

## L-A Dode on Poplar: A Commentary on the “Extraits d’une Monographie Inédite du Genre *Populus*” (1905)

### Introduction

Louis-Albert Dode (1875-1945) was a noted dendrologist and founder of the Société Dendrologique de France. Born at Moulins in the Département of Allier in the Auvergne, he became a Doctor of Law and developed an extensive personal arboretum. He published notable works on *Catalpa*, *Davidia*, *Evodia*, Fagaceae, Juglandaceae, *Platanus*, *Pseudotsuga sinensis* (which he described in 1912), *Phellodendron*, *Populus* and *Salix*, and was particularly active in describing and assessing the material that had been newly introduced into French arboreta from China.

His private plantations were considerable (although very newly established in 1905) consisting, he tells us, of: “approximately 1,500 poplars and willows, species, sexes, varieties, seedlings, hybrids and introductions from all countries of those kinds growing wild or cultivated” (Dode 1905). In addition to studying his own living collections he made extensive use of his own herbarium collection and that of the Musée d’Histoire Naturelle in Paris.

He appears to have been forced to publish prematurely on poplar by the activities of others. In a footnote he writes: “remarkable parallels can be found between this work and that published by another. I cannot condone the prior publication of a number of my own observations, especially since they have been corrupted by errors and gross confusions. Furthermore, my works unpublished or published have been used without being properly cited; they have been the object of general mentions, which would almost make one believe there has been a collaboration by me in a work which, however, I learned of the publication only when it was an accomplished fact.”

The identity of “another” is not clear, but it may in retrospect be fortunate

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that his hand was forced as his promised complete work (“...a comprehensive study of all botanical and horticultural aspects of the genus *Populus*...”) never appeared. We therefore only have his “extract” published in the *Mémoires de la société d’histoire naturelle d’Autun* for 1905 (Dode 1905). This work is most frequently met with in botanical libraries in the form of Dode’s privately published reprint, which he distributed. The copy in the library of the Royal Botanic Garden Edinburgh, for instance, is Dode’s presentation copy to J.H. Gamble, the botanist of British India after whom he named *Populus gamblei*.

### Leaves and Shoots

Dode’s work is notable for a number of reasons, not least for his bold use of leaf characters in classification, despite the notorious heteroblasty in *Populus*. Indeed he includes two plates in the “*Extraits*” with copious close-packed small line drawings of poplar leaves (a page of which is shown in figure 1). He dissects the variable leaf morphology of poplar by constructing an elaborate classification system for leaf type in relation to position on the tree (“young wood”, “old wood”), while noting that leaf morphology is inherently continuous in poplar.

His terminology of auxiblasts, mesoblasts, etc. (Table 1) has not been widely taken up but merits examination. While noting that “it is traditional to affect a certain disdain with regard to this highly variable organ”, he contends that “the poplar leaf varies no more between individuals of the same species than other organs; in each species it only varies greatly with branch-type and the position it occupies on them”. The same shoot type in different species Dode calls “homologues”.

For instance at the extremities of trees (young wood) the terminal shoots are “auxiblasts”, which in turn bear second order shoots (usually “mesoblasts”) which in turn often bear third-order shoots (usually “leptoblasts”). Old wood shoots are classified similarly, and the three old-wood branch-types carry catkins (best developed on the lamproblasts, and least so on the schenioblasts). Shoots of intermediate position are designated “auxilamproblasts”, brachy-lamproblasts” etc., thus incorporating the continuous nature of the variation.

In addition to the shoot types in Table 1, Dode also has ‘discoblasts’ (brachyblasts that form knotty branches consisting of a stack of discs each

