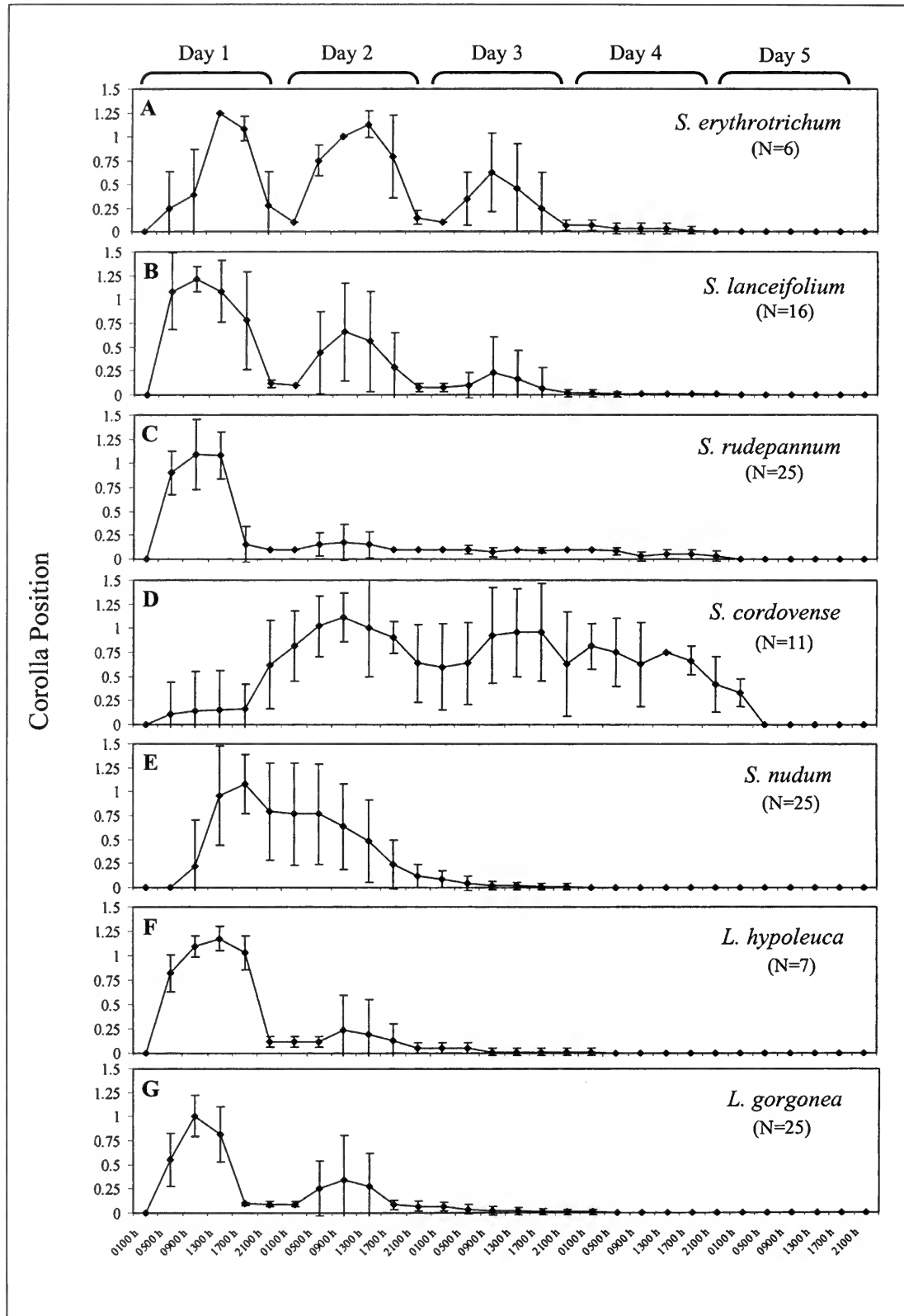
## RESULTS

### Floral phenology

Based on the data collected, the seven species could be divided into two basic groups: those whose flowers opened at sunrise and those whose flowers opened throughout the day and night. The flowers of *Solanum lanceifolium*, *S. rudepannum*, *L. hypoleuca* and *L. gorgonea* opened around 0500 hours, sunrise at Las Cuevas, and closed between 1700 and 2100 hours (Fig. 3B, C, F, G). The flowers of *S. cordovense* and *S. nudum* opened more or less randomly throughout the day and night and remained open through the night, creating the potential for nocturnal pollination (Fig. 3D, E). The corolla of some *S. cordovense* flowers closed partially during the night although never sufficiently to exclude pollinators entirely. *Solanum erythrotrichum* (Fig. 3A) was an intermediate between these two basic groups as its flowers only opened between 0600 and 1300 hours (instead of right around sunrise) and closed at night.

Great variation in the synchrony of flower movements was observed among the seven species. Fig. 3 shows the average position of a corolla of a given species throughout the day. For each data point, standard deviation was calculated to show the variation in corolla position between flowers of the same species. Several species show extreme asynchrony in opening and closing, such as *Solanum cordovense* and *S. nudum*, both of which had long-lived (Fig. 3D, E), small, white flowers less than 1 cm in diameter. This is consistent with the observation that their flowers open randomly throughout the day and night. The large showy white flowers of *S. rudepannum*, *Lycianthes hypoleuca* and *L. gorgonea*, ranging from 1.75 to 2 cm in diameter, opened much more uniformly, particularly on their first day (Fig. 3C, F, G). Flowers of the latter normally opened for one day only (Fig. 3C, F, G), with occasional flowers opening on a second day (perhaps due to lack of pollination).

The flowers of *S. lanceifolium* usually opened to some extent for a second day although they were rarely visited by the bees, which could apparently discern the older flowers (Fig. 3B) (see below). The petals of *S. nudum* remained reflexed for only the first 4 to 12 hours, then the flowers slowly closed over the next day. The petals of *S. cordovense* flowers were reflexed for fewer consecutive hours although they were capable of returning to the reflexed position for several days in a row. This suggests that they continued to be receptive to pollinators for several days after opening or that the reflexed petals act as a pollinator attractant.



**Fig. 3** Corolla movements. Data from up to 25 flowers was combined to produce the graphs. The position of the petals on each flower monitored was recorded every 4 hours using the following scale: 0 = unopened bud (beginning) or flower dead (end); 0.1 = closed but petals not appressed as in the bud; 0.25 = corolla 25% open; 0.50 = corolla 50% open; 0.75 = corolla 75% open; 1.0 = open with petals perpendicular to the pedicel; 1.25 = flowers with petals reflexed. For heterostylous species (*Solanum lanceifolium*, *S. cordovense* and *S. nudum*), only the data from long-styled flowers are shown. Error bars around each point are  $\pm$  one standard deviation. Where no bars appear, the standard deviation is zero.

*Solanum erythrorichum* was an exception to these generalizations. It had flowers of 2 to 2.5 cm in diameter that opened well after sunrise, but they were long-lived, persisting for up to 80 hours (over three days) (Fig. 3A). Each of its flowers opened briefly to the fully reflexed position during late afternoon of its first day before closing for the night. Its flowers then returned to the reflexed position on the second day and occasionally on the third day as well. Old flowers could be distinguished from younger flowers by the purple petals, which darken with age.

## Flower production

All the species flowered at least once during the two-month period of June and July. Two of the species flowered continuously throughout the period: *Solanum nudum* and *S. erythrorichum* (Fig. 4A). *Solanum cordovense*, *S. lanceifolium* and *S. rudepannum* all flowered in late May, paused in mid-June and began to flower again in late June or July (Fig. 4A). The two species of *Lycianthes* were very different from each other in their flowering phenology. *Lycianthes hypoleuca* flowered only during early June (and presumably in late May before monitoring had begun) (Fig. 4A). *Lycianthes gorgonea* flowered for most of June and sporadically in July and still had buds present in late July.

With relation to intensity of flower production, the most prolific bloomers of the seven species were *Lycianthes hypoleuca* and *Solanum nudum*. On average, mature individuals of these species produced around 200 or more flowers (Table 1). Despite the fact that *L. hypoleuca* possesses much larger flowers, the display produced by *S. nudum* overwhelmed that of *L. hypoleuca* because of the sheer number of individuals flowering. While only six of the *L. hypoleuca* individuals monitored flowered, all 25 *S. nudum* individuals flowered, producing a total of 4936 flowers over the 52-day monitoring period. *Solanum lanceifolium* produced the fewest flowers during the monitoring period (Table 1). Considering the number of buds present on individuals at the end of the study, *S. lanceifolium* probably produced quite a large display in August.

Regression analyses revealed significant relationships between canopy cover and flower production for several species. Individuals of both *Solanum cordovense* and *S. lanceifolium* in the shade produced significantly fewer flowers ( $p=0.04$ ,  $p=0.02$  respectively). As colonizers of disturbed areas and secondary forest, these species probably have a low tolerance for shady conditions. Increased canopy cover was also related to a greater proportion of male (short-styled) flowers in the andromonoecious *S. nudum* (Smith & Knapp, in prep.).

## Fruit production

The first species to produce fruit was *Solanum rudepannum*. Its round, green berries were becoming mature in late May and were almost entirely gone by mid-June (Fig. 4B). The fruit of *S. cordovense* were the next to mature, turning from green to a deep purple-black in late June (Fig. 4B). The soft, sweet berries were consumed, probably by birds, in June and July. The fruit of *S. lanceifolium* matured in July, shortly after those of *S. cordovense* (Fig. 4B). Its scarlet berries were not nearly so sweet but quite piquant (pers. obs.). When the berries of *S. lanceifolium* were fully ripe, the fruiting vines attracted large numbers of birds (N. Bol, pers. comm.). *Solanum erythrorichum*, unlike the previous three species, had mature fruit available for the majority of the monitoring period (Fig. 4B). Starting in mid-June, its ripe green fruit began to be taken, although new fruit quickly replaced them. The fruit of the remaining three species were not yet ripe when the monitoring period concluded although it appeared that the fruit of *S. nudum* would mature

first in August, followed by *Lycianthes gorgonea* then *L. hypoleuca* (Fig. 4B).

The amount of fruit produced during June and July varied greatly among the seven species (Table 1). *Solanum nudum* produced the largest number of fruit per individual on average, closely followed by *S. rudepannum*. *Lycianthes gorgonea* produced the fewest, around 13 per individual on average, which was anticipated considering its small floral display (Table 1).

## Flower visitors

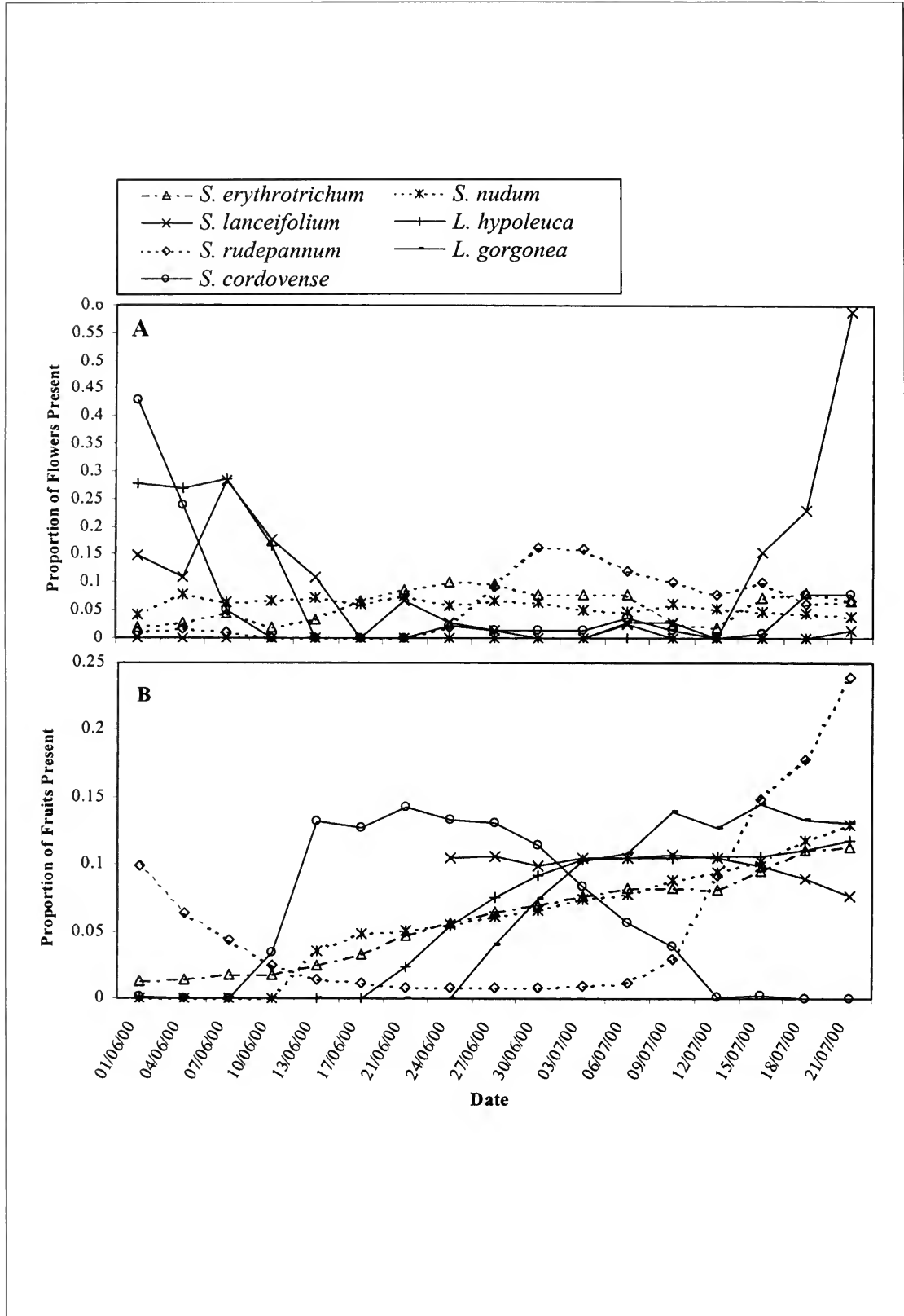
Bees of the families Colletidae, Halictidae and Apidae (Michener, 2000) were the only insects observed to visit, vibrate (buzz) and presumably pollinate the flowers of *Solanum* and *Lycianthes* (listed in Table 2). Pollination is normally effected only by floral visitors that vibrate or buzz the flowers in buzz-pollinated flowers, so we have generally assumed that the visitors we observed were legitimate pollinators of these species. Flowers bagged as part of another study (Smith & Knapp, in prep.) never set fruit. Members of the three bee families we observed at LCRS comprise most of the pollinators of melittophilous Solanaceae (Linsley & Cazier, 1963; Sazima et al., 1993; Raw, 2000). The frequency of visits by the bee species to the study taxa is shown in Table 3. The bees were most active in the morning, and this activity tapered off quickly as the day progressed, a foraging pattern commonly observed in tropical bees (Knapp, 1986; Roubik, 1989). The earliest visitor by far was *Megalopta* sp., which began foraging on *L. hypoleuca* between 0415 and 0430 hours. It was also noted that larger bees tended to be most active early in the morning while smaller bees were active throughout the morning and sometimes into the afternoon (Table 2).

Most bees extracted pollen by buzzing the flower although some small bees obtained pollen by digging into the pores and scavenging on floral parts, as has been observed elsewhere (Anderson & Symon, 1988; Storti, 1988). Bees occasionally dug into the pores after first attempting to buzz the flower, a behaviour that appeared to widen the aperture, allowing the pollen to escape. Neither bees nor other insects were seen to 'rob' pollen by cutting holes into the anthers. In general, large bees visited for shorter periods of time than smaller bees (Table 2), an observation also made by Anderson & Symon (1988). In general, small bees visited small flowers (e.g., those of *Solanum nudum*) while larger bees visited the large flowers (e.g., those of *Lycianthes hypoleuca*).

All bees appeared to locate flowers visually, and were often seen approaching from afar. Once on the flower, bees positioned themselves so that their venter covered the pores of the anthers, and buzzed the anthers to extract the pollen. While buzzing, medium to small bees rotated up to 5 or 6 times to obtain the maximum amount of pollen from each anther. Large bees rotated only once or twice and sometimes not at all. The weight of the large bees was sufficient to invert the flowers, further assisting pollen extraction (Linsley & Cazier, 1963). Bees rarely visited the same flower twice (also noted by Shelly & Villalobos, 2000) and recognition of 'buzzed' flowers may have been assisted by physical changes to the flower. For example, damage by tarsal claws caused bruising on the abaxial anther surface and bees preferentially buzzed flowers free from marks. This preference was tested by bagging flowers on several plants, and allowing the other flowers to be visited and buzzed. When the bags were removed and bees had a choice of buzzed and unbuzzed flowers, only unbuzzed flowers were visited.

The bees observed during this study varied greatly in constancy, as measured by visits to non-conspecifics on a single foraging trip. *Paratetrapedia* sp. was by far the most promiscuous and was observed visiting members of the Melastomataceae, Lamiaceae,





**Fig. 4** Flowering (A) and fruiting (B) phenology from 1 June 2000 to 21 July 2000. Shown is the proportion of flower or fruit present on a given date. This proportion was calculated by summing the total number of flowers or fruit present on all the individuals of a species on a given date and dividing by the total number of flowers or fruit present on all the individuals of a species during the entire monitoring period. Green-fruited species have been given dashed lines; red- or black-fruited species have solid lines.

