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The structure of some *Crataegus* populations in north-eastern France and south-eastern Belgium

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ABSTRACT

There are at least three species of *Crataegus* in north-eastern France and adjoining areas: *C. monogyna* Jacq., *C. laevigata* (Poiret) DC., and *C. curvisepala* Lindman subsp. *lindmanii* (Hrabětová-Uhrová) Byatt (Byatt 1974). In some areas the first two species were found in fairly isolated populations. In large forests, populations of *C. laevigata* were found still relatively uncontaminated by *C. monogyna*. *C. curvisepala* subsp. *lindmanii*, a comparatively rare plant, was only encountered in situations where both *C. monogyna* and *C. laevigata* were also present, and it appeared to hybridise with both these species. Intermediates between *C. laevigata* and *C. curvisepala* subsp. *lindmanii* appeared similar to plants described as *C. macrocarpa* (Hegetschweiler 1840). It is suggested that such plants are hybrids and should therefore be known as *C.* × *macrocarpa* Hegetschw. A key to these species and intermediates is included.

INTRODUCTION

In south-eastern England, the two diploids, *Crataegus monogyna* Jacq. and *C. laevigata* (Poiret) DC., are sympatric and appear to hybridise and produce hybrid swarms (Byatt 1975). While *C. monogyna* still maintains its identity on the scarps of the chalk downs, it is very difficult to find a population of *C. laevigata* which is free from introgression from *C. monogyna*. Apparently, this has resulted from the continued destruction of the habitat of *C. laevigata*, by woodland clearance and the dissection of woodland, thus allowing the two species to come into close contact.

Hence it was decided to examine nearby areas of the Continent to see how far similar conditions prevailed, and to investigate the more complex situation which might be expected where a third species, *C. curvisepala* subsp. *lindmanii*, is also present.

It should be noted that a recent nomenclatural revision (Byatt 1974) has shown that *C. curvisepala* Lindman is the correct name for species 9, *C. calycina* Peterm., in *Flora Europaea* (Franco 1968b), where the latter name was misapplied. In consequence, subsp. 9a becomes *C. curvisepala* subsp. *lindmanii* (Hrabětová-Uhrová) Byatt and subsp. 9b becomes *C. curvisepala* subsp. *curvisepala*.

The most important point of distinction between the two subspecies of *C. curvisepala* is the position of the sepals in the mature fruit (Franco 1968a). The sepals are erect in subsp. *lindmanii* and reflexed in subsp. *curvisepala*. The subspecies also have different geographical ranges. Subsp. *curvisepala* is commonly found from Scandinavia to Yugoslavia and extends eastwards through the northern Balkans and northern Turkey as far as the Caucasus mountains, as well as to other parts of European Russia. This subspecies, which is reported to be a tetraploid, $2n = 68$ (Gladkova 1968), is markedly shade-tolerant, usually growing in deciduous woodlands or sparse pinewoods up to an altitude of 1,800 m. In contrast, subsp. *lindmanii* is confined to central and central-northern Europe and, except possibly in Sweden and Poland where it is sympatric with subsp. *curvisepala*, is apparently rare, having been recorded only occasionally in Czechoslovakia, Germany, France, Belgium, the Netherlands, Latvia and Denmark. The chromosome number is not known, but indirect evidence obtained during this investigation suggests that it is probably also a tetraploid. This lesser-known subspecies grows in woods and wood margins, but apparently not to such high altitudes as subsp. *curvisepala*.

