Populus ilicifolia (Engler) Rouleau and its taxonomic position

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Populus ilicifolia belongs to the most puzzling species within the Salicaceae family. At first it was classed among a totally different family (Ulmaceae), and described as a species of the Celtis genus. Recently, when there has been no doubt whatever of its belonging to the Salicaceae family, it has been recognized as a separate, monotypic genus Tsavo Jarm. No wonder that the number of synonyms of this species has been so considerable.

Populus ilicifolia was found by J. M. Hildebrandt in East Africa, Kenya, along the banks of the rivers Tsavo and Adi, in 1877. In 1895 A. Engler described it for the first time, basing on the herbarium specimen gathered by Hildebrandt. Induced by W. Vatke's remark, placed on the herbarium label, “Celtis”, Engler named this poplar wrongly “Celtis ilicifolia”. Three years later (Engler 1898) he described it again using another herbarium specimen, collected by F. Thomas in Witu, in 1896, but then he named it Populus euphratica Oliv. ssp. Denhardtiorum, in honour of the brothers Denhardt, who organized an expedition to the upper course of the river Tana. Engler failed then to realize that both taxa described by him were identical and only after some years (Engler 1905) he found that he had wrongly classified this poplar among the Celtis genus.

Some years later L. A. Dode (1909) raised the rank of Engler's subspecies to the rank of species, keeping the name “Denhardtiorum”. A minute description, made with the help of E. Battiscombe's herbarium specimens taken along the river Tana (No 207), as well as of drawings of leaves, inflorescences, flowers and fruits, was given by O. Stapf in 1922, while its proper name “ilicifolia”, in conformity with rules of botanical nomenclature, was re-established by E. Rouleau as late as 1945.

Engler as well as Dode and Stapf thought “P. Denhardtiorum” to be a species closely allied to P. euphratica Oliv., which had been classed among the section Turanga by A. Bunge (1852), and to the subgenus of the same name by Dode (1908). Characteristic features of the poplar of the Turanga type are: lack of the terminal bud (sympodial ramification), greatly variable leaves, with a lamina unicoloured on both sides (glaucous or greyish-green) without any marked differentiation into upper and lower side, and a perianth deciduous, deeply dissected or totally divided.

In 1949 A. Jarmolenko placed “P. Denhardtiorum” into a separate genus Tsavo, as Tsavo ilicifolia. The cause of this distinction were the peculiar characteristics of the morphologic structure of inflorescences and female flowers. The
female inflorescences in "P. Denhardtiorum" have several normally developed leaves. The inflorescences of all the other species of poplar (catkins) have no leaves and their base is adapted to be separated from the shoot after the fruit ripens (capsules). It is wholly different in the case of our species where the inflorescence is a clear prolongation of the axis of the lateral shoot and does not fall off after the fruits become ripe.

As I have found examining several herbarium specimens, available to me, the number of leaves on the inflorescence shoot is 1—3. These leaves persist all over the vegetation period and their size is nearly the same as that of the other leaves on sterile short shoots. An inflorescence of this kind must not be named catkin, the name raceme should be given instead. The loose structure of this inflorescence and a few flowers set on long pedicels remind rather of a corymb.

To make sure that the leaved inflorescences of "Tsaeo ilicifolia" are something exceptional indeed, Jarmolenko (1949) examined the herbarium specimens of other species of the poplar of the Turanga type, as well. He stated that one to two leaves at the base of catkins can be met in Populus ariana Dode, though this happens very seldom, but these are leaves with strongly reduced lamina, set on short, thin petioles. They are early deciduous leaves and they do not persist at infructescences. I have also found this kind of leaves in specimens of P. euphratica Oliv. (s.l.) in the herbarium of the Royal Botanic Gardens, Kew, namely: Irak — Rustam, nr. Baghdad, 1929, I. A. Rogers 091; Rustam, 1929, Cowan, Darlington 91; Rustam, thickets along the Diyala River, 1931, Yussaf Layar (?) 1494; Karbala, roadside on canal, 1956, Ali Rawi 15762; U.S.S.R. — Regio transcaspica, Aschabad, prope pagum Gyjaurs, 1900, J. Bornmüller 32; India — Punjab, Herb. Lehmann 1852; Sind, Stocks, Herb. Hooker 1867; Bombay Herb. of the late N. A. Dallzell. In one case highly reduced leaves have been found even on two infructescences (Stocks’ specimen collected at the Indus river).