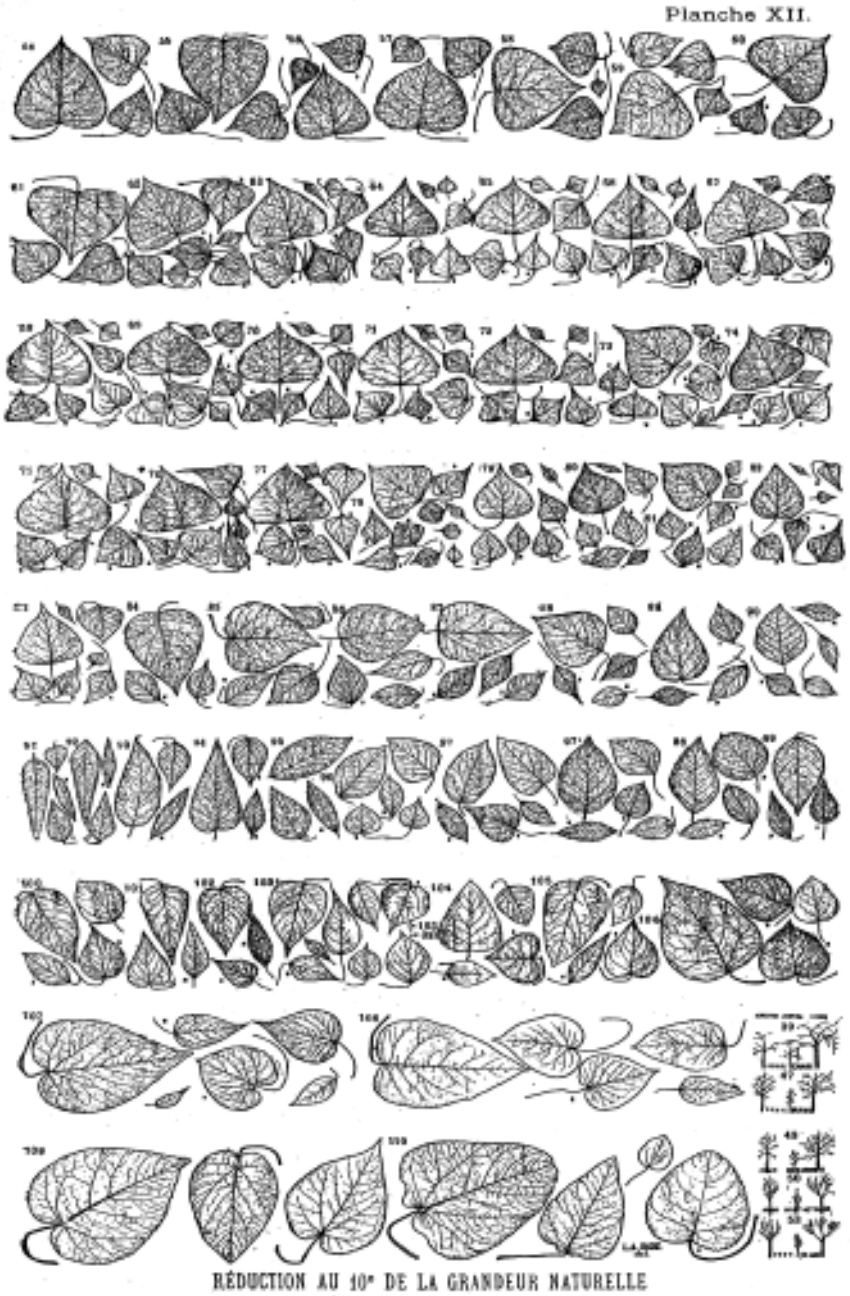


Figure 1. Illustrations from Dode's "Extraits d'une Monographie Inédite du Genre *Populus*" (1905)

representing one year's growth) and 'perissoblasts' (exceptionally vigorous growths, which occur in very vigorous seedlings, or on resprouting stumps, or on trunks or large branches (coppice shoots or "gourmands").

### Dode's Choice of Characters

As noted in the previous section, Dode uses mainly leaf characters in his taxonomic work, particularly leaves from the upper part of auxiblasts (turions), and middle leaves on mesoblasts and brachyblast. On each kind of shoot, basal, middle and top leaves may be distinguished, but when growth is very reduced due to environmental stress, only basal, or basal and middle leaves may be found.

Basal leaves of shoots are rarely used in taxonomic work and the same applies to sucker leaves (which are almost identical in species of the same section). Dode notes that leaf-tip is obliquely- or recurved-acuminate in some aspens and some balsam poplars. When the top is apiculate (e.g. "*P. mexicana*", "*P. europaea*"), this may be lost or aborted rather easily and an obtuse leaf may result.

Dode does not describe stipules as they are caducous, and fall early. He also downplays pubescence as it is environmentally variable and tends to disappear towards autumn. While noting that the species have useful floral characters (pubescence, stigmas, length of pedicels) they are not used by Dode as they are difficult to observe.

