mucilage and traversed by bands of cellulose, *cl.*; *u.e.*, ordinary epidermal cell; *pal.*, commencement of palisade-cells.

Fig. 9. *Crotalaria albida.* Section of upper epidermis, showing very deep mucilage-cells. × 400.

muc., lumen of cell; *iw.*, inner wall of great thickness containing the mucilage with stratified appearance due to bands of unaltered cellulose; *mes.*, mesophyll; *ue.*, ordinary epidermal cell.

Fig. 10. *Glochidion zeylanicum.* Diagram of transverse section of the middle part of internode of stem. × 20.

ep., epidermis; *c.*, cortex; *p.*, pith with central cavity (unshaded).

ph. and *xy.*, phloem and xylem, respectively, of main stele.

$ph._1$ and $xy._1$, „ „ „ of lateral steles.

Fig. 11. *Hedyotis verticillaris.* Longitudinal section of stipular gland. × 100.

ep., epithelial layer of gland; *s.*, stalk of gland; *stip.*, main tissue of stipule; *r.*, raphide-cell.

On the Synanthy in the Genus *Lonicera*.

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The morphological character known as synanthy, or the union of two or more members of an inflorescence, is in nature by no means rare, although it can hardly be said to be of common occurrence. It is exhibited normally in plants belonging to many widely separated orders. Among these, the genus *Lonicera*, belonging to the Caprifoliaceæ, is remarkable both for the number of species which possess this character and for the different ways in which the synanthy is effected.

The genus has recently been divided into three groups as follows *:—

i. *Caprifolium*, DC.
ii. *Nintooa*, Sweet.
iii. *Xylosteum*, DC.†

* Fritsch (1891). The numbers in brackets after the authors' names refer to the date of the memoir, which will be found quoted in the bibliography at the end of this memoir.

† This section was originally founded by Tournefort in 1700 as *Xylosteon*, and this reading has been followed by De Candolle and others. I have, however, adopted here, on the authority of Bentham and Hooker (1873), p. 11, the form *Xylosteum*.

These are separated by the characters of the leaves, inflorescences, and flowers, as well as by the habit. The subgenus *Caprifolium*, which includes the two British climbing Honeysuckles, *L. Caprifolium*, L., and *L. Periclymenum*, L., is easily distinguished from the two other groups by the compound inflorescence, formed of closely compressed 3-flowered dichasia. No synanthy occurs in this group. In the two other subgenera, the inflorescence consists of a simple 2-flowered dichasium, in which the terminal flower is suppressed. The *Nintooa* group includes climbing shrubs, and, so far as is known, synanthy does not occur in any of its species.

The third subgenus, *Xylosteum*, is distinguished by the fact that none of its members are climbers. Usually the habit is that of an erect shrub. In many of the species included in this group, synanthy occurs between the two flowers of the cyme or the two fruits. This group is by far the largest, containing upwards of 70 species *. The great majority of these belong to Eastern Asia, occurring especially in China, the Himalayas, and in other parts of India. A few species belong to North America. Several are European, occurring especially as alpines in the mountains of Southern and Eastern Europe. A single representative of the group, *L. Xylosteum*, L., is a naturalized or possibly indigenous British plant.

The union of the flowers and fruits in certain species of *Lonicera* is well known, and has for many years been used as a character of systematic importance. The main facts relating to the morphology of the flowers and fruits have also been described by various authors, and may be found scattered throughout the systematic literature dealing with this group. At the same time, so far as I am aware, no one has yet undertaken a comparative morphological study of the synanthy in this genus. As little attention appears to have been paid recently to this subject, a comprehensive study of the *Xylosteum* section, from the point of view of the synanthy, may be of interest as a contribution to the morphology of floral structures.

The work has been carried out on the following lines:— Examination of the various stages in the flowers and fruits has been made in the case of a number of species of which material could be obtained. In this way I have worked out, independently

* Fritsch (1891), p. 166.

of previous observers, a series of types to which I believe all or nearly all the species showing synanthy may be referred. I have also examined the whole of the rich collection of dried material in the Kew Herbarium, which I have been able to compare with the types previously dissected. In a few cases, owing to the material being insufficient, or to difficulties inherent to the inspection of dried and mounted specimens, I have not been able to arrive at definite conclusions.

