

*Silene* (Caryophyllaceae) in Greece: a subgeneric and sectional classificationWerner Greuter<sup>1</sup>*Summary*

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Of a world total of c. 700 species of *Silene*, here widely defined to include *Lychnis*, *Cucubalus*, and other generic splits recognized by some authors, 119 are known to be present in Greece. They are grouped in 4 subgenera and 39 sections (some of them new). The sections are keyed out and briefly characterized (mainly on the basis of Greek taxa), and their correct nomenclature is established on the basis of full synonymies and type designations. In many cases the sectional limits remain provisional, and corresponding problems are highlighted. Phylogenetic patterns within the genus, here briefly discussed, are still largely unclear due to frequent character reversals and parallelism.

*Introduction*

*Silene* L. is one of the larger genera of the World's flora. In the wide sense adopted here it comprises c. 700 species, about half of which occur in the Mediterranean area. The S. Balkan Peninsula and S.W. Asia are two of the main centres of diversity for the genus. The present paper, which is a corollary to the *Silene* account prepared for volume 1 of *Flora hellenica* (Phitos & al., in preparation), concerns an area placed at the junction of these two centres.

Problems encountered in Greek *Silene* at the specific and subspecific rank, and their proposed solution, have been discussed elsewhere (Greuter, 1995). According to the *Flora hellenica* account, in Greece alone no less than 119 *Silene* species (including 3 likely casuals) are presently known, of which 37 are endemic to the country and to which several mostly endemic subspecies may be added. This figure compares favourably with species numbers of *Silene* sensu lato known for much larger areas: 92 for N. Africa (Maire, 1963), 122 for Turkey (Davis, 1967), 141 for the *Flora iranica* area (Rechinger, 1988), and 203 for the whole of Europe (Tutin & al., 1993).

The *Flora hellenica* account recognizes generic subdivisions at the ranks of subgenus and section. In preparing it I encountered numerous problems, both of a taxonomic and nomenclatural kind. The latter is not surprising in view of the generally confused state of supraspecific nomenclature, which reflects not only the lack of indexes for names at these ranks but also the rather casual manner in which many authors, past and present, use to treat them. Taxonomic changes resulted both from a revised circumscription of the genus (see below) and from a better understanding of the natural affinities of its Greek representatives.

While fully aware of the unsatisfactory and provisional nature of a classification that is national in coverage, I believe that the assembled material is nevertheless of general relevance. In particular, the identification key and descriptive matter, while subject to regional idiosyncrasies as explained below, are nevertheless essential in

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order to evaluate, criticise and improve the scheme proposed here, and have therefore been included in spite of their length and intrinsic imperfection.

#### *Generic delimitation and classification*

The treatment in *Med-Checklist* (Greuter & al., 1984) on which the *Flora helvetica* accounts normally rely includes a number of taxa within *Silene* that were kept generically distinct in much of this century's European floristic literature, notably *Heliosperma* (Rchb.) Rchb., *Lychnis* L., *Melandrium* Röhl., and *Viscaria* Röhl. (i.e., *Steris* Adans.). Other generic splits recognized by some E. European authors, but which have failed to achieve widespread recognition, are similarly included: *Coronaria* Schaeff., *Oberna* Adans., *Otites* Adans., and *Pleconax* Raf. Furthermore, the monotypic *Cucubalus* L., still kept separate in *Med-Checklist*, has been added to the lot. Following a proposal by Rabeler (1992), *Silene* is now a conserved name (Brummitt, 1994), to avoid transfer of all relevant names to *Lychnis* which would otherwise be necessary under a wide generic concept.

The trend towards reducing the number of genera in the tribe *Sileneae* DC. is not new. *Heliosperma*, *Melandrium*, and other generic splits like *Eudianthe* (Rchb.) Rchb. and *Gastrolychnis* (Endl.) Rchb., have been reduced to *Silene* at various times by various authors, followed by the influential *Flora europaea* treatment (Chater & al. in Tutin & al., 1993) which also merges *Steris* with *Lychnis*. Among the authors who critically discussed the *Silene-Lychnis* relationship, without however drawing formal conclusions, is McNeill (1978). Long before the merger of these two assemblages in *Med-Checklist* (Greuter & al., 1984), Hess & al. (1967) had opted for the same solution, and more recently Melzheimer (in Rechinger, 1988) concurred. The reasons given by these authors are, in essence, that the characters used to define smaller genera in the *Sileneae*, capsule structure in particular, tend to break down when variation patterns are considered on a global scale. Inter-group crossability, as reviewed by McNeill (1978), is far from negligible and often results in fertile offspring, contrary to what one would expect for decent caryophyllaceous genera.

A recent DNA sequencing study by Oxelman & Lidén (1995) lends strong support to the assumption that, not only are *Silene* and *Lychnis* unnatural assemblages as presently delimited, but that, however far one may proceed in recognizing small natural units as segregate genera, inevitably one will be left with a large, polymorphic and highly paraphyletic residue that cannot be reasonably split any further in the present state of our knowledge. Taking Oxelman & Lidén's cladogram at face value (which is perhaps more than its authors would expect) one either ends up with genera that cannot be morphologically defined, and with a classification with little if any predictive value as to the appropriate place of species not yet sequenced; or with the widely circumscribed, single genus *Silene* for which I have opted here. Of all traditionally recognized genera of the tribe, only *Agrostemma* L. and, with a lesser degree of confidence, *Petrocoptis* A. Braun ex Endl. as well as, somewhat surprisingly, *Eudianthe*, withstand the suctional power of the silenean complex, in whose centre are nested hitherto undisputed "genera" such as *Cucubalus* and the Afromontane *Uebelina* Hochst.

The subgeneric and sectional treatment of *Silene* that follows is limited to taxa present in Greece. The key and descriptive matter are based primarily on the Greek

material studied. This limitation must be borne in mind when using the present account. The (estimated) total species number per section, when compared with the number of Greek representatives, shows how thorough the coverage has been in each case. For groups that are well represented on the Greek territory, I have often formalized my own views on natural affinities by the recognition of new or upgraded taxa; in other cases, and in particular when the problems transcend the southern Balkans, I have only discussed them while maintaining the pre-existent classificatory frame.

Three world treatments of *Silene*, or of the whole sileneans, have laid the foundations of our present understanding of the group: those by Otth (in Candolle, 1824), Rohrbach (1867a-b, 1869), and Chowdhuri (1957). Each is remarkable in its kind, especially when seen against the background of prior knowledge, but none is perfect. Other global treatments (Pax in Engler & Prantl, 1889; Williams, 1896) are epigonal in comparison. Much more important are major regional revisions such as those by Boissier (1867), Šiškin (in Komarov, 1936), and Melzheimer (in Rechinger, 1988), to name but the most noteworthy ones. This account has profited from them all.

The classification offered here recognizes four subgenera on the basis of striking and apparently constant morphological differences, of which three are likely monophyletic whereas the fourth and largest one, *Silene* subg. *Silene*, is clearly paraphyletic. At the sectional level I have endeavoured to recognize, or at least foreshadow, truly monophyletic groups. However, the sequence of the sections has been but little modified from that used in *Flora europaea*, and does not claim to reflect natural affinities any better than previous arrangements – as one will find when reading the comments under the individual sectional entries. The reader is therefore warned not to take the present classificatory scheme as definitive, but to understand and use it in the light of the critical remarks made section-wise. Similarly, use of the key should always be made *cum grano salis*, especially when non-Greek taxa are being considered.

### Morphology

No complete overview of morphological features found in *Silene* can be attempted here. I will limit myself to discussing some of the more critical, or unjustly neglected, characters, and will in some cases explain and define the terms used to designate them. Functional traits that reflect upon morphology, such as periodicity and movements in flowering, will also be considered.

*Inflorescence.* – *Silene* offers a wide variety of inflorescence types which have since early times (Otth in Candolle, 1824) been used for the purpose of classification. They can be reduced to the three basic categories, thyrsus (composed of cymes, usually dichasia, arranged in a raceme), dichasium, and monochasium, but these categories are often difficult to use in descriptions and keys because of within-taxon variability and of the fact that, when flower number decreases, they tend to grade into each other. For example, the reduced thyrsus of *S. schwarzenbergeri*, which consists of one terminal and 0-3 alternating lateral dichasia each reduced to a single flower, is easily mistaken for a monochasium as in, e.g., *S. ciliata* when one neglects the fact that, in the former, the lateral flowers are bracteolate. The single flowers prevailing

in *S.* sect. *Saxifragoideae* can be interpreted as basically thyrsoidal only through the few many-flowered members of that group, e.g. *S. linoides*. Taken by themselves, they cannot be told apart from depauperate, one-flowered inflorescences of a monochasial species, e.g. *S. nocturna*, or a dichasial one like *S. cretica*.

Difficulties of interpretation may arise between truly thyrsoidal species and others, e.g. *Silene longipetala*, that bear terminal dichasia on numerous side branches. As long as intercalary leaf pairs exist at the base of a branch it can be identified as such, but when their number is reduced to zero this criterion fails. Distinction between monochasia and dichasia, so easy when the extremes are considered, breaks down completely in view of a full range of intermediate types, ranging from (constant or occasional) twin monochasia with a single dichasial branching and "alar flower" at the base to slightly inaequilaterally branched dichasia in which the last level of branching may become monochasial.

In spite of these difficulties, inflorescence type has its importance in *Silene* classification, and groupings based on it are partly supported by Oxelman & Lidén's (1995) recent sequencing analyses. It is a character to be used with care and discrimination, but not to be dismissed.

*Flowering rhythms.* – Movements of the flower during anthesis can be observed in many species and can as a rule be reliably inferred from dried specimens. Most commonly the flowers become  $\pm$  nodding when they open, whereas the buds and later on the mature capsules take an upright position. The contrary movement, with flowers erect or spreading and capsules  $\pm$  nodding, is rather exceptional but characterizes, i.a., *Silene* sect. *Psammophilae* and a group of species in *S.* sect. *Brachypodae* (q.v.). These shifts in position of the flower are usually associated with bending, or straightening, of the pedicel, examples being the downward-bent flowering and upward-bent fruiting pedicel often seen in *S.* sect. *Behen*, or the basally spreading but apically upcurved fruiting pedicel of *S. sedoides*. The nature of such movements often characterizes species (*S. nutabunda*) or species groups, rarely whole sections.

More important at sectional level, but more difficult to assess on herbarium specimens, are daily flowering rhythms. These have long been known to occur in *Silene*, and are reflected in the names of species such as *S. noctiflora*, *S. nocturna*, and *S. vespertina* Retz. (a synonym of *S. bellidifolia*). The principle has been well described and illustrated by Kerner (1889-1891: 150-152) for *S. nutans*, and provided the main subject of an important comparative study by Lindman (1897). Halket (1931) has investigated the mechanism and its causes in *S. saxifraga*, with conclusions that can probably be generalized for the whole genus. It appears that the opening and closing of *Silene* flowers is a turgor movement, depending on water supply and air humidity not on light, temperature, or endorhythmic control. Whether the same applies to the development of scent (see below) is apparently unknown.

In essence, one can distinguish two kinds of flowering "strategy" in *Silene*, no doubt corresponding to different pollination syndromes. The first type I shall call diurnal, following Lindman (1897), although the term is perhaps not ideal for flowers that remain open not only during the day but, as far as is known, also at night. Diurnal flowers are usually characterized by petal limbs that are not or feebly lobed, are vividly coloured, at least above, in some shade of pink or magenta, and do not inroll under water stress conditions; they may, however, change the angle at which they spread, or may rotate to an oblique position, or even become contorted. Beyond



the cursory observations of Lindman (1897), little is known on the function and possible periodicity of the latter kinds of movement.

What I call vespertine flowers (not nocturnal as Lindman does, since opening usually takes place at some time in the late afternoon or evening) occur in a majority of Greek species. Their petal limbs are characteristically bifid in various degrees, often into narrow lobes, are white to yellow (rarely pink) above and livid to greenish or reddish-brown underneath, and inroll progressively and reversibly under drought. Day periodicity varies due to differences in sensitivity of the regulating mechanism, and irregularities are naturally frequent since the movement is moisture- not day-light-controlled (many species will open their flowers in the middle of a day under a downpour of rain). Development of strong fragrance in the evening and night has been reported for several such species, yet the record is still very incomplete.

*Flower morphology.* – *Silene* flowers, with rare exceptions, function as gamopetalous tubular flowers in spite of their dialypetalous corolla. This is brought about, on the one hand, by the support of a long, synsepalous, often tubular calyx, and on the other hand by the cohesion of the petal claws (which are often expanded above, and sometimes auriculate or ciliate) and/or coronal scales, which together form the corolla mouth.

Calyx features that have been given prominence by earlier authors are, in particular, general shape at the fruiting stage, number, consistency and ramification of the veins, and indumentum. Details of the shape and ciliation of calyx teeth deserve future attention in spite of their variability, which is partly due to the fact that the outer and inner teeth (as seen in valvate aestivation) may differ. The calyx base, whether umbilicate or not, may also be diagnostically important at sectional level. One character that has not yet been adequately studied is indumentum inside the calyx, especially at its base, which is often present as an apparent match of anthophore indumentum and is perhaps functional as an obstacle to nectar predators seeking illicit access through the calyx base, when nectar secretion takes place at the distal end of the anthophore.

Length and pubescence of the anthophore are usually diagnostic for species, the latter sometimes at the sectional level. The anthophore consists of the bases of the corolla and stamens fused among themselves and with the central flower axis. It has often been termed “androgynophore” or “gonophore”, or even “carpopophore” (see Bocquet, 1968a: 162), but all these terms I would consider as misapplied, the latter designating a structure placed between androecium and gynoecium, and the two former, between corolla and androecium, whereas in *Silene* the anthophore separates the attachment of calyx and corolla. One may of course object that, semantically, anthophore is not the right word either, being equivalent to pedicel; but the term as far as I know has never been used in such a sense, and the Greek word *anthos* can stand for the functional unit (blossom) just as well as for flower in the morphological sense of the term.

Corolla features were unjustly neglected in the past in Mediterranean species, perhaps because they are difficult to study on herbarium material. They are, however, of great importance for the correct delimitation of *Silene* taxa. Colour and shape of petal claw and limb are useful characters, but the most significant variation is perhaps linked to the corona. Two free or partly fused (and sometimes further divided) structures are usually found ventrally at the junction of claw and limb, which I term

“coronal scales”. Their size, shape, consistency, degree of hollowness, and position within the flower should, if at all possible, be observed and described on live plants. At present, the data available are unfortunately scant.

*Capsule.* – Capsule size, shape, sometimes consistency, and of course dehiscence type and carpel number, are often used in *Silene* taxonomy, but other useful features are less regularly mentioned. My own data on capsule wall structure and degree of hardening and persistence of the styler bases are unfortunately incomplete. The extent to which the basal septa, always present in the young ovary, are maintained or dissolved at maturity has been used as a generic character in the past, but was surprisingly often neglected within what was considered the core genus, *Silene*. Bocquet (1968a: 168-171) has discussed this feature at length, to dismiss it as of little taxonomic value – which is certainly true at generic but not at sectional level.

*Seed.* – The basic architecture of *Sileneae* seeds is uniform: they are laterally somewhat compressed, reniform to suborbicular or  $\pm$  angular (when densely packed during maturation) in side view, with a ventral hilum at the bottom of a depression (notch or cavity), a curved embryo along the dorsal periphery, and abundant mealy perisperm in the middle. Structural details vary greatly, however, and are useful taxonomic markers, provided that fully mature seeds are available for study. The main limitation of seed features is that they are unknown for several species and, for others, known only from a small sample of populations so that little is known of their variability and reliability.

The terms flanks, shoulders and back were found adequate to describe general seed shape, where the shoulders are defined as the contact zone between flanks and back. Depending on the shape of flanks and back, whether convex, flat or concave, the shoulders may be rounded and  $\pm$  obsolete, or angular, keeled or even winged. A special seed type, characteristic of some of the annual sections, is with small, excavate flanks that are surrounded by broad, laterally bulging shoulders bordering a wide, usually flattish back.

The flanks usually show a regular and distinct radial-concentric cell pattern centred on the hilar region at their ventral edge. The hilum itself lies either on the bottom of a  $\pm$  circular depression, in which case a pad of small-celled tissue shields it from view on both flanks; or in a  $\pm$  narrow transverse groove, so that the hilar region appears as a notch in side view, when the small-celled tissue pad is reduced in size or wanting. There is a full range of intermediate states between these two extremes, and intraspecific variation is considerable, so that this character, while generally informative, should be used with care.

