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THE ORIGIN OF THE CULTIVATED XYLOPHYLLA HYBRID,
 PHYLLANTHUS × ELONGATUS¹

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The most familiar species of *Phyllanthus* (Euphorbiaceae) which are occasionally grown in greenhouses or (in the tropics) out-of-doors are the representatives of section *Xylophylla*. These plants were considered a great curiosity by Linnaeus and his contemporaries because they appeared to produce flowers on the margins of leaves contrary to the "rules" of morphology. This erroneous notion rather generally prevailed until 1824, when Adrien de Jussieu pointed out that the apparent "leaves" were in reality dilated branchlets (phylloclades) with their true leaves reduced to scales. As remarked earlier (Jour. Arnold Arb. 37: 94, 1956), the *Xylophylla* group appears best regarded as a section of *Phyllanthus* rather than as an independent genus; but the species of the section are so distinctive that the word "Xylophylla" may be usefully retained as a common name.

¹ The assistance of Mrs. Nancy Buffler, who prepared the illustrations, and of my wife, Dr. Barbara Webster, is gratefully acknowledged. As much of the work on this paper was done at Harvard University in connection with a revision of the West Indian species of *Phyllanthus*, I wish to thank the staff members of the Harvard Herbaria and Biological Laboratories for providing research facilities.

In an earlier paper (Jour. Arnold Arb. **37**: 4–9. 1956) it was pointed out that the most common weedy species in the genus, *P. amarus*, has been consistently and generally misnamed from Linnaeus's day to the present. A similar fate has befallen the most widespread cultivated *Xylophylla*, whose correct name has not been used for over a century and whose origin has never been properly understood. Before discussing these points the following nomenclatural *résumé* is necessary:

Phyllanthus × **elongatus** (Jacq.) Steud. (pro. sp.). (= *P. arbuscula* × *P. epiphyllanthus*).

Xylophylla elongata Jacq. Pl. Rar. Hort. Schoenbr. **3**: 53, pl. 348. 1798.

Phyllanthus heterophyllus Schneevogt, Allg. Teutsches Gart. Mag. **2**: 420, pl. 27. 1805.

Phyllanthus elongatus (Jacq.) Steud. Nom. Bot. ed. 1, 615. 1821; Lodd. Bot. Cab. **11**: pl. 1091. 1825.

Phyllanthus falcatus β *praelongus* Muell. Arg. Linnaea **32**: 55. 1863.

Phyllanthus angustifolius β *elongatus* (Jacq.) Muell. Arg., *ibid.*

Phyllanthus epiphyllanthus β *praelongus* (Muell. Arg.) Muell. Arg. in DC. Prodr. **15**²: 428. 1866.

This taxon was described from a plant cultivated in the royal gardens at Schönbrunn, and is typified by a specimen of Jacquin's in the herbarium of the Conservatoire botanique (Geneva). Although doubtless the most common xylophylla in cultivation (at least in greenhouses) it is to my knowledge everywhere misidentified. Living plants, mislabelled as *P. speciosus* (i.e., *P. arbuscula*), have been observed in greenhouses at the University of Michigan, Wellesley College, Smith College, and Harvard University; herbarium specimens (under various names) have been seen from the Missouri Botanical Garden, Florida, Cuba, and several European botanical gardens. In the literature the plant has been as completely confused, having been pictured under the names of *Xylophylla montana* (Curtis Bot. Mag. **53**: pl. 2652. 1826), *Phyllanthus angustifolius* (Hegi, Illustr. Fl. Mitt. Eur., fig. 101. 1906), and *Xylophylla epiphyllanthus* (Britton in Addisonia **7**: pl. 240. 1922). Mueller's treatment in the *Prodromus* has probably added to the confusion, for he pigeon-holed specimens into two varieties of different species.