The fresh material for the work was partly collected in Switzerland, and partly obtained from the Botanic Garden at Cambridge. I am indebted to the courtesy of the Director of the Royal Botanic Gardens, Kew, for the material of certain species, and also for permission to work in the Kew Herbarium. I am also indebted to the Keeper of the Herbarium for help during the examination of the dried material.

True Synanthy.

There are two distinct types of synanthy exhibited in the genus. The first, and by far the most common, is one in which the union is effected by the floral organs. This I may distinguish as true synanthy, as opposed to the second type, which is due to the intervention of extra-floral organs, the bracteoles. As will be seen presently, a false synanthy may arise as a corollary to the union of the four bracteoles of the inflorescence into a bracteolar sheath enveloping the ovaries. In true synanthy, the union is effected by the coalescence of the receptacular walls of the two inferior ovaries *.

This coalescence may be partial or complete. We may thus distinguish two types of true synanthy, that of *L. Xylosteum*, L., which is incomplete, and *L. alpigena*, L., in which the union is complete.

Type of *L. Xylosteum*, L.

In a large number of species belonging to the *Xylosteum* group there is no synanthy. Occasionally, however, in some of these very slight union may apparently take place at the base of the

* The walls of inferior ovaries were formerly regarded as almost entirely receptacular. It has been pointed out, however [Goebel (1900), p. 54], that there are good grounds for the belief that the carpels take some share in their formation. I therefore use the term receptacular walls, without implying that the walls are entirely of receptacular origin.

ovaries, e. g., *L. ciliata*, Mühl.*; while in others the two flowers are always free. Such instances as *L. ciliata* form a gradation to the type of *L. Xylosteum*, in which the ovaries are united for rather less than half their length. This union takes place only in one plane, which is the median plane of the inflorescence. In this region, the parenchymatous tissues of the walls of the two inferior ovaries, or of the pericarps of the two berries, are in organic continuity. The fruits are united to a less extent comparatively than the flowers, and thus the two spherical red berries are nearly distinct.

In this species the bracteoles are very small and inconspicuous, and free from one another. In others, however, such as *L. nigra*, L., which possesses the same degree and type of synanthy, they are much larger, and sheath the lower portion of the ovaries. In all the flowers of *L. nigra* which I have examined, the bracteoles are united in pairs on one side, but free laterally. In others the four bracteoles may all be free †. The bracteoles do not, however, increase in size proportionately to the berries, and the fruits of *L. nigra* are similar to those of *L. Xylosteum*.

The following species possess the same type and degree of synanthy as *L. Xylosteum*.

Type of *Lonicera Xylosteum*, L.

L. bracteolaris, Boiss. & Buhse ‡.
L. cærulescens, Dipp. §
L. decipiens, Hook. f. & Thoms.
L. floribunda, Boiss. & Buhse.
L. fragrantissima, Lindl. & Paxt.
L. hellenica, Orph.
L. leiophylla, A. Kern.
L. Maximowiczii, Maxim.
L. nigra, L.
L. phyllocarpa, Maxim. ||
L. Standishii, Hook.
L. Tatarinowii, Maxim. ||

* Dippel (1889), p. 252.
† Koehne (1893), p. 548.
‡ Boissier (1875), p. 9.
§ Dippel (1889), p. 233. I have not seen this species.
|| On the authority of Maximowicz (1859), p. 138.

Type of *L. alpigena*, L.

Species in which the synanthy is complete are somewhat more numerous than those in which the union is only partial, but all gradations may be found between the type of *L. Xylosteum* and that of *L. alpigena*. In both cases, as a rule, the degree of synanthy is constant in the species, but here again exceptions occur. Thus *L. alpigena*, which in Europe has a single berry-like fruit, resulting from the complete union of the two ovaries, occurs also in India, where the two berries are always free *. These variations may possibly have some bearing on the question of the adaptation presented by such a false berry as that of *L. alpigena*.