**Table 1** Flowering and fruiting intensity from 1 June 2000 to 21 July 2000.

|                         |        | Percentage of mature individuals monitored which flowered | Average number of flowers produced per flowering individual | Percentage of individuals monitored which fruited | Average number of fruits produced per fruiting individual |
|-------------------------|--------|---|---|---|---|
| <i>S. erythrorichum</i> | (N=25) | 52%   | 15.85   | 40%   | 13.62   |
| <i>S. lanceifolium</i>  | (N=25) | 32%   | 4.88  | 60%*  | 22.27   |
| <i>S. rudepannum</i>    | (N=10) | 50%   | 51.60   | 40%   | 63.50   |
| <i>S. cordovense</i>    | (N=25) | 52%   | 16.54   | 44%   | 18.55   |
| <i>S. nudum</i>         | (N=25) | 100%  | 197.44  | 80%   | 74.20   |
| <i>L. hypoleuca</i>     | (N=10) | 60%   | 220.00  | 60%   | 33.83   |
| <i>L. gorgonea</i>      | (N=5)  | 80%   | 18.50   | 80%   | 12.75   |

\* A number of individuals of *Solanum lanceifolium* were fruiting when the survey began, remained in fruit and never flowered during the study period.

Piperaceae, and Asteraceae in addition to the Solanaceae. *Paratetrapedia* sp. also flew between study species on a single foraging trip, particularly those which grew side by side, such as *Solanum rudepannum* and *S. nudum*, potentially resulting in interspecific pollen transfer. Some bees visited only solanaceous species, but were not constant to any individual species. For example, *Colletes* sp. visited *S. rudepannum*, *S. nudum* and *S. cordovense* in one foraging trip, but was never observed visiting nearby non-solanaceous species in flower. At the other end of the spectrum were bees like *Xylocopa anthophorides* and *Xylocopa* sp., which were only observed to visit a single study species (Table 2).

### Pollen load analysis

Analysis of pollen loads corroborated field observations that suggested varying levels of constancy among bees. The percentage of pollen from Solanaceae varied from 69.95 to 100.00. More promiscuous pollinators such as *Paratetrapedia* sp. carried lower amounts of solanaceous pollen whereas constant pollinators like *Xylocopa* carried nearly 100% (Table 2). Overall, visitors to the seven study species carried a very high percentage of solanaceous pollen. Unfortunately, it was not possible to distinguish between the pollen of the seven study species.

The size of the pollen load found on the pollinator species generally depended on the size of the bee and how well developed its corbiculae were. Larger bees with well-developed corbiculae such as *Xylocopa* spp. and *Eulaema* sp. carried the most pollen (Table 2), followed by small- and medium-sized apid bees such as *Exomalopsis* sp. 2 and *Melipona* sp. with large corbiculae and hairy bodies (Table 2). The less hairy halictids, which lack corbiculae, carried small amounts of pollen, although *Megalopta* sp. was an exception in foraging only on newly opened, pollen-rich flowers of *Lycianthes hypoleuca*.

## DISCUSSION

### Floral phenology

Patterns of flower movements (i.e., opening and closing of the corolla) often relate to pollination syndrome. Most flower visitation took place in the morning hours, when fresh flowers were presented. Some individuals of *L. hypoleuca* opened their flowers before dawn, allowing pollination by the night-foraging *Megalopta* sp. (Hopkins et al., 2000). Only a few bees foraged throughout the day and these tended to visit plant species that were offering fresh flowers throughout the day, such as *S. nudum*.

Flower movements varied slightly depending on location; e.g., flowers of the individuals of *Lycianthes hypoleuca* near the Las

Cuevas field station opened around 0500 and closed between 1900 and 2100 while those near the observation tower were open between 0430 and 1500 to 1700. The light from the LCRS generator at the former site may account for this difference. Individuals in the sun occasionally had slightly different phenology from those in the shade; e.g., *S. cordovense* in the sun kept their flowers open for a greater number of consecutive days than those in the shade.

Primack (1985) compared the longevity of flowers in major habitat classes and found that most tropical forest species have one-day flowers, regardless of their pollinators. Furthermore, he suggested that within these classes, some variation in longevity within related taxa may be due to flower size. Primack postulated that large flowers would be expected to last longer than small flowers because plants expend more energy to produce them. The present study indicated that the exact opposite is true. The largest-flowered species, with the exception of *S. erythrorichum*, were the most short-lived. This suggests a trade-off between size and longevity where a plant can either maintain energetically-expensive large flowers for a short time or small energetically-inexpensive flowers for a longer time.

### Flower production

Available surveys of flowering phenology in the seasonal tropics indicate that most species exhibit a definite peak or series of peaks in flowering and fruiting at some time during the year (Croat, 1969; Opler et al., 1980; Tanner, 1982; Newstrom et al., 1994). Flowering times for tropical understory herbs and shrubs, like *Solanum* and *Lycianthes*, are often clustered around the transition period from the dry to the wet season (Augspurger, 1983; Knapp, 1986; Oliviera & Gibbs, 2000). This pattern may relate to plants' resource needs such as amount of precipitation (Croat, 1969; Augspurger, 1980, 1983) or their use of environmental cues like temperature to time reproductive activities (Levin, 1978). In the present study, it was only possible to track the study species for two months, an insufficient time to draw conclusions about the phenology over the course of a year or even a season. Locating large numbers of mature individuals in the study area was problematic for the two species of *Lycianthes* and for *S. rudepannum*. Thus, the data presented here provide a preliminary picture of flower production for these seven species.

Plant guilds, i.e., sympatric species sharing a pollination syndrome, may exhibit staggering of flowering times (e.g., Heithaus et al., 1974; Newstrom et al., 1994). Although the buzz-pollinated Solanaceae at LCRS can be considered a guild (Sakai et al., 1999; Murray et al., 2000), there did not appear to be a sequence of flowering times within the study period. Knapp (1986) described a similar situation with eight species of *Solanum* section *Geminata* in Monteverde, Costa Rica, which had randomly distributed and largely overlapping flowering peaks over a year, with some species blooming more than once. Our finding that the multiple buzz-pollinated

**Table 2** Pollinators of *Solanum* and *Lycianthes* species at Las Cuevas. Size classes (length from head to tip of abdomen): Small (<0.75); Medium (0.75–1.25 cm); Large (>1.25 cm).

| Family                   | Species (number observed)              | Size   | Pollen baskets | Time of visits | Average length of visits per flower (seconds) | Number of individuals collected | Average density of pollen | Percent solanaceous pollen | <i>S. erythrorichum</i> | <i>S. lanceifolium</i> | <i>S. rickspanum</i> | <i>S. cordovense</i> | <i>S. nudum</i> | <i>L. hypoleuca</i> | <i>L. gorgonea</i> | Total species visited |
|--------------------------|--|--------|----------------|----------------|---|---------------------------------|---------------------------|----------------------------|-------------------------|------------------------|----------------------|----------------------|-----------------|---------------------|--------------------|-----------------------|
| Colletidae               | <i>Colletes</i> sp. (12)               | Medium | No             | 1000–1320      | 6.9   | 3                               | 2.00                      | 100.00                     | ✓                       | ✓                      | ✓                    | ✓                    | ✓               | ✓                   | ✓                  | 3                     |
| Halictidae               | <i>Lasioglossum</i> sp. (2)            | Small  | No             | 1115           | 1.0   | 1                               | 1.00                      | 94.60                      | ✓                       | ✓                      | ✓                    | ✓                    | ✓               | ✓                   | ✓                  | 2                     |
|                          | <i>Augochloropsis</i> sp. (5)          | Medium | No             | 1020–1200      | 1.1   | 1                               | 1.00                      | 100.00                     |                         |                        |                      |                      |                 |                     |                    | 1                     |
| Apidae                   | <i>Megalopta</i> (16)                  | Medium | No             | 0415–0535      | 6.3   | 4                               | 4.00                      | 99.25                      |                         |                        |                      |                      |                 | ✓                   |                    | 1                     |
|                          | <i>Xylocopa anthiophorides</i> (10)    | Large  | Yes            | 0615–0700      | 3.0   | 1                               | 1.00                      | 98.33                      | ✓                       |                        |                      |                      |                 |                     |                    | 1                     |
|                          | <i>Xylocopa</i> sp. (9)                | Large  | Yes            | 0545–0800      | 2.1   | 1                               | 5.00                      | 100.00                     |                         |                        |                      |                      |                 |                     |                    | 1                     |
|                          | <i>Xylocopa</i> cf. <i>ornata</i> (13) | Large  | Yes            | 0615–0930      | 1.6   | 2                               | 4.00                      | 97.98                      |                         |                        |                      |                      |                 |                     |                    | 1                     |
|                          | <i>Exomalopsis</i> sp. 1 (35)          | Small  | Yes            | 0700–0900      | 9.3   | 4                               | 3.75                      | 99.80                      |                         |                        |                      |                      |                 |                     |                    | 1                     |
|                          | <i>Exomalopsis</i> sp. 2 (1)           | Small  | Yes            | 0800           | 4.0   | 1                               | 1.00                      | 100.00                     |                         |                        |                      |                      |                 |                     |                    | 1                     |
|                          | <i>Paratetrapedia</i> sp. (89)         | Small  | Yes            | 0800–1640      | 8.7   | 4                               | 1.00                      | 72.80                      | ✓                       | ✓                      | ✓                    | ✓                    | ✓               | ✓                   | ✓                  | 6                     |
|                          | <i>Eufriesia</i> sp. (11)              | Large  | Yes            | 0530–1000      | 1.5   | 1                               | 1.00                      | 99.00                      | ✓                       | ✓                      | ✓                    | ✓                    | ✓               | ✓                   | ✓                  | 2                     |
|                          | <i>Euglossa</i> sp. (5)                | Medium | Yes            | 0615–1115      | 1.8   | 1                               | 1.00                      | 96.70                      | ✓                       | ✓                      | ✓                    | ✓                    | ✓               | ✓                   | ✓                  | 2                     |
|                          | <i>Eulaema</i> sp. (8)                 | Large  | Yes            | 0530–0900      | 1.7   | 1                               | 4.00                      | 99.00                      |                         |                        |                      |                      |                 |                     |                    | 1                     |
|                          | <i>Melipona fasciata</i> (12)          | Medium | Yes            | 0630–0900      | 4.1   | 2                               | 3.50                      | 98.50                      |                         |                        |                      |                      |                 |                     |                    | 1                     |
|                          | <i>Melipona</i> sp. (132)              | Medium | Yes            | 0530–1000      | 4.4   | 14                              | 3.54                      | 99.15                      |                         |                        |                      |                      |                 |                     |                    | 2                     |
| <i>Trigona</i> sp. 1     | Small                                  | No     | –              | –              | –   | 1                               | 1.00                      | 100.00                     | ✓                       |                        |                      |                      |                 |                     | 1                  |                       |
| <i>Trigona</i> sp. 2 (1) | Small                                  | No     | 1135           | 2.0            | 2   | 1.00                            | 69.95                     | ✓                          | 5                       | 4                      | 2                    | 1                    | 6               | 9                   | 1                  |                       |

**Table 3** Frequency of pollinator visits on *Solanum* and *Lycianthes* species at Las Cuevas. For each study species, flower hours was calculated from a series of observations (1 to n) using the following equation:  $O = (F_1 \times H_1) + (F_2 \times H_2) + \dots + (F_n \times H_n)$ , where O equals the number of flower-hours, H equals the number of hours a given plant was observed, and F equals the number of flowers present on the plant at the time of observation.

| Species                 | Total number of hours observed | Total number of flowers observed | Number of flower-hours observed | Pollinating visitors per flower-hour | Common pollinators (number which visited during hours observed)  |
|-------------------------|--------------------------------|----------------------------------|---------------------------------|--------------------------------------|--|
| <i>S. erythrorichum</i> | 21.40                          | 61                               | 160.53                          | 0.131                                | <i>Paratetrapedia</i> sp. (17)   |
| <i>S. lanceifolium</i>  | 19.13                          | 79                               | 125.55                          | 0.016                                | <i>Xylocopa anthophorides</i> (10)<br><i>Paratetrapedia</i> sp. (22)<br><i>Eufriesia</i> sp. (10)<br><i>Euglossa</i> sp. (4)   |
| <i>S. rudepannum</i>    | 18.10                          | 242                              | 595.93                          | 0.037                                | <i>Paratetrapedia</i> sp. (16)<br><i>Colletes</i> sp. (5)  |
| <i>S. nudum</i>         | 49.45                          | 1077                             | 2175.77                         | 0.018                                | <i>Paratetrapedia</i> sp. (27)<br><i>Colletes</i> sp. (5)<br><i>Augochloropsis</i> sp. (5)   |
| <i>S. cordovense</i>    | 20.52                          | 82                               | 116.25                          | 0.017                                | <i>Colletes</i> sp. (2)  |
| <i>L. hypoleuca</i>     | 19.52                          | 1190                             | 2017.02                         | 0.116                                | <i>Megalopta</i> sp. (16)<br><i>Xylocopa</i> sp. (9)<br><i>Xylocopa</i> cf. <i>ornata</i> (13)<br><i>Eulaema</i> sp. (8)<br><i>Melipona fasciata</i> (12)<br><i>Melipona</i> sp. (131)<br>inconclusive |
| <i>L. gorgonea</i>      | 19.00                          | 28                               | 71.03                           | 0.014                                |  |

species in the Solanaceae, which share many of the same pollinators, flower simultaneously is consistent with Feinsinger's (1987) observation that pollinator-sharing between sympatric species does not always cause temporal segregation of flower production.

### Fruit production

Vertebrates are the dispersal agents for the majority of Neotropical plant species (Howe & Smallwood, 1982; Janzen, 1983; Murray et al., 2000). For species dependent on biotic dispersal agents, optimization of seed dispersal may involve staggering the time of fruit maturation to avoid interspecific competition for seed-dispersers (Levin, 1978; Fleming, 1985). Staggering of fruiting season has been recorded in the tropical forests of Trinidad in species of *Miconia* (Melastomataceae), whose fruits are dispersed by frugivorous birds (Snow, 1965). At LCRS, it appeared that time of fruit maturation in species potentially sharing the same dispersal agents was somewhat temporally separated. For instance, the brightly-coloured fruit of *Solanum cordovense* matured in late June and early July, those of *S. lanceifolium* in mid-July and those of *Lycianthes gorgonea* in August. By separating the time of fruit maturity, *Solanum* and *Lycianthes* species may maximize seed dispersal and provide a more constant supply of food for frugivorous birds and bats. However, several years of monitoring would be needed to test the staggering of fruit production and dispersal, as variability in seasonal patterns can be high (Wheelwright, 2000).

### Flower visitors

Bees, particularly *Xylocopa*, *Eufriesia*, *Euglossa*, *Eulaema*, *Melipona*, *Trigona* and *Exomalopsis* species, are extremely important pollinators in neotropical forests (Endress, 1994). At La Selva, Costa Rica, for instance, Kress & Beach (1994) record that bees pollinate 38.4% of all plant species, making them the most numerically important pollinators. Our observations at LCRS revealed a diverse array of bees in the Colletidae, Halictidae and Apidae visiting *Solanum* and *Lycianthes*, including many genera observed to pollinate Solanaceae in other tropical habitats (Knapp, 1986; Storti, 1988). Large showy white-flowered species, like *S.*

*lanceifolium* and *L. hypoleuca*, attracted mainly medium and large bees. As the flowers of these two species usually lasted for one day only and opened around sunrise, flower visitors could depend on fresh flowers full of pollen each day and responded by returning daily to forage early in the morning. Longer-lived flowers did not draw such a loyal following. The flowers of *S. erythrorichum* and *S. nudum*, for example, attracted mostly *Paratetrapedia* sp., the small promiscuous bee. Because the flowers opened more or less at random and remained open for several days, bees could not depend on a reliable supply of fresh pollen at a certain time of day. Thus, foraging activity on these species with 'long-lived' flowers was spread throughout the morning and early afternoon.

The pollination ecology of two study species remains unclear. Very few visits were observed on individuals of *Solanum cordovense*. Although its flowers are morphologically similar to *S. nudum*, its small display failed to attract a similar suite of flower visitors. No visitors to *Lycianthes gorgonea* were observed during the study. Its few scattered individuals also produced a small display, never more than ten flowers at a time.

Pre-dawn pollination, as observed in *Lycianthes hypoleuca*, is not unknown in buzz-pollinated Solanaceae. Linsley & Cazier (1963) recorded pollination of *Solanum elaeagnifolium* Cav. and *S. rostratum* Dunal by *Ptiloglossa* and *Caupolicana* (Colletidae) up to an hour before dawn in desert habitats in Arizona. Our finding that flowers of *Lycianthes hypoleuca* open in the darkness and are pollinated before sunrise is particularly interesting because some members of the genus appear to open exclusively at night. Many white-flowered species of *Lycianthes* are nocturnal or crepuscular bloomers (Benítez & D'Arcy, 1997), and flowers are closed during the day (Nee, 1981). No studies of flower longevity or movements have been undertaken with these species however, so it is unclear whether *L. hypoleuca* is unusual in its floral phenology. Members of *Lycianthes* section *Meizodontae*, a small group of primarily Mexican herbs, have flowers that open at dawn and close during the day (Dean, pers. comm., July 2000). These flowers are pollinated by small solitary bees, and open and close over the course of several days. This diversity of floral phenologies in the genus *Lycianthes* suggests adaptive radiation to access different suites of pollinators.