### Dode's Taxonomy and Nomenclature

In the *Extraits* he describes numerous new species. Some, like *P. yunnanensis* Dode, (Figure 2), are still in use but most are now considered insignificant varieties or clone groups of hybrid origin. He included descriptions in French only, but as they are published before January 1<sup>st</sup> 1935, Latin diagnoses are not required and the names are all validly published. However, Dode seems to have been aware of the deficiencies with respect to convention and the following year (Dode, 1906) published the names with Latin descriptions.

He admits that many of his species are microspecies, but attempts to exclude hybrid clones from treatment as species by requiring his species to be known in the wild and as both sexes. He does concede however that lumpers will wish to treat his "groups" as species and his "species" as

subspecies. His nomenclature was revolutionary, following the rule of priority where possible while being scathing of the confusions and inadequate descriptions of his botanical predecessors, and hugely multiplying the known species. Nevertheless only a few of his many species epithets are in use at present.

### Dode's Classification of Poplar

Dode's classification of poplar is also interesting as he is the first to recognize subgenera (as well as sections) in the genus. He raises section *Turanga* of Bunge (then including only *P. euphratica* and *P. pruinosa*) to subgenus *Turanga* (Bunge) Dode, convinced of the distinctiveness of these two species. Wesmael (1868) had previously classified these species with the aspens in section *Leuce*. This distinction was supported by the later discovery of the even more unusual related species *Populus ilicifolia* (Engler) Rouleau from the Tana and Tsavo rivers in Kenya. Although this species was known in Dode's lifetime, Engler had described this unpoplar-like poplar as a *Celtis*. Browicz (1966) used subgenus *Balsamiflua* (Griff.) Browicz for the turanga poplars as a whole, and recognized a section *Tsavo* (Jarn.) Browicz for *P. ilicifolia* and section *Turanga* Bunge for the other turanga poplars.

Dode's conspectus of the genus *Populus* in the *Extraits* (including his key to sections with sectional notes) contains many useful observations, and is reproduced here in translation. This translation excludes his species accounts and keys to species and species groups, as the species concept he uses is very different from that currently adopted, and translation of species accounts would need elaborate annotation to equate Dode's information to taxa used in other treatments. I am indebted to Bénédicte Wenden for assistance with certain points of translation.

### Genus *Populus*: A Conspectus of the Subgenera

1. Leaves coriaceous, glaucous, concolorous, never tomentose below, upper and lower surfaces identical, entire (at least in turion leaves), variable, much shorter on the old wood than on the young; foliar glands not far projecting, mamillate, often with a hole at the tip and as a consequence bowl-shaped; petioles round; buds small, short, blunt, often showing only one scale, seldom viscid. Pubescence better developed on young or old wood according to the group. Perianth caducous, deeply divided, with acute teeth. Stigmas large,

carmine, 3. Stamens approximately 12. Capsules coriaceous, elongated

**...Subgenus *Turanga***

2. Leaves green above, lighter and sometimes tomentose below, sometimes lobed, almost always of varying type, with petioles less compressed on turion leaves than on the brachyblasts; foliar glands projecting, bowl-shaped, sometimes even situated on the petiole, often absent; buds average, more or less acute, not or a little viscid, with several obvious scales. Pubescence better developed on young wood than on old. Perianth persistent, sinuous, obliquely truncate. Stigmas pale pink to carmine, 2. Stamens 5-20. Capsules rather slender, small, elongated

**...Subgenus *Leuce***

Catkins always rather compact.

3. Leaves green above, lighter and sometimes pubescent below, teeth never very deep, never lobed, more or less different in outline (often very little), according to the nature of the branches; foliar glands irregularly bowl-shaped or as a perforated ridge; petioles more or less compressed laterally, or with a quadrangular or rectangular section; buds rather large, acute, viscid, with many very obvious scales. Pubescence more developed on old wood than young. Perianth persistent, sinuous or more or less deeply toothed, truncate ?right. Stigmas greenish, with many to few more or less pigmented warts, 2-4. Stamens many, 8-8. Capsules rather coriaceous, elliptic-globular.

**...Subgenus *Eupopulus***

No transition exists between the subgenera, which can, in particular subgenus *Turanga*, be regarded as true genera.