In *L. alpigena*, at least in European examples, the coalescence is complete in the median plane throughout the entire, or nearly the entire, length of the ovaries. As Vidal † has already pointed out, this union is effected by the parenchymatous tissues of the receptacular walls or pericarps, which are in organic continuity.

Fig. 1.

L. alpigena, L.—The pseudocarp resulting from the complete union of the two berries. The scars of the two calyx-rings are seen towards the apex of the fruit. ×3.

The synanthy is even more marked in the fruit than in the flowers, for as the pseudocarp ripens it becomes globose, and the distinction between the two ovaries, from which it originates, is lost (fig. 1). This particular kind of pseudocarp may be termed a false berry.

* Hooker (1882), vol. ii. p. 16. † Vidal (1897), p. 14.

In *Lonicera alpigena* the bracteoles are small, while in *L. oblongifolia*, Hook., and *L. microphylla*, Will., they are usually absent altogether. In other species possessing the same type of synanthy they form by their union a well-developed bracteolar sheath, which may be quite two-thirds as long as the ovaries, *e. g. L. angustifolia*, Wall. *

In the following species the synanthy is complete or nearly complete both in the flowers and fruits :—

Type of *Lonicera alpigena*, L.

L. angustifolia, Wall.
L. calcarata, Hemsl.†
L. caucasica, Pall.‡
L. Chamissoi, Bunge.
L. conjugalis, Kell.
L. discolor, Lindl.
L. Glehni, F. Schmidt.
L. glutinosa, Vis.
L. Kesselringi, Regel §.
L. microphylla, Willd.
L. oblongifolia, Hook.
L. orientalis, Lam. ‖
L. parvifolia, Edgew.
L. Schmitziana, Dipp.¶
L. szechuanica, Batal.
L. tangutica, Maxim.
L. tomentella, Hook. f. & Thoms.

False Synanthy.

In many species of *Lonicera* the bracteoles are well developed and more or less completely united into a sheath, by the fusion of the four bracteoles of the cyme in the median and lateral planes. This bracteolar sheath may completely envelop the ovaries, especially in species in which the bracteoles are all united. In this case the external appearance of the flowers and

* Koehne (1893), p. 543.
† Hemsley (1901), pl. 2632.
‡ Jaubert & Spach (1842), tab. 72, p. 135.
§ Koehne (1893), p. 548. I have not seen this species.
‖ Jaubert & Spach (1842), tab. 71, p. 134.
¶ Koehne (1893), p. 548. I have not seen this species.

the young fruits is apt to be misleading. In *L. iberica*, Bieb. (*cf.* fig. 2), the two corollas appear superficially to spring from a single inferior ovary, whereas the two ovaries are really free from one another, though closely enwrapped by the bracteolar sheath. This sheath has, in fact, been mistaken for completely fused ovaries. C. Koch* was apparently the first to discover that, in *L. iberica* and *L. chlamydophora*, C. Koch, the two ovaries are free. Again, Boissier† states that, in the case of *L. cærulea*, there are no bracteoles; although in other species he recognized the existence of a bracteolar sheath. As we shall see, bracteoles play a very important part in this species. Other authors, notably Jaubert and Spach ‡, Dippel §, and especially Koehne ‖, have called attention to the fusion of the bracteoles into a sheath enveloping the ovaries.

In the great majority of species in which a completely fused sheath is present, the two ovaries are entirely free from one another and there is no synanthy. A few exceptions occur, such as those which exhibit true synanthy, as already mentioned. In one species, *L. cærulea*, the presence of a bracteolar sheath has given rise to a form of synanthy which is distinct from that above described.