The profound confusion with regard to the identity of this plant is understandable, since most botanists have tacitly assumed that the common greenhouse specimens of it are the descendants of a wild species native to the West Indies. However, on the basis of morphological characters alone it is clear that *P. elongatus* is probably a hybrid, and this supposition is confirmed by the evidence of its sterility and the history of its origin, as discussed below.

On casual inspection plants of *P. × elongatus* appear to be not unlike *P. angustifolius* or *P. arbuscula*; they differ, however, in having a floriferous prolongation of the primary (penultimate) axis of the branchlet or compound phylloclade². In *P. angustifolius* and *P. arbuscula* the primary axis either ends abruptly at the last lateral phylloclade or projects only a very few millimeters as a sterile tip (Fig. G). The floriferous tip of *P. × elongatus* is evidently an inheritance from its parent *P. epiphyllanthus*, which has a simple phylloclade (phylogenetically derived by reduction from the "compound" one of *P. angustifolius*)

² Cf. Jour. Arnold Arb. **39**: 181. 1958. The simple phylloclade of *P. epiphyllanthus* is homologous with the entire branchlet of *P. arbuscula*, including its lateral axes; it is convenient, even if not strictly correct, to call the branchlet of the latter a "compound phylloclade".

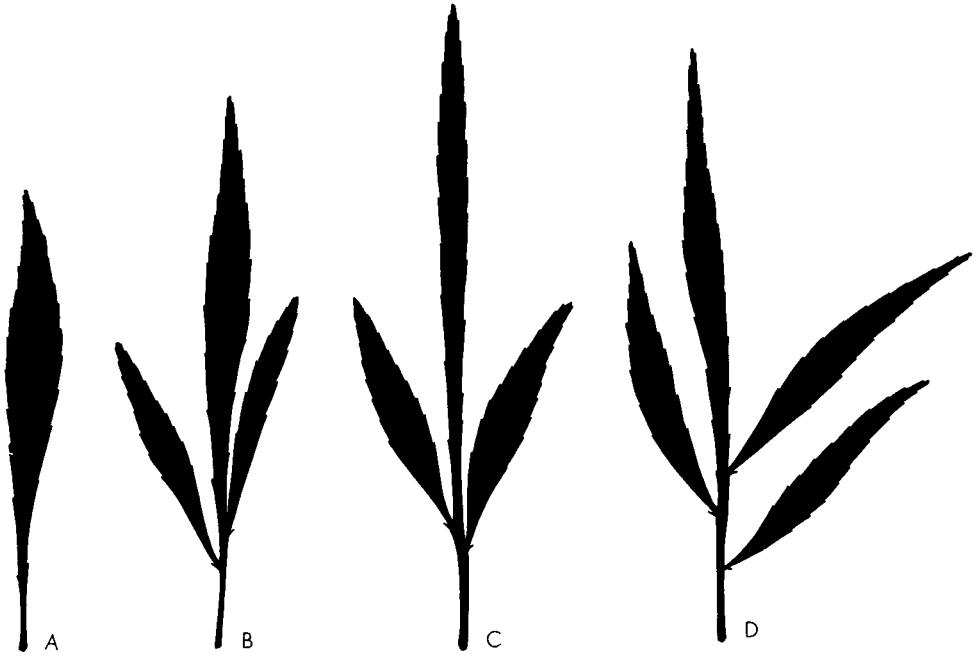
flowering from base to tip (Fig. A). The phylloclades of *P. ×elongatus* thus exhibit the intermediate nature to be expected of a hybrid, most branchlets on a plant having the form shown in Fig. F (but often with the floriferous prolongation even shorter). The most interesting feature of the hybrid, however, is its extraordinary variability, for all of the branchlets shown in Figs. A–G were taken from a single plant growing in the greenhouse of the Biological Laboratories at Harvard. A more or less continuous series may be traced from the simple phylloclade of Fig. A, which is essentially indistinguishable from one of *P. epiphyllanthus*, to the compound phylloclade of Fig. G, which can scarcely be distinguished from one of *P. arbuscula*.³ In both of the parental species there is some genetic and ontogenetic variation, but over a much narrower range. This striking morphological instability of *P. ×elongatus* evidently reflects a genetic imbalance and suggests its hybrid nature as compellingly as does its morphological intermediacy.