**ACKNOWLEDGEMENTS.** We thank Chris Minty and Nicodemas 'Chapal' Bol for facilitating fieldwork at LCRS; George Else (The Natural History Museum) and Chris O'Toole (University of Oxford) who kindly identified the flower visitors; the Belizean Ministry of Natural Resources for permission to collect voucher specimens; and the helpful comments provided by two anonymous reviewers. SS would like to express her immense gratitude to Dr Barbara Pickersgill for patient and critical review of her Master's thesis on this subject, to Dr Roger Smith for his support and editorial assistance during the development of this paper, and to Stephen Hague for technical assistance at LCRS during part of the study. This work formed part of a MPhil degree awarded by the University of Reading and the University of Birmingham, and was supported by the Marshall Aid Commemoration Commission.

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# The diatom type slides and bibliography of John Carter (1908–1993)

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## CONTENTS

|  |     |
|--|-----|
| Introduction .....                               | 137 |
| Carter's new taxa: types and illustrations ..... | 137 |
| Bibliography .....                               | 150 |
| References .....                                 | 150 |

**SYNOPSIS.** An inventory of John Carter's diatom type slides is given along with a complete bibliography. Details of the whereabouts of Carter's type slides are included along with their geography, references to sources of additional illustrations, and nomenclatural notes.

## INTRODUCTION

'In the heighday of the amateur naturalist nearly everyone who possessed a microscope, however humble the instrument, treasured in his cabinet of slides a few diatom specimens' (Carter, 1971*b*: 66). So wrote John Carter in a short but significant piece on the role of amateur diatomists and the legacy of good specimen collections (Carter, 1971*b*). After his death in 1993 (Marson, 1994; Hartley, 1994), Carter's diatom collection was donated to The Natural History Museum, where it now resides. Carter's collections have added significantly to the data on the British diatom flora, of which Carter's collection is largely composed. In all, the collection consists of some 5000 microscope slides and 4000 bottled samples, along with a variety of notebooks and a card index. The early part of the collection consists of representative material from Rev. Dingley Fuge, an early inspiration for Carter. This material consists of some 1200 bottles that were never made into slides for Carter's collection. Fuge's collection will be the subject of a further paper.

The documentation included with the material makes the collections relatively easy to work with and, along with the recently published collection of drawings (Sims, 1996), forms a major record for the British freshwater diatom flora, spanning a period of six decades (1930–1990).

Carter did not just study the British diatom flora but made a contribution to diatom taxonomy in many areas of the world, including places that have never received attention before. As a consequence of these activities, as well as the detailed study of the British flora, Carter inevitably described a large number of new taxa.

This paper presents a compilation of all new taxa Carter described with details of type specimens and slides. In most cases it was relatively easy to trace the holotype specimen(s) if it was not stated at the time of publication. In Carter's earlier papers where the holotype was not usually cited, slides that may be types have been noted. In most cases a lectotype has not been selected, as that task is best left to those more familiar with the particular diatom under consideration. In some cases, for instance, the comprehensive *Süßwasserflora von Mitteleuropa* (Krammer & Lange-Bertalot, 1986–1991), lectotypes have already been selected and these are indicated in the text below.

In some early papers, Carter noted that some slides were sent to the Quekett Microscopical Society Club. A preliminary examination of those collections has not revealed the material. We have marked these types as 'holotype?' simply because, if found, the Quekett material may very well be the holotype. In most cases we have discovered identical material in the NHM collections which may serve as lectotypes should the need arise.

The nomenclature has been revised in cases where necessary.

## CARTER'S NEW TAXA: TYPES AND ILLUSTRATIONS

### *Achnanthes* Bory 1822

*A. aperta* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 529, pl. 2, fig. 8.

*Holotype*: 'collection Carter, Shet. No. 68a' = BM 87975.

*Locality*: 'In Chumlie Loch, Shetland.'

*Additional illustrations*: Lange-Bertalot & Krammer (1989: 113, taf. 89, figs 13–13') as *Achnanthes oestrupii* var. *aperta* (J.R. Carter) Lange-Bert., '...Holotypus, Coll. Carter Shetland 65A [sic, 68a], Chumlie Loch'; Krammer & Lange-Bertalot (1991a: 82, 344, taf. 48, figs 15–16) as *Achnanthes oestrupii* var. *aperta* (J.R. Carter) Lange-Bert., '...Holotypus'; Sims (1996: 18–19, fig. 3; 2 images).

*Note*: Lange-Bertalot & Krammer (1989: 113) place this taxon in *Achnanthes oestrupii* var. *aperta* (J.R. Carter) Lange-Bert.

*A. atalanta* J.R. Carter 1966: 444, pl. 1, figs 15–16, 19–20.

*Syntypes*: BM 77591-2.

*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae ... Sample No. 6. Crater Lake, on moss, 6500 feet above sea level.' [BM 77591] 'Sample No. 7. As number 6 but on algae.' [BM 77592].

*Additional illustrations*: Lange-Bertalot & Krammer (1989: 23, 63, 204, taf. 19, figs 21–25'), as a possible synonym of *Achnanthes helvetica* (Hust.) Lange-Bert., 'Typenpräp. BM 77591, Tristan da Cunha.'



- A. cassida* J.R. Carter 1970b: 608, pl. 1, figs 17–18.  
*Holotype*: BM 77780.  
*Locality*: ‘Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.’  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 37, 133, taf. 48, figs 9–21), ‘...Holotypus (von *A. cassida*) BM 77780...’ as *Achnanthes rossi* Hust.  
*Note*: Bukhtiyarova & Round (1996: 12) place this taxon in *Psammothidium rossi* (Hust.) Bukht. & Round.
- A. curtissima* J.R. Carter 1963: 200, pl. 1, fig. 3.  
*Holotype*: Not given.  
*Lectotype*: BM 93606. Carter 2630 ‘Fell Loch Wigstow-shire, 3/63’, see below.  
*Locality*: ‘Fell Loch, Wigtownshire. Fresh water, probably not a rare form.’  
*Additional illustrations*: Krammer & Lange-Bertalot (1991a: 21, 344, taf. 11, fig. 8), ‘Holotypus, coll. Carter 2630, Schottland’ = BM 93606. Slide marked as lectotype by Carter. It is worth noting that on slide 4774 (BM 96179, ‘Sheigra, Shetland, Bog’) Carter wrote in his index ‘I still have difficulty with this form [*A. curtissima*]. These specimens are my idea of it.’ This material is not related to type material; Sims (1996: 20–21, pl. 2, fig. 13, 4 images).
- A. didyma* f. *gibbosa* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 530, pl. 23, figs 17–18.  
*Holotype*: Not given.  
*Locality*: Not given.  
*Additional illustrations*: Sims (1996: 22–23, pl. 3, fig. 3A, 2 images).  
*Note*: As synonym of *A. rosenstockii* Lange-Bert. (Lange-Bertalot & Krammer, 1989: 131, no illustrations).
- A. exiloides* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 532, pl. 1, figs 40–43.  
*Holotype*: ‘collection Carter, Shet. No. 35’ = BM 87947.  
*Locality*: ‘In Kirk Loch, Shetland.’  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: taf. 67, figs 20–23’) as ‘*A. expressa* Carter (syn. *A. exiloides* Carter)...Holotypus, Coll. Carter, Kirk Loch/Shetland’; Krammer & Lange-Bertalot (1991a: taf. 31, figs 13–18), ‘Typenpräparat von *A. exiloides* Carter *nom. nov.* = *A. expressa* ...’; Sims (1996: 22–23, pl. 3, fig. 10, 2 images).  
*Notes*: Noted in Lange-Bertalot & Krammer (1989: 55) as ‘*A. expressa* Carter *in litt.*’ and in Krammer & Lange-Bertalot (1991a) as ‘*A. expressa* Carter *nom. nov.*’ but, in fact, the correct citation is *A. expressa* J.R. Carter in Hartley (see below).
- A. expressa* J.R. Carter in Hartley 1986: 606 = *A. exiloides* J.R. Carter in J.R. Carter & Bailey-Watts (1981) non *A. exiloides* Chlonoky (1963).
- A. fugeii* J.R. Carter 1963: 203, pl. 1, fig. 7.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Locality*: ‘Estuary of the Forth. Probably a brackish water form.’  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 58, taf. 32, figs 24–24’), ‘Coll. Carter 39A, Burkwell/Shetland.’ Not type material; Sims (1996: 24–25, pl. 4, fig. 7, 2 images).  
*Note*: There are no relevant slides in Carter’s collection.
- A. fulla* J.R. Carter 1970b: 608, pl. 1, figs 19–20.  
*Holotype*: BM 77780.  
*Locality*: ‘Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic ... collected by Mr. J. Broadhead during the summer of 1966 and 1967.’
- A. hirta* J.R. Carter 1970b: 609, pl. 1, figs 10–11.  
*Holotype*: BM 77780.  
*Locality*: ‘Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.’  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 65, taf. 40, figs 10–12), ‘Holotypus, BM 77780, Andorra’, taf. 31, figs 3–4, ‘...Population aus den Pyrenäen/Andorra (leg. J. Carter)’; Krammer & Lange-Bertalot (1991a: taf. 18, figs 1–4), ‘Holotypus von *A. hirta* Carter, Andorra.’
- A. interrupta* J.R. Carter 1961b: 18, figs 49–50.  
*Holotype*: Not given.  
*Locality*: ‘Found in Strath Farrar in a sphagnum bog at 2000 feet above sea level.’  
*Notes*: Three slides in Carter’s BM collection seem appropriate for selection of a lectotype: BM 93089, ‘W Strath Farrar, 2276’, BM 93090, ‘Strath Farrar, 2276A’, BM 93091, ‘N Strath Farrar, 2276F’. These slides are from the same material (Carter 2276) although in the accompanying notebook the drawings given in the publication are not included in the notes for sample 2276.
- A. investians* J.R. Carter 1966: 445, pl. 1, figs 23–28.  
*Lectotype*: BM 77587. After Lange-Bertalot & Krammer (1989; see below).  
*Syntypes*: BM 77588, BM 77593, BM 77594.  
*Locality*: ‘In aquis dulcibus insulae Tristan da Cunha dictae... Sample No. 2. Above Burntwood, stream at 1800 feet above sea level.’ [BM 77587] ‘Sample No. 3. As number 2 but a little upstream in a pool’ [BM 77588] ‘Sample No. 8. Salt beach at sea level.’ [BM 77593] ‘Sample No. 9. Hottentot Gulch, stream pool, 2000 feet above sea level.’ [BM 77594].  
*Additional illustrations*: Carter (1966: 483) as *A. investians* n. sp. forma, pl. 8, figs 13–14 ‘...form from Gough Island sample 12...Gough Island sample 1006, Steam Gonydale, 1400 feet a.s.l.’ [BM 77600]. Lange-Bertalot & Krammer (1989: 71, taf. 18, figs 27–29’), ‘Typenpräp. BM 77587, Tristan da Cunha’.  
*Note*: Bukhtiyarova & Round (1996: 26) place this taxon in *Psammothidium investians* (J.R. Carter) Bukht. & Round.
- A. lanceolata* f. *rhombica* J.R. Carter 1966: 446, pl. 1, figs 17–18.  
*Holotype*: BM 77586.  
*Locality*: ‘Sample No. 1. Pigbite, stones in running water at sea level.’
- A. lintonensis* J.R. Carter 1961a: 325, figs 15–16.  
*Holotype*: Not given.  
*Locality*: ‘This species is rare and local to areas of the Cheviots.’  
*Additional illustrations*: Sims (1996: 26–27, pl. 5, fig. 11, 2 images).  
*Note*: One slide in Carter’s collection might be an appropriate lectotype: BM 94111, ‘Cheviots, 3019’.
- A. lucana* J.R. Carter 1970b: 609, pl. 1, figs 8–9.  
*Holotype*: BM 77780.  
*Locality*: ‘Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.’
- A. microcephala* f. *scotia* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 534, pl. 1, fig. 31.

- Holotype*: Not given.  
*Locality*: Not given.  
*Lectotype*: BM 94890 (Carter 3665), after Lange-Bertalot in Lange-Bertalot & Krammer (1989: 300). Carter noted on slide 3665 'fo. *scotia* in plenty.'  
*Locality*: Ardislaigh Lochan, June '76.  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 106, taf. 55, figs 11–12), as *Achnanthes minutissima* var. *scotica* (J.R. Carter) Lange-Bert., 'Achnanthes microcephala f. *scotia* Carter, Coll. Carter 3665.' = BM 94890 and Taf. 67, figs 35–36, 'Coll. Carter 3665 Ardislaigh Lochan/Schottland.' = BM 94890; Krammer & Lange-Bertalot (1991a, taf. 31, figs 1–6), 'Coll. Carter aus Schottland und Brunnsee/Oberbayern.' [Not indicated which figures are from Carter material.]  
*Notes*: Lange-Bertalot & Krammer (1989: 106) placed this taxon in *Achnanthes minutissima* var. *scotia* (J.R. Carter) Lange-Bert. and later elevate it to species-level, as *Achnanthes scotia* (J.R. Carter) Lange-Bert. (Lange-Bertalot, 1993: 8). However, *Achnanthes scotia* had already been used by Flower & Jones (1989: 228) hence Lange-Bertalot proposed the substitute name *Achnanthes caledonica* Lange-Bert. in Lange-Bertalot & Moser (1994: 95).
- A. minima** J.R. Carter 1961b: 21, figs 65–66.  
*Holotype*: Not given.  
*Locality*: 'I have found this species in Perthshire and Galloway but only as single cells.'
- A. miota** J.R. Carter & Denny 1982: 286, pl. 1, fig. 9.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone] ... phytoplankton.'  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 107, taf. 87, figs 5–9) as *Achnanthes lanceolata* var. *apiculata* R.M. Patrick, '...Typenpräg. BM 78107, Sierra Leone'; Krammer & Lange-Bertalot (1991a: taf. 46, figs 19–21), 'Typenpräg. Sierra Leone/Afrika.'  
*Note*: As *Achnantheopsis miota* (J.R. Carter) Lange-Bertalot (1997: 207) and *Planothidium miotum* (J.R. Carter) Lange-Bertalot (1999: 278), the latter being the current, accepted name.
- A. natrata** J.R. Carter 1966: 446, pl. 1, figs 1–2.  
*Holotype*: BM 77593.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae ... Sample No. 8. Salt beach at sea level.'
- A. parallela** J.R. Carter 1963: 200, pl. 1, fig. 4.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Syntype?*: BM 93945 = Carter 2904, 'Lindean – on Burrweed', specimen marked.  
*Locality*: 'Well distributed but never in plenty in the hill lochs of the Southern Scottish uplands and the mountainous districts of south-west Scotland.'  
*Additional illustrations*: Krammer & Lange-Bertalot (1991a: taf. 37, figs 24–27), 'Coll. Carter 2904, Schottland' as *A. petersenii* Hust.; Sims (1996: 32–33, pl. 8, fig. 5, 4 images).  
*Notes*: *A. sonyda* J.R. Carter = *A. parallela* J.R. Carter non *A. parallela* Castr. (1886). As *Achnanthes petersenii* Hust. in Lange-Bertalot & Krammer (1989: 117). Carter 2904 is noted on Carter's card file as 'type material' and in the accompanying notebook as 'Pub as parallela JQMC 1963 Vol. 29.'
- A. perfida** J.R. Carter 1963: 200, pl. 1, fig. 2.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Locality*: 'Loch Hempton on the surface of peat, fresh water, not common.'
- Additional illustrations*: Sims (1996: 30–31, pl. 7, fig. 5, 2 images).  
*Notes*: See *Navicula perfidissima* Lange-Bert. There are two slides in Carter's collection which may also be type material: BM 93425, 'Loch Hempton, 2497, BM 93597, 'Loch Hempton, on Weed, 2625, 5/63'.
- A. pericava** J.R. Carter 1966: 447, pl. 1, figs 5–8.  
*Holotype*: BM 77593.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae...Sample No. 8. Salt beach at sea level.'  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 116, 162, taf. 79, figs 40–44'), 'Holotypus, BM 77593, Tristan da Cunha.'; Krammer & Lange-Bertalot (1991a: taf. 40, figs 14–16), 'Holotypus, Tristan da Cunha.'  
*Note*: As *Achnantheopsis pericava* (J.R. Carter) Lange-Bert. (1997: 207) and *Planothidium pericavum* (J.R. Carter) Lange-Bert. (1999: 278), the latter being the current, accepted name.
- A. piafica** J.R. Carter & Denny 1982: 286, pl. 1, fig. 10.  
*Holotype*: BM 78108.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone] ... phytoplankton.'  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 119, taf. 85, fig. 9 and taf. 87, fig. 10), both 'Typenpräg. BM 78108, Sierra Leone.'  
*Note*: Possible synonym of *Achnanthes lanceolata* var. *rostrata* (Østrup) Hust. according to Lange-Bertalot & Krammer (1989: 90).
- A. pictii** J.R. Carter 1963: 203, pl. 1, fig. 8.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Locality*: 'Solway mud flats, not uncommon.'  
*Notes*: Synonym of *Achnanthes linkei* Hust. (Lange-Bertalot & Krammer, 1989: 97, see also p. 119). There are two slides in Carter's BM collection which may also be type material: BM 93583, 'Solway, Mud flats, 2623, 5/63', BM 93584, 'Solway, Mud flats, 2623a, 5/63.'
- A. plana** J.R. Carter 1963: 201, pl. 1, fig. 6.  
*Holotype*: Not given.  
*Lectotype*: BM 93605 = Carter 2629, 'L. Eidrig, 5/63', marked on Carter's card file as 'type slide'.  
*Locality*: 'Loch Eidrig, fresh water, very rarely.'  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 90, 120, taf. 88, figs 22–23), '...Holotypus, Coll. Carter 2629 Loch Eidrig/Schottland' as *Achnanthes lanceolata* var. *robusta* Hust.; Sims (1996: 30–31, pl. 7, fig. 7, 2 images).
- A. pseudoswazi** J.R. Carter 1963: 201, pl. 1, fig. 5.  
*Holotype*: Not given.  
*Locality*: 'Perhaps widely distributed in the larger northern lakes but always odd cells. I have it from regions as far apart as L. Tummel in the north to the Border Country.'  
*Additional illustrations*: Lange-Bertalot & Krammer (1989: 25, taf. 45, figs 37–38), not type material; Krammer & Lange-Bertalot (1991a: taf. 24, figs 1–2), 'Holotypus.' Krammer & Lange-Bertalot do not identify a holotype and, as it was not given in the original description, these illustrations may not be from type material; Sims (1996: 30–31, pl. 7, fig. 12, 3 images).  
*Note*: Bukhtiyarova & Round (1996: 20) place this taxon in *Psammothidium pseudoswazi* (J.R. Carter) Bukht. & Round.
- A. pyropa** J.R. Carter 1970b: 610, pl. 1, figs 1–2.  
*Holotype*: BM 77780.  
*Locality*: 'Sample No. 2 from a ditch near Llorts which is in the