Before, however, proceeding to discuss the condition of affairs in this interesting species, it may perhaps be well to point out how different species of *Lonicera* exhibit different stages in the formation of a complete bracteolar sheath such as that of *L. iberica*. In *L. nigra* we have in some forms a very incomplete sheath, which, in the flowering stage, does not cover more than half the length of the ovaries. In *L. involucrata*, Banks, a North American species with large leaf-like bracts, the two free ovaries are completely covered by large bracteoles, which are united in pairs medially, but remain free laterally. Other species similar in this respect to *L. involucrata* are *L. Maacki*, Maxim., *L. arborea*, Boiss., *L. flavescens*, Dipp.¶, and *L. spinosa*, Jacq.**

In *L. iberica*, as already stated, the four bracteoles are completely fused. Other species with a complete bracteolar sheath, and with the ovaries free from one another and from the

* C. Koch (1851), p. 478.
† Boissier (1875), p. 9.
‡ Jaubert & Spach (1842), p. 137.
§ Dippel (1889), p. 254, &c.
‖ Koehne (1893), p. 545, &c.
¶ Koehne (1893), fig. 313 *c-f*.
** Koehne (1893), fig. 313 *a-c*.

bracteolar sheath, are *L. Aucheri*, Jaub. & Spach *, *L. gynochlamydea*, Hemsl.†, *L. hypoleuca*, Decne., *L. quinqueloculariis*, Hardw., and *L. Ferdinandi*, Franch. ‡

The function of the bracteolar sheath is, no doubt, to afford protection to the young fruits. In all the above-mentioned species the fruits as they mature either grow out of the sheath, usually splitting it laterally (*L. iberica*), or where the bracteoles are free laterally the sheath becomes reflexed (*L. involucrata*).

In at least two other species, *L. ligustrina*, Wall., and *L. pileata*, Oliver, additional protective coverings to the ovaries and young fruits are found. The flowers of *L. ligustrina*, Wall., an East-Indian species which Koehne § has figured, possess in addition to the bracteolar sheath a further and still outer integument, which is developed from the region of the calyx-tube, and which grows downwards, overlapping the bracteolar sheath. When the fruits are ripe they project beyond the bracteolar sheath, as in *L. iberica*, and bear at the apices the withered remains of the upper integument. The two fruits, as also the two ovaries, are quite free from one another and from the bracteolar and upper sheaths. In *L. pileata* the upper and outer envelope is also present ‖, and probably also in *L. vesicaria*, Komar ¶. I have not, however, seen this latter species.

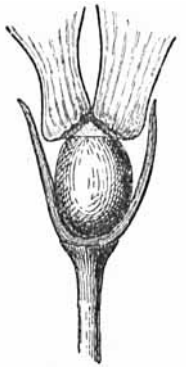
Type of *L. cærulea*, L.

In those species which possess a more or less well-developed bracteolar sheath, we have seen that the two ovaries and the two fruits are entirely free from one another. We have also traced the fate of the bracteolar sheath when the fruits mature. We are now in a position to understand the origin of the false synanthy in the isolated type, *L. cærulea*, L., a common European alpine, and a species of great morphological interest. A completely fused bracteolar sheath is present in this species surrounding the two ovaries (fig. 2). The ovaries are, as in *L. iberica*, quite free from one another, although externally they appear to be completely fused.

* Jaubert & Spach (1842), tab. 73, p. 137.
† Forbes & Hemsley (1888), p. 362.
‡ Also ? *L. minuta*, Batal., *vide* Batalin (1892), p. 170.
§ Koehne (1891), p. 167, fig. 57 *f–j*.
‖ Figured by Oliver (1887), pl. 1585.
¶ Komarov (1901), p. 427.

The two ovaries are, however, united with the bracteolar sheath in certain planes. The condition of affairs is best explained by means of the diagrammatic sketches in fig. 3.

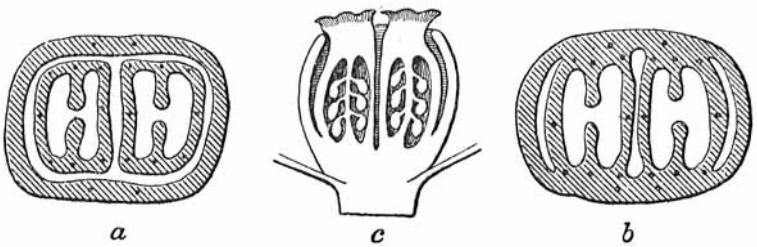
Fig. 2.