TABLE 1. COMPARISON OF SOME CHARACTERS OF *CRATAEGUS MONOGYNA*, *C. CURVISEPALA* SUBSP. *LINDMANII* AND *C. LAEVIGATA*

	C. monogyna	*C. curvisepala* subsp. *lindmanii*	*C. laevigata*
Axillary spines	Often frequent and may exceed 11 mm	Few, up to 11 mm	Few, up to 11 mm
Mature leaf-shape	Laciniate, often 5- to 7-lobed	Somewhat laciniate, commonly 5-lobed	Shallowly 3- to 5-lobed to ± entire
Lowest lateral leaf-sinus	In lower ⅓ of leaf-blade, often extending more than ⅔ to midrib	In lower ½ of leaf-blade, extending about ⅔ to midrib	In upper ½ of leaf-blade, extending less than ⅔ to midrib
Lowest lateral leaf-lobes	Acute or subobtuse, longer than broad, spreading somewhat laterally, sometimes slightly recurved towards base	Acute, longer than broad, pointing obliquely forward	Obtuse, broader than long, usually pointing obliquely forward
	Lower margin ± entire	Lower margin serrulate nearly to base	Lower margin serrate nearly to base
Hairs of vein axils of abaxial leaf surface	Present	Present	Absent
Stipules on leaves of old wood	Entire	Serrate	Serrate
Pedicel + peduncle length	Usually less than 30 mm	Usually more than 30 mm	Usually less than 30 mm
Sepal length/breadth ratio	*c* 1:1	*c* 2:1	*c* 1:1
Sepals in mature fruit	Reflexed	Erect, connivent	Reflexed
Style or 'fruit stone' number	1	1	2–3
Hypanthium	Glabrous to villous	Villous	Glabrous
Fruit length/breadth ratio	*c* 1:0·85	*c* 1:0·6	*c* 1:1

TABLE 2. SUMMARY OF SITES SAMPLED

Site number	Locality	Altitude (approx.)	Soil	Community	*Crataegus* species and hybrids present					
					mon.	*curv.*	*laev.*	*c.* × *m.*	*c.* × *l.*	*l.* × *m.*
2	Falmignoul, Belgium	365m	Limestone and clay, pH 6·8	Scrub on cliff and *Quercus* wood	+	−	+	−	−	+
5	Langaumburg, Moselle, France	300m	Clay, pH 6·5	Wet *Quercus* forest	−	−	+	−	−	?
12	Cernay, Haut-Rhin, France	375m	Clay, pH 5·9	*Betula*/*Quercus* forest	+	+	+	+	+	?
13	Mirecourt, Vosges, France	300m	Chalk marl, pH 8·0	Mixed *Quercus* wood and hedgerow	+	+	+	+	?	−
15	Goviller, Vosges, France	350m	Clay	*Quercus*/*Fraxinus*/ *Carpinus* wood	+	−	+	−	−	−

\+ Taxon present
− Taxon absent
? Plant most like taxon shown, but identity not certain

m., *mon.* – *C. monogyna*
c., *curv.* – *C. curvisepala* subsp. *lindmanii*
l., *laev.* – *C. laevigata*