**Key to Sections and Sectional Notes**

**Subgenus *Turanga***

I. Pubescence less developed on young wood than on old; perianth with divisions scarcely exceeding half the height

**...Group *Euphratica***

II. Pubescence more developed on young wood than on old; perianth

with divisions almost reaching its base, more reudit

### ...Group *Pruinosa*

It is on the newly developed brachyblastes and on the buds that one can best note the pubescence of the old wood growth. The poplars of the two groups live on banks of saline rivers of desert areas; they are definitely halophilous, and their tissues can absorb salt in great quantity. Fossil forms of the subgenus frequently have been encountered, in particular *P. mutabilis* Heer of the European Tertiary period, rather little different from the extant *P. mauritanica* [*P. euphratica*]. The illustrations of leaves given for this subgenus are far from covering all the variation: no other tree shows such foliar polymorphism. The turangas differ besides by their overall appearance from all other trees and distantly recall certain willows (*persicae*, *longifoliae*, *purpureae*). Their leaves are sometimes opposite, the appearance of their capsules, and their reduced and caducous perianth also bring them closer to the willows (in which the perianth is missing), as well as the presence of small leaves at the base of the catkins.

The cultivation of turangas has often been abandoned. These failures have been caused by an insistence on propagating them by cuttings (an unsuitable procedure for them—at least in the open air) or by grafting (they appear to be unable to live grafted on poplars proper). However, the four species cultivated by the author grow vigorously and *P. mauritanica* also is grown at Angers by Mr Allard. Saline localities (maritime areas) will be particularly appropriate for them (although a little salt can easily be applied to seedlings cultivated in normal soil).

The turangas are of average size, with tough and decorative leaves, and their wood, it appears, has some merit. The author proposes to call them generally by the name “turangas”, as one says “aspens” and “white poplars” for subgenus *Leuce* and “balsam poplars” for section *Tacambacae*.

### Subgenus *Leuce*

I. Mature turion leaves woolly below, more or less lobed; young brachyblast leaves more or less woolly below. Floral bracts little or somewhat divided. Multiplication by cuttings

### ...Section *Albidae*

(*P. alba*, *P. tomentosa*, etc.)

It is important for the study of the species of this section, to remember that in very bright and dry situations, the trees have a whiter trunk, with greater cracking, whiter, more pubescent leaves; in very shady situations, all things being equal, the trunks are smoother, more green, the foliage greener and the look of the species of the *nivea* group approaches that of the species of the *alba* group, as in the first case those of the *alba* group resembles those of the *nivea* group.

**II.** Turion leaves glabrescent, silky-hairy or with rough hairs, more or less irregularly serrate-toothed; brachyblast leaves developing at first with more or less abundant silky hairs. Floral bracts deeply divided. Ordinary methods of vegetative propagation by cuttings are unsuccessful

### ...Section *Trepidae*

(*P. grandidentata*, *P. tremula*, etc.)

The mesoblast leaves of the species of this section often greatly resembling each other. The brachyblast leaves are usually wider, and those at the top of the shoot often entire. One should not seek distinctive characters on the young suckers (nor on the other wayward growths), for example the pubescence is similar on these shoots, whether they belong to a very pubescent species or to a very glabrous species. In aspens as in the other poplars, the foliar glands, in a given species, are more prevalent on leaves of vigorous growth.

### Subgenus *Eupopulus*

**I.** Petioles more or less compressed laterally, those of the turion leaves noticeably so and all proportions remaining equal in extent to those of the brachyblast leaves; leaves more or less glaucous below; foliar glands rather ridge-shaped

### ...Section *Aigiri*

(*P. fremontii*, *P. nigra*, etc.)

They are the poplars “par excellence”. They generally live in colonies, where usually only one species of the section is represented, on the banks of the important rivers. The rachis, the pedicels and the capsules are glabrous or pubescent according to the groups and species. In the foliage of these poplars one meets some narrow leaves, varying in frequency and

pronouncement according to the group and species. These leaves are recognized by having their base and their top attenuated and have their top more or less oblique: these leaves are known by the name of “comma leaves”.

**II.** Petioles quadrangular in cross section, usually less compressed, those of the turion leaves constant in shape, usually shorter than those of the brachyblast leaves; leaves glaucous, whitish or white below; foliar glands rather bowl-shaped

...**Section Tacamahacae**

(*P. trichocarpa*, *P. laurifolia*, *P. ciliata*, etc.)