Lonicera cærulea, L.—Lower portion of the inflorescence, showing the bracteolar sheath investing the two gynæcea.

Fig. 3, *a*, shows the two free ovaries surrounded by the bracteolar sheath, to which, in their upper portion, they are

Fig. 3.



Lonicera cærulea, L.—(*a*) Diagram of a transverse section through the upper portion of the ovaries; (*b*) transverse section through the lower portion of the ovaries; (*c*) diagram of a longitudinal section through the lower portion of the inflorescence in the plane of the bracts.

not united. At a lower level, figs. *b*, *c*, they are united in the median plane of the inflorescence with the sheath, but remain free laterally. The longitudinal section* in the plane of the

* A similar diagram of Koehne's (1891), fig. 57 *e*, is not quite correctly drawn, at least as regards the specimens which I have examined.

bracts, fig. 3 *c*, shows that the two ovaries are not united with one another.

The result of this fusion is that, as the fruit matures, the growth of the bracteolar sheath keeps pace with the growth of the true berries which it encloses, and contributes to the pericarp in addition to the walls of the two ovaries. The pseudocarp which results is not very dissimilar in appearance, except in colour and size, to that of *L. alpigena* (fig. 1), although it is morphologically quite distinct. We see, therefore, that the presence of a bracteolar sheath may give rise to a false synanthy in which the union is effected by organs external to the flowers themselves.

Conclusions.

We have seen that two different types of synanthy occur in the *Xylosteum* section of the genus *Lonicera*. True synanthy is effected by the partial or complete fusion of the receptacular walls of the inferior ovaries or fruits, and the bracteoles play no part in its formation. Where the synanthy is complete, the resulting fruit is a false berry, in which the pericarp is formed from the walls of the two ovaries. Dr. Masters * states that this type of synanthy occurs in *Pomax* and *Opercularia* among Rubiaceæ, in *Eucalyptus Lehmanni* among Myrtaceæ, and in *Lycopersicum esculentum* (Solanaceæ). He terms this particular form of synanthy (in which "the pistils of different flowers may coalesce more or less without much alteration in the other parts of the flowers, as happens normally in many Caprifoliaceæ") *Syncarpy*. This is a most inappropriate and misleading term in this connection. If some such term is really necessary, we might perhaps coin a word such as *Syngyny*, or speak of these as cases of *Syngynœcea*.

It has been shown, as has already been pointed out by various authors, that in many species the gynæcea are enveloped by a bracteolar sheath, and that, as a rule, there is no synanthy in such cases. The object of the fusion of the bracteoles into a sheath is no doubt to protect the young fruits. Their function would thus seem to be very similar to that of the bracteoles in *Castanea* and *Fagus*. As a rule, this sheath plays no part in the formation of the pericarp of the fruit.

In one species, however, the presence of a bracteolar sheath

* Masters (1869), pp. 38 and 45.

may give rise to a false synanthy. So far as I am aware, this occurs only in the case of *L. cærulea*, though it is not improbable that other species may eventually be found which possess this character. The false synanthy in *L. cærulea* is effected by the union of the two gynæcea in certain planes with the bracteolar sheath, the gynæcea themselves remaining quite free from one another. The fruit in this species is a pseudocarp and a false berry, in which the bracteoles as well as the ovarian walls contribute to the pericarp.

There can be little doubt that there is some special biological significance expressed in the false berries of *L. alpigena* and *L. cærulea*, and that these forms of synanthy, although morphologically distinct, are both adaptations to some particular conditions of the plants' environment. What these conditions are, in the case of these two species, are questions which can hardly be answered without a special study of the subject. It would seem possible, however, that the adaptations have some connection with the alpine conditions under which these species thrive.

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