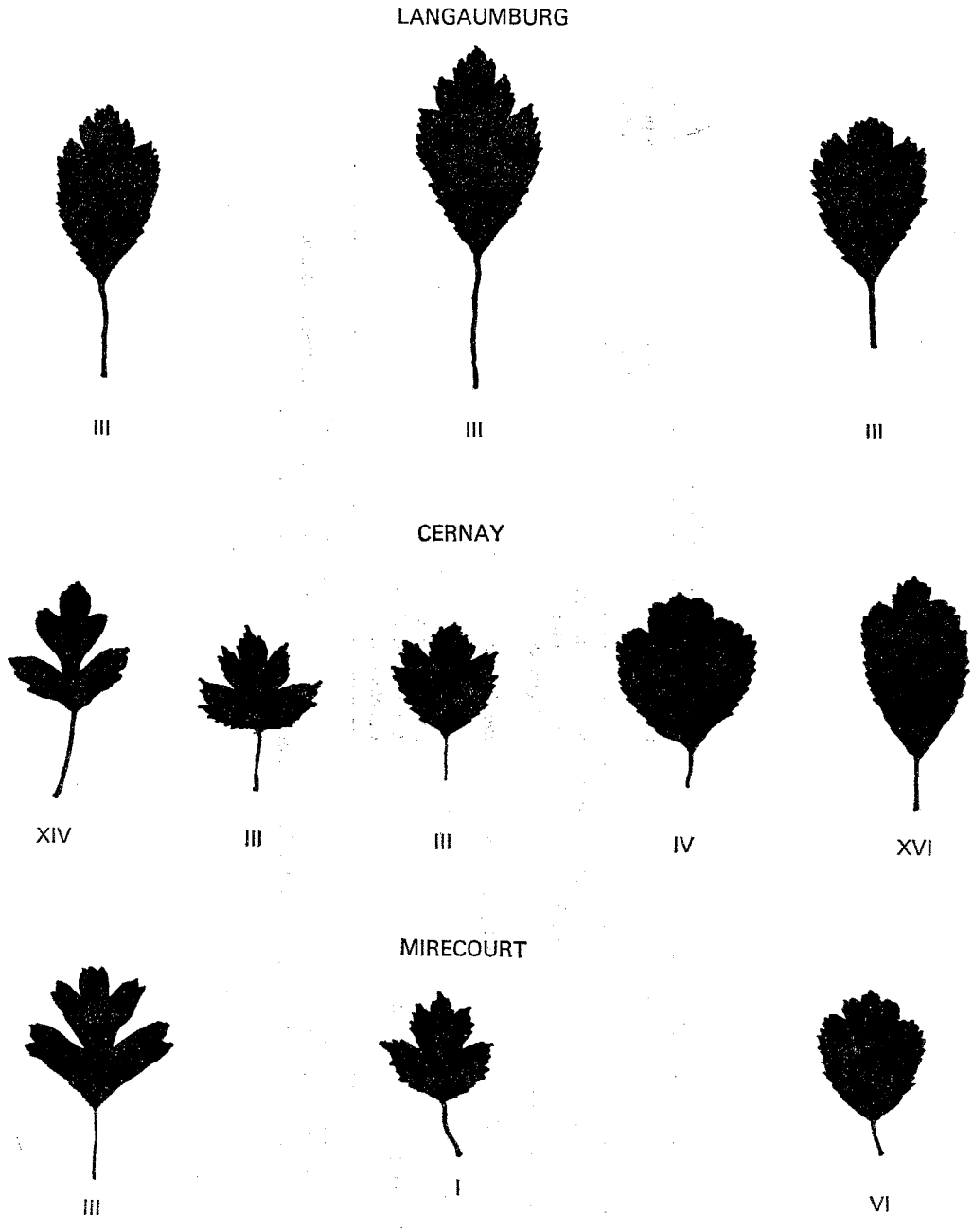


FIGURE 1. Representative leaves from some populations sampled.

Langaumburg: III *C. laevigata.*
Cernay: XIV *C. monogyna*; III *C. curvisepala* subsp. *lindmanii*; IV and XVI *C. laevigata.*
Mirecourt: III *C. monogyna*; I *C. curvisepala* subsp. *lindmanii*; VI *C. laevigata.*
Numbers refer to individual plants.

RESULTS

Figure 1 shows representative leaves and Table 1 summarises these and other important distinguishing characters of the three species considered in this paper. It will be seen that no single character can be used to separate them; hence several of the most clearly recognized characters have been selected and plotted on the scatter diagrams. Some characters, for example the diameter of flowers, have not been used because they are unduly affected by environmental factors or are too seasonal. The ratios obtained were multiplied by 100 to maintain whole numbers. The method of leaf-measurement was the same as explained earlier (Byatt 1975). Fig. 2 shows the locations of the five sites where plants were examined and Table 2 gives some details concerning the populations present. Fig. 3 comprises scatter diagrams of these populations and, for comparison, a scatter diagram of two English populations, one of *C. monogyna* growing outside the present area of natural distribution of *C. laevigata* (Earl's Hill, Salop) and one of a population which is the nearest to pure *C. laevigata* so far found in England (Horish Wood, W. Kent).

The Continental populations of *C. monogyna* encountered were not very extensive or well isolated from other *Crataegus* species, and were not therefore considered suitable for detailed population study.