Shape and structure of the testa cells have received considerable attention lately, especially in the works of Melzheimer (1977, 1980, 1987, and in Rechinger, 1988). Not all characters used by Melzheimer have, however, proved to be useful. Oxelman's (1995: 149) statement, that the shape of the testa cell margin is of little importance in *Silene* sect. *Sedoideae*, can be generalized for the other sections as well. I have found a number of allegedly diagnostic features, such as cell shape in surface view, the presence of mamillae, and cell surface granularity, to be quite variable within certain species or even populations while constant and reliable in others. In a general way, testa cells tend to be elongated to various degrees in a radial sense on the flanks, and transversely on the back. The individual cells may be flat, or

bulging as a whole, but more often they possess a single, central or decentral, conical or truncate-conical mamilla that is particularly pronounced in peripheral cells and usually small or absent in the perihilar ones.

A structure of which I could find no mention in the literature is what I have termed apiculum: a minute, perhaps secretory extrusion, usually single and central or eccentric in each cell (and often though not always in the centre of the mamilla, when present), which may take the form of a dark dot or acumen, or, particularly in the small perihilar cells, of a stipitate "gland". This structure appears to be constantly present in *Silene* sect. *Italicae*, but is found in other species, too. *S. graeca* has several minute dark dots on each testa cell, which may perhaps be similar in structure and function. More observations are needed.

### Nomenclature

Several general questions of a nomenclatural kind have cropped up during the preparation of this survey. Some of them (e.g. the unranked status of the so-called sections of *Silene* in Boissier, 1867) have been addressed by Rabeler (1993) in his recent update of caryophyllaceous infrageneric nomenclature, and need not be mentioned here. Others, however, require explanation.

*Dates.* – Establishing the relative priority of competing names is fortunately easy in our group. The only tricky problem, merely of correct citation, is with a set of names published twice, almost simultaneously, by one and the same author (Rohrbach, 1867a, b). Both publications appeared at the end of 1867 (or perhaps early in 1868), but no exact date could be established for either. One is in the December issue of the *Annales des sciences naturelles*, the other in an appendix of the 1867 Berlin seed list presumably distributed at the turn of the year (Appendix 3 of that list, almost certainly published simultaneously, includes reference to a paper published on 23 Nov 1867 in the *Gardener's chronicle*). I have found no better solution than citing both sources in each case. Incidentally, Rohrbach's names of subdivisions of *Silene* are almost invariably (and incorrectly) cited from his monograph (Rohrbach, 1869), which was published a full year later, on 1 Jan 1869.

*Valid publication.* – All names mentioned in the synonymies below have been checked and found to be validly published under the current *Code*. No problems were encountered, except that a few names have no nomenclatural status because they contravene Art. 21.3 (prefix *Eu-*). One intriguing individual case is discussed under *Silene* sect. *Otites*.

*Legitimacy.* – The number of illegitimate names is surprisingly small in spite of extensive homotypy and frequent disregard of earlier names by many authors. This is mainly due to the fact that early names were often not published in a definite rank (see below) and therefore (a) cannot be superfluous under Art. 52.1, which applies only at definite ranks, and (b) can in turn serve as a legitimate basionym thus, under Art. 52.3, conferring legitimacy to names in definite ranks that are in effect superfluous. A second provision that proves beneficial in many cases is the newly phrased Art. 52.2, which rules that inclusion of a subsequently designated type does not by itself cause illegitimacy. Now that this point has been clarified, and since types, in

most cases, have been designated only recently, Art. 52 is but rarely applicable except when either the original or automatic type of a priorable name was included in the protologue, or when the name itself is cited.

For the sake of completeness, one may add that the Art. 53.5 situation (homonymy at the same or at different ranks) has been encountered only once (see *Silene* subsect. *Nutantes*, under sect. *Brachypodae*).

*Ranks.* – Brizicky's (1969) pioneer paper on early use of subgeneric and sectional ranks has proved an important and reliable guideline in almost every case (see also Rabeler, 1993). There is a single instance in which, after reflection, I have preferred a different answer to Brizicky's: I have concluded that Endlicher (1840, 1842), in the *Caryophyllaceae* treatment influenced by Fenzl (see below), consistently uses two different, definite ranks, subgenus (lettered in Latin script) and section (with Greek letters). Such an interpretation, while compatible with the provisions of the *Code* (see below), is preferable to Brizicky's (no definite ranks) in this case, in the interest of nomenclatural stability and historical fairness [although I do not question Brizicky's conclusion for the non-caryophyllaceous portions of Endlicher's book].

Technically, the answer depends on whether one accepts that Endlicher's *Genera plantarum* and its supplements are parts of one and the same publication, as defined in Art. 35.4. The question of supplements is not directly addressed in that provision, where "same title, same author, same edition" are the three stated criteria. In our case, one may question that the *Genera* and Supplement 2 (*Mantissa plantarum sistens Generum plantarum supplementum secundum*) have the same title. My answer is: they do have the same main title (*Genera plantarum*, although it is in the genitive case in the Supplement, for grammatical reasons), although the Supplement has a different subtitle (*supplementum secundum*) and an alternative title (*Mantissa plantarum*, which stands first but in somewhat smaller type). Perhaps more importantly, Supplement 2 is one of a series of five, the first of which is by all evidence part of the main publication (continued pagination, no title page of its own).

The reason why this is important is that the 1840 treatment does not mention ranks in the case of the *Caryophyllaceae*, whereas the 1842 supplement does, and consistently so, in the sense mentioned above. Under Art. 35.4 the 1840 names, which would otherwise be unranked (and are often not taken up again in 1842), can thus be accepted in definite ranks.

*Typification.* – I have avoided the customary (mis-)use of the terms holotype, syntype and lectotype for supraspecific names (*Code*, Art. 10 Note 1). The term "type" stands either for original type (single included element, or originally designated type, or automatic type under Art. 22.5), in which case no qualification is added; or for subsequently designated type, when reference to the first known designation is added. When no previous designation is known, the type is considered as newly designated here. In designating types, I have been careful to relegate to synonymy names that are either unused or ambiguous in view of their earlier use, but to keep such names available as may later be found useful for designating more narrowly defined units, e.g. at the subsectional level.

Types are mentioned only once, at the end, for each homotypic block of synonyms. Frequently, however, homotypy is not a primary quality of names but the

result of later type designation. Different names of the same homotypic group may therefore have had their type designated at different times and by different authors. It must be understood that the reference given at the end of a paragraph, within the type entry, relates to the first listed name of the block (or to its basionym, as the case may be); all other type designations (including new ones) are indicated under the individual synonyms.

*Author citation.* – Clarification of Art. 46 at the Tokyo Congress has left little ambiguity in this field. The only tricky issue is, again, in Endlicher's (1840, 1842) work. The *Caryophyllaceae* treatment, there, has obviously been taken largely from an unpublished thesis by Fenzl, repeatedly quoted as one of Endlicher's sources in 1840 (e.g. as "Fenzl *dissert. inedit.*", under *Saponaria*). Names of some of the new taxa, but not the descriptions, are ascribed to Fenzl, so that the author citation is "Fenzl ex Endl." New combinations or transfers, however, though usually attributed to Fenzl by later authors, are credited only to the basionym author. Accepting that the *Genera* and its supplements are parts of one publication under Art. 35.4 (see above), one may nevertheless accept Fenzl as the author of those transfers which, usually in synonymy, are ascribed to him in Supplement 2 (see Art. 46.6), where extensive quotations also demonstrate that he "contributed in some way to that publication" (Art. 46.2).

Autonyms (Art. 22.1) are now treated as validly published names (Art. 32.7) with priority at their rank (Art. 11.6), and it is often desirable to cite them in order to justify the choice of a name as correct. Since they are not to be followed by an author citation (Art. 46.1), citation poses problems, and the *Code* gives no relevant guidance. I have chosen to add reference to the place of valid publication (or establishment) of an autonym in square brackets, with insertion of the preposition *per* ahead of the name of the validating (or establishing) author.

*Spelling.* – Under Art. 61 of the *Code*, later orthographical variants of a name are not validly published, and, whenever they appear in print, are to be treated as if they were printed in their correct form (Art. 61.4). By consequence, it is inappropriate to even parenthetically cite such incorrect variants in synonymies, and I have as a rule ignored them even though their use may in its time have been deliberate (as was doubtless the case with *Conoimorpha* being spelled *Coniomorpha* or *Conomorpha*, and *Melandrium*, *Melandryum* or *Melandrum*).

I made an exception to that rule in the case of plural vs. singular epithets, either both used as nouns (*Atocia* vs. *Atocion*) or one adjectival and the other substantival (*Otiteae* vs. *Otites*). It may need explanation why the two former are indeed correctable orthographical variants. The first case is straightforward, since a plural noun as epithet, in the name of a subdivision of a genus, is contrary to Art. 21.2 and correctable under Art. 32.6 (such epithets must either be plural adjectives or have "the same form as a generic name", i.e., be singular nouns under Art. 20.1). The second case may appear more tricky, since a singular noun and a plural adjective are not just two different spelling or inflectional forms of an epithet, and so do not fall under the definition of variants in Art. 61.2. In this case, however, Art. 61.5 applies: *Otites* and *Otiteae*, when used as epithets under the same generic name to designate the same plants, are doubtless confusingly similar and must therefore be treated as if they were variants in the strict sense.

*Key to subgenera and sections of Greek Silene*

1. Capsule opening by 5 entire teeth ..... 2.
- Capsule opening by 6 or sometimes 10 teeth, or indehiscent ..... 4.
2. Capsule septate for most of its length, its teeth alternisepalous, alternating with the styles which are upright at the base; inflorescence thyrsoïdal (subg. *Viscaria*) ..... 3. sect. *Viscaria*
- Capsule not septate, its teeth alternipetalous, terminated by the styles which are divaricate-reflexed at the base; inflorescence thyrsoïdal (subg. *Lychnis*) . . . 3.
3. Plants tomentose, with monopodial growth and lateral stems; petal limb rounded to emarginate ..... 1. sect. *Agrostemma*
- Plants subglabrous, with sympodial growth and terminal stems; petal limb 4-lobed or 4-fid ..... 2. sect. *Coccyganthe*
4. Calyx with 15-60 unbranched, parallel veins; commissural veins often absent or forking early; plants always annual (subg. *Conoimorpha*) ..... 5.
- Calyx (5-)10-veined, or if  $\pm$  20-veined, plants perennial and veins branched and anastomosing; commissural veins normally present (subg. *Silene*) ..... 6.
5. Calyx pubescent but not hirsute, truncate or invaginate and not adnate to the corolla at the base; staminal filaments hairy at the base, glabrous above ..... 38. sect. *Conoimorpha*
- Calyx pubescent and hirsute, with patent setae, rounded and shortly adnate to the corolla at the base; staminal filaments glabrous at the base but ciliate in the middle ..... 39. sect. *Lydiae*
6. Fruit indehiscent, black, berry-like, pergamentaceous; calyx reflexed at maturity, with 5 faint veins ..... 19. sect. *Cucubalus*
- Fruit a capsule (sometimes tardily dehiscent but then hard), never black; Calyx sometimes split or retracted but never reflexed, with 10-20 veins .... 7.
7. Capsule lacking septa, or with narrow septal remains at the base; calyx pubescent to villous ..... 8.
- Capsule with well developed septa at least in its lower half, or if with reduced septa, then calyx glabrous ..... 12.
8. Biennial or perennial, or if annual then capsule hard and firm ..... 9.
- Annual, with a thin and fragile,  $\pm$  translucent capsule ..... 11.
9. Seeds with long papillae forming a distinct crest on the back; calyx feebly 10-veined ..... 25. sect. *Heliosperma*
- Seeds smooth or tuberculate, but never with long, crest-forming papillae; calyx with 10-20 markedly anastomosing veins ..... 10.
10. Calyx vesicular-campanulate, inflated; leaves 1-3-veined ..... 17. sect. *Odontopetalae*
- Calyx ellipsoidal to ovate or fusiform, not inflated at maturity; leaves pinnately veined ..... 4. sect. *Elisanthe*



11. Seeds globular, with indistinct shoulders ..... 28. sect. *Atocion*  
 – Seeds reniform, with flattish flanks and bluntly angular shoulders  
 ..... 27. sect. *Sedoideae* p.p.
12. Annual ..... 13.  
 – Biennial or perennial ..... 23.
13. Calyx glabrous and smooth (except for ciliation of teeth) ..... 14.  
 – Calyx hairy or scabrous ..... 16.
14. Anthophore pubescent (if imperceptibly so, then calyx 5-7 mm); gynophore,  
 above the stamen insertion, absent ..... 26. sect. *Rigidulae*  
 – Anthophore glabrous (exceptionally pubescent, in plants with a short gynophore  
 above the stamen insertion); calyx at least 7 mm ..... 15.
15. Calyx narrowed apically at least in fruit (if indistinctly so, anthophore  
 pubescent) ..... 30. sect. *Behenantha*  
 – Calyx not narrowed apically; anthophore always glabrous  
 ..... 23. sect. *Compactae* p.p.
16. Seeds with small, excavate flanks and laterally bulging shoulders ..... 17.  
 – Seeds with depressed to convex flanks, and rounded to angular or winged  
 shoulders ..... 19.
17. Inflorescence a secund monochasium with or without one basal dichasial  
 branching ..... 37. sect. *Silene*  
 – Inflorescence dichasial, sometimes inaequilaterally so ..... 18.
18. Calyx antrorsely eglandular-scabrid ..... 32. sect. *Lasiocalycinae* p.p.  
 – Calyx glandular-pubescent ..... 36. sect. *Rubellae*
19. Seeds with depressed flanks, and shoulders produced into wavy wings  
 ..... 34. sect. *Dipterospermae*  
 – Seeds with flat to convex flanks and rounded to angular shoulders ..... 20.
20. Calyx feebly veined, lacking membranous bands, evenly pubescent with  
 (mostly glandular) hairs ..... 27. sect. *Sedoideae* p.p.  
 – Calyx with 10 prominent veins or costae separated by membranous bands .. 21.
21. Calyx eglandular, covered with coarse hairs or asperities, especially on the  
 costae ..... 32. sect. *Lasiocalycinae* p.p.  
 – Calyx glandular-pubescent ..... 22.
22. Anthophore glabrous; calyx  $\pm$  inflated in fruit ..... 29. sect. *Psammophilae*  
 – Anthophore pubescent; calyx not inflated ..... 35. sect. *Nicaeenses*
23. Inflorescence monochasial or, if dichasial at the base, ending in long  
 monochasial branches ..... 24.  
 – Inflorescence thyrsoidal or dichasial (sometimes inaequilaterally so), or  
 flowers solitary ..... 25.

- 24. Inflorescence few-flowered, monochasial; fruiting calyx clavate, inflated; anthophore pubescent . . . . . 33. sect. *Fruticulosae*
- Inflorescence dichasial, with long monochasial branches; fruiting calyx ellipsoidal, not inflated; anthophore glabrous . . . . . 31. sect. *Dichotomae*
- 25. Leaf margins with a dense fringe of short, recurved hairs (the upper face or both faces glabrous) . . . . . 26.
- Leaf margins  $\pm$  ciliate, scabrid, or glabrous, but not with dense, short, recurved hairs . . . . . 27.
- 26. Calyx glandular-pubescent . . . . . 6. sect. *Paradoxae*
- Calyx glabrous . . . . . 11. sect. *Coronatae* p.p.
- 27. Calyx up to 7 mm; flowers numerous . . . . . 28.
- Calyx longer than 7 mm or, if shorter, flowers solitary or in pairs . . . . . 29.
- 28. Leaves filiform; flowers hermaphrodite, in loosely pyramidal inflorescences . . . . . 10. sect. *Tunicoideae*
- Leaves wider, spatulate to elliptic; flowers unisexual, clustered in verticillasters or heads . . . . . 15. sect. *Otites*
- 29. Calyx glabrous (except for ciliation of teeth) or at most minutely eglandular-scabrid . . . . . 30.
- Calyx pubescent, with or without glandular hairs . . . . . 40.
- 30. Flowers in regular or inaequilateral dichasia terminating the stems and branches, sometimes condensed into heads . . . . . 31.
- Flowers in often impoverished thyrsoidal inflorescences, or single . . . . . 34.
- 31. Flowers nodding at anthesis; petal limb deeply bifid . . . . . 32.
- Flowers upright; petal limb entire or emarginate . . . . . 33.
- 32. Anthophore pubescent; staminal filaments hirsute; calyx clavate, not inflated . . . . . 9. sect. *Lasiostemones* p.p.
- Anthophore and staminal filaments glabrous; calyx ellipsoidal or wider, inflated at anthesis . . . . . 18. sect. *Behen*
- 33. Plants monocarpic or stoloniferous, tall (30-100 cm) . . . . . 23. sect. *Compactae* p.p.
- Plants caespitose, dwarf (to 25 cm) . . . . . 22. sect. *Rupifraga*
- 34. Capsule septate only at the base; calyx turbinate-obconical, widened above . . . . . 24. sect. *Barbeyanae*
- Capsule septate at least in its lower half; calyx clavate . . . . . 35.
- 35. Petal limb emarginate; calyx viscid . . . . . 14. sect. *Tataricae*
- Petal limb bilobed to bifid; calyx not viscid . . . . . 36.