- only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'
- Additional illustrations:* Lange-Bertalot & Krammer (1989: 128, taf. 67, figs 19–19'), 'Coll. Carter 13926, Pyrenäen/Andorra' = BM 77780.
- A. *saccula*** J.R. Carter in J.R. Carter & Bailey-Watts 1981: 535, pl. 24, fig. 6.  
*Holotype:* 'collection Carter, Shet. No. 25.' = BM 87942.  
*Locality:* 'At Punds, Shetland.'  
*Additional illustrations:* Lange-Bertalot & Krammer (1989: 134, taf. 27, figs 20–20'), 'Holotypus, Coll. Carter Shetland 25, "Punds"' = BM 87942; Krammer & Lange-Bertalot (1991a: taf. 15, figs 19–20), '...Holotypus, Shetland.'; Sims (1996: 32–33, pl. 8, fig. 1, 2 images).  
*Note:* Bukhtiyarova & Round (1996: 27) place this taxon in *Psammothidium saccula* (J.R. Carter) Bukht. & Round.
- A. *sonyda*** J.R. Carter in Hartley 1986: 606 = *A. parallela* Carter non *A. parallela* Castr. (1886).
- A. *sphacelata*** J.R. Carter 1970b: 611, pl. 1, figs 41–44.  
*Holotype:* BM 77780.  
*Locality:* 'Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'  
*Additional illustrations:* Lange-Bertalot & Krammer (1989: 143, taf. 67, figs 10–13), 'Holotypenpräp. BM 77780'.
- A. *sumara*** J.R. Carter 1966: 447, pl. 1, figs 21–22.  
*Holotype:* BM 77586.  
*Locality:* 'In aquis dulcibus insulae Tristan da Cunha dictae... Sample No. 1. Pigbite, stones in running water at sea level.'  
*Note:* As *Achnanthes petersenii* Hust. in Lange-Bertalot & Krammer (1989: 117).
- A. *sutura*** J.R. Carter 1970b: 611, pl. 1, figs 39–40.  
*Holotype:* BM 77780.  
*Locality:* 'Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'  
*Additional illustrations:* Lange-Bertalot & Krammer (1989: 145, 149, taf. 21, figs 4–4'), '...Typenpräp. BM 77780' as *Achnanthes subatomoides* (Hust.) Lange-Bert. & R.E.M. Archibald.
- A. *taiaensis*** J.R. Carter & Denny 1982: 288, pl. 1, figs 11–15.  
*Holotype:* BM 78107.  
*Locality:* 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'  
*Additional illustrations:* Lange-Bertalot & Krammer (1989: 150, taf. 67, figs 25–28), 'Holotypus, BM 78107, Sierra Leone'.
- A. *tuma*** J.R. Carter 1970b: 612, pl. 1, figs 35–36.  
*Holotype:* BM 77780.  
*Locality:* 'Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'  
*Additional illustrations:* Lange-Bertalot & Krammer (1989: 154, taf. 67, figs 14–18), 'Holotypenpräp. BM 77780.'
- A. *umara*** J.R. Carter 1970b: 612, pl. 2, figs 1–2.  
*Holotype:* BM 77780.  
*Locality:* 'Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'  
*Additional illustrations:* Lange-Bertalot & Krammer (1989: 145, 154, taf. 21, figs 3–3'), '...Typenpräp. BM 77780' as *Achnanthes subatomoides* (Hust.) Lange-Bert. & R.E.M. Archibald; Sims (1996: 32–33, pl. 8, fig. 13, 4 images).
- A. *wickenensis*** J.R. Carter 1963: 199, pl. 1, fig. 1.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Lectotype:* BM 93539 = Carter 2591 (see below).  
*Locality:* 'Found very sparingly in Wicken Lode. Fresh water July.'  
*Additional illustrations:* Lange-Bertalot & Krammer (1989: 122, 156, taf. 41, figs 17–17'), '...Coll. Carter 3591 [sic, 2591] "Wicken",' as *Achnanthes ploensis* var. *gessneri* (Hust.) Lange-Bert.; Sims (1996: 32–33, pl. 8, fig. 14, 2 images).  
*Note:* There are four slides in Carter's BM collection which may also be type material: BM 93586, 'Wicken Lode, Cambs'. BM 93587, 'Wicken Lode, Cambs', BM 93588, 'Wicken Lode, Cambs', BM 93539, 'Wicken Lode, 2591a.'
- Amphora*** Ehrenb. ex Kütz. 1844
- A. *eximia*** J.R. Carter in Haworth 1974: 48, figs 3, 14.  
*Holotype:* BM 77902.  
*Locality:* 'Loch Leven, 20cm.'  
*Additional illustrations:* Sims (1996: 52–53, pl. 18, figs 8–9, 5 images).
- A. *incurvata*** J.R. Carter 1966: 448, pl. 3, figs 29–31.  
*Holotype:* BM 77593.  
*Locality:* 'In aquis dulcibus insulae Tristan da Cunha dictae...Sample no. 8. Salt beach at sea level.'
- Anomoeneis*** E. Pfitzer 1871
- A. *serians*** var. *brachysira* f. *minuta* J.R. Carter 1961d: 75, fig. 13.  
*Holotype:* Not given  
*Locality:* '...from the bed of Loch na Cuilic.'  
*Note:* There are a number of slides in the collection from this locality. A possible lectotype is BM 93364, which is the sample cleaned by Mr S. Meakin which 'he has separated the very light forms' (Carter 1961d: 74) although in Carter's notebook there is no mention of a new form in relation to this slide. Another possible lectotype is BM 93297-8. These are the slides Carter prepared from the cleaned material and in his notebook he wrote 'list for publication...list sent 17/6/61.' The list does not include f. *minuta* but does note the occurrence of a new variety.
- Asterionella*** Hassall 1850
- A. *contorta*** J.R. Carter & Denny 1987: 234, pl. 1, figs 7–8.  
*Holotype:* BM 81159.  
*Locality:* '...coastal strip of South-Western Sierra Leone...Sample 68 (16<sup>th</sup> April 1976)...Phytoplankton horizontal haul...Lake Mape.'
- Berkella*** R. Ross & P.A. Sims 1978
- B. alpina*** J.R. Carter ex D.M. Williams *nov. sp.*  
*Description:* In Carter (1993a: 106, figs 24–25).  
*Holotype:* BM 94636 = Carter no. 3462. As *Berkella alpina* (Amossé) J.R. Carter in Carter (1993a: 106, figs 24–25) and *Berkella spicula* (Amossé) J.R. Carter in J.R. Carter & Bailey-Watts (1981: 539, pl. 2, fig. 38, pl. 24, fig. 12).  
*Locality:* 'Etrick Valley, S. Scotland; August 1974.'  
*Additional illustrations:* Sims (1996: 84–85, figs 8–15, 16 images as *Berkella spicula* var. *alpina* Amossé); Krammer & Lange-Bertalot (1986: 634, fig. 7), 'Shetlands, Pr. Carter') as *Frustulia spicula* Amossé.  
*Notes:* Ross & Sims (1978: 156) described the new genus *Berkella* R. Ross & P.A. Sims basing it on specimens of *B. linearis* R. Ross

& P.A. Sims, discovered in Loch Poit na h'I. Mull, Scotland. Although they write that their species 'was first described by Amossé under the name *Frustulia spicula* var. *alpina*...' his name was invalid as 'he did not designate a type'. They continue: '[we have] adopted a new epithet to make it quite clear that we are not basing our species on Amossé's variety' (Ross & Sims, 1978: 158). Carter concluded, after examination of a variety of specimens, that *Frustulia spicula* var. *alpina* was indeed another species of *Berkella*, distinct from *B. linearis*. Carter described his *Berkella alpina* as a new combination but as *Frustulia spicula* var. *alpina* had no designated type, it should have been described as a new species.

*Caloneis* Cleve 1894

*C. borealis* J.R. Carter 1971a: 660, pl. 1, figs 1–3.

*Syntypes*: BM 77777-8.

*Locality*: 'Devil's Hole Cave. '...Kinraig Hill at the south-western extremity of Kilconquhar parish, Fife...collected by the late Mr. Geo. West of University College, Dundee, in the second decade of this century [1920s].'

*Additional illustrations*: Sims (1996: 96–97, pl. 40, figs 9–10, 6 images).

*C. continua* J.R. Carter 1964: 225, pl. 2, fig. 9.

*Holotype*?: Slides in Quekett Microscopical Society Collections.

*Locality*: 'Loch Maben Dumfriesshire, fresh water, seemingly somewhat rare.'

*Note*: There are nine slides in Carter's BM collection which may be type material: BM 92993, 'Loch Maben, 2204', BM 93261, 'Loch Maben, Mud, 2371', BM 93262, 'Mabon, 2371A, BM 93263, 'Loch Maben, Mud, 2371C', BM 93264, 'Loch Maben, 2371P', BM 93265, 'Loch Maben, 2371R', BM 93282, 'Loch Maben, Mud, 2387', BM 93569, 'Loch Maben, 2612, BM 93570, 'Loch Maben, 2613'.

*C. inliberalis* J.R. Carter & Denny 1992: 164, pl. 1, fig. 23.

*Holotype*: BM 81522.

*Locality*: 'Lake Popei...sample 54 [Sierra Leone].'

*C. lauta* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 540, pl. 23, figs 6, 8.

*Holotype*: 'collection Carter, Shet. 11.' = BM 87928.

*Locality*: 'In Burga Water, Shetland.'

*Additional illustrations*: Krammer & Lange-Bertalot (1986: 389, taf. 173, fig. 3), 'Holotypus Shetlands, Burga Water, Coll. Carter'; Sims (1996: 100–101, pl. 42, fig. 8, 4 images).

*C. lepidiformis* J.R. Carter & Denny 1987: 235, pl. 1, fig. 12.

*Holotype*: BM 81147.

*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 5 (18<sup>th</sup> Feb. 1976)...Periplankton scraped from *Vossia* stems...Lake Mape.'

*C. liophilla* J.R. Carter 1966: 448, pl. 8, fig. 20.

*Holotype*: BM 77599.

*Locality*: 'In aquis dulcibus insula Gough Island ...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'

*C. toxsa* J.R. Carter 1966: 449, pl. 2, fig. 19.

*Holotype*: BM 77595.

*Locality*: 'In aquis dulcibus insulae Tristan da Cunha...Sample No. 10. New lava field, stream and moss.'

*C. transepta* J.R. Carter 1966: 449, pl. 2, fig. 18.

*Holotype*: BM 77595.

*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae...Sample No. 10. New lava field, stream and moss.'

*Cocconeis* Ehrenb. 1837

*C. confusa* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 542, pl. 3, fig. 34.

*Holotype*: 'collection Carter, Shet. No. 54a.' = BM 87963.

*Locality*: 'In Hevdadale Water, Shetland.'

*Additional illustrations*: Lange-Bertalot & Krammer (1989: 72, taf. 67, figs 34–34'), '...Holotypus, Coll. Carter [Shet.] 54A, Hevdadale/Shetland' as *Achnanthes johncarteri* Lange-Bert.; Krammer & Lange-Bertalot (1991a: taf. 18, figs 22–23) as *Achnanthes johncarteri* Lange-Bert., '...Holotypus, Shetland'; Sims (1996: 118–119, pl. 51, fig. 4, 2 images).

*C. diversa* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 544, pl. 3, fig. 33.

*Holotype*: 'collection Carter, Shet. No. 22.' = BM 87939.

*Locality*: 'In Spiggie Loch, Shetland.'

*Additional illustrations*: Lange-Bertalot (1989: 130, taf. 70, figs 2–2'), '...Holotypus, Coll. Carter Shet. 22, Spiggie Loch' as *Achnanthes reversa* Lange-Bert. & Krammer; Krammer & Lange-Bertalot (1991a: taf. 18, figs 20–21) as *Achnanthes reversa* Lange-Bert. & Krammer, '...Holotypus, Shetland'; Sims (1996: 118–119, pl. 51, fig. 13, 2 images).

*Note*: Bukhtiyarova & Round (1996: 23) place this taxon in *Psammothidium reversum* (Lange-Bert. & Krammer) Bukht. & Round.

*C. leonis* J.R. Carter & Denny 1987: 236, pl. 1, fig. 14.

*Holotype*: BM 81147.

*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 5 (18<sup>th</sup> Feb. 1976)...Periplankton scraped from *Vossia* stems...Lake Mape.'

*C. toxsa* J.R. Carter & Denny 1987: 236, pl. 1, figs 16–17.

*Holotype*: BM 81154.

*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'

*Cyclotella* (Kütz.) Bréb. 1838

*C. bastowii* J.R. Carter 1961d: 75, fig. 7.

*Holotype*: Not given.

*Locality*: '...from the bed of Loch na Cuilic.'

*Notes*: There are a number of slides from Loch na Cuilic in Carter's collection. The most likely lectotype is slide 2457 in Carter's collection (BM 93364, 'Loch na Cuilic, 2457'). In Carter's notebook entry for sample 2457 he notes '[new] *Cyclotella*' with a slide finder reference number. Thus it would seem that sample 2457 was type material. The entry has been crossed out in pencil with the words 'slide broken' added. BM 93364 is a strewn slide that happens to be broken. The break is on the glass slide and appears not to have damaged the coverslip. However, the slide has been mended with adhesive tape, which harbours a faint impression of a coverslip suggesting that the existing coverslip was moved or re-mounted after the break occurred. One other slide made from Carter's 2457 material (BM 93365) is a selected slide with no specimens of *Cyclotella*.

*C. cyclopuncta* Håk. & J.R. Carter 1990: 155, figs 6–8.

*Holotype*: Carter Collection no. 4112 [=BM 95423].

*Locality*: 'Plitvicer See, tree-trunk.'

*Additional illustrations*: Håkansson in Krammer & Lange-Bertalot (1991b: taf. 51, figs 10–14), 'Baumstamm, Plitvicer See, Typenmaterial.'

*C. delicatissima* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 545, pl. 4, fig. 14A.