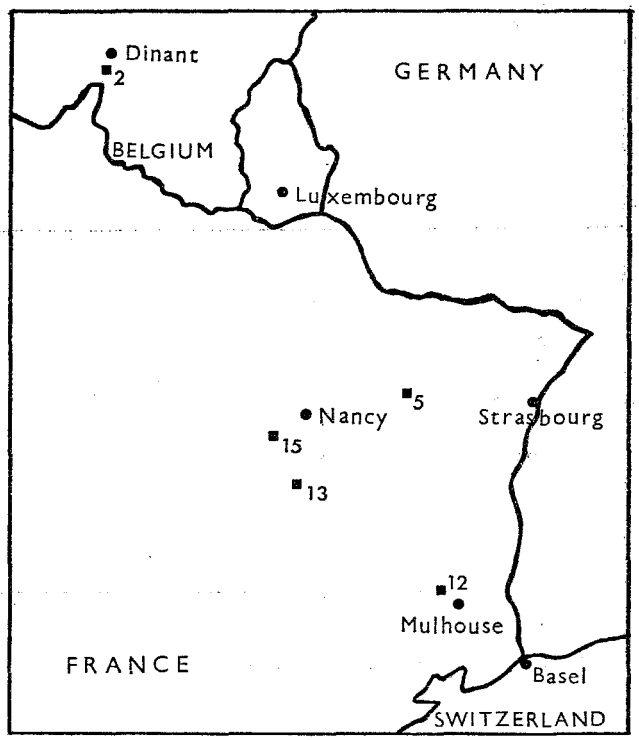


FIGURE 2. Map showing sites sampled.

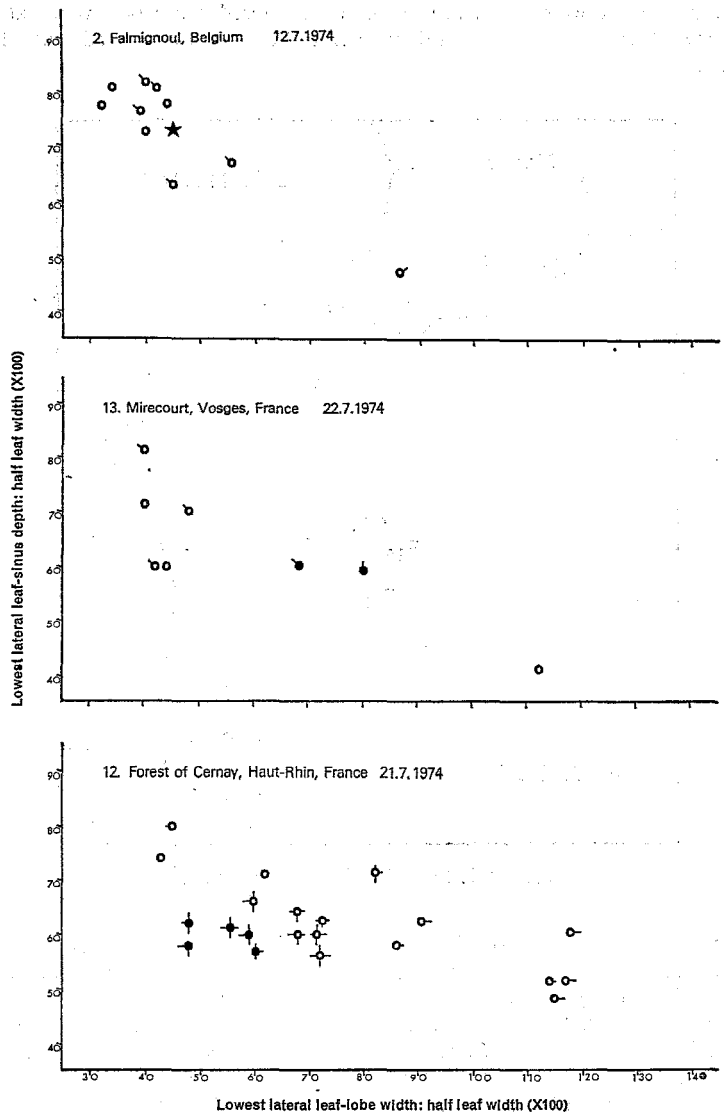
However, two good examples of woods with relatively isolated populations of *C. laevigata* were found: site 5, the forest of Langaumburg, and site 15, near Goviller. The population at Langaumburg consists almost entirely of typical plants of *C. laevigata*. No plants of *C. monogyna* were found and only one or two plants, those plotted farthest to the left on the scatter diagram, show any signs of possible introgression from *C. monogyna*. It can be seen from the scatter diagram that plants of this population have leaves with leaf-lobe: half leaf width ratios higher than those of the English populations at Horish Wood, although sinus depth: half leaf width ratios do not differ so