Another feature Jarmolenko drew attention to, is the structure of female flowers, more properly, the structure of the style. Jarmolenko’s observations, however, based on one herbarium specimen (isotypus), which had been collected
when the style was badly preserved, led the author to wrong conclusions. Jarmolenko did not know Stapf’s paper either, and there the structure of the female flower has been splendidly represented in Table 3050. There the bottlelike ovary of P. ilicifolia has a distinct style with three strongly elongated and deeply divaricate stigma lobes (Fig. 1). The ends of these divarications are again secondarily lobed, too (2–3 lobes). Jarmolenko took them as free ends of pistils. As such a structure was not known in any of the species of poplars it was used by Jarmolenko to separate a new genus.

Jarmolenko’s “stylodium” is really nothing else as an exceptionally long and divaricate stigma. Nevertheless such a type of stigma is a real peculiarity in the *Populus* genus and is markedly different from the short and only shallowly reniform stigma lobes of other poplars of the *Turanga* type (Fig. 1). Thus the shape of stigma, and leafed female inflorescences are such marked features that they allow to separate poplars of the *Turanga* type into two sections. Among the first, for which I keep Jarmolenko’s generic name — *Tsavo* — I class only one species — *P. ilicifolia*, and all the other species belong to the other — section *Turanga* Bunge (subgenus acc. to Dode). The following table shows the differences between these sections:

<table>
<thead>
<tr>
<th>Section Tsavo</th>
<th>Section Turanga</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trees to 30 m high</td>
<td>Trees to 15 m high.</td>
</tr>
<tr>
<td>Female inflorescences and infructescences supported by 1—3 normally shaped leaves</td>
<td>Inflorescences and infructescences without leaves, or with minute, greatly reduced, deciduous leaves, at the most</td>
</tr>
<tr>
<td>Female flowers usually no more than 10</td>
<td>Female flowers up to 40 or even more</td>
</tr>
<tr>
<td>Stigma much elongated divaricate. Ramification with 2–3 lobes of second order</td>
<td>Stigma short, reniformly retuse</td>
</tr>
</tbody>
</table>

Common features of these sections are: shape and structure of leaves, sympodial ramification of shoots, and dissected perianth, falling off (is it so in all species?). This group of species is, owing to these features, so distinctly opposed to the other species of poplars, that the division of the genus *Populus* into two subgenera is wholly justified. I propose the name *Balsamiflua* to the subgenus represented by the sections *Tsavo* and *Turanga*. This name, as a generic one, had been used, for the first time, by W. Griffith in 1848, i.e. some years before Bunge described the section *Turanga*. To the genus *Balsamiflua*, according to Griffith, belongs *B. deltooides* Griff. from Afghanistan (Griffith 1854); this species is just *Populus euphratica*.

The name *Balsamiflua* became forgotten and it was not until 1939 that it was applied by A. Kimura to the poplar of *Turanga* type; the year before (Kimura 1938) it was separated into a single genus *Turanga* (Bunge) Kimura. There is no proper reason to distinguish a separate genus from the *Populus* genus, because it is mainly based on characteristics of vegetative organs, and not on generative ones. Kimura (1938) writes: “Cum genere *Populo multa communia habet, sed ramificatione sympodiiali, cortice interniore scleroblastis carente, foliis isolateralibus, perigonis deciduis profunde vel ad basim usque dentato-laciniatis generice distinguendum*. 
Within the genus *Balsamiflua* Kimura placed *P. illicifolia* to the section *Euphratica* (Dode) Kimura, but it is quite wrong, because *P. illicifolia*, as mentioned above, differs remarkably from *P. euphratica*.