- 36. Inflorescence narrow, raceme-like; flowers numerous, nodding, usually singly in reduced dichasia paired at each node; calyx veins faint and irregular ..... 13. sect. *Chloranthae*
- Inflorescence usually ample and/or few-flowered, if narrow then with up-right flowers single at most nodes; calyx veins distinct ..... 37.
- 37. Lower leaves pubescent, obovate-spathulate ..... 8. sect. *Italicae* p.p.
- Leaves glabrous and ciliolate, more rarely scabrid or farinose-papillate, but then linear to lanceolate ..... 38.
- 38. Flowers usually several, in an often depauperate thyrsoidal inflorescence; either leaves mostly in sterile basal tufts, or upper cauline leaves cordate-amplexicaul; calyx rather firm ..... 39.
- Flowers 1-2(-3) at the end of the stems and branches, or if forming a thyrsoidal inflorescence then most or all leaves cauline and subulate to lanceolate; calyx thin, membranous ..... 21. sect. *Saxifragoideae* p.p.
- 39. Anthophore, staminal filaments and styles glabrous; leaves glabrous (ciliolate at the margin), glaucous ..... 12. sect. *Sclerocalycinae*
- Anthophore, staminal filaments and styles hairy; leaves farinose-papillate, green ..... 9. sect. *Lasiostemones* p.p.
- 40. Calyx narrowed at the base; coronal scales linear-subulate ..... 5. sect. *Siphonomorpha*
- Calyx truncate-umbilicate at the base; coronal scales not linear-subulate, often small or absent ..... 41.
- 41. Leaves succulent, glandular-pubescent; coronal scales large, papery; calyx glandular-pubescent outside and within ..... 7. sect. *Succulentae*
- Leaves not succulent (or, if so, not glandular); coronal scales never large and papery, usually small or absent; calyx eglandular within ..... 42.
- 42. Leaves filiform to linear-lanceolate (up to 2.5 mm wide) ..... 43.
- Leaves narrowly spatulate to obovate ..... 45.
- 43. Flowers single or in pairs ..... 21. sect. *Saxifragoideae* p.p.
- Flowers several, in (often irregular) thyrsoidal inflorescences ..... 44.
- 44. Plants caespitose, with most leaves in sterile basal tufts ..... 20. sect. *Brachypodae* p.p.
- Plants suffruticose, the leaves all cauline ..... 16. sect. *Spergulifoliae*
- 45. Flowers 1-4, in a pseudo-racemose inflorescence; calyx eglandular-pubescent; coronal scales prominent, horn-like ..... 11. sect. *Coronatae* p.p.
- Flowers more numerous, in paniculate thyrsoidal inflorescences, and/or calyx with glandular hairs; coronal scales minute or absent ..... 46.
- 46. Flowers usually in laxly paniculate thyrsoidal inflorescences, or if in glomerules and pseudoverticillasters then plants monocarpic; anthophore 3-12 mm long ..... 8. sect. *Italicae* p.p.
- Plants caespitose to suffrutescent; either flowers in verticillasters and terminal glomerules, or anthophore 1-3 mm long .... 20. sect. *Brachypodae* p.p.

*Synopsis of Greek Silene*

*Silene* L., Sp. Pl.: 416 (1753), nom. cons. against *Lychnis*. – Synonyms and type: see under *S.* sect. *Silene*.

Unless the contrary is specified in the individual sectional and subgeneric descriptions, the flowers are normally hermaphrodite and protandrous (occasional female plants are found in many species but are not mentioned specially); the calyx is 10-veined, with 5 main and 5 commissural veins; the styles are three, upright at the base and glabrous on the back; the capsule opens by 6 teeth and is septate in at least its proximal half; and the seeds are rounded, orbicular to reniform in side view.

- A. *Silene* subg. *Lychnis* (L.) Greuter, **comb. nov.**  $\equiv$  *Lychnis* L., Sp. Pl.: 436. 1753, nom. rej. in favour of *Silene* L.  $\equiv$  *Lychnis* L. subg. *Lychnis* [per Reichenbach, Consp. Regn. Veg.: 207. 1828-1829]. – Type (designated by Britton & Brown, 1913(2): 68): *L. chalcidonica* L. (*S. chalcidonica* (L.) E. H. L. Krause).

Capsule not septate at the base, opening by 5 teeth that alternate with the petals; styles 5, terminal to the capsule teeth, with a divaricate-reflexed base appressed to the ovary.

1. *Silene* sect. *Agrostemma* (DC.) Greuter, **comb. nov.**  $\equiv$  *Coronaria* Guett. in Hist. Acad. Roy. Sci. Mém. Math. Phys. 1750: 229. 1754 (type designated here)  $\equiv$  *Lychnis* sect. *Agrostemma* DC. in Lamarck & Candolle, Fl. Franç., ed. 3, 4: 763. 1805  $\equiv$  *L.* subg. *Muscipula* Riv. ex Rchb., Consp. Regn. Veg.: 207. 1828-1829 (type designated here)  $\equiv$  *C.* sect. *Pseudagrostemma* A. Braun in Flora 26: 368. 1843  $\equiv$  *L.* sect. *Pseudagrostemma* (A. Braun) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(1b): 73. 1889  $\equiv$  *S.* sect. *Lychnidiformes* Melzh. in Rechinger, Fl. Iran. 163: 478. 1988, nom. illeg. – Type (designated here): *L. coronaria* (L.) Desr. (*Agrostemma coronaria* L., *C. tomentosa* L. ex A. Br., *S. coronaria* (L.) Clairv.).

Grey- to white-tomentose, eglandular, short-lived perennials with a monopodial rosette and lateral stems. Inflorescence dichasial; flowers showy, diurnal, upright. Calyx silky-villous, 10-costate by unbranched veins anastomosing apically, with deep grooves in-between, narrowed to rounded at the base. Anthophore glabrous. Petal claw glabrous to sparsely ciliate, not auriculate; limb rounded to shallowly emarginate; coronal scales present. Staminal filaments densely pubescent at the widened base, glabrous above. Seeds subglobular, with convex flanks and back, and indistinct shoulders, the hilar notch not visible in side view. – S. Europe to N. Iran; species 1: *Silene coronaria* (L.) Clairv.

*Nomenclature.* – Candolle's section is based on *Agrostemma* L. pro parte, as emended by later authors to exclude *Githago* Adans. (i.e. *Agrostemma* s.str. of modern authors, with *A. githago* L. as type). Under Art. 48, *Lychnis* sect. *Agrostemma* DC. is to be considered the name of a new taxon, not as a combination based on the Linnean type.

2. *Silene* sect. *Coccyganthe* (Rchb.) Greuter, **comb. nov.**  $\equiv$  *Lychnis* [unranked] *Coccyganthe* Rchb., Fl. Germ. Excurs.: 825. 1832  $\equiv$  *Coccyganthe* (Rchb.) Rchb., Handb. Nat. Pfl.-Syst.: 298. 1837  $\equiv$  *L.* subg. *Coccyganthe* (Rchb.) A.

Braun in Flora 22: 319. 1839  $\equiv$  *Coronaria* sect. *Coccyganthe* (Rchb.) A. Braun in Flora 26: 368. 1843  $\equiv$  *L.* sect. *Coccyganthe* (Rchb.) Godr. in Grenier & Godron, Fl. France 1: 223. 1847  $\equiv$  *Coronaria* subg. *Coccyganthe* (Rchb.) Devyatov & V. N. Tikhom. in Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 97: 122. 1992. – Type: *L. flos-cuculi* L. (*Coccyganthe flos-cuculi* (L.) Fourr., *S. flos-cuculi* (L.) Clairv.).

Subglabrous, rhizomatous perennials with underground stolons ending in leaf rosettes and terminal stems. Inflorescence dichasial (or a short, corymbose thyrsus); flowers diurnal, upright. Calyx glabrous, with distinct, simple veins anastomosing apically, membranous in-between, narrowed to rounded at the base. Anthophore glabrous, or nil. Petal claw glabrous, not auriculate; limb 4-fid or 4-lobed; coronal scales present. Staminal filaments glabrous. Seeds with the hilar notch not visible in side view, with flattish flanks, a convex back, and rounded shoulders. – Europe to Central Asia; species 2, one widespread the other endemic to the Central Balkans: *Silene flos-cuculi* (L.) Clairv., *S. subintegra* (Hayek) Greuter.

**B.** *Silene* subg. *Viscaria* (DC.) Greuter, **comb. nov.** – Basionym and type: see below.

Calyx 10-veined, commissural veins present. Capsule septate for most of its length, opening by 5 teeth that alternate with the sepals; styles 5, alternating with the capsule teeth, their base upright.

**3.** *Silene* sect. *Viscaria* (DC.) Greuter, **comb. nov.**  $\equiv$  *Steris* Adans., Fam. Pl. 2: 255, 607. 1763  $\equiv$  *Lychnis* sect. *Viscaria* DC. in Lamarck & Candolle, Fl. Franç., ed. 3, 4: 761. 1805  $\equiv$  *Viscaria* (DC.) Röhl., Deutschl. Fl., ed. 2, 2: 37, 275. 1812  $\equiv$  *L.* subg. *Viscaria* (DC.) Rchb., Consp. Regn. Veg.: 207. 1828-1829. – Type: *L. viscaria* L. (*V. vulgaris* Röhl., *Silene viscaria* (L.) Jess.).

Subglabrous, caespitose perennials with terminal stems arising from the previous or present year's leaf rosettes. Inflorescence thyrsoidal; flowers hermaphrodite or unisexual (the sexes variously distributed), diurnal, spreading. Calyx glabrous or glandular-pubescent, with weak veins anastomosing apically or ending free, membranous in-between, umbilicate at the base. Anthophore glabrous. Petal claw glabrous, expanded and auriculate above; limb rounded to slightly emarginate; coronal scales present. Staminal filaments glabrous. Seeds with the hilar notch scarcely visible in side view, with flat flanks and back, and bluntly keeled shoulders. – Central Europe to Caucasia and W. Siberia; species 2, one widespread the other endemic to the S. Balkans; in Greece: *Silene atropurpurea* (Griseb.) Greuter & Burdet.

**C.** *Silene* L. subg. *Silene*. – Synonyms and type: see under *S.* sect. *Silene*.

Calyx (5-)10-veined, or  $\pm$  20-veined in some perennials but then veins branched, anastomosing at least in the distal part, and submarginal vein continuous. Styles 3 (rarely 5); capsule opening by 6 (rarely 10) teeth.

**4.** *Silene* sect. *Elisanthe* (Fenzl ex Endl.) Ledeb., Fl. Ross. 1: 314. 1842  $\equiv$  *Saponaria* sect. *Elisanthe* Fenzl ex Endl., Gen. Pl.: 972. 1840 (vide Endlicher, Gen. Pl., Suppl. 2: 78. 1842)  $\equiv$  *Saponaria* subg. *Silenanthe* Fenzl ex Endl., Gen. Pl.: 972. 1840 (vide Endlicher, Gen. Pl., Suppl. 2: 77. 1842) (type designated here)  $\equiv$

*Silene* subg. *Elisanthe* (Fenzl ex Endl.) Fenzl in Endlicher, Gen. Pl., Suppl. 2: 78. 1842 = *Melandrium* sect. *Elisanthe* (Fenzl ex Endl.) A. Braun in Flora 26: 371. 1843 = *Silene* [unranked] *Melandriformes* Boiss., Fl. Orient. 1: 568. 1867 *Lychnis* sect. *Pseudagrostemma* (A. Braun) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(1b): 73. 1889 = *Silene* sect. *Melandriformes* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957. – Type (designated by Pfeiffer, 1871-1875: 1186): *Silene noctiflora* L.

- = *Melandrium* Röhl., Deutschl. Fl., ed. 2, 2: 37, 274. 1812 = *Lychnis* [unranked] *Melandrium* Rchb., Fl. Germ. Excurs.: 824. 1832 = *L.* subg. *Melandrium* (Röhl.) A. Braun in Flora 22: 319. 1839 = *Saponaria* subg. *Melandrium* (Röhl.) Fenzl in Endlicher, Gen. Pl.: 972. 1840 (vide Endlicher, Gen. Pl., Suppl. 2: 78. 1842) = *M.* sect. *Melandrium* [per A. Braun in Flora 26: 371. 1843] = *Silene* sect. *Melandrium* (Röhl.) Rabeler in Contr. Univ. Michigan Herb. 19: 161. 1993. – Type (designated by Rabeler, 1993: 161): *M. sylvestre* (Schkuhr) Röhl. (*L. dioica* var. *sylvestris* Schkuhr, *Silene sylvestris* (Schkuhr) Clairv.).

Annuals, biennials or perennials with eglandular and glandular hairs, wide, pinnately veined leaves, and herbaceous bracts. Inflorescence ± irregularly dichasial; flowers vespertine, hermaphrodite, or unisexual on dioecious plants, ± upright. Calyx hairy, with 10-20 veins that are branched and anastomosing in the distal half, rounded at the base. Anthophore glabrous to pubescent, or nil. Petal claw glabrous to ciliate, ± auriculate-expanded above; limb bifid; coronal scales present. Staminal filaments glabrous or pubescent. Capsule 1-locular, lacking basal septa; styles 3 or 5. Seeds with the hilar notch not visible in side view, with convex flanks and back, and rounded shoulders. – Eurasia and N. Africa, naturalized elsewhere; species c. 15 (mostly Asian); in Greece: *Silene latifolia* Poir., *S. heuffelii* Soó, *S. noctiflora* L.

*Taxonomy.* – The 3-stylous, usually annual hermaphrodite *Silene noctiflora* and the complex of 5-stylous, dioecious perennials centred around the polymorphic *S. latifolia* are strikingly different, yet their relationship is close enough to ask for some kind of common umbrella. Contrary to what Sandbrink & al. (1989) have concluded on the basis of chloroplast DNA restriction fragment analysis, I have therefore decided to maintain *S.* sect. *Elisanthe* in its traditional circumscription, while recognizing that division at subsectional level may be appropriate. This appears to be compatible with results of nuclear rDNA sequence analysis (Oxelman & Lidén, 1995).

5. *Silene* sect. *Siphonomorpha* Otth in Candolle, Prodr. 1: 377. 1824 = *S.* subg. *Siphonomorpha* (Otth) Endl., Gen. Pl.: 973. 1840 = *S.* sect. *Cymosae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854 (type designated here), nom. illeg. = *S.* ser. *Nutantes* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 5. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 381. 1867 = *S.* subsect. *Nutantes* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 315. 1899. – Type (designated by Chowdhuri, 1957: 234): *S. nutans* L.
- = *Silene* [unranked] *Viridiflorae* Boiss., Fl. Orient. 1: 574. 1867. – Type: *S. viridiflora* L.

Perennials with eglandular and glandular hairs and wide, pinnately veined leaves. Inflorescence thyrsoidal; flowers vespertine, nodding at anthesis. Calyx pubescent, with simple veins anastomosing apically, narrowed at the base. Anthophore pubescent. Petal claw glabrous, not auriculate; limb deeply bifid, with narrow lobes;



coronal scales solid, fleshy, linear-subulate. Staminal filaments glabrous. Seeds with the hilar notch not obvious in side view, with flat to convex flanks and back, and bluntly keeled shoulders. – Europe to Central Asia; species 2; in Greece: *Silene viridiflora* L.