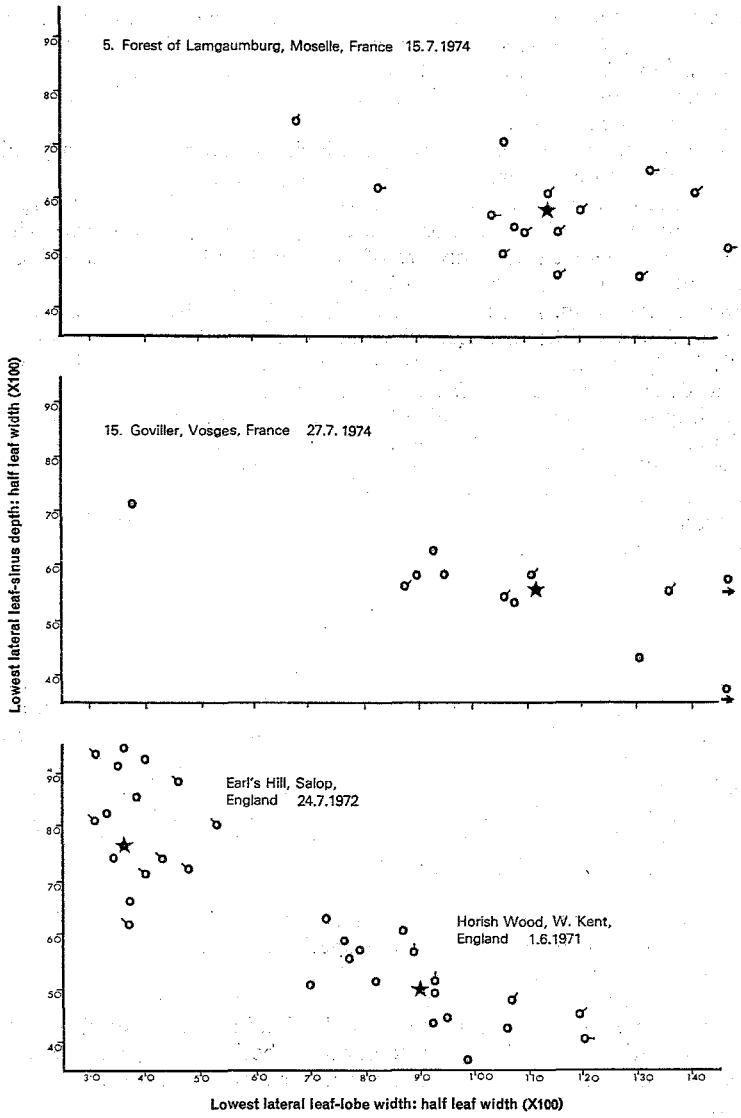
greatly. The bulk of English populations nearest to pure *C. laevigata* have most plants with leaf-lobe width: half leaf width ratios between 70 and 90, and fewer plants with higher ratios. The French populations have many plants with leaf-lobe width: half leaf width ratios above 90. The population at Goviller is similar to that at Langaumburg, the majority of the plants being *C. laevigata*, although an isolated plant of *C. monogyna* was found at the margin of the wood.

At Falmignoul, site 2, the area of woodland is very small and has *C. monogyna* growing just outside. In the wood only one plant of *C. laevigata* could be found, the others being either *C. monogyna* or plants which, although near to *C. monogyna*, are outside its normal range of variation and probably represent plants introgressed by *C. laevigata*.

No isolated populations of *C. curvisepala* subsp. *lindmanii* were found, but at site 13, near Mirecourt, and site 12, the forest of Cernay, mixed populations containing all three *Crataegus* species were encountered, together with apparent intermediates.