It is difficult to provide a character that infallibly assigns a species to a particular section. The balsam poplars (*Tacamahacae*) may sometimes be recognised by their leaves being white below, sometimes by their large petioles, sometimes by the number of carpels greater than two. (One does not find numerous carpels in the section *Aegiri*, unlike in the large foliage species: the balsam poplars always have some of their flowers at least with 3 carpels.)

The balsam poplars are generally characterized by very variable foliage, and very resinous and odorous buds; their growth is fast, but it would be undoubtedly an error to plant these poplars for the production of wood; they do not usually reach a large-size; they are to the poplars what the sallows (*Capreae*) are to the willows. On the same branch, the length of the petioles varies greatly in certain species: some have at the top of the shoots (especially on the lamproblasts), a rosette of large terminal leaves which are very long petiolate (e.g., *P. elongata*).

As a general phenomenon in the poplars, the perissoblast leaves tend to assume the shape of the brachyblast leaves, but with much greater dimensions. The mesoblast leaves are usually strongly narrowed, the turion leaves less so. The teeth are in general rounder (scalloped) than those of the *Aegiri*. The pubescence (as in the latter) is much better developed and more persistent on the old wood than on the young (the notes given refer to the young adult wood). On short shoots where growth has aborted, the pubescence is particularly dense.

**III.** Petioles round-subquadrangular in cross-section, turion-leaf petioles notably so, and all proportions remaining equal in extent to those of the brachyblast leaves; leaves white-woolly below when young, then only glaucous;

foliar glands rather bowl-shaped

**...Section Leucoideae**

(*P. lasiocarpa*, *P. heterophylla*)

These poplars are not in fact similar to white poplars, even though the only species known until recently (*P. heterophylla*) has almost always been placed with them. They are propagated with great difficulty. Their foliage and their branching recalls the balsam poplars and their floral characters especially recall the group *ciliata* [i.e., sect. *Tacamabacae* - *P. ciliata*, *P. jacquemontiana*]. They also have some affinity with the group *Carolinensis* [i.e., sect *Aegiri* - *P. carolinensis*, *P. angulata*, *P. besseyana*].

**References**

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Young Wood	Old Wood
<p>Annual growth which is separated from wood more than three years old by a rather long distance, that is to say current-year growth, two-year old growth, or three year old growth that is sufficiently long</p>	<p>Annual growth positioned on parts of the tree aged five or at least six years, or growth that is separated from old wood by short branches only</p>
<p>(1) <b>Turion</b> or <b>auxiblast</b> (growth shoot)</p>	<p>(1) <b>Lamproblast</b> (super-shoot)</p>
<p>Ordinary vigorous shoots, produced at the tips of the young wood</p>	<p>Growth of the old wood, corresponding to the auxiblasts, but much shorter and almost always very large, with characteristic vigour and robust handsome leaves; they usually bear very large buds containing flowers.</p>
<p>(2) <b>Mesoblast</b> (intermediate shoots)</p>	<p>(2) <b>Schenioblast</b> (thin shoots)</p>
<p>Shoots characterised by their slenderness, and their smaller buds and leaves.</p>	<p>Old wood shoots corresponding to the mesoblasts, usually produced in summer from spring short shoots; when there is no cessation of growth the two types of shoots are only separated by a few badly-formed leaves</p>
<p>(3) <b>Leptoblast</b> (weak shoots)</p>	<p>(3) <b>Brachyblast</b> (short shoots on old wood)</p>
<p>Shoots hardly exceeding 5 to 10 cm, and often not persistent. Leptoblasts are generally produced from the buds of the mesoblasts, the latter themselves often coming from turion buds, except in very young seedlings.</p>	<p>A word coined by <b>Hartig</b> (<i>Voll. Naturg. D. forstl. Kulturpfl. 1851</i>), and which Dode used as a model for coining the other terms. It appears to have been applied by Hartig to short shoots in a general way.</p>

**Table 1.** Shoots characteristics of old and young wood, after Dode (1905). This classification of shoot types with their characteristic leaves is central to Dode's system. He calls shoots of the same type on different trees "homologues".



Figure 2. *Populus yunnanensis* at the Royal Botanical Gardens, Kew (2004).