*Taxonomy.* – As here redefined, this section is much smaller and more natural than as delimited in, e.g., Tutin & al. (1993). Homogeneous species groups recognized by Jeanmonod (1985), such as the *Silene paradoxa* and *S. italica* groups, are better treated as separate sections. Chowdhuri (1957), while separating *S. sect. Italicæ* (as sect. *Paniculatae*), included several probably unrelated species in *S. sect. Siphonomorpha*, whose appropriate placement requires further study.

6. *Silene* sect. **Paradoxæ** Greuter, sect. nov. – Type: *S. paradoxa* L. – *Proxima* *S. sect. Italicis et Siphonomorphae*, sed differt foliis angustioribus, in faciebus glabris, margine et in carina dense retrorse ciliolatis, nec non capsula firmiore, basin annulatim tumescente.

Perennials with eglandular- and glandular-hairs. Leaves lacking apparent side veins, glabrous except for the densely retrorsely pubescent margins and keel. Inflorescence thyrsoidal; flowers vespertine, upright or spreading. Calyx glandular, fusiform-clavate, distinctly narrowed above, umbilicate at the base, its veins unbranched below but anastomosing in the distal part. Anthophore pubescent. Petal claw glabrous, not or feebly auriculate; limb bilobed, with obovate lobes; coronal scales small, mostly triangular-subulate, often two-tipped. Staminal filaments glabrous. Capsule firm, with a thickened, shallowly 10-lobed rim at the base. Seeds with flat or slightly concave flanks and back and bluntly to acutely keeled shoulders. – Central and E. Mediterranean; species 2: *Silene fruticosa* L., *S. paradoxa* L.

7. *Silene* sect. **Succulentæ** (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957 ≡ *S.* [unranked] *Succulentæ* Boiss., Fl. Orient. 1: 576. 1867. – Type: *S. succulenta* Forssk.

Perennials with eglandular and glandular hairs. Leaves succulent, densely pubescent, lacking apparent side veins; bracts leafy. Inflorescence asymmetrically dichasial, with one branch usually single-flowered; flowers vespertine, upright. Calyx glandular-pubescent both outside and within, clavate, not narrowed above, umbilicate at the base, its veins unbranched below but anastomosing in the distal part. Anthophore pubescent. Petal claw glabrous or dorsally pubescent at the base, not auriculate; limb bilobed, with obovate lobes; coronal scales present. Staminal filaments glabrous. Capsule membranous; styles glandular-pubescent in the proximal half. Seeds with the hilar notch not visible in side view, with somewhat convex flanks, an indistinctly furrowed back, and rounded shoulders. – S.E. Mediterranean, Corsica and Sardinia; species 1: *Silene succulenta* Forssk.

*Taxonomy.* – Misused by Chowdhuri (1957) as a dustbin taxon comprising four unrelated species of three different sections (*Silene* sect. *Psammophilæ*, sect. *Spergulfoliæ*, and sect. *Succulentæ*), all of them specialists of sandy seashores. The closest relationship of *S. succulenta* is perhaps with *S. sect. Spergulfoliæ* but most likely not with its present neighbours.

8. *Silene* sect. *Italicae* (Rohrb.) Schischk. in Komarov, Fl. SSSR 6: 675. 1936  $\equiv$  *S.* [unranked] *Paniculatae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854 (type designated by Chowdhuri, 1957: 233)  $\equiv$  *S.* ser. *Italicae* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 5. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 382. 1867  $\equiv$  *S.* subsect. *Italicae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 317. 1899  $\equiv$  *S.* sect. *Paniculatae* (Willk.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 233. 1957  $\equiv$  *S.* subsect. *Patulae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 233. 1957, nom. illeg. – Type: *S. italica* (L.) Pers. (*Cucubalus italicus* L.).

Perennials with eglandular and usually glandular hairs. Lower leaves membranous, pinnately veined, the upper 1-3-veined. Inflorescence thyrsoidal, sometimes compound; flowers usually vespertine and whitish (rarely diurnal, then pink), upright to spreading. Calyx membranous, variously pubescent, rarely glabrous, papery, clavate, umbilicate at the base, not conspicuously narrowed above, with 10 veins loosely anastomosing (rarely densely reticulate-veined) in the distal half. Anthophore pubescent (rarely glabrous). Petal claw glabrous, sometimes sparsely pubescent at the base or ciliate above (rarely villous), not or feebly auriculate; limb bifid, with spathulate to obovate lobes; coronal scales minute or reduced. Staminal filaments glabrous (rarely villous). Capsule firm but lacking a thickened basal rim. Seeds with the hilar notch visible or concealed in side view, with  $\pm$  flat flanks, a flat to shallowly furrowed back, and keeled shoulders; testa cells each with a minuscule, dark, central or eccentric punctiform apiculum. – Mediterranean, mainly in the west; species c. 30; in Greece: *Silene italica* (L.) Pers. subsp. *italica*, subsp. *peloponnesiaca* Greuter, *S. damboldtiana* Greuter & Melzh., *S. sieberi* Fenzl, *S. spinescens* Sm., *S. cythnia* (Halácsy) Walters, *S. goulimyi* Turrill, *S. gigantea* (L.) L. subsp. *gigantea*, subsp. *hellenica* Greuter, subsp. *rhodopea* (Janka) Greuter, *S. niederi* Boiss.

*Taxonomy.* – When reduced to the *Silene italica* group (Jeanmonod, 1985) this becomes a very natural and homogeneous section. The inclusion of *S. gigantea*, however, is problematic and must be regarded as provisional. While in floral characters *S. gigantea* comes close enough to small-flowered *S. italica* populations, the inflorescence rather recalls *S. congesta* and its relatives in *S.* sect. *Brachypodae*. Perhaps *S. gigantea*, especially in view of the very high pedicel-peduncle ratio that characterizes even its laxly paniculate variants, would find a more natural place in the latter section. *S. niederi* is a further species of uncertain affinity whose present placement is unsatisfactory (as is its former placement, in *S.* sect. *Lasiostemones*).

9. *Silene* sect. *Lasiostemones* (Boiss.) Schischk. in Komarov, Fl. SSSR 6: 631. 1936  $\equiv$  *S.* [unranked] *Lasiostemones* Boiss., Fl. Orient. 1: 574. 1867  $\equiv$  *S.* ser. *Lasiostemones* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 5. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 381. 1867  $\equiv$  *S.* subsect. *Lasiostemones* (Boiss.) Gürke in Richter, Pl. Eur. 2: 315. 1899. – Type (designated by Chowdhuri, 1957: 234): *S. longipetala* Vent.

Perennials with eglandular but no glandular hairs. Leaves filiform to lanceolate, variously veined. Inflorescence thyrsoidal or compound-dichasial; flowers vespertine, often nodding at anthesis. Calyx glabrous, firm, clavate, umbilicate at the base, with robust veins simple below but reticulately anastomosing in the distal part. Anthophore  $\pm$  pubescent. Petal claw not auriculate, in its lower part hirsute on the margins and on either side along the veins; limb bifid for most of its length, with

long, narrow lobes; coronal scales robust, linear, somewhat fleshy. Staminal filaments hirsute below. Styles hispid at the base. Seeds often somewhat angular in side view, with flat flanks, a widely furrowed back, and keeled shoulders. – S.W. Asia, just extending to Greece (see Jeanmonod, 1985, on the possible inclusion of the Central Mediterranean *Silene catholica* (L.) W. T. Aiton); species c. 25; in Greece: *S. guicciardii* Boiss. & Heldr., *S. longipetala* Vent.

10. *Silene* sect. *Tunicoideae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957  $\equiv$  *S.* [unranked] *Tunicoideae* Boiss., Fl. Orient. 1: 577. 1867. – Type: *S. tunicoides* Boiss.

Perennial with eglandular but no glandular hairs. Leaves linear-subulate. Inflorescence thyrsoidal; flowers minute, probably diurnal, not nodding. Calyx glabrous, obconical-campanulate, narrowed at the base, with robust veins ending free or occasionally anastomosing in the distal part. Anthophore glabrous. Petal claw glabrous, not auriculate; limb narrow, entire; coronal scales absent. Staminal filaments glabrous. Seeds unknown. – Rhodes and S.W. Anatolia; species 1, of uncertain affinity: *Silene tunicoides* Boiss.

11. *Silene* sect. *Coronatae* (Chowdhuri) Greuter, **stat. nov.**  $\equiv$  *S.* subsect. *Coronatae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957. – Type: *S. reichenbachii* Vis.

Subglabrous to pubescent perennials lacking glandular hairs. Leaves firm, lanceolate to orbicular-spathulate, without conspicuous side veins. Inflorescence narrowly thyrsoidal, often few-flowered, seemingly racemose; flowers vespertine, upright or somewhat nodding at anthesis. Calyx glabrous or pubescent, umbilicate at the base, with robust, simple veins anastomosing apically. Anthophore pubescent. Petal claw glabrous or hairy, not auriculate; limb bifid, with  $\pm$  linear lobes; coronal scales minute,  $\pm$  conical, to prominent and horn-like. Staminal filaments glabrous or hairy. Seeds rounded to  $\pm$  triangular and with the hilar notch mostly not conspicuous in side view, with flat flanks, a widely furrowed back, and acutely keeled shoulders. – S. Balkans; species 5; in Greece: *Silene radicata* Boiss. & Heldr., *S. oligantha* Boiss. & Heldr. subsp. *oligantha*, subsp. *pseudoradicosa* (Rech. f.) Greuter, subsp. *parnesia* Greuter, *S. melzheimeri* Greuter, *S. schwarzenbergeri* Halácsy.

*Taxonomy.* – Chowdhuri (1957) subordinated this taxon to *Silene* sect. *Chloranthae* and included two unrelated species in it: *S. genistifolia* Halácsy (a synonym of *S. multicaulis* subsp. *sporadum*, in sect. *Saxifragoideae*) and *S. lycaonica* Chowdhuri (probably a member of sect. *Sclerocalycinae*). The group as here delimited is very natural except for the (provisional) inclusion of *S. schwarzenbergeri*, an isolated taxon of uncertain affinity.

12. *Silene* sect. *Sclerocalycinae* (Boiss.) Schischk. in Komarov, Fl. SSSR 6: 636. 1936  $\equiv$  *S.* [unranked] *Sclerocalycinae* Boiss., Fl. Orient. 1: 575. 1867  $\equiv$  *S.* ser. *Sclerocalycinae* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 4. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 378. 1867  $\equiv$  *S.* subsect. *Sclerocalycinae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 310. 1899  $\equiv$  *S.* subsect. *Longiflorae* Schischk. ex Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957, nom. illeg. – Type (designated by Chowdhuri, 1957: 235): *S. bupleuroides* L.

- = *Silene* subsect. *Chlorifoliae* Schischk. ex Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957. – Type: *S. chlorifolia* Sm.

Glabrous, glaucous perennials. Leaves linear to orbicular-cordate, firm, scabrid-ciliolate, lacking apparent side veins. Inflorescence thyrsoidal, few-flowered, mostly appearing racemose; flowers vespertine, upright. Calyx glabrous, narrowly clavate, not narrowed above, umbilicate at the base, with distinct veins anastomosing in the distal half. Anthophore usually glabrous. Petal claw glabrous, not auriculate; limb bifid, the lobes  $\pm$  spatulate; coronal scales small, triangular, somewhat fleshy. Staminal filaments glabrous. Seeds rounded to  $\pm$  angular and with the hilar notch not visible in side view, with flat to slightly concave flanks, a flat to furrowed back and keeled to almost winged, prominent shoulders. – S.W. Asia, extending to S.E. Europe (2 species) and S.W. Africa (1 species); species c. 30; in Greece: *Silene chlorifolia* Sm., *S. bupleuroides* L. subsp. *bupleuroides*, subsp. *staticifolia* (Sm.) Chowdhuri.

13. *Silene* sect. *Chloranthae* (Rohrb.) Schischk. in Komarov, Fl. SSSR 6: 616. 1936  $\equiv$  *S.* ser. *Chloranthae* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 4. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 378. 1867  $\equiv$  *S.* subsect. *Chloranthae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 310. 1899  $\equiv$  *S.* subsect. *Ecoronatae* Schischk. ex Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957, nom. illeg. – Type: *S. chlorantha* (Willd.) Ehrh. (*Cucubalus chloranthus* Willd.).

Glabrous, glaucous perennials. Leaves narrow, scabrid-ciliolate, sometimes obscurely pinnately veined. Inflorescence thyrsoidal, elongate, of few-flowered (in Greece: 1-flowered) dichasia; flowers vespertine, spreading horizontally at anthesis (which is almost synchronous). Calyx glabrous, cylindrical in flower, fusiform-clavate in fruit, umbilicate at the base, with 10-15 faint, irregular veins anastomosing in the distal two-thirds. Anthophore pubescent to almost glabrous. Petal claw glabrous, not auriculate; limb deeply bifid, with linear lobes; coronal scales minute or absent. Staminal filaments glabrous. Seeds [immature] with the hilar notch visible in side view, with flat or concave flanks, a furrowed back, and prominently keeled (perhaps winged) shoulders. – E. and S.E. Europe to Central Asia; species 3 (perhaps more); in Greece: *Silene frivaldszkiana* Hampe.

*Taxonomy.* – A quite natural section when *Silene viscosa* (L.) Pers., placed here by Chowdhuri (1957), is excluded.

14. *Silene* sect. *Tataricae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 236. 1957  $\equiv$  *S.* subsect. *Tataricae* (Chowdhuri) Devyatov & V. N. Tikhom. in Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 97: 122. 1992. – Type: *S. tatarica* (L.) Pers. (*Cucubalus tataricus* L.).

Pubescent perennials lacking glandular hairs. Leaves lanceolate, 3-veined and sometimes with an apparent pinnate venation. Inflorescence thyrsoidal; flowers vespertine, erecto-patent. Calyx glabrous, umbilicate at the base, with simple veins not conspicuously anastomosing apically. Anthophore pubescent. Petal claw ciliolate all along, not auriculate; limb broadly linear, emarginate; coronal scales minute or absent. Staminal filaments pubescent at the base. Seeds with the hilar notch visible in side view, with flat flanks, a shallowly furrowed back, and acute, prominently keeled

shoulders. – From E. Europe to E. Asia; species c. 10; in Greece: *Silene skorpilii* Velen.

15. *Silene* sect. *Otites* (Adans.) Otth in Candolle, Prodr. 1: 369. 1824  $\equiv$  *Otites* Adans., Fam. Pl. 2: 255. 1763  $\equiv$  *S.* subg. *Otites* (Adans.) Rchb., Consp. Regn. Veg.: 207. 1828-1829  $\equiv$  *S.* [unranked] *Verticillatae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854  $\equiv$  *S.* sect. *Botryosilene* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 4. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867, nom. illeg.  $\equiv$  *S.* ser. *Otites* ('*Otiteae*') (Adans.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 4. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 379. 1867  $\equiv$  *S.* subsect. *Otites* ('*Otiteae*') (Adans.) Gürke in Richter, Pl. Eur. 2: 312. 1899. – Type: *Cucubalus otites* L. (*S. otites* (L.) Wibel).
- = *Silene* sect. *Albopetalae* Panov in Dokl. Bulg. Akad. Nauk 27: 1571. 1974. – Type: *S. roemerii* Friv.

Pubescent to villous, usually dioecious perennials lacking glandular hairs. Leaves narrowly spatulate to obovate, indistinctly pinnately veined. Inflorescence thyrsoidal, often compound; flowers small, diurnal, (functionally) unisexual, upright to spreading. Calyx glabrous to puberulous, narrowed to umbilicate at the base, wide at the mouth, with slender, simple veins inconspicuously anastomosing apically or ending free. Anthophore glabrous to hairy, or absent. Petal claw glabrous or ciliate, not auriculate; limb linear to cuneate, entire or bilobed; coronal scales absent. Staminal filaments glabrous or ciliate. Seeds rounded to angular and with the hilar notch visible or  $\pm$  concealed in side view, with flat flanks, a flat to shallowly furrowed back, and bluntly to acutely keeled shoulders. – Europe and S.W. Asia; species c. 12 (or more, but ill-defined); in Greece: *Silene roemerii* Friv. subsp. *roemerii*, subsp. *macrocarpa* (Vandas) Greuter, *S. sendtneri* Boiss. subsp. *balcanica* (Formánek) Greuter., *S. otites* (L.) Wibel, *S. exaltata* Friv.