The division of the genus *Populus* may be now represented as follows:

Subgenus 1. *Balsamiflua* (Griff.) Browicz, comb. nov.


Terminal bud missing. Sympodial ramification. Dimorphic leaves, unicoloured on both sides, without a distinct differentiation on upper and lower side. Perianth falling off, deeply dissected, or completely divided.

Sectio 1. *Tsavo* (Jarm.) Browicz, comb. nov.


Sectio 2. *Turanga* Bunge, Pl. Lehmannianae 322(1852)


Subgenus 2. *Populus*


Terminal bud present. Monopodial ramification. Leaves entire or dimorphic, distinctly differentiated into upper and lower side, bicoloured. Perianth persistent, cut out or toothed.

Sectio 1. *Populus*


There is only one species belonging to the new section *Tsavo*, namely:

*Populus illicifolia* (Engler) Rouleau

Rhodora 47:362 (1945); Dale, Greenway, Kenya Trees Shrubs 493 (1961)


Fig. 2. Variability of leaves of *Populus ilicifolia*: (seedlings) 1—2 Sampson 68C, 3—4 — Bally 1710; (long shoots) 5—6 — Dummer 5026; 7 — Sampson 68; 8 — Greenway 8858; 9 — Hildebrandt 2608; (short shoots) 10 — Sampson 68 A; 11 — Greenway 8858; 12 — S. Paulo 477; 13 — Thomas 49.


A thorough description of this species is given by Stapf (1922), only a description of leaves of seedlings Stapf did not know should be added to it, as well as the description of leaves (especially their sizes) should be completed.

Leaves of seedlings about 6 cm long and 5—10 mm broad are clearly acuminate at both ends, edges distinctly, shallowly toothed with 2—4 teeth on each side, placed on short petioles (2—5 mm). This type of leaves with a lamina, much longer than it is wide, can be found, too, in older plants on long shoots of strong growth. They are totally distinct from leaves on shortened shoots. Leaves to 12 cm long and to 4.5 cm wide (in the broadest part), acute or acuminate, with a cuneate base, on a petiole to 3.5 cm long. Leaves of short shoots are roundish or broadly obovate in outline, with a short acute apex more or less as long as lateral teeth, broadly cuneiform at the base, to 6 cm long and to 5 cm wide. Both the leaves of short shoots and long shoots have 2—4 pairs of teeth, they are, however, more clearly marked and more acute than in leaves of seedlings (Fig. 2).

The height of trees is defined in different ways. According to Engler (1898) this poplar gets 25—30 m high, according to Stapf (1922) 18—30 m. Other authors and collectors usually note 50—80 feet, i.e. 16—26 m more or less. When young the crown is almost columnar, later it becomes more rounded.

Specimens examined:


Distribution:

Populus ilicifolia is limited in its occurrence to east and partly central part of Kenya, almost from the equator to about 3 degrees of south latitude. G. Cufo-
dontis (1953) records that it probably occurs in S-SE Ethiopia, i.e. north of the equator, but this supposition has not been confirmed either in literature or in herbaria (Fig. 3).

*P. ilicifolia* grows along valleys of the river systems: Tana, Tsavo, Athi and Uaso Nyiro, in sandy soil from the sea level up to about 1150 m a.s.l. (Dale, Greenway 1961). Its seedlings grow only on exposed river banks at the beginning of November, and every year they are almost wholly washed out by floods (Rawlins, in sched.). Along the river Tana at the water line they grow accompanied by seedlings of *Cyperaceae, Sphaeranthus* and *Gnaphalium* while older individuals from littoral forests together with: *Acacia spirocarpa, A. sp.*, *Trichilia emetica, Borassus, Phoenix, Hyphane, Garcinia, Cordia gharaf, Minusops, Ficus gnaphalocarpa* (Greenway, in sched). A picture of such a forest is given by E. Battiscombre (1926).

The wood of *P. ilicifolia* works easily, therefore the trunks are favoured by natives for dug-out canoes (Dale, Greenway 1961).