The evidence of sterility in *P. ×elongatus*, although not conclusive in itself, does lend support to the morphological evidence. No capsules have ever been seen on any of several cultivated plants, which have produced thousands of flowers during four years of observation. Of course, this may not be decisive, for the plants could be self-sterile, as many woody species of *Phyllanthus* appear to be. Examination of pollen grains, however, shows clear evidence of sterility; three counts of over 200 grains for each sample gave the following percentages of abortive or misshapen grains: Harvard Greenhouse, 28%; Missouri Botanical Garden, 58%; Florida, 75%. The percentage of sterility may well be much higher than this, however, as many plump pollen grains were pale in color and were probably inviable. Certainly propagation of *P. ×elongatus* has always been by cuttings and never by seed.

Fortunately, this morphological and reproductive evidence for the hybrid nature of *P. ×elongatus* is given strong support by a unique historical record of the origin of the plant, which leaves little doubt that it does indeed represent the offspring of a cross between *P. arbuscula* and *P. epiphyllanthus*. G. V. Schneevogt, a Dutch nurseryman, discussed this subject in an interesting manner in an article in the *Allgemeines Teutsches Garten-Magazin* for 1805. Although ignored or overlooked by almost all subsequent authors, Schneevogt's observations are so well recorded that they leave little doubt as to the correctness of his descriptions, even though he failed to interpret his data correctly. According to his preliminary remarks, Schneevogt's father—who was then managing a nursery at Harlem—had some years before received from England a plant of *P. epiphyllanthus*, which was followed in 1789 or 1790 by one labelled *Xylophylla latifolia*. By the time of his 1805 article, G. V. Schneevogt was aware that this "*Xylophylla latifolia*" which he had illustrated in his *Icones plantarum rariorum* (1793) actually was conspecific with *P. speciosus* and *P. arbuscula*.

During the summer of 1800 Schneevogt was surprised to find, on his return from a trip to England, that some seedlings of seed gathered from *P. epiphyllanthus* were very different from the parent plant. His description and illustration of the "leaves" (phylloclades) as very irregular—hardly any two alike—with the last "leaflet" (branchlet axis) prolonged, give an accurate impression of the habit and variability of the plant. In describing this plant as a new

³ A plant of *P. ×elongatus* in the University of Michigan Botanical Gardens was not observed to produce simple phylloclades (as in Fig. A) normally, but did do so when the limbs were wounded by pruning.



species, *P. heterophyllus*, Schneevogt remarked that of more than 20 plants raised from seed produced by an individual of *P. epiphyllanthus*, all represented *P. heterophyllus* rather than the mother plant. Even though he admitted that the production of a new species from seed taken from a different one was unusual, he apparently did not suspect the possibility of a hybrid origin for *P. heterophyllus*. The fact that *P. arbuscula* was being grown in the same nursery—perhaps quite nearby—did not strike his attention, for although he discussed *P. arbuscula* in his article it was only from the standpoint of its nomenclature and generic affinity. However, if it is assumed that the plants of *P. heterophyllus* represent a cross between *P. arbuscula* and *P. epiphyllanthus*, the puzzling aspects of his report can be explained. The irregularity of phylloclade development of *P. heterophyllus* is a striking but not unexpected manifestation of the morphogenetic instability characteristic of many hybrids between morphologically distinct species (W. H. Wagner, ined.). The failure of *P. epiphyllanthus* to reproduce its own kind in the nursery requires further investigation but may prove to be due to self-incompatibility.