*Taxonomy.* – While this is a well circumscribed and natural section, it comprises two equally well delimited species groups, perhaps best recognized at subsectional level. The first group, widespread throughout the sectional range, consists of slender plants of steppic or sandy habitats, with upright, linear petals. The second, of two Balkano-Apenninic mountain species (*Silene roemerii*, *S. sendtneri*), is characterized by spreading, cuneate petal limbs and is coextensive with *S.* sect. *Albopetalae*.

*Nomenclature.* – A curious situation arises with "*Otites* sect. *Albopetalae*" as published by Rabeler (1993: 162). In the introduction, Rabeler makes it clear that he is dealing with nine genera, to be treated in alphabetical order. *Otites* is not one of these nine genera, and the corresponding entry is placed under *Silene*. The conclusion, reinforced by circumstantial evidence of a taxonomic nature, is that Rabeler does not accept *Otites* Adans. as a distinct genus, and only makes the transfer for the benefit of others who might accept it. The combination is not therefore validly published under Art. 34.1 (a)-(b) of the Code.

16. *Silene* sect. *Spergulfoliae* (Boiss.) Schischk. in Komarov, Fl. SSSR 6: 652. 1936  $\equiv$  *S.* [unranked] *Spergulfoliae* Boiss., Fl. Orient. 1: 572. 1867  $\equiv$  *S.* ser. *Spergulfoliae* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 5. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 380. 1867  $\equiv$  *S.* subsect. *Spergulfoliae*

(Boiss.) Gürke in Richter, Pl. Eur. 2: 314. 1899  $\equiv$  *S.* subsect. *Polyphyllae* Schischk. ex Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 238. 1957, nom. illeg. – Type: *S. spergulifolia* (Willd.) M. Bieb. (*Cucubalus spergulifolius* Willd.).

- = *Silene* ser. *Suffruticosae* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 4. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 379. 1867  $\equiv$  *S.* subsect. *Suffruticosae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 311. 1899  $\equiv$  *S.* sect. *Suffruticosae* (Rohrb.) Schischk. in Komarov, Fl. SSSR 6: 646. 1936. – Type (designated by Chowdhuri, 1957: 239): *S. suffrutescens* M. Bieb.
- = *Silene* subsect. *Supinae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 239. 1957. – Type: *S. supina* M. Bieb.

Mostly gynomonoecious or gynodioecious perennials with glandular and eglandular hairs. Leaves narrow, single-veined. Inflorescence thyrsoidal, often few-flowered; flowers vespertine, often dimorphic (hermaphrodite and female), suberect. Calyx coarsely glandular-hairy, umbilicate at the base, apically narrowed in fruit, with simple, distally anastomosing veins. Anthophore pubescent at least below. Petal claw glabrous, not or indistinctly auriculate; limb bifid, with linear-spathulate lobes; coronal scales conspicuous or reduced. Staminal filaments glabrous. Seeds with the hilar notch not visible in side view, with flattish flanks, somewhat convex back, and rounded shoulders. – Asia (mainly in the S.W.), extending to E. Europe and N.W. North America; species c. 20; in Greece: *Silene spergulifolia* (Willd.) M. Bieb., *S. supina* M. Bieb.

17. *Silene* sect. *Odontopetalae* Schischk. ex Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 240. 1957  $\equiv$  *S.* subsect. *Dentatae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 240. 1957. – Type: *S. odontopetala* Fenzl

Perennials with eglandular and glandular hairs. Leaves lanceolate, 1- or indistinctly 3-veined. Inflorescence dichasial, few-flowered; flowers diurnal, upright. Calyx glandular-pubescent, vesicular-campanulate, umbilicate at the base, not narrowed apically, often c. 20-veined due to 10 weak additional veins present at the base and dissolving in a dense reticulum of anastomoses in the distal half. Anthophore glabrous or sparsely pubescent. Petal claw glabrous, auriculate; limb 2(-4)-fid, with wide lobes; coronal scales conspicuous. Staminal filaments glabrous. Capsule without septa except at the base and along the wall. Seeds  $\pm$  angular and with the hilar notch visible or concealed in side view, with flat flanks and back, and acutely keeled shoulders (but often irregularly formed). – Mountains of Asia and S. Europe; species c. 15; in Greece: *Silene auriculata* Sm.

18. *Silene* sect. *Behen* Dumort., Fl. Belg.: 107. 1827  $\equiv$  *Oberna* Adans., Fam. Pl. 2: 255, 583. 1763 (type designated by Ikonnikov, 1976: 119)  $\equiv$  *Behen* Moench, Methodus: 709. 1794 [non Hill 1762]  $\equiv$  *S.* subg. *Physalocalyx* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854 (type designated here)  $\equiv$  *S.* [unranked] *Inflatae* Boiss., Fl. Orient. 1: 573. 1867  $\equiv$  *S.* subg. *Behen* (Dumort.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 1. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 369. 1867  $\equiv$  *S.* sect. *Inflatae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957  $\equiv$  *S.* subsect. *Latifoliae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957. – Type: *Behen vulgaris* Moench (*Cucubalus*



*behen* L., *S. inflata* Sm., nom. illeg., *S. cucubalus* Wibel, nom. illeg., *S. vulgaris* (Moench) Garcke, *Oberna behen* (L.) Ikonn.).

Glabrous to sparsely eglandular-pubescent, often glaucous, hermaphrodite (rarely gynodioecious) perennials or sometimes biennials. Leaves lanceolate to orbicular, distinctly or indistinctly pinnately veined. Inflorescence a symmetrically or asymmetrically branched dichasium, often many-flowered but sometimes reduced to a single or few flowers (and then occasionally monochasial); flowers vespertine (sometimes indistinctly so), hermaphrodite (or female), nodding at anthesis but upright at maturity. Calyx glabrous, inflated at anthesis, umbilicate at the base, with 10 or c. 20 veins which branch from near the base and anastomose in the distal part. Anthophore glabrous, or nil. Petal claw glabrous, auriculate; limb bifid to the base, with linear-spathulate to obovate lobes; coronal scales conspicuous, linear, or reduced. Staminal filaments glabrous. Seeds with the hilar notch concealed in side view, with flat to convex flanks and back, and rounded to bluntly keeled shoulders. – Throughout Europe and extratropical Asia, N. Africa, Atlantic Islands, naturalized elsewhere; species c. 8; in Greece: *Silene fabaria* (L.) Sm. subsp. *fabaria*, subsp. *domokina* Greuter, *S. ionica* Halácsy, *S. fabarioides* Hausskn., *S. caesia* Sm., *S. samothracica* (Rech. f.) Greuter, *S. variegata* (Desf.) Boiss. & Heldr., *S. vulgaris* (Moench) Garcke subsp. *macrocarpa* Turrill, subsp. *suffrutescens* Greuter & al., subsp. *megalosperma* (Sart. ex Heldr.) Hayek, subsp. *prostrata* (Gaudin) Schinz & Thell., subsp. *bosniaca* (G. Beck) Greuter & al., subsp. *vourinensis* Greuter.

*Taxonomy.* – The section consists of two subunits which may or may not be closely related: the extremely difficult complex of *Silene vulgaris*, which I consider to consist of a single, widespread, polymorphic species; and the *S. fabaria* group, centred on the S. Balkans and extending to Anatolia and S. Russia. The latter is distinguished, i.a., by its prominent corona and thinly membranous, usually 10-veined calyx – not, however, by a thyrsoidal inflorescence as Melzheimer (1980) claims, having completely misunderstood the characteristic, inaequilaterally branching dichasium of all these taxa. Another point on which I disagree with Melzheimer is when he (in Rechinger, 1988) includes *S. vulgaris* and the *S. odontopetala* group (*S. sect. Odontopetaleae*) in one and the same section (*S. sect. Inflatae*). The true relationships of *S. fabaria* and its allies may well be with the annuals around *S. behen* (*S. sect. Behenantha*, q.v.), and one might in the future consider transferring them to the latter section, suitably amended, leaving *S. vulgaris* alone in *S. sect. Behen*.

19. *Silene* sect. *Cucubalus* (L.) Greuter, **comb. & stat. nov.**  $\equiv$  *Cucubalus* L., Sp. Pl.: 414. 1753. – Type (designated by Pfeiffer, 1871-1875: 937): *C. baccifera* L. (*S. baccifera* (L.) Roth).

Perennials with glandular and eglandular hairs. Leaves ovate-lanceolate to broadly elliptic, acuminate, pinnately veined. Inflorescence thyrsoidal; flowers probably diurnal, nodding. Calyx pubescent, obconical during the male phase, later becoming saucer-shaped, then reflexed at maturity, with 5 faint veins. Anthophore glabrous. Petal claw glabrous, not auriculate, adnate to its epipetalous stamen for up to half its length; limb bifid, with linear lobes; coronal scales present. Staminal filaments glabrous. Fruit indehiscent, black, globular, 1-locular except for basal remains of the membranous septa. Seeds with the hilar notch concealed in side view,

evenly convex without differentiation into flanks, back, and shoulders. – Europe, S. Asia from Anatolia to Japan; species 1: *Silene baccifera* (L.) Roth.

*Taxonomy.* – Usually treated as a monotypic genus but in fact a specialized offshoot nested within *Silene*, being distinguished mainly by calyx and fruit features that appear to be part of a specialized dispersal syndrome (see Rohweder & Urmi, 1978).

20. *Silene* sect. *Brachypodae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957  $\equiv$  *S.* [unranked] *Brachypodae* Boiss., Fl. Orient. 1: 575. 1867  $\equiv$  *S.* ser. *Brachypodae* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 3. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 375. 1867  $\equiv$  *S.* subsect. *Brachypodae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 303. 1899  $\equiv$  *S.* subsect. *Nutantes* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957 [non *S.* ser. *Nutantes* Rohrb. 1867], nom. illeg. – Type (designated by Chowdhuri, 1957: 241): *S. grisea* Boiss.

= *Silene* subsect. *Erectae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957. – Type: *S. flavescens* Waldst. & Kit.

Perennials with eglandular and usually glandular hairs. Leaves linear to spatulate, lacking apparent side veins. Inflorescence thyrsoidal, simple or compound, or of few-flowered di- or monochasia in a  $\pm$  paniculate synflorescence, or few- to single-flowered; flowers vespertine or diurnal, upright to spreading at anthesis but often nodding in fruit. Calyx pubescent, clavate to ellipsoid in fruit, umbilicate at the base, not narrowed above, the veins simple below and anastomosing in the distal part. Anthophore pubescent to glabrous. Petal claw glabrous or ciliate, not auriculate; limb bilobed or bifid, with linear to spatulate lobes; coronal scales small or absent. Staminal filaments glabrous. Seeds irregularly angular and with the hilar notch concealed in side view (rarely regularly reniform and with a wide hilar sinus), with flat flanks, a narrow, furrowed back, and acutely keeled shoulders. – S.E. Europe, S.W. Asia, Ethiopia; species c. 12; in Greece: *Silene adelphiae* Runemark, *S. congesta* Sm., *S. cephalenia* Heldr. subsp. *cephallenia*, subsp. *epirotica* Melzh., *S. flavescens* Waldst. & Kit. subsp. *flavescens*, subsp. *thessalonica* (Boiss. & Heldr.) Nyman, subsp. *dictaea* (Rech. f.) Greuter, *S. leptoclada* Boiss., *S. orbelica* Greuter.

*Taxonomy.* – More than half of the known taxa of this section occur in Greece. They appear to fall into two groups on the basis of inflorescence features (pseudover-ticillate vs. lax), correlated with position of the fruiting capsule (nodding vs. upright). This correlation does not hold outside Europe, however, and the type of Chowdhuri's *Silene* subsect. *Nutantes*, *S. grisea*, with nodding capsules, is closely akin to *S. flavescens* with upright capsules. The section as a whole shows affinities with *S.* sect. *Italicae*, through its pseudover-ticillate representatives (e.g., *S. cephalenia*) and *S. gigantea*, which latter may however, as stated above, be misplaced in its present position.

21. *Silene* sect. *Saxifragoideae* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854  $\equiv$  *S.* ser. *Macranthae* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 2. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 374. 1867 (type designated by Chowdhuri, 1957:

243)  $\equiv$  *S.* subsect. *Macranthae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 299. 1899  $\equiv$  *S.* sect. *Macranthae* (Rohrb.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957  $\equiv$  *S.* subsect. *Saxifragae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957, nom. illeg. – Type: *S. saxifraga* L.

Glabrous to pubescent perennials with eglandular (exceptionally also glandular) hairs. Leaves linear to lanceolate, 1-veined (rarely pinnately and reticulately veined). Flowers usually single or in pairs at the end of the stem and branches, rarely in an irregular thyrsoidal inflorescence; vespertine, hermaphrodite, upright. Calyx glabrous or slightly scabrid-pubescent, rarely glandular, narrowly clavate, umbilicate at the base, not conspicuously narrowed above, the veins unbranched below but anastomosing in the distal part. Anthophore glabrescent to puberulous. Petal claw glabrous or ciliate, auriculate or not; limb bilobed to bifid for one third to halfway, with linear to obovate lobes; coronal scales absent or small and conical. Staminal filaments glabrous (rarely pubescent). Seeds rounded to angular and with the hilar notch partly or totally concealed in side view, with flat flanks, a flat to shallowly furrowed back, and keeled shoulders. – *S.* Europe, Anatolia, ?Morocco; species 15 to 25; in Greece: *Silene falcata* Sm., *S. urvillei* Schott ex d'Urv., *S. waldsteinii* Griseb., *S. saxifraga* L., *S. taygetea* Halácsy ex Vierh., *S. dirphyia* Greuter & Burdet, *S. antri-jovis* Greuter & Burdet, *S. conglomeratica* Melzh., *S. parnassica* Boiss. & Spruner subsp. *parnassica*, subsp. *serbica* (Vierh. & Adamović) Greuter, subsp. *pindicola* (Hauskn.) Greuter, subsp. *vourinensis* Greuter, subsp. *dionysii* (Stoj. & Jordanov) Greuter, *S. orphanidis* Boiss., *S. multicaulis* Guss. subsp. *multicaulis*, subsp. *sporadum* (Halácsy) Greuter & Burdet, *S. linoides* Otth.

*Taxonomy.* – In Greece this section is represented by a polymorphic, natural core of 7 species centred on *Silene saxifraga*, plus the somewhat less closely related *S. waldsteinii* and the similarly well defined species pair *S. multicaulis-linoides*. What remains are two species of isolated position, *S. urvillei* and *S. falcata*, which both belong to an Anatolian complex that is not well understood, their presumed relatives, and they themselves, having often been placed in a different section (*S. sect. Pinifoliae* Chowdhuri). All these species are in need of further study.

22. *Silene* sect. *Rupifraga* Otth in Candolle, Prodr. 1: 375. 1824  $\equiv$  *S.* subg. *Rupifraga* (Otth) Endl., Gen. Pl.: 973. 1840  $\equiv$  *S.* ser. *Brachyanthae* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 3. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 375. 1867 (type designated here)  $\equiv$  *S.* subsect. *Brachyanthae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 303. 1899. – Type (designated by Chowdhuri, 1957: 244): *S. rupestris* L.

= *Silene* [unranked] *Decumbentes* Boiss., Fl. Orient. 1: 576. 1867. – Type (designated here): *S. lerchenfeldiana* Baumg.

Glabrous perennials. Leaves lanceolate, 1-veined (rarely 3-5-veined). Inflorescence dichasial; flowers diurnal, upright. Calyx glabrous, clavate, umbilicate at the base, not narrowed above, its veins unbranched below and feebly anastomosing in the distal part. Anthophore glabrous. Petal claw glabrous, not auriculate; limb truncate to emarginate; coronal scales conical. Staminal filaments glabrous. Seeds with the hilar notch concealed in side view, with flat flanks and back, and bluntly keeled

shoulders. – Europe, N. America; species 7; in Greece: *Silene lerchenfeldiana* Baumg.