- Holotype*: 'collection Carter, Shet. No. 32a.' = BM 87945.  
*Locality*: 'In Mussell Loch, Shetland.'  
*Additional illustrations*: Sims (1996: 132–133, pl. 58, fig. 5, 1 image).
- C. minima** H.G. Barber & J.R. Carter 1970: 272, figs 8–9.  
*Holotype?*: 'Typus in collectione Quekett Microscopical Club.'  
*Locality*: '...fossil diatomaceous earth situated in Gordon Road, Auckland, New Zealand at co-ordinates 225,110E, 656,720N, Square G.7 of New Zealand M.S. 17, 1962 Edition 'Auckland'.'
- C. stelligeroides f. irregularis** J.R. Carter 1966: 450, pl. 8, fig. 17.  
*Holotype*: BM 77599.  
*Locality*: 'In aquis dulcibus insulae Gough Island dictae...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'
- Cymbella** C. Agardh 1830
- C. citrus** J.R. Carter in J.R. Carter & Bailey-Watts 1981: 548, pl. 6, figs 26–29.  
*Holotype*: 'collection Carter, Shet. No. 42b.' = BM 87952.  
*Locality*: 'Loch, west of Funzie, Shetland.'  
*Additional illustrations*: Krammer & Lange-Bertalot (1985: 23, taf. 8, figs 9–11), 'Typenpräparat Carter 428/1978 [sic, 42 b], Shetlands', as *Cymbella amphicephala* var. *citrus* (J.R. Carter in J.R. Carter & Bailey-Watts) Krammer; Krammer & Lange-Bertalot (1986: 335, taf. 142, figs 15–16), 'Typenpräp. Shetlands, Coll. Carter 42 B/1978', as *Cymbella amphicephala* var. *citrus* (J.R. Carter in J.R. Carter & Bailey-Watts) Krammer; Sims (1996: 140–141, pl. 64, fig. 2, 3 images).
- C. diavola** J.R. Carter 1971a: 662, pl. 1, figs 6–8.  
*Syntypes*: BM 77777–8.  
*Locality*: 'Devil's Hole Cave.' '...Kincaig Hill at the south-western extremity of Kilconquhar parish, Fife...collected by the late Mr. Geo. West of University College, Dundee, in the second decade of this century [1920s].'  
*Additional illustrations*: Krammer & Lange-Bertalot (1985: 26, taf. 6, fig. 16), 'Isotypus...', as *Cymbella falaisensis* (Grunow) Krammer & Lange-Bert.; Krammer & Lange-Bertalot (1986: taf. 134, fig. 19), 'Typenpräp...' as *Cymbella falaisensis* (Grunow) Krammer & Lange-Bert.  
*Note*: As *Encyonopsis falaisensis* (Grunow) Krammer in Krammer (1997b: 116).
- C. difficilis f. capitata** J.R. Carter & Denny 1992: 167, pl. 1, figs 42–43.  
*Holotype*: BM 81522.  
*Locality*: 'Lake Popei...sample 54 [Sierra Leone].'
- C. ioica** J.R. Carter & Denny 1982: 291, pl. 2, fig. 43.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- C. lembus** J.R. Carter & Denny 1992: 167, pl. 1, fig. 44, pl. 2, fig. 12.  
*Holotype*: BM 81506.  
*Locality*: 'In sample 3, a stream near Lake Sonfon [Sierra Leone].'
- C. umara** J.R. Carter & Denny 1982: 291, pl. 1, fig. 40.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'  
*Additional illustrations*: In Krammer (1997a: taf. 97, fig. 10), reproduction of Carter & Denny (1982: pl. 1, fig. 40).  
*Note*: As *Encyonema umara* (J.R. Carter & Denny) Krammer in Krammer (1997b: 83).
- Diploneis** Ehrenb. ex Cleve 1894
- D. volsella** J.R. Carter & Denny 1987: 239, pl. 1, fig. 36.  
*Holotype*: BM 81157.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 67 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul near Bandako...River Malen.'
- Eunotia** Ehrenb. 1837
- E. ambigua** J.R. Carter 1966: 451, pl. 2, figs 11–15, 20.  
*Holotype*: BM 77587.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae...Sample No. 2. Above Burntwood, stream at 1800 feet above sea level.'
- E. cantica** J.R. Carter & Denny 1992: 171, pl. 3, fig. 26.  
*Holotype*: BM 81507.  
*Locality*: 'In sample 4... [Sonfon swamp, Sierra Leone].'
- E. diverta** J.R. Carter 1966: 452, pl. 9, figs 6–7.  
*Holotype*: BM 77599.  
*Locality*: 'In aquis dulcibus insula Gough Island dictae...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'
- E. germainii** J.R. Carter 1990: 14, pl. 1, figs 1–56.  
*Holotype*: 'BM 81621' (sic) = BM 81622.  
*Locality*: 'In Avoca, Hibernia, inventa...Avoca, County Wicklow, Irish Free State...June 1975...'  
*Additional illustrations*: Sims (1996: 206–207, figs 2–6, 27 images).
- E. incurva** J.R. Carter 1966: 453, pl. 2, figs 7–8, 16.  
*Syntypes*: BM 77591–2.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha...Sample No. 6. Crater Lake on moss, 6500 feet above sea level.' [BM 77591] 'Sample No. 7. As number 6 but on algae.' [BM 77592].
- E. johncarterii** D.M. Williams, *nom. nov.* = *E. pectinoides* J.R. Carter (1966: 454, pl. 9, figs 4–5) non *E. pectinoides* Zimmermann (1915: 35, fig. 9).
- E. marginistriata** J.R. Carter & Denny 1992: 172, pl. 3, figs 13–14.  
*Holotype*: BM 81509.  
*Locality*: 'In sample 5 [Lake Sonfon, stream, Sierra Leone].'
- E. morbida** J.R. Carter 1966: 453, pl. 9, figs 23–24.  
*Holotype*: BM 77599.  
*Locality*: 'In aquis dulcibus insula Gough Island dictae...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'
- E. pectinoides** J.R. Carter 1966: 454, pl. 9, figs 4–5, 22.  
*Holotype*: BM 77599.  
*Locality*: 'In aquis dulcibus insula Gough Island ...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'  
*Notes*: non *E. pectinoides* Zimmermann (1915); see *E. johncarterii* D.M. Williams, *nom. nov.*
- E. pirla** J.R. Carter & Flower 1988: 2, figs 17–48, 51–53, 55–56, 57–62.  
*Holotype*: BM 17870, Kützing coll. 'Pitchdale, Trinidad, ex Kruger, Kutz. 29'.  
*Syntypes*: BM 81400–2, BM 95889.  
*Locality*: 'Woolmer Pond, a strongly acid pool in Hampshire, England...'  
*Additional illustrations*: Krammer & Lange-Bertalot (1991a: 556, taf. 163, figs 8–13), ('Typenmaterial, Coll. Carter 5415 [sic,

- = 4514], Woolmer Pond/East Hampshire' = BM 95889) as *E. veneris* (Kütz.) De Toni.
- E. rica** J.R. Carter & Denny 1987: 240, pl. 2, figs 9–10.  
*Holotype*: BM 81157.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 67 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul near Bandako ...River Malen.'
- E. testula** J.R. Carter & Denny 1987: 242, pl. 2, fig. 14.  
*Holotype*: BM 81154.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'
- Fragilaria** Lyngb. 1819
- F. brevistriata** f. *australis* J.R. Carter 1966: 454, pl. 7, fig. 10.  
*Holotype*: BM 77593.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha...Sample No. 8. Salt beach at sea level.'
- F. taiaensis** J.R. Carter & Denny 1982: 296, pl. 3, fig. 82.  
*Holotype*: BM 78110.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from submerged wood.'
- F. telum** J.R. Carter & Denny 1987: 243, pl. 11, fig. 25.  
*Holotype*: BM 81154.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'
- Gomphonema** C. Agardh 1824
- G. asymmetricum** J.R. Carter 1966: 455, pl. 6, figs 8–10, 17.  
*Holotype*: BM 77595.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae...Sample No. 10. New lava field, stream and moss.'  
*Note*: non *G. asymmetricum* Gutw. (1890: 28, pl. 1, fig. 24). See *G. johncarterii* D.M. Williams, *nov. nom.*
- G. dintara** J.R. Carter & Denny 1982: 298, pl. 3, figs 100–102.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- G. johncarterii** D.M. Williams, *nov. nom.* = *G. asymmetricum* J.R. Carter (1966: 455–456, pl. 6, figs 8–10, 17) non *G. asymmetricum* Gutw. (1890: 28, pl. 1, fig. 24).
- G. invidia** J.R. Carter & Denny 1982: 298, pl. 3, figs 94–95.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- G. parvulissima** J.R. Carter 1970b: 616, pl. 3, figs 10–12.  
*Holotype*: BM 77780.  
*Locality*: 'Sample No. 2 from a ditch near Lloris which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'
- G. spatulum** J.R. Carter : 1966: 456, pl. 6, fig. 12, pl. 7, fig. 23.  
*Holotype*: BM 77590.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae... Sample No. 5. Big Waterburn, stones in stream, 100 feet above sea level.'
- G. subula** J.R. Carter & Denny 1982: 299, pl. 4, fig. 107.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- G. taiaensis** J.R. Carter & Denny 1982: 299, pl. 3, figs 97–99.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- G. tholus** J.R. Carter & Denny 1992: 177, pl. 4, figs 12–13.  
*Holotype*: BM 81506.  
*Locality*: 'In sample 3 [Lake Sonfon, Sierra Leone].'
- Gomphonitzschia** Grunow 1868
- G. taiaensis** J.R. Carter & Denny 1982: 300, pl. 4, fig. 108.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- Gyrosigma** Hassall 1845
- G. algoris** J.R. Carter in J.R. Carter & Bailey-Watts 1981: 569, pl. 10, figs 6–8.  
*Holotype*: 'collection Carter, Shet. No. 4b.' = BM 87922.  
*Locality*: 'In Moo Water, Shetland.'  
*Additional illustrations*: Krammer & Lange-Bertalot (1986: taf. 116, fig. 1), 'Syntypus, Shetlands' as *G. obscurum* (W. Sm.) J.W. Griff. & Henfr.; Sterrenberg (1993: 450, figs 5, 8, 10–13, '...type material, Moo Waters, Shetland...'); Sims (1996: 244–245, pl. 114, fig. 3, 2 images).
- Krasskella** R. Ross & P.A. Sims 1978
- K. hyalina** J.R. Carter & Denny 1992: 178, pl. 4, figs 15–15a.  
*Holotype*: BM 81509.  
*Locality*: 'Rarely in sample 5 [Lake Sonfon, stream, Sierra Leone].'
- Melosira** C. Agardh 1824
- M. dispersa** J.R. Carter 1966: 457, pl. 8, fig. 16.  
*Holotype*: BM 77599.  
*Locality*: 'In aquis dulcibus insula Gough Island dictae...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'
- M. incorrupta** J.R. Carter 1966: 458, pl. 8, fig. 18.  
*Syntypes*: BM 77599-77600.  
*Locality*: 'In aquis dulcibus insula Gough Island dictae...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.' [BM 77599] 'Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.' [BM 77600].
- M. johncarterii** D.M. Williams, *nov. nom.* = *M. setosa* J.R. Carter (1966: 458, pl. 9, figs 12–14) non *M. setosa* Grev. (1866: 436, pl. 6, figs 17–19).
- M. setosa** J.R. Carter 1966: 458, pl. 9, figs 12–14.  
*Syntypes*: BM 77599-600.  
*Locality*: 'In aquis dulcibus insula Gough Island dictae...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.' [BM 77599] 'Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.' [BM 77600].  
*Note*: non *M. setosa* Grev. (1866: 436, pl. 6, figs 17–19), see *Melosira johncarterii*.
- M. transitus** J.R. Carter & Denny 1987: 247, pl. 4, fig. 9.  
*Holotype*: BM 81154.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'
- Navicula** Bory 1822
- N. abica** J.R. Carter 1966: 458, pl. 9, fig. 9.  
*Holotype*: BM 77599.  
*Locality*: 'In aquis dulcibus insula Gough Island dictae...Sample No. 11. Gough Island sample 1003, Cave Bell Rocks, sea level.'



- N. amerinda* J.R. Carter 1966: 459, pl. 3, figs 1–6.  
*Holotype*: BM 77586.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha...Sample No. 1. Pigbite, stones in running water at sea level.'
- N. anca* J.R. Carter 1964: 227, pl. 2, fig. 15.  
*Holotype*: Not given.  
*Locality*: 'Several lochs in the southern Scottish Uplands.'
- N. armata* J.R. Carter 1964: 228, pl. 2, fig. 16.  
*Holotype*: Not given.  
*Lectotype*: BM 92964 ('Rubens Law, 2188, April, 1953'). This slide is the only one that Carter refers to in his index.  
*Locality*: 'Growing in wet vegetation on the cliffs, Bewickshire.'  
*Additional illustrations*: Sims (1996: 278–279, pl. 131, fig. 3, 2 images).
- N. arvensiformis* J.R. Carter 1970*b*: 617, pl. 2, fig. 18.  
*Holotype*: BM 77782.  
*Locality*: 'Sample No. 4 from a clear stream near Soldeu...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'
- N. aspergilla* J.R. Carter & Denny 1992: 181, pl. 6, figs 1–5.  
*Holotype*: BM 81509.  
*Locality*: 'In sample 5 quite commonly [Lake Sonfon, stream, Sierra Leone].'
- N. bacillum* f. *delicatula* J.R. Carter & Denny 1982: 302, pl. 5, fig. 175.  
*Holotype*: Not given.  
*Locality*: Not given.  
*Note*: This taxon should belong in the genus *Sellaphora* Mereschk.
- N. belsesiensis* J.R. Carter 1984: 134, figs 5–7*a*.  
*Holotype*: BM 81188.  
*Locality*: '...small ditch near Belses on the Scottish side of the Border.'
- N. bintila* J.R. Carter & Denny 1982: 302, pl. 6, fig. 190.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- N. bottnica* f. *acuta* J.R. Carter & Denny 1992: 181, pl. 5, fig. 2.  
*Holotype*: BM 81508.  
*Locality*: '...in sample 4...[Lake Sonfon, Sierra Leone]'
- N. brockmannii* f. *concava* J.R. Carter 1966: 460, pl. 3, fig. 14.  
*Holotype*: BM 77590.  
*Locality*: 'Sample No. 5. Big Waterburn, stones in stream, 100 feet above sea level.'
- N. caenosus* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 574, pl. 11, fig. 41.  
*Holotype*: 'collection Carter, Shet. No. 16*a*.' = BM 87933.  
*Locality*: 'In Houlma Water, Shetland.'  
*Additional illustrations*: Sims (1996: 282–283, pl. 133, fig. 5, 2 images; 356–357, pl. 170, fig. 11, 1 image).
- N. carterii* VanLand. (1975: 2520) see *N. dispersa* J.R. Carter.
- N. chaspula* J.R. Carter & Denny 1982: 304, pl. 6, fig. 191.  
*Syntypes*: BM 78108, BM 78112.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from phytoplankton.' [BM 78108] 'River Jong (Taia) at Njala [Sierra Leone]...from rotting leaves.' [BM 78112].
- N. claytoni* J.R. Carter 1987: 633, figs 1–10.  
*Syntypes*: BM 81413–4.  
*Locality*: 'In Gala Water inventa...In February 1986 Mr John Clayton...took a sample of diatoms from the tributary of the River Tweed, the Gala Water.'
- Additional illustrations*: Sims (1996: 284–285, pl. 134, fig. 5, 2 images).
- N. cocconeoides* J.R. Carter 1964: 227, pl. 2, fig. 13.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Syntypes*: BM 93582, 'Madingly Brick Pit, Cambridge, 2622, 5/63'; BM 93794, 'Maddingly, Brick Pit, on Liverworts, 2777, 5/63.'  
*Locality*: 'Madingly Brick Pit, Cambridge.'  
*Additional illustrations*: Sims (1996: 286–287, pl. 135, fig. 2, 1 image).  
*Notes*: non *Navicula cocconeoides* (Rabenh.) Ralfs in A. Pritch. (1861: 909). Although the spelling of the specific epithet for Carter's taxon is similar to that of Ralfs, the two taxa would be hard to confuse. While there may be justification in re-naming Carter's taxon, we have chosen to retain it.
- N. concentrica* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 576, pl. 11, fig. 7.  
*Holotype*: 'collection Carter, Shet. No. 2.' = BM 87920.  
*Locality*: 'In Blister Punds, Shetland and several other locations.'  
*Additional illustrations*: Sims (1996: 286–287, pl. 135, fig. 6, 3 images).  
*Note*: non *N. concentrica* Bailey (1844: 139, pl. 3, figs 13–15). Inspection of Bailey's illustrations of his *Navicula concentrica* clearly show specimens of *Goniothecium* Ehrenb. while Carter's *Navicula concentrica* is certainly a species of *Navicula sensu stricto*. Nevertheless, Bailey's name still has priority hence Carter's taxon is renamed here as *Navicula johncarterii* D.M. Williams, *nov. nom.*
- N. crepitacula* J.R. Carter & Denny 1982: 304, pl. 6, fig. 189.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- N. cuvella* J.R. Carter & Denny 1982: 306, pl. 6, figs 193–194, 218.  
*Holotype*: BM 78108.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from phytoplankton.'
- N. decissa* J.R. Carter 1966: 461, pl. 3, fig. 11.  
*Holotype*: BM 77587.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae... Sample No. 2. Above Burntwood, stream at 1800 feet above sea level'.
- N. dispersa* J.R. Carter 1964: 225, pl. 2, fig. 10.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Locality*: 'Loch Hempton in the peat, fresh water, not common.'  
*Additional illustrations*: Sims (1996: 282–283, pl. 133, fig. 12, 1 image).  
*Note*: *N. carterii* VanLand. (1975: 2520) = *N. dispersa* J.R. Carter non *N. dispersa* Grove & Sturt (1887: 132, pl. 10, fig. 10) nec *N. dispersa* Manguin (1942: 137, pl. 2, fig. 32). Should the Quekett slides not materialize then BM 93597 will be a suitable lectotype: 'Loch Hempton, on Weed, 2625, 5/63, *Navicula carterii*.'
- N. diverta* J.R. Carter 1966: 461, pl. 3, figs 19–20.  
*Holotype*: BM 77591.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae... Sample No. 6. Crater Lake on moss, 6500 feet above sea level.'
- N. eidrigiana* J.R. Carter 1979: 78, figs 58–64, 70–72.  
*Holotype*: BM 78083.