At Mirecourt, the plants are growing in a small copse and adjacent hedgerow. Of the plants





Key to symbols

All sites except Forest of Cernay (site 12)

- Style number unknown
- One style
- Both one and two styles
- Two styles
- Both two and three styles
- ● Fruit breadth/length ratio less than 0·64
- ★ Population mean (not given where three species present)

Forest of Cernay (site 12)

- ● Fruit breadth/length ratio less than 0·64
- hairs in leaf-axils — long narrow sepals — high style number — finely serrate, acute leaf-lobes
- Lines absent—characters absent
- Half-lines—characters intermediate
- Typical plant of *Crataegus monogyna*
- Typical plant of *C. curvisepala*
- Typical plant of *C. laevigata*

FIGURE 3. Scatter diagrams of populations.

in the hedgerow, three appear to be *C. monogyna* and one *C. curvisepala* subsp. *lindmanii*. In the copse one plant is clearly *C. laevigata*, another appears like *C. curvisepala* subsp. *lindmanii* but is possibly introgressed by *C. laevigata*, while two others, the plants shown farthest to the left of the scatter diagram with a sinus depth: half leaf width ratio of 60, have some characters of *C. monogyna* and some of *C. curvisepala* subsp. *lindmanii*.

At Cernay there is a strip of *C. monogyna* scrub, including some hybrids, adjoining the forest. The population inside the forest consists mainly of plants which are either *C. curvisepala* subsp. *lindmanii*, with a long, narrow fruit and a single style (plotted on the scatter diagram near to 60 on both the horizontal and vertical axes), or apparent hybrids of this subspecies with *C. laevigata*. The latter have either two-styled or a mixture of one-styled and two-styled fruits, and, having a leaf-lobe width: half leaf width ratio between 65 and 90, are mostly grouped on the scatter diagram nearer to *C. curvisepala* subsp. *lindmanii* than to *C. laevigata*. The plants shown on the scatter diagram with a leaf-lobe width: half leaf width ratio greater than 80 have some or all of the characters of *C. laevigata*. Also, a few plants growing near the wood-margin have a mixture of *C. monogyna* and *C. curvisepala* subsp. *lindmanii* characters.

A test for viability was made on the pollen from a small number of plants from Cernay which were intermediate between *C. curvisepala* subsp. *lindmanii* and *C. laevigata*. Although some samples had a low pollen viability, others showed a viability of over 90%.

Chromosome numbers were also determined in root-tips of five seedlings collected from the middle of the forest at Cernay. Of these, two had a chromosome number of $2n = 52$ and three of $2n = 34$. These are discussed later.

DISCUSSION

The difference between the leaf-lobe width: half leaf width ratios of plants of *C. laevigata* from English and French populations may be the result of their prolonged isolation and consequent divergence, but another possible explanation is the gradual disappearance of the more extreme leaf-forms in England owing to widespread hybridization with *C. monogyna*. Plants in English populations which appear to be hybrids, since they show intermediate characters, have leaves with leaf-lobe width: half leaf width ratios frequently up to 90 but only very rarely beyond this value. In France, where isolating factors between the two species appear to be operating more effectively and the chances of hybridization are less, plants of *C. laevigata* have leaves with higher ratios.

The presence of these comparatively uncontaminated populations of *C. laevigata* appears to be related to the size of the woodlands in which this species occurs. Only a single plant referable to *C. laevigata* was found in the small woodland at Falmignoul, the rest of the population consisting mainly of *C. monogyna* or plants closely resembling that species. Thus, this population is similar to many found in south-eastern England where suitable habitats for *C. laevigata* are also limited. In contrast, the populations of *C. laevigata* examined at both Langaumburg and Goviller occur within large forest areas and in consequence are more or less isolated from and uncontaminated by *C. monogyna*.

Another factor which may have an effect on the continued existence of relatively pure populations of shade-tolerant species such as *C. laevigata* is the extent and nature of roads through the forests. For example, at Horish Wood, W. Kent, the survival of the *Crataegus* population nearest to *C. laevigata* so far found by the author in England is threatened not only by the nearby occurrence of native *C. monogyna* but also by the building of a motorway that now bisects the wood, since the wide, open bank of this road has been planted with a hedge of a cultivated variant of *C. monogyna* and it also provides a suitable habitat for the natural establishment of this species close to the existing population of *C. laevigata*. Insufficient time has elapsed for changes to be apparent so far, but the final destruction of this *C. laevigata* population in the future seems inevitable, although its survival may be extended through the maintenance of suitable habitats in the wood itself, because no coppicing, tree-felling or path-clearing has taken place in recent years.