Although Jacquin, in his description of *P. elongatus* (1798), gave no details of its origin, his excellent colored plate is incontestably that of a hybrid plant with the same parentage as Schneevogt's *P. heterophyllus*; consequently, his name must be adopted on grounds of priority. Since Jacquin's plate was published two years before Schneevogt's discovery of seedlings of *P. heterophyllus*, his plant from the Schönbrunn gardens must have originated from an independent hybridization (herbarium specimens from the Naturhistorisches Museum, Vienna, show that in fact *P. arbuscula* and *P. epiphyllanthus* were both cultivated there at about the time of Jacquin's publication). The plant illustrated in Curtis's *Botanical Magazine*, which was growing in the garden of the Count de Vandes in Bayeswater in 1822, may have been yet another independently produced hybrid. If, as seems not unlikely, *P. arbuscula* and *P. epiphyllanthus* are both self-incompatible, the common cultivation of both species in European greenhouses must have been conducive to interspecific crossing.

At present *P. ×elongatus* is the only cultivated Xylophylla hybrid whose identity and origin are reasonably well established. Although it is possible that other Xylophylla hybrids may have been introduced into cultivation, none has been recognized. Aside from *P. ×elongatus* the hybrid most likely to occur in cultivation would be *P. angustifolius* × *P. epiphyllanthus*. It is possible that a collection from near Miami (*Small et al.* 10201) which was cited as a cultivated specimen of *P. angustifolius* (*Jour. Arnold Arb.* 39: 195. 1958) may actually represent that cross, but the specimen is too incomplete for certain identification. Field experience in Jamaica suggests that other interspecific crosses such as *P. angustifolius* × *P. arbuscula* may occur in the wild (*Jour. Arnold Arb.* 39: 192. 1958), but because of the closer resemblance of the parental species, these would not be morphologically outstanding.

FIG. 1. Series of branchlets taken from an individual plant of *Phyllanthus ×elongatus*; approximately ½ natural size.

Because of its importance as an ornamental, it has seemed appropriate to designate the hybrid of Schneevogt and Jacquin with a binary name, rather than a formula. However, it must be admitted that future hybridizations may upset this tidy nomenclatural picture. The two parental species both show a considerable geographic variation, *P. ×elongatus* apparently being the offspring of a cross between the pale-flowered Blue Mountains race of *P. arbuscula* with the common subsp. *epiphyllanthus* of *P. epiphyllanthus*. If the depauperate red-flowered race of *P. arbuscula* were to be crossed with the Cuban subsp. *dilatatus* of *P. epiphyllanthus*, a radically different-looking hybrid would probably be obtained; and several other crosses are conceivable. Unless careful records were kept, the cultivated offspring of all these matings might become inextricably confused. However, the discomfiture to systematic book-keeping would probably be offset by the attractiveness of some of the progeny, and by the interesting studies which could be made on the cytological and morphogenetic effects of hybridity.

THE GLUME PIT OF ANDROPOGON BARBINODIS¹

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The glandular depression or "pit" in the first glume of the sessile spikelet in many North American species of *Andropogon*, section *Amphilophis* (genus *Bothriochloa*) has been discussed by the writer (1957) and its phylogenetic significance noted. The glume pit (Figs. 1-4), as far as known, has no functional value. It does provide, however, a marker character for tracing relationships of Old World and New World taxa of this group and when properly used is a reliable taxonomic character.

Grasses of Sect. *Amphilophis* are separable into three groups on the basis of the presence or absence of the glume pit: 1. Glumes never pitted; 2. First glume of sessile spikelet always pitted; and 3. Glume pit irregular in occurrence on different plants or even different parts of the same panicle.

It can be seen from Table 1 that New World taxa with irregularly pitted glumes are all highly polyploid, with chromosome complements of $2n = 120$ and $2n = 180$. Presumably they have arisen from crosses and backcrosses between plants with pitted and non-pitted glumes. The situation in respect to the Old World taxa probably is similar, but data to substantiate this observation are unavailable.

The name *Andropogon perforatus* was proposed by Trinius (1886) for plants with pitted spikelets, belonging to the *A. barbinodis* complex. The type collec-

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