23. *Silene* sect. *Compactae* (Boiss.) Schischk. in Komarov, Fl. SSSR 6: 615. 1936 ≡ *S.* [unranked] *Compactae* Boiss., Fl. Orient. 1: 569. 1867 ≡ *S.* ser. *Compactae* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 3. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 375. 1867 ≡ *S.* subsect. *Compactae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 303. 1899. – Type: *S. compacta* Fisch.  
= *Silene* [unranked] *Armerioideae* Boiss., Fl. Orient. 1: 576. 1867. – Type: *S. asterias* Griseb.

Glabrous annuals, biennials or perennials. Leaves lanceolate to ovate, 1-7-veined from the base and pinnately veined above, or with obsolete secondary veins. Inflorescence dichasial, often compact; flowers diurnal, upright. Calyx glabrous, clavate, narrowed or umbilicate at the base, not narrowed above, its veins unbranched below and feebly anastomosing in the distal part. Anthophore glabrous. Petal claw glabrous, not auriculate; limb entire or emarginate; coronal scales prominent or minute to obsolete. Staminal filaments glabrous. Seeds with the hilar notch concealed in side view, with flat or convex flanks, a furrowed or convex back, and keeled or rounded shoulders. – Central and E. Europe, S.W. Asia; species 4; in Greece: *Silene asterias* Griseb., *S. compacta* Fisch., *S. armeria* L.

*Taxonomy.* – The section is very homogeneous except for *Silene asterias* which, as a stoloniferous hemicryptophyte, occupies an isolated position and may well deserve at least a subsection of its own.

24. *Silene* sect. *Barbeyanae* Greuter, sect. nov. – Type: *S. barbeyana* Boiss. – *Inter S. sect. Saxifragoideis et Heliospermate quasi intermedia sed differt a priore calycibus obconico-turbinatis apice expansis et floribus diurnis, ab altera habitu dense pulvinato et seminibus non papilloso-cristatis, ab ambabus capsula ad basin, sed ad basin tantum, triloculari.*

Glabrous perennials with monopodial innovations. Leaves linear-spathulate, indistinctly 3-veined. Flowers solitary, diurnal, upright. Calyx glabrous, turbinate, subtruncate to umbilicate at the base, widened above, its veins unbranched below and feebly ramulose but scarcely anastomosing in the distal part. Anthophore glabrous. Petal claw glabrous, not auriculate; limb shallowly bifid, with broadly obovate lobes; coronal scales present. Capsule thin and fragile, 3-locular only at the base. Staminal filaments glabrous. Seeds with the hilar notch visible in side view, with flat flanks, a narrow, furrowed back, and keeled shoulders. – Mountains of Central Greece; species 1: *Silene barbeyana* Boiss.

25. *Silene* sect. *Heliosperma* (Rchb.) Ledeb., Fl. Ross. 1: 317. 1842 ≡ *S.* [unranked] *Heliosperma* Rchb., Fl. Germ. Excurs.: 817. 1832 ≡ *Saponaria* sect. *Heliosperma* (Rchb.) Fenzl in Endlicher, Gen. Pl. 972. 1840 (vide Endlicher, Gen. Pl., Suppl. 2: 78. 1842) ≡ *Heliosperma* (Rchb.) Rchb., Deut. Bot. Herb.-Buch: 206. 1841 ≡ *Silene* subg. *Heliosperma* (Rchb.) Endl., Gen. Pl., Suppl. 2: 78. 1842. – Type (designated by Chowdhuri, 1957: 244): *Silene quadrifida* (L.) L. (*Cucubalus quadrifidus* L.).

Glabrous or glandular- and eglandular-pubescent perennials. Leaves linear-spathulate to elliptical, with usually indistinct reticulate venation and submarginal veins. Inflorescence dichasial or 1-flowered; flowers diurnal, upright. Calyx turbinate to clavate, subtruncate to umbilicate at the base, not narrowed above, with faint veins that may show some inconspicuous branching and anastomosing. Anthophore glabrous. Petal claw glabrous, not auriculate; limb 4-lobed, with two larger, forwardly directed median lobes and two small, tooth-like or angular, sometimes obsolete lateral lobes; coronal scales present. Staminal filaments glabrous. Capsule thin and fragile, 1-locular, lacking basal septa. Seeds with the hilar notch not or scarcely visible in side view, with convex flanks, no obvious shoulders, and an often narrow back crested with prominent protuberances. – Central and S. Europe, especially Balkans; species 3 (or more, depending on circumscription); in Greece: *Silene pusilla* Waldst. & Kit. subsp. *albanica* (K. Maly) Greuter & Burdet, subsp. *chromodonta* (Boiss. & Reut.) Greuter, subsp. *tymphaea* Greuter, *S. intonsa* Greuter & Melzh.

26. *Silene* sect. *Rigidulae* (Boiss.) Schischk. in Komarov, Fl. SSSR 6: 681. 1936 ≡ *S.* [unranked] *Rigidulae* Boiss., Fl. Orient. 1: 571. 1867 ≡ *S.* ser. *Rigidulae* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 3. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 376. 1867 ≡ *S.* subsect. *Rigidulae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 306. 1899. – Type: *S. rigidula* Sm. [non L.] [= *S. corinthiaca* Boiss. & Heldr.].

Annuals, partly with eglandular but lacking glandular hairs. Rosular leaves ovate-spathulate; bracts small, with scarious margins or sheath. Inflorescence regularly dichasial, lax; flowers vespertine, upright. Calyx glabrous outside, obconical in flower, clavate in fruit, minutely umbilicate at the base, not narrowed apically, with simple veins anastomosing in the distal part. Anthophore pubescent or subglabrous. Petal claw glabrous, expanded above but not auriculate; limb bifid, with linear lobes; coronal scales well developed. Staminal filaments glabrous. Seeds with the hilar notch visible in side view, often oblique, with flat flanks and back, and bluntly to acutely keeled shoulders. – Circum-mediterranean, extending W. to Macaronesia and E. to Pakistan; species c. 20; in Greece: *Silene pinetorum* Boiss. & Heldr. subsp. *pinetorum*, subsp. *sphaciotica* Oxelman & Greuter, *S. echinosperma* Boiss. & Heldr., *S. corinthiaca* Boiss. & Heldr., *S. echinospermoides* Hub.-Mor.

27. *Silene* sect. *Sedoideae* Oxelman & Greuter in Willdenowia 25: 150. 1995. – Type: *S. sedoides* Poir.

Annuals with glandular and eglandular hairs and fleshy (sometimes succulent) leaves. Rosular leaves spathulate; bracts leafy, never scarious. Flowers in often asymmetrical dichasia sometimes passing into monochasia, diurnal, upright. Calyx pubescent (mostly glandular), cylindrical to obconical or clavate, umbilicate at the base, not or scarcely narrowed apically, usually feebly veined, with inconspicuous secondary venation. Anthophore glabrous. Petal claw glabrous (exceptionally ciliate), not auriculate; limb entire to emarginate; coronal scales present. Staminal filaments glabrous. Capsule 3-locular at least in its lower half (exceptionally only at the base). Seeds with the hilar notch visible or concealed in side view, with flat to subconvex flanks and a furrowed back, and bluntly to acutely keeled shoulders. –

Greece, but one species circum-mediterranean; species 6 (Oxelman, 1995): *Silene sedoides* Poir. subsp. *sedoides*, subsp. *runemarkii* Oxelman, *S. aegaea* Oxelman, *S. pentelica* Boiss., *S. haussknechtii* Hausskn., *S. laconica* Boiss. & Orph., *S. integripetala* Bory & Chaub. subsp. *integripetala*, subsp. *elaphonesiaca* Oxelman, subsp. *lidenii* Oxelman, subsp. *greuteri* (Phitos) Akeroyd.

28. *Silene* sect. *Atocion* Otth in Candolle, Prodr. 1: 383. 1824  $\equiv$  *S.* subg. *Ocymastrum* Riv. ex Rchb., Consp. Regn. Veg.: 207. 1828-1829 (type designated here)  $\equiv$  *Silene* subg. *Atocion* (Otth) Endl., Gen. Pl.: 973. 1840  $\equiv$  *S.* sect. *Dichasiosilene* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 2. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 373. 1867, nom. illeg.  $\equiv$  *S.* ser. *Atocion* ('*Atocia*') (Otth) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 3. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 376. 1867  $\equiv$  *S.* subsect. *Atocion* ('*Atocia*') (Otth) Gürke in Richter, Pl. Eur. 2: 304. 1899. – Type: *S. atocion* Jacq. [= *S. aegyptiaca* (L.) L. f., *Cucubalus aegyptiacus* L.].  
 = *Silene* subsect. *Delicatulae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 245. 1957, nom. illeg. – Type: *S. aegyptiaca* (L.) L. f. (*Cucubalus aegyptiacus* L.).

Annuals with glandular and sparse eglandular hairs. Rosular leaves rhombic-spathulate; bracts leafy, never scarious. Flowers in monochasia, rarely with an odd dichasial branching at the base, diurnal, suberect. Calyx glandular-pubescent, cylindrical becoming ellipsoidal or clavate, minutely umbilicate at the base, not or scarcely narrowed apically, usually feebly veined, with inconspicuous secondary venation. Anthophore glabrous or pubescent. Petal claw glabrous, not auriculate; limb truncate to faintly emarginate; coronal scales present. Staminal filaments glabrous. Capsule thin and fragile, 1-locular, lacking basal septa. Seeds nearly globular, with a depressed circular hilum not visible in side view, evenly convex, without differentiation into flanks, back, and shoulders. – E. Mediterranean, extending to Iran; species 6; in Greece: *Silene insularis* Barbey, *S. salamandra* Pamp.

*Taxonomy.* – The section is here much restricted with respect to its traditional acceptance, in which it was very heterogeneous. Main sectional characters are the globular seeds and a weak capsule lacking septa. With these E. Mediterranean species as well as the Greek representatives of *Silene* sect. *Sedoideae* (see above) removed, what remains of the former section consists of mainly W. Mediterranean annuals with excavate seed flanks, here assigned to *S.* sect. *Rubellae* (q.v.).

*Nomenclature.* – One may wonder why I do not, as for *Silene* sect. *Otites*, consider *S.* sect. *Atocion* as based on Adanson's earlier generic name, *Atocion* (Adanson, 1763: 254, ['*Atokion*'] 522). The fact is that *Otites* (Adanson, 1763: 255, 586) has *S. otites* as its original type, being the only binomial element included in the protologue (as "*Cucubalus*. 10. Lin. Sp. 415"), while *S.* sect. *Otites* is automatically typified by the same element under Art. 22.5. *S. atocion*, the obligate type of *S.* sect. *Atocion*, is not however an original element of *Atocion* Adans. The latter includes a single reference, to a polynomial from Tournefort's (1703: 24) *Corollarium*, "*Lychnis graeca, bellidis folio, verna, flore parvo, dilute purpurascens*", which I consider of doubtful identity and of which no material appears to have survived. True, it is included in the protologue of *S. orchidea* L. f., today considered a



synonym of *S. aegyptiaca* along with *S. atocion*. But *S. aegyptiaca* is a rather poor match of Tournefort's diagnostic phrase, and has never been collected in Greece. All in all, *Atocion* Adans. is best left untypified and of uncertain application.

**29. *Silene* sect. *Psammophilae* (Talavera) Greuter, **stat. nov.**  $\equiv$  *S.* subsect. *Psammophilae* Talavera in Lagasalia 8: 150. 1979. – Type: *S. littorea* Brot.**

Annuals with glandular and eglandular hairs. Rosular leaves lanceolate-spathulate; bracts herbaceous. Inflorescence monochasial; flowers diurnal, upright at anthesis but spreading to recurved in fruit. Calyx glandular-pubescent,  $\pm$  tubular in flower, obovoid-clavate and conspicuously inflated in fruit, umbilicate at the base, scarcely narrowed apically, keeled by prominent, essentially unbranched veins. Anthophore glabrous. Petal claw glabrous, not auriculate; limb obcordate, bilobed; coronal scales conspicuous. Staminal filaments glabrous. Seeds with the hilar notch not visible in side view, with flattish to convex flanks and back, and blunt to rounded shoulders. – W. and S.E. Mediterranean (elsewhere, as in Greece, only subsponaneous); species 6; in Greece: *Silene pendula* L.

*Taxonomy.* – Talavera (1979), when describing this taxon at subsectional level, already pointed out the conspicuous differences that separate it from *Silene* sect. *Erecto-refractae* Chowdhuri. Testa cell shape (subisodiametric vs. elongate) and flowering rhythm (diurnal vs. vespertine) can be added to these differences, making them important enough to warrant sectional rank. The S.E. Mediterranean *S. villosa* Forssk., misplaced by Chowdhuri (1957) in *S.* sect. *Succulentae* along with *S. littorea*, and not mentioned by Talavera, also appears to belong here.

**30. *Silene* sect. *Behenantha* Otth in Candolle, Prodr. 1: 367. 1824  $\equiv$  *Silene* subg. *Behenantha* (Otth) Endl., Gen. Pl.: 973. 1840  $\equiv$  *S.* [unranked] *Leiocalycinae* Boiss., Fl. Orient. 1: 569. 1867 (type designated here)  $\equiv$  *S.* ser. *Leiocalycinae* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 3. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867  $\equiv$  *S.* subsect. *Leiocalycinae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 307. 1899  $\equiv$  *S.* subsect. *Muscipulae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957, nom. illeg. – Type (designated by Chowdhuri, 1957: 245): *S. behen* L.**

= *Silene* [unranked] *Sparsiflorae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854  $\equiv$  *S.* subsect. *Creticae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 245. 1957. – Type (designated here): *S. cretica* L.

= *Silene* [unranked] *Viscosissimae* Batt. in Battandier & Trabut, Fl. Algérie, Dicot.: 136. 1888. – Type (designated here): *S. muscipula* L.

Annuals lacking glandular hairs, glabrous or pubescent below, glabrous above. Rosular leaves lanceolate to obovate-spathulate; bracts all herbaceous or the upper membranous. Inflorescence dichasial (sometimes only once at the base, then monochasial); flowers diurnal or vespertine, upright to nodding. Calyx glabrous, tubular to fusiform or top-shaped or clavate,  $\pm$  umbilicate (rarely narrowed) at the base, usually narrowed apically at least in fruit, white-membranous at least below between the veins which anastomose for most of its length or only apically. Anthophore glabrous (rarely pubescent). Petal claw glabrous, only rarely auriculate; limb from entire to obcordate to deeply bifid, with orbicular to linear lobes; coronal scales well developed to rudimentary. Staminal filaments glabrous. Seeds rounded (rarely angular)

and with the hilar notch visible or concealed in side view, with flat flanks, a flat to slightly convex or shallowly furrowed back, and bluntly angular (rarely rounded) shoulders. – Circummediterranean and Macaronesian, ? N. and S. America; species c. 15; in Greece: *Silene muscipula* L., *S. cretica* L., *S. tenuiflora* Guss., *S. ungeri* Fenzl, *S. behen* L., *S. pseudobehen* Boiss., *S. holzmannii* Boiss., *S. reinholdii* Heldr., *S. graeca* Boiss. & Spruner, *S. nutabunda* Greuter.

*Taxonomy.* – Even when one excludes the New World cleistogamous *Silene antirrhina* L., whose similarity with the Mediterranean species is perhaps due to convergence, this section remains very heterogeneous and should probably be split. The four following species groups can be recognized on the basis of, i.a., flowering rhythm, shape of the calyx and invagination of the calyx base, and seed testa cell elongation: (1) the W. Mediterranean *S. muscipula* group (*S. muscipula* and *S. stricta* L.), which is probably not native to Greece; (2) the Central and E. Mediterranean *S. cretica* group, absent from N. Africa and only naturalized further to the west, with *S. cretica*, *S. tenuifolia*, *S. ungeri*, and *S. gemmata* Meikle (the last-named doubtfully distinct from *S. tenuifolia*); (3) the E. and S. Mediterranean to Macaronesian *S. behen* group, with *S. behen*, *S. pseudobehen*, *S. holzmannii*, *S. reinholdii*, and *S. laevigata* Sm., which has obvious links with the *S. fabaria* group in *S. sect. Behen* (q.v.); and (4) the S. Balkanic *S. graeca* group, with *S. graeca* and the newly described *S. nutabunda*.

31. *Silene* sect. *Dichotomae* (Rohrb.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957 ≡ *S. ser. Dichotomae* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 1. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 370. 1867 ≡ *S. subsect. Dichotomae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 290. 1899. – Type: *S. dichotoma* Ehrh.