- Locality*: 'Loch Eidrig, south west Scotland...' (Carter, 1979: 78).  
*Additional illustrations*: Sims (1996: 296–297, fig. 1, 9 images); Lange-Bertalot (2001: 34, pl. 43, figs 1–6).
- N. friska** J.R. Carter 1966: 462, pl. 3, figs 7–10.  
*Syntypes*: BM 77587-8.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae... Sample No. 2. Above Burntwood, stream at 1800 feet above sea level.' [BM 77587] 'Sample No. 3. As number 2 but a little upstream in a pool' [BM 77588].
- N. glomus** J.R. Carter in J.R. Carter & Bailey-Watts 1981: 578, pl. 13, fig. 17.  
*Holotype*: 'collection Carter, Shet. No. 39a' = BM 87950.  
*Locality*: 'At Burkwell, Shetland.'  
*Additional illustrations*: Krammer & Lange-Bertalot (1986: taf. 71, fig. 39), 'Typenpräg. Coll. Carter Shetland 39 a.'
- N. gralana** J.R. Carter & Denny 1982: 306, pl. 6, fig. 195.  
*Holotype*: BM 78108.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from phytoplankton.'
- N. insepia** J.R. Carter & Denny 1982: 307, pl. 6, figs 197–198.  
*Holotype*: BM 78108.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from phytoplankton.'
- N. inexpectans** J.R. Carter 1964: 227, pl. 2, fig. 12.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Locality*: 'Loch Mochrum fresh water as isolated cells.'  
*Additional illustration*: Sims (1996: 308–309, pl. 146, fig. 10, 1 image).  
*Note*: Two additional slides in the Carter collection may be type material: BM 93573, 'Loch Mochrum, on stones, 2616, 5/63'; BM 93578, 'Loch Mochrum, mud, 2619, 5/63.'
- N. involata** J.R. Carter & Denny 1982: 307, pl. 6, fig. 199.  
*Syntypes*: BM 78111-2.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.' [BM 78111] 'River Jong (Taia) at Njala [Sierra Leone]...from rotting leaves.' [BM 78112].
- N. johncarterii** D.M. Williams, *nov. nom.* = *N. concentrica* J.R. Carter in J.R. Carter & Bailey-Watts (1981: 576, pl. 11, fig. 7) non *N. concentrica* Bailey (1844: 139, pl. 3, figs 13–15).
- N. laevissima** var. *semi-aperta* H.G. Barber & J.R. Carter 1971b: 82, fig. 97.  
*Holotype?*: 'Typus in collectione Quekett Microscopical Club.'  
*Locality*: '...fossil diatomaceous earth situated in Gordon Road, Auckland, New Zealand at co-ordinates 225,110E, 656,720N, Square G.7 of New Zealand M.S. 17, 1962 Edition 'Auckland.'  
*Note*: This taxon should belong in the genus *Sellaphora* Mereschk.
- N. lapila** J.R. Carter in J.R. Carter & Bailey-Watts 1981: 582, pl. 14, figs 34–35.  
*Holotype*: 'collection Carter, Shet. No. 4' = BM 87922.  
*Locality*: 'In Moo Water, Shetland.'  
*Additional illustration*: Sims (1996: 310–311, pl. 147, fig. 14, 1 image).
- N. lapsa** J.R. Carter & Denny 1992: 184, pl. 5, figs 11–15.  
*Holotype*: BM 81509.  
*Locality*: 'In sample 5 [Lake Sonfon, stream, Sierra Leone].'
- N. lupula** J.R. Carter & Denny 1982: 308, pl. 6, fig. 200.  
*Holotype*: BM 78112.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from rotting leaves.'
- N. lurinda** J.R. Carter & Denny 1982: 308, pl. 6, fig. 201.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- N. malica** J.R. Carter & Denny 1982: 308, pl. 6, figs 202–204.  
*Syntypes*: BM 78107-8.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.' [BM 78107] 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.' [BM 78108].
- N. menda** J.R. Carter in J.R. Carter & Bailey-Watts 1981: 582, pl. 24, fig. 27.  
*Holotype*: 'collection Carter, Shet. No. 12' = BM 87929.  
*Locality*: 'In Voxterby, Shetland.'  
*Additional illustrations*: Sims (1996: 312–313, pl. 150, fig. 2, 2 images).  
*Notes*: Haworth & Offer (1986: 446) suggested two further slides as lectotypes '[B]ecause the original description is based upon just one specimen...'. This reason is not a valid justification for the designation of lectotype material as Carter did identify the holotype slide and that has to remain so, regardless of how many specimens were consulted for the description. The two slides suggested by Haworth & Offer (BM 81209-10) may act as useful, additional non-type examples.
- N. mintracta** J.R. Carter & Denny 1982: 309, pl. 6, fig. 205.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- N. nabrona** J.R. Carter & Denny 1982: 309, pl. 6, fig. 206.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- N. nabrona** f. *ovalis* J.R. Carter & Denny 1982: 309, pl. 6, fig. 207.  
*Holotype*: Not given.  
*Locality*: Not given.  
*Lectotype*: BM 78107 ('River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.').  
*Note*: Carter writes 'occurs mixed with the type.' This seems to suggest that BM 78107 is the most suitable lectotype.
- N. nienta** J.R. Carter 1966: 464, pl. 3, fig. 17.  
*Holotype*: BM 77590.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae... Sample No. 5. Big Waterburn, stones in stream, 100 feet above sea level.'
- N. nutata** J.R. Carter & Denny 1982: 309, pl. 6, figs 208–210.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- N. orbita** J.R. Carter 1966: 464, pl. 3, fig. 12.  
*Holotype*: BM 77594.  
*Locality*: 'In aquis dulcibus insulae Tristan da Cunha dictae... Sample No. 9. Hottentot Gulch, stream pool, 2000 feet above sea level.'
- N. orbis** J.R. Carter in J.R. Carter & Bailey-Watts 1981: 584, pl. 24, fig. 34.  
*Holotype*: 'collection Carter, Shet. No. 39a' = BM 87950.  
*Locality*: 'At Burkwell, Shetland.'  
*Additional illustration*: Sims (1996: 320–321, pl. 152, fig. 11, 1 image).

- N. patrina* J.R. Carter & Denny 1982: 310, pl. 6, fig. 211.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- N. perfidissima* Lange-Bert. in Lange-Bertalot & Krammer (1989: 162, taf. 70, figs 22–25', ?26, 27).  
*Holotype*: BM 93708 = Carter 2716, 'Devils Hole (Tay Dist.) West Coll. A.W. Round no. 35' (Carter, 1971a: 659, *Achnanthes perfida*), two specimens marked (Lange-Bertalot & Krammer, 1989: taf. 70, figs 22–25), 'Als *Achnanthes perfida* Carter in Coll. Carter 2716, Devil's Hole/Schottland.' BM 93708 is not type material of *A. perfida*, see above.
- N. petilina* J.R. Carter & Denny 1982: 310, pl. 6, fig. 212.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- N. pseudoclamans* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 585, pl. 14, fig. 7.  
*Holotype*: 'collection Carter, Shet. No. 4a' = BM 87922.  
*Locality*: 'In Moo Water, Shetland.'  
*Additional illustrations*: Sims (1996: 328–329, pl. 156, fig. 12, 2 images).
- N. pseudomenisculus* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 585, pl. 14, fig. 8.  
*Holotype*: 'collection Carter, Shet. No. 36' = BM 87948.  
*Locality*: 'In Loch of Cliff, Shetland.'  
*Additional illustration*: Sims (1996: 328–329, pl. 156, fig. 19, 1 image).  
*Note*: non *N. pseudominiscula* Fusey (1950: 156, fig. 22). Although the spelling of the specific epithet for Carter's taxon is remarkably similar to that of Fusey, these two taxa would be hard to confuse. While there may be justification in re-naming Carter's taxon, we have chosen to retain it.
- N. pseudostundlii* H.G. Barber & J.R. Carter 1971b: 83, fig. 122.  
*Holotype?*: 'Typus in collectione Quekett Microscopical Club.'  
*Locality*: '...fossil diatomaceous earth situated in Gordon Road, Auckland, New Zealand at co-ordinates 225,110E, 656,720N, Square G.7 of New Zealand M.S. 17, 1962 Edition 'Auckland'.'
- N. resecta* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 586, pl. 12, fig. 55.  
*Holotype*: 'collection Carter, Shet. No. 36' = BM 87948.  
*Locality*: 'In Loch of Cliff, Shetland.'  
*Additional illustrations*: Sims (1996: 336–337, pl. 160, fig. 4, 2 images).
- N. retrica* J.R. Carter & Denny 1982: 311, pl. 6, figs 214–215.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- N. retrocurvata* J.R. Carter ex R. Ross & P.A. Sims 1978: 159, figs 14–16.  
*Holotype*: BM 78070.  
*Locality*: '...ex rivulo 'on the links behind Sandside Bay, Mainland' in Orcades, J.R. Carter 3369 lectus.'  
*Additional illustrations*: Sims (1996: 312–313, pl. 148, fig. 11, 3 images; 336–337, pl. 160, fig. 6, 2 images).  
*Note*: = *Hippodonta lesmonensis* (Hust.) Lange-Bert., Metzeltin & Witkowski (1996: 261).
- N. riparta* J.R. Carter 1966: 465, pl. 8, fig. 19.  
*Holotype*: BM 77599.  
*Locality*: 'In aquis dulcibus insula Gough Island dictae...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'
- N. rotesta* J.R. Carter 1970b: 620, pl. 2, figs 14, 32–33.  
*Holotype*: BM 77783.  
*Locality*: 'Sample No. 5 from the Rio d'Envalira...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'
- N. sarolata* J.R. Carter & Denny 1982: 311, pl. 6, figs 216–217.  
*Holotype*: Not given.  
*Lectotype*: BM 78107.  
*Locality*: 'A few specimens seen. 11, 20' = 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.' [Sample 11, BM 78107] 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.' [Sample 11, BM 78108]; 'River Jong (Taia) at Njala [Sierra Leone]...from stones.' [Sample 20, BM 78111].
- N. sarolata f. capitata* J.R. Carter & Denny 1992: 185, pl. 5, figs 38–39.  
*Holotype*: BM 81506.  
*Locality*: 'In sample 3 only [Lake Sonfon, Sierra Leone].'
- N. scalpia* J.R. Carter 1966: 466, pl. 8, fig. 15.  
*Holotype*: BM 77600.  
*Locality*: 'In aquis dulcibus insula Gough Island dictae...Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.'
- N. scela* J.R. Carter & Denny 1982: 312, pl. 6, figs 187–188.  
*Holotype*: BM 78112.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from rotting leaves.'
- N. scirpus* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 586, pl. 24, figs 29–30a.  
*Holotype*: 'collection Carter, Shet. No. 26' = BM 87943.  
*Locality*: 'In North Vementry, Shetland.'  
*Additional illustrations*: Sims (1996: 340–341, pl. 162, fig. 8, 5 images).
- N. sequens* H.G. Barber & J.R. Carter 1971b: 83, fig. 110.  
*Holotype?*: 'Typus in collectione Quekett Microscopical Club.'  
*Locality*: '...fossil diatomaceous earth situated in Gordon Road, Auckland, New Zealand at co-ordinates 225,110E, 656,720N, Square G.7 of New Zealand M.S. 17, 1962 Edition 'Auckland'.'
- N. sponsa* J.R. Carter 1964: 226, pl. 2, fig. 11.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Locality*: 'I have found this form in three locations in the Cheviots in every case on the surface of mud in high level springs.'  
*Additional illustration*: Sims (1996: 344–345, pl. 164, fig. 13, 1 image).
- N. subexilissima* J.R. Carter 1970b: 620, pl. 2, fig. 13.  
*Holotype*: BM 77780.  
*Locality*: 'Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'
- N. subvasta* J.R. Carter 1970b: 621, pl. 2, fig. 20.  
*Holotype*: BM 77780.  
*Locality*: 'Sample No. 2 from a ditch near Llorts which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'  
*Notes*: non *N. subvasta* Hust. Hustedt illustrated his *N. subvasta* in Schmidt's *Atlas* (1936: pl. 403, figs 49–50) but provided no description. While Hustedt did eventually provide a description, first he placed it under the name *Navicula rivularis* Hust. (1942:

- 112) and second, in 1945 (930, pl. 41, figs 38–40), he included it in *Navicula helensis* P. Schulz. *Navicula helensis* is now correctly referred to as *Fallacia helensis* D.G. Mann (in Round et al. 1990: 668). As neither of Hustedt's descriptions can be understood as validly published and as the illustration in Schmidt's *Atlas* is after 1908, Carter's name is the first valid use of *Navicula subvasta*.
- N. sulta* J.R. Carter & Denny 1982: 314, pl. 8, fig. 290.  
*Holotype*: BM 78110.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from submerged wood.'
- N. suspica* J.R. Carter & Denny 1992: 186, pl. 5, fig. 45.  
*Holotype*: BM 81522.  
*Locality*: 'In sample 54 rarely [Lake Popei, Sierra Leone].'
- N. tauta* J.R. Carter & Denny 1982: 314, pl. 8, fig. 293.  
*Holotype*: BM 78108.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- N. toxa* J.R. Carter 1960*b*: 284, fig. 6.  
*Holotype*: Not given.  
*Lectotype*: BM 92981 = Carter 2198, 'Woodhead Loch, Ancrum, Small Nav....'  
*Locality*: 'Abundant in Woodhead Loch, Roxburghshire, usually on the surface of mud.'
- N. variolinea* J.R. Carter 1971*a*: 668, pl. 2, fig. 71, pl. 3, fig. 95.  
*Syntypes*: BM 77777-8.  
*Locality*: 'Devil's Hole Cave.' '...Kinraig Hill at the south-western extremity of Kilconquhar parish, Fife...collected by the late Mr. Geo. West of University College, Dundee, in the second decade of this century [1920s].'  
*Additional illustrations*: Sims (1996: 350–351, pl. 167, fig. 1, 3 images).
- N. vatinata* J.R. Carter & Denny 1982: 315, pl. 5, fig. 180.  
*Holotype*: BM 78112.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from rotting leaves.'
- N. vincita* J.R. Carter & Denny 1982: 315, pl. 5, fig. 182.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- N. virosa* J.R. Carter & Denny 1992: 188, pl. 4, fig. 43.  
*Holotype*: BM 81506.  
*Locality*: '...in sample 3... [Lake Sonfon, Sierra Leone].'
- N. visitanda* J.R. Carter 1970*b*: 621, pl. 2, figs 15–16.  
*Holotype*: BM 77780.  
*Locality*: 'Sample No. 2 from a ditch near Lloris which is in the only side valley of the republic...collected by Mr. J. Broadhead during the summer of 1966 and 1967.'
- N. vitila* J.R. Carter & Denny 1982: 316, pl. 5, figs 176–77.  
*Holotype*: BM 78108.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- N. vula* J.R. Carter 1971*a*: 669, pl. 2, fig. 84.  
*Holotype*: 'Typus: praeparatum No. 2716C in collectione Carter' = BM 93709.  
*Locality*: 'Devil's Hole Cave' '...Kinraig Hill at the south-western extremity of Kilconquhar parish, Fife...collected by the late Mr. Geo. West of University College, Dundee, in the second decade of this century [1920s].'  
*Additional illustrations*: Sims (1996: 350–351, pl. 167, fig. 9, 2 images).
- N. wavella* J.R. Carter & Denny 1982: 316, pl. 5, fig. 178.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- N. wustula* J.R. Carter & Denny 1982: 318, pl. 5, fig. 179.  
*Holotype*: BM 78112.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from rotting leaves.'
- N. zipila* J.R. Carter & Denny 1982: 318, pl. 5, fig. 181.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- Neidium* Pfitzer 1871
- N. juba* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 592, pl. 24, fig. 35.  
*Holotype*: 'collection Carter, Shet. No. 39a' = BM 87950.  
*Locality*: 'In Burkwell, Shetland.'  
*Additional illustrations*: Krammer & Lange-Bertalot (1986: 269, taf. 99, fig. 11), 'Holotypus, Coll. Carter Shetland 39 A'; Sims (1996: 372–373, pl. 178, fig. 5, 1 image).
- N. lentis* J.R. Carter & Denny 1987: 254, pl. 5, fig. 3.  
*Holotype*: BM 81154.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'
- N. miopsa* J.R. Carter & Denny 1992: 189, pl. 6, fig. 26.  
*Holotype*: BM 81514.  
*Locality*: 'In sample 9 rarely [Lake Sonfon, Sierra Leone].'
- N. plexum* J.R. Carter & Denny 1987: 254, pl. 5, fig. 6.  
*Holotype*: BM 81156.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'
- N. popeiensis* J.R. Carter & Denny 1992: 189, pl. 6, fig. 27.  
*Holotype*: BM 81522.  
*Locality*: 'Not rare in sample 54... [Lake Popei, Sierra Leone].'
- N. tabletta* J.R. Carter & Denny 1992: 190, pl. 6, figs 29–30.  
*Holotype*: BM 81522.  
*Locality*: 'Not rarely in sample 54... [Lake Popei, Sierra Leone].'
- N. taiaensis* J.R. Carter & Denny 1982: 319, pl. 6, fig. 219.  
*Holotype*: 'BM 7811' (sic) = BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- N. testa* J.R. Carter in J.R. Carter & Bailey-Watts 1981: 593, pl. 24, fig. 36.  
*Holotype*: 'collection Carter, Shet. No. 66' = BM 87973.  
*Locality*: 'At Housetter, Shetland.'  
*Additional illustrations*: Krammer & Lange-Bertalot (1986: 268, taf. 99, fig. 10), 'Holotypus, Coll. Carter Shetland W66'; Sims (1996: 374–537, pl. 179, fig. 3, 1 image).
- Nitzschia* Hassall 1845
- N. disputata* J.R. Carter 1971*a*: 670, pl. 1, figs 38–40.  
*Syntypes*: BM 77777-8.  
*Locality*: 'Devil's Hole Cave' '...Kinraig Hill at the south-