A similar situation is found in the forest of Cernay, which has been divided by a dual carriageway with wide, cleared areas on either side. Although no hedgerows have been planted, clearance has been followed by the natural establishment of a population of *C. monogyna*. The forest of Langaum-

burg is also divided by a main road but this appears to have had little effect on the *Crataegus* present. It is a single carriageway without footpaths; the forest-trees grow to their full height right up to the road and no *Crataegus* was found growing at its margins. Therefore, it can be reasonably concluded that, as a result of the continued spread of man's activities, *C. laevigata*, at least in its present form, will only survive for a limited time in Europe unless it is possible to conserve large areas of woodland well isolated from *C. monogyna*.

Populations where not two but three species of *Crataegus* are growing in close proximity are also of great interest. The mixing of *C. curvisepala* subsp. *lindmanii* with *C. laevigata* does not depend upon man's activities to the same extent as does that of *C. monogyna* and *C. laevigata*, because they have very similar habitat preferences, both being shade tolerant and able to grow in sparse woodland. Most of the intermediates in the small copse at Mirecourt appear to be hybrids between *C. monogyna* and *C. curvisepala* subsp. *lindmanii*. At Cernay similar intermediates occur only near the margin of the forest, whereas those commonly found within the forest appear to be hybrids between *C. curvisepala* subsp. *lindmanii* and *C. laevigata*. This situation may have arisen because the whole of small areas of woodland tends to be marginal, with resultant penetration of *C. monogyna* and its hybrids, but in much larger areas the margins form a less important part of the whole and only the true woodland species survive within.

On the scatter diagrams of the sample from Cernay (Fig. 3), the group of plants with characters intermediate between *C. curvisepala* subsp. *lindmanii* and *C. laevigata* is nearer to the former than to the latter. This raises the question whether *C. curvisepala* subsp. *lindmanii* exists here as a pure taxon or whether all plants represented by the central group on the diagram should be considered as a single variable taxon. However, there is a marked tendency for single styles to be associated with long, narrow fruits with erect sepals, and this agrees with the original description of the species by Lindman (1904, 1918). Such one-styled plants also tend to group together on the scatter diagram, well away from *C. laevigata*.

C. laevigata is a diploid species (Gladkova 1968, Byatt 1976), but, as *C. curvisepala* subsp. *curvisepala* is known to be a tetraploid (Gladkova 1968), it is probable that subsp. *lindmanii* is also a tetraploid. Some evidence in support of the view that these are the parental species of the intermediates is provided by the near triploid chromosome numbers of two of the seedlings growing under such plants at the forest of Cernay. It is very likely that they are progeny of the mature intermediates which, in spite of probably being triploids, have a high pollen fertility and show every sign of producing a normal crop of fruit. As has been shown in closely related species of other genera (Vardi 1971, 1974), triploids are not necessarily completely sterile.

This last population may also help to elucidate the confusing published descriptions of *C. macrocarpa* Hegetschw., a species originally described from Switzerland (Hegetschweiler 1840). A very similar plant, *C. calycina* Peterm., which in *Flora Europaea* (Franco 1968b) was the name wrongly applied to *C. curvisepala*, was later described from the Leipzig area of Germany (Petermann 1849), but it is now considered to be conspecific with *C. macrocarpa* (Hrabětová-Uhrová 1968, Byatt 1974).

The flowers of both these plants were described as having variable style numbers. The illustration in Petermann's Flora shows a long, narrow fruit without styles but with erect sepals, similar to those occurring on both one-styled and two-styled flowers of plants at Cernay. Existing Petermann herbarium specimens (**LAU, S**) have flowers with two styles, and leaves with many characters of *C. curvisepala*. Flowering specimens (**herb. A. Roubal, PRC**) from populations near Kladno in Czechoslovakia, where they were apparently growing near *C. laevigata*, also show many features of *C. curvisepala*; of the ten specimens (with one exception), those with a single style were determined by Roubal as *C. curvisepala* and those with a higher number of styles as *C. macrocarpa*. This character seems an insufficient foundation for a specific distinction, especially as there is no spatial separation between the taxa, and those plants with flowers having the higher number of styles are most likely hybrids between *C. curvisepala* and *C. laevigata*, with a tendency to favour *C. curvisepala* in their conspicuous vegetative features, as do the plants at Cernay. Many other herbarium specimens from different areas of Europe also show this combination of features of *C. curvisepala* and *C. laevigata*. In some examples the leaf-lobe width: half leaf width ratio is intermediate between that of the two species. Such specimens are usually named either *C. macrocarpa* Hegetschw. or *C.* × *schumacheri* Raunk., a name applied in *Flora Europaea* (Franco 1968b) to hybrids between *C. laevigata* and *C. curvisepala*. *C.* × *schumacheri* was described from Denmark