Pubescent to villous biennials or short-lived perennials (or rarely annuals), lacking glandular hairs. Leaves linear-lanceolate to obovate-lanceolate; bracts herbaceous to membranous. Inflorescence usually dichasial at the base, always ending in long monochasial branches; flowers vespertine, hermaphrodite, nodding at anthesis but suberect in fruit. Calyx hairy, cylindrical to fusiform in flower, ± ellipsoidal in fruit, truncate at the base, narrowed apically, prominently 10-angled, with veins anastomosing only apically. Anthophore glabrous. Petal claw glabrous, not conspicuously auriculate; limb bifid for most of its length, with obovate to spatulate lobes; coronal scales well developed to rudimentary. Staminal filaments glabrous. Seeds with the hilar notch not visible in side view, with flat flanks, a shallowly furrowed back, and bluntly to acutely keeled shoulders. – E. Europe and S.W. Asia; species c. 6; in Greece: *Silene dichotoma* Ehrh., *S. euxina* (Rupr.) Hand.-Mazz.

32. *Silene* sect. *Lasiocalycinae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957 ≡ *S. [unranked] Lasiocalycinae* Boiss., Fl. Orient. 1: 569. 1867 ≡ *S. ser. Lasiocalycinae* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 4. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 ≡ *S. subsect. Lasiocalycinae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 309. 1899 ≡ *S. subsect.*

*Squamatae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957, nom. illeg. – Type (designated by Chowdhuri, 1957: 246): *S. squamigera* Boiss.

- = *Silene* subsect. *Papillosae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957. – Type: *S. papillosa* Boiss.

Pubescent and often hirsute annuals lacking glandular hairs. Leaves spatulate-lanceolate to linear; bracts herbaceous. Inflorescence dichasial or monochasial; flowers usually diurnal, upright. Calyx covered with coarse hairs or asperities on the 10 prominent costae, membranous in-between, narrowly cylindrical or fusiform or clavate in flower and more widely so in fruit, not inflated, umbilicate at the base, narrowed distally, the veins not normally anastomosing except apically. Anthophore glabrous or pubescent. Petal claw glabrous (rarely ciliolate), not or inconspicuously auriculate; limb entire, emarginate, or  $\pm$  bifid with obovate lobes; coronal scales present. Staminal filaments glabrous. Seeds with the hilar notch visible or concealed in side view, with flat (rarely excavate) flanks, a flat to convex back, and keeled, rounded or laterally bulging shoulders. – Central and E. Mediterranean, N.W. Africa; species c. 10; in Greece: *Silene remotiflora* Vis., *S. gallinyi* Heuff. ex Rchb., *S. squamigera* Boiss., *S. papillosa* Boiss., *S. crassipes* Fenzl.

*Taxonomy.* – This is probably a heterogeneous section, here accepted in the circumscription of Chowdhuri (1957) except for exclusion of the unrelated *Eudianthe* and addition of *Silene remotiflora*, transferred from the foregoing section. *S. crassipes* should probably better be transferred to *S. sect. Silene* on account of its seeds with excavate flanks. Even so, further study is required to assess true relationships within and among sections, for this and other annual groups.

33. *Silene sect. Fruticulosae* (Willk.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957  $\equiv$  *S.* [unranked] *Fruticulosae* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854  $\equiv$  *S.* ser. *Fruticulosae* (Willk.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 2. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 372. 1867  $\equiv$  *S.* subsect. *Fruticulosae* (Willk.) Gürke in Richter, Pl. Eur. 2: 298. 1899. – Type (designated here): *S. ciliata* Pourr.

- = *Silene* [unranked] *Unilaterales* Boiss., Fl. Orient. 1: 574. 1867. – Type (designated here): *S. graefferi* Guss. (*S. ciliata* subsp. *graefferi* (Guss.) Nyman).

Pubescent perennials lacking glandular hairs. Leaves lanceolate, lacking apparent side veins; bracts herbaceous. Inflorescence monochasial; flowers vespertine, upright. Calyx pubescent, clavate and inflated at anthesis and in fruit,  $\pm$  truncate at the base, scarcely narrowed above, with main veins anastomosing in the distal third or only apically, membranous in-between. Anthophore velvety-pubescent. Petal claw glabrous, auriculate; limb bifid, with linear, blunt lobes; coronal scales present. Staminal filaments glabrous. Seeds with a deep hilar notch visible in side view, with flat to slightly concave flanks and back, and keeled shoulders. – Mountains of S. Europe, N. and Tropical Africa; S. Africa; species c. 12; in Greece: *Silene ciliata* Pourr. subsp. *graefferi* (Guss.) Nyman.

*Nomenclature.* – Chowdhuri (1957), when rising the present taxon to sectional rank, ascribed the basionym to Rohrbach (1869) and designated *Silene burchellii* Othth as the type. Here as elsewhere I have applied Art. 33.3 generously and disre-

garded what I consider an “error of bibliographic citation”, since the conditions for valid publication (reference to a published Latin description) were otherwise fulfilled by Chowdhuri. Rohrbach (1867a or b) first published the alleged basionym a year earlier, but even there it was not an entirely new name. Although Rohrbach never cites previous authors for the names of his series, it is clear from the context that he often re-uses earlier names, usually at a new rank. Unless one accepts that his names are homotypic with the earlier ones, which are thus their implicit basionyms, they would be illegitimate later homonyms under Art. 53.5.

In the present case Rohrbach adopted the epithet of an unranked taxon from Willkomm, and included in the corresponding series all three of Willkomm’s original species (*Silene elegans* Link ex Brot., *S. ciliata* Pourr., and *S. legionensis* Lag.). Unfortunately, Chowdhuri’s type is not among them. Taking his type designation at face value, one would have to conclude that his sectional name is an illegitimate later homonym, and that the correct combination is newly published here. This would make little sense, however, especially in view of the fact that Chowdhuri explicitly included the three original species in the same section. It is much more reasonable to treat Chowdhuri’s type designation as a formal error, to be superseded by the one proposed above.

34. *Silene* sect. *Dipterospermae* (Rohrb.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 248. 1957  $\equiv$  *S.* [unranked] *Dipterospermae* Rohrb., Monogr. *Silene*: 69. 1869  $\equiv$  *S.* subsect. *Dipterospermae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 296. 1899. – Type (designated by Chowdhuri, 1957: 248): *S. colorata* Poir.
- = *Silene* [unranked] *Pterospermae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854  $\equiv$  *S.* [unranked] *Bipartitae* Boiss., Fl. Orient. 1: 571. 1867  $\equiv$  *S.* ser. *Bipartitae* (Boiss.) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 1. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 371. 1867. – Type (designated here): *S. bipartita* Desf. [= *S. colorata* Poir.].

Pubescent annuals lacking glandular hairs. Leaves obovate to linear, lacking apparent side veins; bracts herbaceous. Inflorescence a monochasium with occasional dichasial branching at the base; flowers diurnal to vespertine or cleistogamous, upright. Calyx pubescent to villous, clavate or urceolate, not inflated,  $\pm$  rounded at the base, not conspicuously narrowed above, the main veins separated by membranous bands and faintly anastomosing in the distal part. Anthophore pubescent. Petals, when produced, with a claw not conspicuously auriculate, eciliate but scabrid along the midvein above, deeply bifid limb with  $\pm$  spatulate lobes, and prominent coronal scales. Staminal filaments glabrous. Seeds with a  $\pm$  deep hilar notch visible in side view, with depressed flanks, a deeply and narrowly furrowed back, and shoulders produced into wavy wings. – Circummediterranean (centred on the west and south), spreading to Macaronesia, Arabia and W. Pakistan; species 8; in Greece: *Silene colorata* Poir., *S. apetala* Willd.

*Nomenclature.* – This is the only case in which Rohrbach changed his mind, and his nomenclature, between the *Conspectus systematicus* (1867a-b) and the *Monographie* (1869). This change has been misunderstood by Rabeler (1993) who, under *Silene* sect. *Scorpioideae*, claims that Rohrbach, in 1869, “replaced without explanation” his former *S.* ser. *Bipartitae* with *S.* ser. *Scorpioideae*, so that the latter would

be illegitimate. Rohrbach (1869: 54, footnote), in fact, explained perfectly what he did, and why. He had removed *S. colorata* Poir. and a few related species from the bulk of *S. ser. Bipartitae*, and together with them *S. bipartita* Desf., cited in synonymy of *S. colorata*, which is the basis of the series name and under Art. 22.5 provides its automatic type. Renaming the bulk of the former series was therefore mandatory under our present rules, although it was a surprisingly far-sighted action in 1869. As to the “typical” portion of the former series, Rohrbach raised it to an indefinite rank above series (to parallel *S. [unranked] Apterospermae*, comprising *S. ser. Dichotomae* and *ser. Scorpioideae*) and (again legitimately as it happens, thanks to the shift in rank) changed its epithet from *Bipartitae* to *Dipterospermae*.

35. *Silene* sect. *Nicaeenses* (Rohrb.) Talavera in *Anales Jard. Bot. Madrid* 45: 361. 1988  $\equiv$  *S. [unranked] Fasciculatae* Willk., *Icon. Descr. Pl. Nov.* 1: 74. 1854 (type designated here)  $\equiv$  *S. ser. Nicaeenses* Rohrb. in *App. Alt. Ind. Sem. Hort. Bot. Berol.* 1867: 3. 1867; et in *Ann. Sci. Nat., Bot., ser. 5*, 8: 375. 1867  $\equiv$  *S. subsect. Nicaeenses* (Rohrb.) Gürke in *Richter, Pl. Eur.* 2: 304. 1899. – Type: *S. niceensis* All.

Annuals (sometimes biennials) with glandular and eglandular hairs. Leaves somewhat succulent, narrowly spatulate; bracts herbaceous. Inflorescence a monochasium or asymmetrical dichasium; flowers vespertine, upright. Calyx glandular- and sometimes also eglandular-pubescent, clavate, not inflated, truncate or umbilicate at the base, not conspicuously narrowed above, the main veins separated by membranous bands and faintly anastomosing in the distal part. Anthophore pubescent. Petal claw  $\pm$  glabrous, not conspicuously auriculate; limb bifid, with linear-spatulate lobes; coronal scales present. Staminal filaments glabrous. Seeds with a deep to shallow hilar notch in side view, with flat flanks, a furrowed back, and blunt shoulders. – Circummediterranean; species c. 10; in Greece: *Silene niceensis* All., *S. discolor* Sm.

36. *Silene* sect. *Rubellae* (Batt.) Oxelman & Greuter, **stat. nov.**  $\equiv$  *S. [unranked] Rubellae* Batt. in *Battandier & Trabut, Fl. Algérie, Dicot.*: 137. 1888  $\equiv$  *S. subsect. Rubellae* (Batt.) Chowdhuri in *Notes Roy. Bot. Gard. Edinburgh* 22: 245. 1957. – Type: *S. rubella* L., nom. utique rej. [= *S. bergiana* Lindm.].
- = *Silene* [unranked] *Divaricatae* Batt. in *Battandier & Trabut, Fl. Algérie, Dicot.*: 138. 1888  $\equiv$  *S. subsect. Divaricatae* (Batt.) Chowdhuri in *Notes Roy. Bot. Gard. Edinburgh* 22: 245. 1957. – Type: *S. divaricata* Clemente ex Lag. [non Sm.] [= *S. aellenii* Sennen].

Annuals with glandular and eglandular hairs. Lower leaves lanceolate-spathulate, the upper ovate-lanceolate; bracts herbaceous. Inflorescence inaequilaterally dichasial; flowers diurnal, upright. Calyx glandular-pubescent, cylindrical becoming clavate, not inflated, umbilicate at the base, not conspicuously narrowed apically, the veins simple, without conspicuous anastomoses. Anthophore glabrous. Petal claw glabrous, not auriculate; limb oblong-cuneate, truncate to retuse; coronal scales elongate, laterally fused. Staminal filaments glabrous. Seeds with the hilar notch not visible in side view, with small, excavate flanks, a flat to shallowly furrowed back, and widely rounded, laterally bulging shoulders. – Mediterranean (mainly in the

west), one species extending to Iran; in Greece only as an erratic weed; species c. 12; in Greece: *Silene fuscata* Brot.

*Taxonomy.* – This is the fairly homogeneous residue of the former *Silene* sect. *Atocion*, once *S. sect. Sedoideae* and the core group around *S. aegyptiaca* have been removed (see under *S. sect. Atocion*). The three sections recognized here, mainly characterized by seed morphology, show nicely coherent distributional patterns.

37. *Silene* sect. *Silene*  $\equiv$  *Viscago* Zinn, Cat. Pl. Hort. Gott.: 188. 1757 (type designated here)  $\equiv$  *S. sect. Stachyomorpha* Otth in Candolle, Prodr. 1: 371. 1824 (type designated here)  $\equiv$  *S. subg. Viscago* (Zinn) Rchb., Consp. Regn. Veg.: 207. 1828-1829  $\equiv$  *S. sect. Viscago* (Zinn) W. D. J. Koch, Syn. Fl. Germ. Helv.: 100. 1835  $\equiv$  *S. subg. Stachyomorpha* (Otth) Endl., Gen. Pl.: 973. 1840  $\equiv$  *S. sect. Racemosae* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854 (type designated here)  $\equiv$  *S. [unranked] Coelospermae* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854 (type designated here)  $\equiv$  *S. sect. Cincinnosilene* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 1. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 370. 1867 (type designated here). – Type (designated by Britton & Brown 1913(2): 62): *S. anglica* L. [= *S. gallica* L., nom. cons. prop.].

= *Silene* [unranked] *Gallicae* Batt. in Battandier & Trabut, Fl. Algérie, Dicot.: 131. 1888. – Type: *S. gallica* L.

= *Silene* [unranked] *Nocturnae* Batt. in Battandier & Trabut, Fl. Algérie, Dicot.: 132. 1888  $\equiv$  *S. subsect. Nocturnae* (Batt.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957. – Type: *S. nocturna* L.

Annuals with eglandular and mostly glandular hairs. Lower leaves obovate-spatulate; bracts herbaceous (or the upper ones minute and membranous). Inflorescence a secund monochasium with or without a single dichasial branching at the base; flowers diurnal or vespertine or cleistogamous, upright throughout or spreading at anthesis. Calyx pubescent to hirsute, with or without glandular hairs, tubular to fusiform in flower, variously shaped in fruit, not inflated, rounded or narrowed at the base, slightly to markedly tapering above in fruit, the main veins branching almost from the base or only in the distal third. Anthophore pubescent. Petals sometimes rudimentary or wanting, when well developed with a glabrous, non-auriculate claw, an entire to bifid limb, and conspicuous coronal scales. Staminal filaments glabrous or barbellate in the lower half. Seeds with a hilar notch visible in side view, with excavate flanks, a flat to furrowed back, and widely rounded, laterally bulging shoulders. – Circummediterranean (centred on N.W. Africa), extending to Macaronesia and Pakistan, introduced elsewhere; species c. 20; in Greece: *Silene nocturna* L., *S. bellidifolia* Jacq., *S. gallica* L., *S. sclerocarpa* Dufour.

*Taxonomy.* – Species placed here were formerly partly assigned to *Silene* sect. *Scorpioideae* (Rohrb.) Chowdhuri, typified by *S. hirsuta* Lag. non Poir. [= *S. scabriflora* Brot.]. That section should, to my mind, be restricted to species with flat seed flanks, whereas all those with excavate flanks fit nicely together in *S. sect. Silene*, whether they have genuine monochasia (most species) or twin monochasia arising from a basal dichotomy (as in *S. bellidifolia* and *S. disticha* Willd.). The special case of *S. crassipes*, with regular dichasia but excavate seed flanks, has been mentioned before (under *S. sect. Lasiocalycinae*).



**Unplaced as to section:** *Silene samia* Melzh. & Christod.

Annual with eglandular and mostly glandular hairs. Rosular leaves roundish spatulate, petiolate; bracts lanceolate. Inflorescence inaequilaterally dichasial, very lax; flowers cleistogamous, upright; Calyx glandular-pubescent, broadly ovoid in fruit, rounded at the base, not narrowed above, with distinct, simple veins. Anthophore  $\pm$  absent. Petals included in the calyx; limb oblong-cuneate, bilobed; coronal scales minute. Seeds with flat to concave flanks and a flat back. – Samos (E. Aegean) and Marmaris Peninsula (S.W. Anatolia); an isolated species, difficult to relate to an extant section due to its reduced flower features (cleistogamy).