- western extremity of Kilconquhar parish, Fife...collected by the late Mr. Geo. West of University College, Dundee, in the second decade of this century [1920s].'  
*Additional illustrations*: Krammer & Lange-Bertalot (1988: 51, taf. 40, figs 9–15), not type material, as *N. epithemoides* var. *disputata* (J.R. Carter) Lange-Bert. in Lange-Bertalot & Krammer (1987: 16); Sims (1996: 384–385, pl. 184, fig. 1, 3 images).
- N. epressa* J.R. Carter 1966: 467, pl. 6, figs 24–25.  
*Holotype*: BM 77590.  
*Locality*: 'Tristan da Cunha inventa aqua dulci...Sample No. 5. Big Waterburn, stones in stream, 100 feet above sea level.'
- N. inimasta* J.R. Carter & Denny 1982: 320, pl. 7, figs 230–230a.  
*Holotype*: BM 78107.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phyto-plankton.'
- N. jamiesoni* H.G. Barber & J.R. Carter 1972: 147, fig. 207.  
*Holotype?*: 'Typus in collectione Quekett Microscopical Club.'  
*Locality*: '...fossil diatomaceous earth situated in Gordon Road, Auckland, New Zealand at co-ordinates 225,110E, 656,720N, Square G.7 of New Zealand M.S. 17, 1962 Edition 'Auckland'.'
- N. navia* J.R. Carter 1966: 468, pl. 7, figs 1, 7.  
*Holotype*: BM 77593.  
*Locality*: 'Tristan da Cunha inventa aqua dulci...Sample No. 8. Salt beach at sea level.' [BM 77593].
- N. oscilla* J.R. Carter 1966: 468, pl. 7, figs 21–22.  
*Holotype*: BM 77589.  
*Locality*: 'Tristan da Cunha inventa aqua dulci...Sample No. 4. Rookery Gulch, wet rock, with gelatinous algae (Nostoc sp.)'
- N. palmida* J.R. Carter 1966: 468, pl. 9, figs 27–28.  
*Holotype*: BM 77600.  
*Locality*: 'Gough Island inventa aqua dulci...Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.'
- N. petulla* J.R. Carter 1966: 469, pl. 6, figs 18–23.  
*Holotype*: BM 77593.  
*Locality*: 'Tristan da Cunha inventa aqua dulci...Sample No. 8. Salt beach at sea level.'
- N. pistilla* J.R. Carter 1966: 469, pl. 7, fig. 5.  
*Holotype*: BM 77590.  
*Locality*: 'Tristan da Cunha inventa in aqua dulci...Sample No. 5. Big Waterburn, stones in stream, 100 feet above sea level.'
- N. rotula* J.R. Carter 1966: 470, pl. 7, fig. 19, 26.  
*Holotype*: BM 77586.  
*Locality*: 'Tristan da Cunha inventa aqua dulci...Sample No. 1. Pigbite, stones in running water at sea level.'
- N. salta* J.R. Carter 1966: 470, pl. 7, fig. 24.  
*Holotype*: BM 77595.  
*Locality*: 'Tristan da Cunha inventa in aqua dulci...Sample No. 10. New lava field, stream and moss.'
- N. serpentiformis* J.R. Carter 1966: 470, pl. 9, fig. 10.  
*Holotype*: BM 77599.  
*Locality*: 'Gough Island inventa aqua dulci...Sample No. 11. Gough Island sample 1003, Cave Bell Rocks, sea level.'
- N. sonora* J.R. Carter 1966: 470, pl. 8, figs 21–22.  
*Holotype*: BM 77600.  
*Locality*: 'Gough Island inventa in aqua dulci...Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.'
- N. tantata* J.R. Carter & Denny 1992: 192, pl. 7, fig. 17.  
*Holotype*: BM 81509.  
*Locality*: 'In sample 5 only [Lake Sonfon, stream, Sierra Leone].'
- N. wodensis* J.R. Carter 1964: 228, pl. 2, fig. 17.  
*Holotype?*: Slides in Quekett Microscopical Society Collections.  
*Locality*: Woden Loch on the surface of dead wood, fresh water, not very common.'  
*Notes*: If the Quekett slides are not available, BM 93522 ('Woden Loch, on dead wood, 2582, 9/62') would serve as lectotype.
- Opephora* P. Petit 1888
- O. taiaensis* J.R. Carter & Denny 1982: 321, pl. 5, fig. 185.  
*Holotype*: BM 78111.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...from stones.'
- Pinnularia* Ehrenb. 1843
- P. carminata* H.G. Barber & J.R. Carter 1978: 305, text-figs p. 306.  
*Holotype*: BM 78064.  
*Locality*: '...inter muscos in rivulo montoso ad 'Tai Newddion, Nant Ffrancon, Gwynedd', Cambriam, Barber – Cleaning No. 537 lectus.'  
*Additional illustrations*: Krammer (1992: 140, taf. 55, fig. 5), 'Loch Enoch, Schottland, leg. Carter. Präp. 574B, IOK'; Krammer (2000: 153, pl. 133, fig. 5), 'Loch Enoch, Schottland, leg. Carter. slide 574B IOK'; Sims (1996: 434–435, pl. 209, fig. 3, 3 images).
- P. dispersa* J.R. Carter 1966: 472, pl. 5, figs 7–9.  
*Holotype*: BM 77593.  
*Locality*: 'Tristan da Cunha inventa in aqua dulci...Sample No. 8. Salt beach at sea level.'  
*Note*: non *P. dispersa* Østrup (1901: 273, fig. 37), see *P. johncarterii* D.M. Williams, *nov. nom.*
- P. extenda* J.R. Carter 1966: 473, pl. 4, figs 3–4.  
*Holotype*: BM 77590.  
*Locality*: 'Tristan da Cunha inventa in aqua dulci ...Sample No. 5. Big Waterburn, stones in stream, 100 feet above sea level.'
- P. graphica* J.R. Carter & Denny 1992: 194, pl. 8, fig. 5.  
*Holotype*: BM 81509.  
*Locality*: 'In sample 5 only, not common [Lake Sonfon, stream, Sierra Leone].'
- P. impassa* J.R. Carter 1966: 473, pl. 4, figs 5–6.  
*Holotype*: BM 77590.  
*Locality*: 'Tristan da Cunha inventa in aqua dulci ...Sample No. 5. Big Waterburn, stones in stream, 100 feet above sea level.'
- P. johncarterii* D.M. Williams, *nov. nom.* = *P. dispersa* J.R. Carter (1966: 472, pl. 5, fig. 7–9) non *P. dispersa* Østrup (1901: 273, fig. 37).
- P. leptosomiformis* J.R. Carter 1966: 474, pl. 8, fig. 6.  
*Holotype*: BM 77600.  
*Locality*: 'Gough Island inventa in aqua dulci...Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.'
- P. mica* J.R. Carter & Denny 1987: 258, pl. 5, figs 19–22.  
*Holotype*: 'BM 91146' (sic) = BM 81146.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)... )...Periplankton scraped from *Vossia* stems...Lake Mape.'
- P. mondinia* J.R. Carter & Denny 1992: 198, pl. 8, fig. 6.  
*Holotype*: BM 81522.  
*Locality*: 'In sample 54... [Lake Popei, Sierra Leone].'
- P. posita* J.R. Carter 1966: 475, pl. 8, figs 7–8.

- Holotype*: BM 77599.  
*Locality*: 'Gough Island inventa in aqua dulci...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'
- P. redunda*** J.R. Carter 1966: 475, pl. 8, figs 10–11.  
*Holotype*: BM 77600.  
*Locality*: 'Gough Island inventa in aqua dulci...Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.'
- P. restituta*** J.R. Carter 1966: 475, pl. 8, figs 3–5.  
*Holotype*: BM 77599.  
*Locality*: 'Gough Island inventa in aqua dulci...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'
- P. ritarda*** J.R. Carter 1966: 476, pl. 4, fig. 21.  
*Holotype*: 'in collectione Carter, Hawick, Scotland.' = BM 77590.  
*Locality*: 'Tristan da Cunha inventa in aqua dulci...Sample No. 5. Big Waterburn, stones in stream, 100 feet above sea level.'
- P. seriata*** J.R. Carter 1966: 476, pl. 8, fig. 12.  
*Holotype*: BM 77600.  
*Locality*: 'Gough Island inventa in aqua dulci...Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.'
- P. sistassa*** J.R. Carter 1966: 477, pl. 5, figs 3–6.  
*Syntypes*: BM 77586–7.  
*Locality*: 'Sample no. 1. Pigbite, stones in running water at sea level.' [BM 77586] 'Tristan da Cunha inventa in aqua dulci...Sample No. 2. Above Burntwood, stream at 1800 feet above sea level.' [BM 77587].  
*Additional illustrations*: Sims (1996: 474–475, pl. 229, fig. 6, 7 images).
- P. statua*** J.R. Carter & Denny 1987: 260, pl. 8, figs 2–3, 10.  
*Holotype*: BM 81154.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'
- P. subcapitata* f. *plana*** J.R. Carter 1966: 478, pl. 8, figs 2–3.  
*Holotype*: Not given.  
*Lectotype*: BM 77599, 'Sample 11 not rare.'  
*Locality*: 'Tristan da Cunha inventa in aqua dulci...Sample No. 11 Gough Island sample 1003, Cave Bell Rocks, sea level.'
- P. suplica*** J.R. Carter & Denny 1987: 262, pl. 7, fig. 8.  
*Holotype*: BM 81154.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'
- P. taiaensis*** J.R. Carter & Denny 1982: 324, pl. 8, fig. 265.  
*Holotype*: BM 78109.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...surface Flotsam.'
- P. trudis*** J.R. Carter & Denny 1992: 199, pl. 9, fig. 11.  
*Holotype*: BM 81508.  
*Locality*: 'In sample 4... [Lake Sonfon, Sierra Leone].'
- P. trulla*** J.R. Carter & Denny 1987: 262, pl. 7, fig. 15.  
*Holotype*: BM 81154.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'
- P. unca*** J.R. Carter & Denny 1987: 263, pl. 8, fig. 14.  
*Holotype*: BM 81160.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul from near Manobotma...Lake Mape.'
- P. vacua*** J.R. Carter & Denny 1992: 196, pl. 9, fig. 7.  
*Holotype*: BM 81521.  
*Locality*: 'In sample 54 only [Lake Popei, Sierra Leone].'
- P. vapilla*** J.R. Carter 1966: 478, pl. 4, figs 1–2.  
*Syntypes*: BM 77593, BM 77595.  
*Locality*: 'Tristan da Cunha inventa in aqua dulci...Sample No. 8. Salt beach at sea level.' [BM 77593] 'Sample No. 10. New lava field, stream and moss.' [BM 77595].
- Pseudoeunotia*** Grunow in Van Heurck 1881
- P. duplex*** J.R. Carter 1966: 479, pl. 9, fig. 29.  
*Holotype*: BM 77600.  
*Locality*: 'Gough Island inventa in aqua dulci...Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.'
- P. linearis*** J.R. Carter 1966: 479, pl. 9, figs 15–19.  
*Holotype*: BM 77600.  
*Locality*: 'Gough Island inventa in aqua dulci...Sample No. 12. Gough Island sample 1006, Stream Gonydale, 1400 feet a.s.l.'
- Stauroneis*** Ehrenb. 1843
- S. bulla*** J.R. Carter & Denny 1987: 264, pl. 9, figs 16–20, pl. 11, figs 14–15.  
*Holotype*: BM 81160.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul from near Manobotma...Lake Mape.'
- S. capula*** J.R. Carter & Denny 1992: 200, pl. 10, fig. 10.  
*Holotype*: BM 81511.  
*Locality*: 'A few cells in sample 7 [Lake Sonfon, Sierra Leone].'
- S. didacta*** J.R. Carter & Denny 1992: 200, pl. 10, fig. 9.  
*Holotype*: BM 81506.  
*Locality*: 'Occasional in sample 3, rarely in sample 54... [Lake Sonfon, Sierra Leone].'
- S. impenda*** J.R. Carter & Denny 1992: 202, pl. 10, fig. 8.  
*Holotype*: BM 81509.  
*Locality*: 'In samples 5 [Lake Sonfon, Sierra Leone] and 54 [Lake Popei, Sierra Leone]... Sample 5 is holotype material, sample 54 represents syntype material.'
- S. singula*** J.R. Carter & Denny 1992: 202, pl. 10, fig. 5.  
*Holotype*: BM 81522.  
*Locality*: 'Not rarely in sample 54... [Lake Popei, Sierra Leone].'
- Surirella*** Turpin 1828
- S. subtilis*** J.R. Carter & Denny 1992: 204, pl. 11, fig. 6.  
*Holotype*: BM 81522.  
*Locality*: 'In sample 54... [Lake Popei, Sierra Leone].'
- S. taiaensis*** J.R. Carter & Denny 1982: 325, pl. 8, fig. 274.  
*Holotype*: BM 78108.  
*Locality*: 'River Jong (Taia) at Njala [Sierra Leone]...phytoplankton.'
- S. terebra*** J.R. Carter & Denny 1987: 268, pl. 9, fig. 30.  
*Holotype*: BM 81154.  
*Locality*: '...coastal strip of South-Western Sierra Leone...Sample 66 (3<sup>rd</sup> April 1976)...Phytoplankton horizontal haul...Lake Mabesi.'

*Synedra* Ehrenb. 1830

*S. capilla* J.R. Carter & Denny 1992: 204 = *S. filiformis* J.R. Carter & Denny non *S. filiformis* Grunow (1880).

*S. filiformis* J.R. Carter & Denny 1987: 270, pl. 9, fig. 32.

*Holotype*: BM 81159.

*Locality*: '...coastal strip of South-Western Sierra Leone... Sample 68 (16<sup>th</sup> April 1976) ... Phytoplankton horizontal haul... Lake Mape.'

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**ACKNOWLEDGEMENTS.** We would like to thank Karen Webb, whose initial investigations into John Carter's diatom collections instigated this work, and Dr E.Y. Haworth for information.

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# The typification, defining features and geographical range of *Calymperes couguiense* Besch. (Calymperaceae, Musci)

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**SYNOPSIS.** A neotype is proposed for *Calymperes couguiense* Besch. and the features are outlined by which the species may be distinguished from *C. subintegrum* Broth. and *C. porrectum* Mitt. Owing to its confusion with these latter species, most reports of its occurrence in Malesia are erroneous. The distribution of *C. couguiense* includes NE Australia and the islands of the Pacific as far east as the Tuamotu Archipelago.

Research for this paper was inspired by the discovery that, contrary to citations in the literature, the holotype of *Calymperes couguiense* Besch. is not in Bescherelle's herbarium (BM). An examination of many specimens identified as *C. couguiense* revealed a long-standing confusion of this species with some forms of *Calymperes porrectum* Mitt. and *Calymperes subintegrum* Broth. These problems of typification and identification are addressed below.

*Calymperes couguiense* Besch. in *Ann. Sci. Nat. Bot. sér. 5*, **18**: 206 (1873). Type: New Caledonia, Balade, Vieillard 1776 (BM!-neotype, designated here; S!-isotype?).

*Calymperes setosum* Müll. Hal. in *J. Mus. Godeffroy* **3**(6): 64 (1874). Type: Samoa, Upolu, Graeffe s.n. (BM!, S!-isotypes).

*Calymperes marginatum* Dixon in *Proc. Linn. Soc. New South Wales* **55**: 275 (1930). Type: Fiji, Vanua Levu, 3000 ft, December 1922, Greenwood 474 (BM!-holotype).

*Calymperes pseudopodianum* E.B. Bartram in *Occas. Pap. Bernice Pauahi Bishop Mus.* **10**(10): 7 (1933). Type: Pacific Islands, Tuamotu Archipelago, Makatea, 3 March 1930, Emory s.n. (FH-holotype).

## Typification

There has been some misapprehension with regard to the typification of *Calymperes couguiense* Besch. In the protologue, Bescherelle (1873) cited a type specimen from New Caledonia – ‘Ad cortices in monte Cougui (BALANSA)’. Reese & Mohamed (1985) and Reese & Stone (1995) cited this specimen as being housed in BM. However, the holotype of *Calymperes couguiense* (Balansa s.n.) is not in Bescherelle's herbarium (BM) and isotypes have not been found in BM or in other likely herbaria elsewhere (FH, H, L, MEL, MO, NY, PC, S). Hitherto, a non-type collection in BM, identified as *C. couguiense* by Bescherelle (1895), appears to have been mistaken for the type specimen. Although annotated as type material by recent authorities, it is clearly labelled ‘Nov. Caled. Balade Vieillard No. 1776’. In Möller's herbarium (S) there is an apparent duplicate of Vieillard 1776 which has also been mistaken for type material. The outer packet of this specimen is marked ‘Vieillard 1776’ and stamped ‘TYPUS’. Confusingly, the inner packet bears a label with the collection details of Vieillard 1776 followed immediately by those of Balansa s.n. This is possibly a rendition of the specimen citation published by Bescherelle (1895) rather than a specific reference to the contents of the packet. The true origin of this specimen remains uncertain.

In the absence of material clearly identifiable as Balansa's collec-

tion, *Calymperes couguiense* requires neotypification. The authentic material, Vieillard 1776 in Bescherelle's herbarium (BM), is here proposed as the neotype.

## Taxonomy

*Calymperes subintegrum* Broth., *C. porrectum* Mitt. and *C. couguiense* Besch. all possess similar strongly dimorphic leaves (i.e. erect, linear gemmiferous leaves, largely consisting of thick costae (Fig. 1b) which project above a canopy of vegetative leaves with narrower costae and relatively broad laminal blades (Fig. 1a)).