by Raunkiaer (1933), and the labelling of intermediate plants in herbaria as *C. macrocarpa* or *C.* × *schumacheri* depends largely on the locality, those from nearer Switzerland carrying the former name and those from nearer Denmark the latter.

The strongest evidence for considering *C. macrocarpa* as a distinct species is Hegetschweiler's original description of the fruit, which is followed in *Flora Europaea* (Franco 1968b). He described the fruit as large with five protuberances at its base. If *C. curvisepala* is one of the parents, the fruit might be expected to be large, but the presence of protuberances at the base of the fruit has been considered diagnostic for several European species. My own investigations of herbarium specimens have shown that such protuberances occur fairly frequently in plants otherwise typical of *C. curvisepala*. One of the most typical examples of *C. curvisepala* subsp. *lindmanii* at Cernay shows this feature clearly, while another plant with intermediate characters also has protuberances. Therefore, it appears that this character is not an adequate basis for distinguishing *C. macrocarpa* as a separate species.

Some of the plants at Cernay agree well with descriptions in various Floras of *C. macrocarpa* Hegetschw. This fact, together with evidence from herbarium specimens from other parts of Europe, suggests that plants known as *C. macrocarpa* Hegetschw. are probably of hybrid origin. Cinovskis (1971) came to a similar conclusion. In the absence of convincing evidence that such plants form a distinct species, they are probably better designated as *C.* × *macrocarpa* Hegetschw.

It will be seen from the scatter diagrams based on the assortment of some selected characters in mixed populations that the precise identification of individual plants may be difficult. Therefore an attempt has been made below to construct a key incorporating those characters which have been found most useful in practice. However, where hybridization is suspected, it is necessary to look at as many characters as possible, since individual plants may have an unusual assortment of characters. Although the identification of the majority of plants will be quite straightforward, a few may prove very difficult to determine with any degree of certainty. Quite apart from the normal variation encountered in the parent species, some plants may be the result of more complex hybridization than it is possible to allow for in a key only dealing with distinct species and their obvious intermediates. The hybrid binomials used in the key refer to the following:

C. × *macrocarpa* Hegetschw. = *C. curvisepala* × *C. laevigata*
C. × *heterodonta* Pojark. = *C. curvisepala* × *C. monogyna*
C. × *media* Bechst. = *C. laevigata* × *C. monogyna*

1. Leaves with at least some acute, finely serrate lobes; fruit breadth/length ratio usually less than 0·75
   2. Styles 1-2 or 2; lowest lateral sinus about midway along leaf, occasionally lower .. .. *C.* × *macrocarpa*
   2. Styles always 1; lowest lateral sinus in lower half of five-lobed leaves
      3. Leaf-lobes finely serrate to base; sepals twice as long as broad .. .. *C. curvisepala*
      3. Leaf-lobes serrate only in distal half; sepals not much longer than broad .. .. *C.* × *heterodonta*

1. Leaves without acute, finely serrate lobes; fruit breadth/length ratio greater than 0·75
   4. Leaf-lobes entire or with a few teeth; main lateral veins curving downwards; lowest lateral leaf sinus more than half way to mid-vein; style 1 .. .. *C. monogyna*
   4. Leaf-lobes distinctly serrate; main lateral veins straight or curving upwards; lowest lateral leaf sinus not more than half way to mid-vein; styles at least sometimes more than 1
      5. Leaf-lobes coarsely serrate in distal half; main lateral veins straight; lowest lateral leaf sinus about half way to mid-vein; styles usually 1-2 .. .. *C.* × *media*
      5. Leaf-lobes coarsely serrate ± to base; main lateral veins curving upwards; lowest lateral leaf sinus less than half way to mid-vein; styles 2 or 2-3 .. .. *C. laevigata*

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