**D. *Silene* subg. *Conoimorpha* (Otth) Endl., Gen. Pl.: 973. 1840. – Basionym and type: see below.**

Petal claw with protracted auricles. Calyx with 15-60 unbranched, parallel veins joined only at their tip; commissural veins often wanting or forking early, so that the submarginal vein is interrupted in the sinuses.

**38. *Silene* sect. *Conoimorpha* Otth in Candolle, Prodr. 1: 371. 1824  $\equiv$  *Pleconax* Raf., Autik. Bot.: 24. 1840  $\equiv$  *S.* subg. *Conocalyx* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854, nom. illeg.  $\equiv$  *S.* [unranked] *Conosilene* Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 1. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 370. 1867  $\equiv$  *Conosilene* (Rohrb.) Fourr. in Ann. Soc. Linn. Lyon 16: 344. 1868 *S.* subg. *Conosilene* (Rohrb.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(1b): 70. 1889. – Type (designated by Chowdhuri, 1957: 248): *S. conica* L. (*Pleconax striata* Raf., nom. illeg.).**

**= *Pleconax* sect. *Macrodonatae* Ikonn. in Novosti Sist. Vyss. Rast. 14: 77. 1977. – Type: *P. macrodonta* (Boiss.) Sourková (*Silene macrodonta* Boiss.).**

**= *Silene* [unranked] *Ammophilae* Boiss., Fl. Orient. 1: 568. 1867  $\equiv$  *Pleconax* sect. *Ammophilae* (Boiss.) Ikonn. in Novosti Sist. Vyss. Rast. 14: 77. 1977. – Type: *S. ammophila* Boiss. & Heldr.**

Annuals with eglandular and usually glandular pubescence, never hirsute. Lower leaves spatulate to linear, the upper usually smaller, often 3(-9)-veined at the base; bracts herbaceous. Inflorescence an inaequilateral, dichasium (rarely a monochaesium); flowers diurnal or vespertine, suberect. Calyx pubescent, usually with glandular hairs, tubular to narrowly conical in flower, wider and sometimes inflated in fruit, umbilicate at the base (often narrowly invaginate, simulating an anthophore), usually tapering above (seldom wide open). Anthophore and invaginate calyx base, when present, hairy (rarely subglabrous). Petal claw pubescent at the base, glabrous above; limb obovate to cordate, entire to bilobed; coronal scales conspicuous. Staminal filaments hairy at the base (rarely in their lower half). Seeds with a hilar notch in side view, with flat flanks, a flat (sometimes depressed) to convex back, and keeled to rounded shoulders. – Circummediterranean, extending to most of Europe and through S.W. Asia to the Himalayas; California; species 11; in Greece: *Silene ammophila* Boiss. & Heldr. subsp. *ammophila*, subsp. *carpathae* Chowdhuri, *S. sartorii* Boiss. & Heldr., *S. grisebachii* (Davidov) Pirker & Greuter, *S. conica* L., *S. subconica* Friv., *S. conoidea* L., *S. macrodonta* Boiss.

*Taxonomy.* – This section has its main centre of diversity in Greece (Pirker & Greuter, 1995). It is characterized by a basic chromosome number ( $x = 10$ ) that differs from the one found elsewhere throughout the genus ( $x = 12$ ). The number of calyx veins offers a convenient if perhaps somewhat artificial criterion for further subdividing the section, as proposed by Ikonnikov (1977) at sectional level. An apparently more meaningful difference has been found in a single species formerly included here, which leads to the recognition of the following new section.

**39. *Silene* sect. *Lydiae* Greuter, sect. nov.** – Type: *S. lydia* Boiss. – A *S. sect. Conoimorpha differt calyce praeter pubescentiam hirsuto, basin rotundato (nec invaginato) et basi petalorum staminumque breviter adnato.*

Annuals with eglandular and glandular pubescence, and with long, villous eglandular setae on the calyces. Rosular leaves lanceolate-spathulate, the bracts and upper leaves ovate-subulate, with 5-9 strong parallel veins. Inflorescence an inaequilateral dichasium; flowers diurnal, upright. Calyx pubescent and hirsute, narrowly conical in flower, pyriform and not inflated in fruit, rounded at the base, tapering above, with c. 30 veins. Anthophore lacking, the petals and stamens shortly adnate to the calyx at the base. Petal claw glabrous; limb cuneate-obovate, emarginate; coronal scales conspicuous. Staminal filaments glabrous at the base but ciliate in the middle. Seeds with the hilar notch concealed in side view, with somewhat convex flanks and back, and broadly rounded shoulders. – S.E. Balkans, W. Anatolia; species 1: *Silene lydia* Boiss.

*Taxonomy.* – *Silene lydia* is characterized, primarily, by what one might call a “negative anthophore”: instead of being stalked above the calyx base, the corolla and petal insertion is briefly adnate to it, so as to appear broadly sessile. Whether a second difference, on the chromosomal level, holds when more data become available remains to be seen: Pirker (unpublished) has counted  $2n = 22$  chromosomes on material from Mt Ossa (Greece), which contradicts the single previous count ( $2n = 20$ ; Löve & Kjellkvist, 1972) made on plants from Evvia – where the species has never been collected by others, the voucher itself having disappeared. Whether or not the section will prove to have its own, unique chromosome number, *S. lydia* remains an intriguing, quite isolated species.

*Conclusion: some thoughts on caryophylloid phylogeny*

Bocquet (1968b), basing himself on his experience with *Silene* sect. *Physolychnis* (Benth.) Bocquet and on general, partly intuitive considerations, has “polarized” a large number of characters for that section and, by implication, for the caryophylloid genera as a whole. A primitive, or unspecialized, member of the group would, in summary, be a short-lived, branched hemicryptophyte of medium size, with glabrescent, membranous, elliptic leaves, a thyrsoidal inflorescence, a tubular to campanulate, 10-veined calyx, a short anthophore, livid (vespertine?), upright flowers, 5 carpels, a capsule with persistent septa and opening by 5 teeth, and numerous small, globular, tuberculate seeds. Except for the livid flowers, this is a faithful description of *Silene viscaria*.

In Oxelman & Lidén’s (1995) phylogenetic tree, which is based on an entirely different, objective set of data, we find little support for a basal position of *Silene*

subg. *Viscaria* in the silenean complex. Their tree rather supports the assumption of *S.* subg. *Lychnis* being a taxon close to the root of the tribe. Turning back to Bocquet's portrait, we can make it match, say, *S. flos-cuculi* by changing the polarity of just two characters (in addition to flower colour): a dichasial rather than thyrsoidal inflorescence, and absence of septa in the capsule, would then be the more "primitive" state.

All this, however, is not very convincing as long as virtually nothing can be said on the phyletic relationships among the sections of *Silene* as a whole. The problem, there, is that the variational pattern we observe is highly reticulate and can only be explained by repeated character reversals and widespread parallelism. Take capsule septation as an example. Its absence is the general condition prevailing in the *Caryophyllaceae*, and is apparently one of the basal apomorphies distinguishing this family from its presumed sister group, the *Molluginaceae*, and from the other centrosperous families (see for example Cronquist, 1988: fig. 6.4; Bocquet's (1968b) hypothesis of the *Caryophyllaceae* being a primitively gamosepalous group derived from the *Primulales* sounds rather adventurous). Yet in the *Sileneae* the basal septa in the capsule are almost omnipresent (their absence being due to dissolution during ontogeny), and they must have been lost, and perhaps reacquired, repeatedly and independently, not only at early evolutionary stages (*S.* subg. *Lychnis*) but also at the ultimate branching stages (*S. sedoides*, within *S.* sect. *Sedoideae*). The loss is apparently correlated with two diametrically opposite capsule conditions: firm and wide in the former case, papery and tiny in the latter.

A natural system of *Silene* sensu lato remains utopia, and I have no solution to offer. What I have tried to outline, in this paper, is a series of natural groups that one can recognize within the genus. They are the background against which the results of molecular studies, and in particular the comparative sequencing of various (!) DNA segments, can be interpreted and tested. It is my hope that, once the data from the latter field become sufficiently abundant and complete in coverage, combining their results with those from a traditional morphological approach may provide a definite if not definitive answer to our questions.

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#### Literature cited

- Adanson, M. 1763. *Familles des plantes*. Paris.  
 Bocquet, G. 1968a. *Physolychnidum* morphologica catalecta. *Candollea* 23: 151-176.  
 – 1968b. De evolutione annotamenta aliqua *Silenis* et imprimis earum sectione *Physolychnide* inducta. *Arch. Sci.* 21: 239-262.

- Boissier, E. 1867. *Flora orientalis sive enumeratio plantarum in Oriente a Graecia et Aegypto ad Indiae fines hucusque observatarum*, 1. Basel & Genève.
- Britton, N. L. & Brown, A. 1913. *An illustrated flora of the Northern United States, Canada and the British Possessions ...*, ed. 2, 1-3. New York.
- Brizicky, G. K. 1969. Subgeneric and sectional names: their starting points and early sources. *Taxon* 18: 643-660.
- Brummitt, R. K. 1994. Report of the Committee for Spermatophyta: 41. *Taxon* 43: 271-277.
- Candolle, A.-P. de, 1824. *Prodromus systematis naturalis regni vegetabilis*, 1. Paris, Strasbourg & London.
- Chowdhuri, P. K. 1957. Studies in the genus *Silene*. *Notes Roy. Bot. Gard. Edinburgh* 22: 221-278.
- Cronquist, A. 1988. *The evolution and classification of flowering plants*, ed. 2. – Bronx, NY.
- Davis, P. H. 1967. *Flora of Turkey and the East Aegean Islands*, 2. Edinburgh.
- Endlicher, S. 1840. Tribus II. *Lychnideae* Fenzl msc. Pp. 971-974 in: Endlicher, S. L., *Genera plantarum secundum ordines naturales disposita*. Wien.
- 1842. *Mantissa plantarum sistens Generum plantarum supplementum secundum*. Wien.
- Engler, A. & Prantl, K. (ed.), 1889. *Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere der Nutzpflanzen*, 3(1b). Leipzig.
- Greuter, W. 1995. Studies in Greek *Caryophylloideae*: *Agrostemma*, *Silene*, and *Vaccaria*. *Willdenowia* 25: 105-142.
- , Barrie, F. R., Burdet, H. M., Chaloner, W. G., Demoulin, V., Hawksworth, D. L., Jørgensen, P. M., Nicolson, D. H., Silva, P. C., Trehane, P. & McNeill, J. 1994. International code of botanical nomenclature (Tokyo Code) adopted by the Fifteenth International Botanical Congress, Yokohama, August-September 1993. *Regnum Veg.* 131.
- , Burdet, H. M. & Long, G., 1984. *Med-Checklist. A critical inventory of vascular plants of the circum-mediterranean countries*, 1. Genève & Berlin.
- Halket, A. C. 1931. The flowers of *Silene saxifraga*, L., an inquiry into the cause of their day closure and the mechanism concerned in effecting their periodic movements. *Ann. Bot. (Oxford)* 45: 15-37.
- Hess, H. E., Landolt, E. & Hirzel, R. 1967. *Flora der Schweiz und angrenzender Gebiete*, 1. Basel & Stuttgart.
- Ikonnikov, S. S. 1976. Zametki o gvozdičnyh (*Caryophyllaceae*), 3. *Novosti Sist. Vysš. Rast.* 13: 113-120.
- 1977. Zametki o gvozdičnyh (*Caryophyllaceae*), 5. *Novosti Sist. Vysš. Rast.* 14: 74-79.
- Jeanmonod, D. 1985. Révision de la section *Siphonomorpha* Otth du genre *Silene* L. (*Caryophyllaceae*) en Méditerranée occidentale. V: Synthèse. *Candollea* 40: 35-56.
- Kerner von Marilaun, A. 1889-1891. *Pflanzenleben*, 2. Leipzig & Wien.
- Komarov, V. L. 1936. *Flora SSSR*, 6. Moskva & Leningrad.
- Lindman, C. A. M. 1897. Remarques sur la floraison du genre *Silene* L. *Acta Horti Berg.* 3(1B): 3-28.
- Löve, A. & Kjellqvist, 1972: Cytotaxonomical vindication of the genus *Conosilene*. *J. Indian Bot. Soc.* 50A: 366-376.
- Maire, R. 1963. Flore de l'Afrique du Nord (Maroc, Algérie, Tunisie, Tripolitaine, Cyrénaïque et Sahara), 10. *Encycl. Biol.* 62.
- McNeill, J. 1978. *Silene alba* and *S. dioica* in North America and the generic delimitation of *Lychnis*, *Melandrium*, and *Silene* (*Caryophyllaceae*). *Canad. J. Bot.* 56: 297-308.
- Melzheimer, V. 1977. Biosystematische Revision einiger *Silene*-Arten (*Caryophyllaceae*) der Balkanhalbinsel (Griechenland). *Bot. Jahrb. Syst.* 98: 1-92.
- 1980. Revision einiger balkanischer Arten von *Silene* sect. *Inflatae* (*Caryophyllaceae*). *Bot. Jahrb. Syst.* 101: 153-190.
- 1987. On the taxonomic position of *Silene thebana* (*Caryophyllaceae*). *Pl. Syst. Evol.* 155: 251-256.
- Oxelman, B. 1995. A revision of the *Silene sedoides*-group (*Caryophyllaceae*). *Willdenowia* 25: 143-169.

- & Lidén, M. 1995. Generic boundaries in the tribe *Sileneae* (Caryophyllaceae) as inferred from nuclear rDNA sequences. *Taxon* 44: 525-542.
- Pfeiffer, L. K. G. 1871-1875. *Nomenclator botanicus*, 1. Kassel.
- Pirker, B. & Greuter, W. 1995. *Silene* subg. *Coniomorpha* (Caryophyllaceae) in Greece. *Bocconeia* (in press).
- Rabeller, R. K. 1992. (1034) Proposal to conserve 2490 *Silene* L. against *Lychnis* L. (Caryophyllaceae). *Taxon* 41: 126-128.
- 1993. Infrageneric nomenclature: corrections and additions in the Caryophyllaceae. *Contr. Univ. Michigan Herb.* 19: 149-164.
- Rechinger, K. H. (ed.), 1988. *Flora iranica. Flora des iranischen Hochlandes und der umrahmenden Gebirge*, 163. Graz.
- Reichenbach, H. G. L. 1828-1829. *Conspectus regni vegetabilis per gradus naturales evoluti tentamen*. Leipzig.
- Rohrbach, P. 1867a. Conspectus systematicus specierum generis *Silenes* (*Heliospermatis* atque *Elisanthes* generibus exclusis). *Ann. Sci. Nat., Bot.*, ser. 5, 8: 369-382.
- 1867b. Conspectus systematicus specierum generis *Silenes* (*Heliospermatis* atque *Elisanthes* generibus exclusis). *Appendix altera ad indicem seminum in horto botanico berlinensi anno 1867 collectorum*. Berlin.
- 1869. *Monographie der Gattung Silene*. Leipzig.
- Rohweder, O. & Urmi, E. 1978. Centrospermen-Studien. 10. Untersuchungen über den Bau der Blüten und Früchte von *Cucubalus baccifer* L. und *Drypis spinosa* L. (Caryophyllaceae-Silenoideae). *Bot. Jahrb. Syst.* 100: 1-25.
- Sandbrink, J. M., Geurts, L. J. N. M., Gadella, T. W. J. & Brederode, J. van, 1989. Chloroplast DNA variation in *Silene* section *Elisanthe* demonstrates *Silene noctiflora* L. is not properly classified. *Biochem. Syst. Ecol.* 17: 539-549.
- Talavera, S. 1979. Revisión de la sect. *Erectorefractae* Chowdhuri del género *Silene*. *Lagasalia* 8: 135-164.
- Tournefort, J. P. de, 1703. *Corollarium institutionum rei herbariae...* Paris.
- Tutin, T. G., Burges, N. A., Chater, A. O., Edmondson, J. R., Heywood, V. H., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (ed.) 1993. *Flora europaea*, ed. 2, 1. Cambridge.
- Williams, F. N. 1896. A revision of the genus *Silene*, Linn. *J. Linn. Soc., Bot.* 32: 1-196.