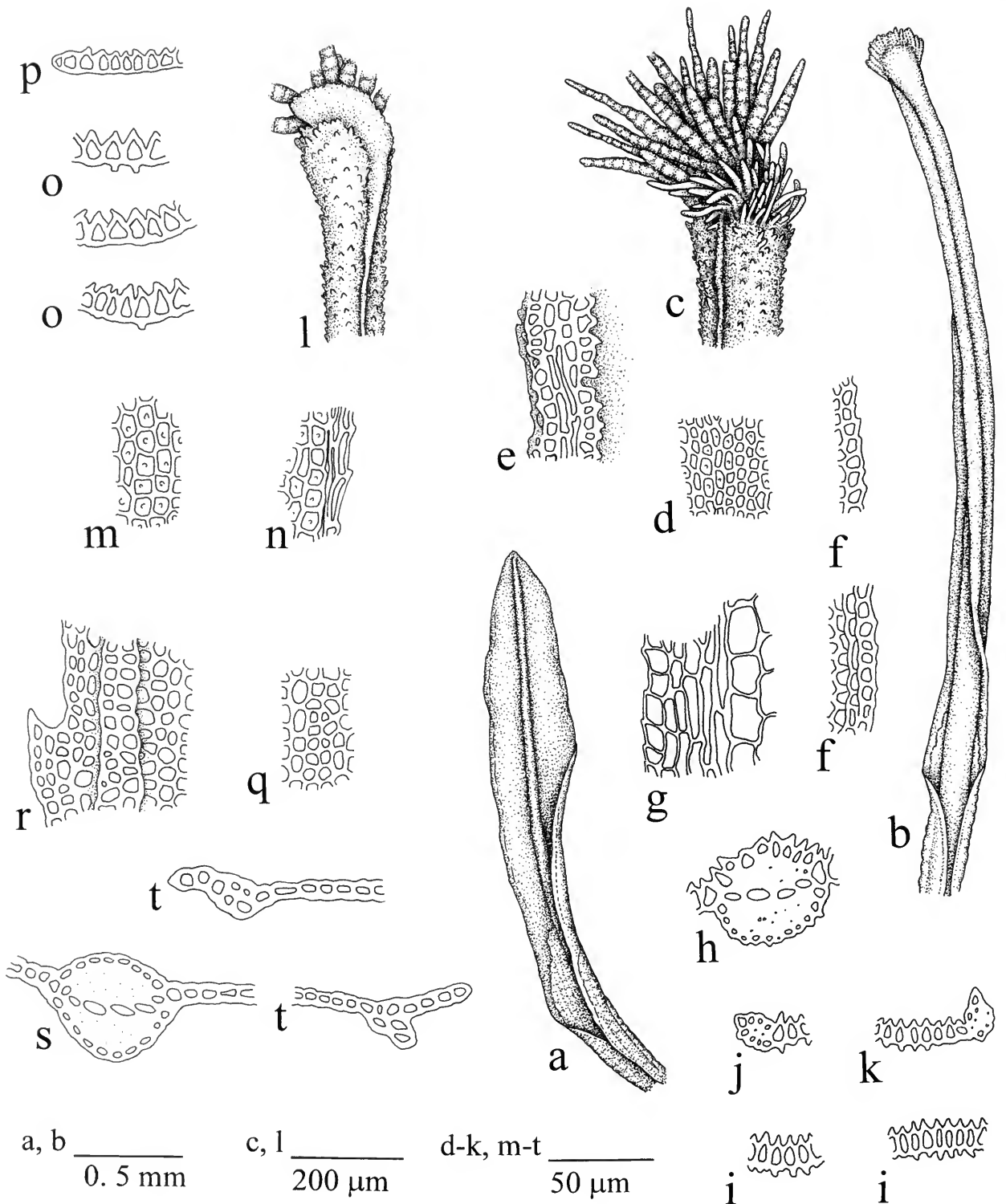
Collections of *Calymperes subintegrum* and of diminutive forms of *Calymperes porrectum* have often been misidentified as *C. couguiense*. This has led to a misrepresentation of the latter species both in herbaria and in recent literature. For example, the illustrations of *C. couguiense* by Eddy (1990) mostly depict leaf features of *C. porrectum*, and Reese, Koponen & Norris (1986) cited only misidentified material in their account of the species.

The distinguishing features of *Calymperes couguiense*, *C. porrectum* and *C. subintegrum* are outlined in a key and discussed in detail below.

## Key features of *Calymperes porrectum* Mitt., *C. subintegrum* Broth. and *C. couguiense* Besch.

- |   |   |                               |
|---|---|-------------------------------|
| 1 | Non-gemmiferous leaves recurved, costa smooth, cells of chlorophyllose lamina smooth and flat; leaf margin with intramarginal polystratose rib, serrate (Fig. 1r, t) .....  | <b>Calymperes porrectum</b>   |
|   | Non-gemmiferous leaves erect to spreading, costa scabrid to some degree, cells of chlorophyllose lamina projecting from the ventral and/or dorsal surfaces of the leaf; leaf margin with or without rib, subtire to denticulate ..... | 2                             |
| 2 | Cells of chlorophyllose lamina 7.5–15(–>20) × 5–10(–12.5) µm, dorsally flat (occasionally unipapillose) (Fig. 1m, o) .....  | <b>Calymperes subintegrum</b> |
|   | Cells of chlorophyllose lamina <5–10(–12.5) × 5–7.5(–10) µm, dorsally unipapillose (invariably) (Fig. 1d, i) .....  | <b>Calymperes couguiense</b>  |

For an illustrated account of *Calymperes porrectum* Mitt. with synonymy see Eddy (1990), and see Ellis (1991) for a similar treatment of *Calymperes subintegrum* Broth. Recent useful accounts of *Calymperes couguiense* Besch. include those by Reese & Mohamed (1985), Reese, Koponen & Norris (1986) and Reese & Stone (1995).



**Fig. 1** a–k. *Calymperes couguiense* Besch. a–c. leaves (a: non-gemmiferous leaf, b: gemmiferous leaf (gemmae missing), c: apex of gemmiferous leaf in lateral view); d–g. cells of leaf in surface view (d: chlorophyllose lamina (ventral view), e, f: margin of chlorophyllose limb (ventral view), g: margin at mid hyaline base), h–k. cross-sections of chlorophyllose limb (h: costa, i: lamina, j, k: margin). l–p. *Calymperes subintegrum* Broth. l. apex of gemmiferous leaf in lateral view, m, n. cells of chlorophyllose limb in surface view (m: lamina (ventral view), n: margin), o, p. cross-sections of chlorophyllose limb (o: lamina, p: margin). q–t. *Calymperes porrectum* Mitt. q, r. chlorophyllose limb in surface view (q: lamina, r: margin), s, t. cross-sections of chlorophyllose limb (s: costa, t: lamina and margin). a, c. Drawn from Society Islands, *De Sloover* 20962 (H). b, e, g–j. Drawn from New Caledonia, *Veillard* 1776 (BM). d. Drawn from Australia, *Stone* 18577 (MEL). f, k. Drawn from Samoa, *Graeffe* s.n. (BM). l, m, o. Drawn from Australia, *Stone* 23095 (MEL). n, p. Drawn from New Guinea, *Zanten* 149c (BM). q–t. Drawn from New Ireland, *Eddy* 6333 (BM).

**DISCUSSION.** Shoots of *Calymperes porrectum* possess strongly recurved non-gemmiferous leaves with a smooth costa (Fig. 1s) and chlorophyllose lamina (Fig. 1t). The laminal chlorocysts form a largely flat surface, but are sometimes very slightly protuberant ventrally. In surface view they reach  $<5-10(-12.5) \times <5-10(-12.5) \mu\text{m}$ , smaller on average, and more irregularly polygonal or rounded, than those in *C. subintegrum* (see below). A differentiated rib lies well within the margin of the leaf, and extends from the leaf base to near the apex. Above the hyaline lamina it becomes polystratose and projects slightly from the dorsal leaf surface (Fig. 1t). Adjacent to this rib, a narrow, unistratose marginal lamina, (2-)3-5(->6) cells wide, is formed, which at intervals gives rise to subtriangular, often multicellular, teeth (Fig. 1r). In gemmiferous leaves the costa is scabrid and slightly excurrent; gemmae are produced in a cluster from the costal apex. Adjacent to the cluster of gemmae some superficial costal cells become elongated and finger-shaped.

In *Calymperes subintegrum* the non-gemmiferous leaves are erect to spreading and possess more or less scabrid costae. The cells of the chlorophyllose lamina are flat dorsally (occasionally unipapillose), but project acutely from the ventral surface of the leaf (Fig. 1o). In surface view they reach  $7.5-15(->20) \times 5-10(-12.5) \mu\text{m}$ , and are mostly subrectangular (Fig. 1m). A narrow, intramarginal, unistratose (rarely bistratose) rib of linear cells is usually apparent. Adjacent to this, a single row of subrectangular cells (ventrally and dorsally flat) forms a subentire to denticulate margin (Fig. 1n, p). Unlike in *C. porrectum* and *C. couguiense*, the costa in the gemmiferous leaves of *C. subintegrum* ceases just below the leaf apex. This is formed by a narrow band of lamina, and gemmae are produced only from the ventral surface of the costal tip (Fig. 1l). Adjacent to the clustered gemmae a few elongated, finger-like cells may protrude from the surface of the costa. Unfortunately, the disposition of gemmae and lamina is often obscured by damage, or in well-developed leaves, by the backward flexing of the leaf tip. In practical terms, this slightly limits the value of the apices of gemmiferous leaves as a reliable distinguishing feature.

In *Calymperes couguiense* the non-gemmiferous leaves have a similar disposition to those in *C. subintegrum* and are never notably recurved. They have scabrid costae (Fig. 1h), and the cells of the chlorophyllose lamina are ventrally acutely protuberant and dorsally unipapillose (Fig. 1i). Superficially they are visibly smaller than those of *C. porrectum* and *C. subintegrum*, reaching  $<5-10(-12.5) \times 5-7.5(-10) \mu\text{m}$  (Fig. 1d). Above the hyaline lamina, the leaf margins are often formed by a subentire to denticulate, polystratose rib (Fig. 1e, j, k). This sometimes appears to be intramarginal, particularly when seen in surface view. In the leaves of many specimens the marginal/intramarginal rib is poorly developed to absent (Fig. 1f). The gemmiferous leaves possess apices similar to those of *C. porrectum*, with an excurrent, scabrid costa and gemmae produced in a cluster from the costal tip. The lamina narrows into the costal apex, its distal-most cells, and the distal-most superficial cells of the costa are elongated, finger-like with rounded ends; they form a regular to irregular fringe at the base of the crown-like cluster of gemmae (Fig. 1c). These sterile, projecting cells are a consistently well-developed feature in collections of *C. couguiense*.

**HABITAT.** *Calymperes couguiense* Besch. evidently flourishes in habitats ranging from undisturbed forest to cultivated gardens, and has mostly been collected from sea level to below 500 m. Both *Calymperes porrectum* and *Calymperes subintegrum* occur within this altitudinal range, but records of these species extend to over 1000 m. *Calymperes couguiense* also shares some substrate

preferences with *C. porrectum* and *C. subintegrum*, occurring on tree boles, twigs and dead wood. Well-developed turfs of *C. couguiense* have also been collected on sandy soil.

**DISTRIBUTION.** *Calymperes couguiense* Besch. is largely a species of the Pacific islands and northeastern Australia. Reports of its occurrence in Java and New Guinea (Reese, Koponen & Norris, 1986; Reese & Stone, 1987, 1995) appear to be unsupported by specimens. Misidentified collections from the Malay Peninsula (*Spare* 3213b, BM), Java (*Fleischer* 70, BM, FH, NY; *Schiffner* 3, BM) New Ireland (*Eddy* 6165, BM), and New Guinea (*Zanten* 190a, NY) represent a diminutive form of *Calymperes porrectum* Mitt. A further wrongly determined collection from New Guinea (*Zanten* 149c, BM) is *Calymperes subintegrum* Broth. Of the material seen for this present study, only a single collection from New Britain (*Streimann* 40215, NY) indicates the presence of *Calymperes couguiense* in Malaysia.

Orbán (1995) identified specimens from the Seychelles as *C. couguiense* and Reese & Stone (1987) cited Mauritius as a station. Unfortunately, the material on which the latter citation is presumably based (*Balfour* s.n., NY) represents a form of *Calymperes hispidum* Renaud & Cardot.

**SPECIMENS EXAMINED.** *Calymperes couguiense* Besch. **Australia.** Queensland: Cook, Cairns, Crystal Cascades, 16° 55' S 145° 46' E, July 1979, *Stone* 15334 pro parte (MEL), 15349 pro parte (MEL); Cook, Bellenden Ker National Park, Goldsburgh Track, The Boulders, 6 km W. of Babinda, 17 July 1987, *Stone & Reese* 24451 (MEL); Cook, rainforest in saddle between Bartle Frere and Bellenden Ker ranges, 8 km W. of Babinda, 7 July 1987, *Reese, Stone & Stone* 17038 (NY); Cook, Mt Bellenden Ker, 17° 16' S 145° 51' E, 4 September 1986, *Stone* 24121 (MEL), 24122 (MEL), 24123 (MEL); Cook, Mossman Gorge, 16° 28' S 145° 21' E, 1 September 1986, *Stone* 24061 (MEL), 24045 (MEL); Cook, Mossman Gorge, May 1975, *Stone* 8837 pro parte (MEL), 12037 pro parte (MEL); Cook, Mossman, Rex Creek, 16° 28' S 145° 16' E, 30 June 1982, *Stone* 19642 pro parte (MEL); Cook, Woornooran National Park, Josephine Falls, 17° 25' 58" S 145° 51' 32" E, 19 August 1986, *Stone* 23904 (MEL); Cook, Cardstone, Tully, 17° 55' S 145° 55' E, 20 May 1985, *Stone* 23113 (MEL); North Kennedy, Kennedy Bay, 17° 58' S 146° 04' E, 16 May 1982, *Stone* 18573 pro parte (MEL), 18577 (MEL); 9 July 1982, *Stone* 19987 (MEL), 20000 (MEL); North Kennedy, Cardwell, Conn Creek, 18° 15' S 145° 43' E, 8 August 1980, *Stone* 16337 (MEL); North Kennedy, Cardwell, Stoney Creek, 18° 35' S 145° 48' E, 21 July 1979, *Travers* 14876 pro parte (MEL), 20 May 1982, *Stone* 18666 pro parte (MEL); North Kennedy, Tully, Kooroomool Creek, 17° 52' S 145° 42' E, 25 May 1982, *Stone* 18803 pro parte (MEL). **New Britain.** Hoskins, town area, 5° 26' S 150° 25' E, 16 February 1989, *Streimann* 40215 (NY). **Mariana Islands.** Guam, limestone forest 6 miles N. of Agana, 13 November 1945, *Holland* 21 (FH). **New Caledonia.** Balade, *Vieillard* 1776 (BM, S). **Fiji.** Viti Levu, Suva, 25 January 1923, *Greenwood* 477 (FH); Vanua Levu, December 1922, *Greenwood* 474 (BM). **Samoa.** Tutuila, Vatia, *Bryan Jr* s.n. (FH); Tau, 4 October 1939, *Yuncker* 9243 (FH!); Tau, Judd's Crater, NW rim, 27 July 1938, *Harris* 413 (FH), 414 (FH); Upolu, Mataulu village, Lefaga Bay, 24 October 1953, *Irwin* 122 (FH). **Tuamotu Archipelago.** Makatea, 3 March 1930, *Emory* s.n. (FH). **Society Islands.** Tahiti: Gaugin Museum, 26 May 1988, *Hegewald & Hegewald* 11477 (MO); Insel Huahine, *Hegewald & Hegewald* 11442 (MO); Mooréa, au-dessus du point de vue du Belvédère, 11 July 1975, *De Sloover* 20962 (H, NY).

**SPECIMENS MISIDENTIFIED AS CALYMPERES COUGUIENSE BESCH.** *Calymperes boulayi* Besch. – **Australia.** Queensland: along 'Sullivan's Track', c. 6 km WNW of Cardwell, 22 July 1987, *Reese, Stone & Stone* 17168 (MO).

*Calymperes hispidum* Renaud & Cardot – **Mauritius.** *Balfour* s.n. (NY). *Calymperes moluccense* Schwägr. **New Caledonia.** Ilot au Sud de l'île, May 1988, *Martin* s.n. (PC). *Calymperes porrectum* Mitt. – **Malay Peninsula.** Perak, Kampong Ijok,

25 August 1940, *Spare* 3213b (BM!). **Java**. Buitenzorg, Botanic Garden, March 1899, *Fleischer* 70 (BM, FH, NY), March 1894, *Schiffner* 3 (BM). **New Ireland**. East coast, Danfu Valley, 2 February 1970, *Eddy* 6165 pro parte (BM!). **Papua New Guinea**. Kau River, below Star Mountains, Woropko, Zanten 190a (NY).

*Calymperes strictifolium* (Mitt.) G. Roth (forma) (*C. francii?*) – **New Caledonia**. Rivière Bleu Reserve, near bridge over Rivière Bleu, 7 September 1981, *Crosby* 14325 (NY).

*Calymperes subintegrum* Broth. – **Australia**. Queensland, Cook, Wooroonooran National Park, Josephine Falls, 17° 25' 58" S 145° 51' 32" E, 19 August 1986, *Stone* 23905 pro parte (MEL). **Fiji**. Viti Levu, hills between Navua and Suva, May 1943, *Greenwood* 903 (BM), 976 (BM). **Papua New Guinea**. Ajerok, 24 May 1959, *Zanten* 149c (BM).

**ACKNOWLEDGEMENTS.** I am grateful to the curators of FH, H, L, MEL, MO, NY, PC and S for the loan of specimens.

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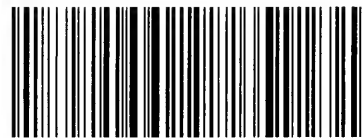
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## CONTENTS

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*N.K.B. Robson*
- 125 The natural history of reproduction in *Solanum* and *Lycianthes* (Solanaceae) in a subtropical moist forest  
*S.D. Smith and S. Knapp*
- 137 The diatom type slides and bibliography of John Carter (1908–1993)  
*D.M. Williams and G. Reid*
- 153 The typification, defining features and geographical range of *Calymperes couguiense* Besch. (Calymperaceae: Musci)  
*L.T. Ellis*

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0968-0446(200211)32:2;1-K

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Vol. 32, No. 2, November 2002