**DISCUSSION**

Species of poplars of subgenus *Balsamiflua* are not properly worked out so far, and are often described under the name of *P. euphratica* (in several varieties and forms). They belong to the most xeromorphic representatives of the genus *Populus*, and their area is limited to dry territories (deserts) of north Africa: Morocco, Al-
geria, Tunisia, Libya, Egypt; south-west Asia: Israel, Jordan, Syria, Iraq, Turkey, Iran and central Asia: U.S.S.R. (Middle Asia), Afghanistan, West Pakistan, India.

Farthest to the east they reach Mongolia (Grubov 1955), Tibet, and the province Kansu in West China (Walker 1941). One species occurs in the Caucasus, too (P. transcaucasica Jarm.). Besides, in 1908, Dode described a new species of such a poplar from Europe, from SE Spain (near Elche, on saline soils); it was named P. ilicifolia Dode. C. Viciouso (1951) suggests, however, that this species is identical with P. euphratica, and according to J.A. Franco (1964) it does not grow wild in Spain, but is naturalized, but this seems rather doubtful, as poplars of the Balsamiflua subgenus do not propagate vegetatively from cuttings and their seeds lose their power of germination rather quickly.

Thus we see the area of the Balsamiflua subgenus is the most south-eastern part of the general area of the genus Populus. It is a typically broken area, with a number of smaller or larger concentrations of localities, especially in north Africa. The latter localities of P. ilicifolia, as well as the isolated ones, south of the equator, clearly show, that the southern line of the area, before Sahara’s becoming dry, ran further south in the Tertiary, than it occurs nowadays. Poplars of the Balsamiflua type occurred during the Tertiary, in Europe (southern and central Europe) and in North America, as well, evidence given by fossil remains of leaves of P. mutabilis Heer, a species, as Engler (1898), mentions, considered by a large number of palaeobotanists as ancestor of the contemporary P. euphratica. The disruption and contraction of the area in this group took place with the climate getting drier and drier in the territory of north Africa and Old Mediterranean, to which the poplars of the Balsamiflua subgenus are nearly totally limited. The dryness of the climate caused simultaneously the appearance of a number of xeromorphic features in this poplar, such as the drying up of the terminal bud, leaves becoming coriaceous, change of colour, lack of clear differentiation of lamina to lower and upper side, and the diminution of the size of the tree; e.g. in the section Turanga the poplars become about 15 m high, and in extremely dry conditions they grow in the form of trees only some meters high, with a crooked and low trunk. P. ilicifolia is the only exception, growing up to 30 m, thus reminding in its size of the sizes of a number of species from the subgenus Populus; some species of the latter subgenus reach even 60 m in height (P. trichocarpa Hook.).

P. ilicifolia is the only tropical species of the poplar. Its isolated area far to the south of the area of other species of poplar, as well as some morphologic differences clearly show, that we have here to do with a taxon forming an important link in the evolution process of the whole Populus genus. P. ilicifolia has some specific features that show its dissimilarity to all other poplars. These features are: leaved inflorescences of a raceme type, infructescences persistent after ripening, and an elongate and divaricate stigma. The first feature is the most important one.

The occurrence of leaves on inflorescences, as has been already discussed, has been also found in other representatives of the subgenus Balsamiflua. These observations, however, show very clearly that this feature so strongly expressed in P. ilicifolia, gets less developed in the Turanga section, where the inflorescence leaves,
in a reduced form, appear only from time to time and fall off early. This feature can, therefore, be considered as phylogenetically older in the Turanga section. The inflorescences, as well, fall off in this section after ripening. We can conclude, therefore, that the evolution of the structure of inflorescences in the subgenus Balsamiflua, and most likely in the whole Populus genus, has run from a leafed inflorescence of the raceme or corymb type to the leafless catkin, which has lost its power to persist on the shoot after the ripening of fruits.

Further changes in the structure of flowers and inflorescences have been seen: 1. in the shortening of pedicels which are 7 mm long in P. ilicifolia, a little shorter in the Turanga section, while in the Tacamahaca section the flowers are subsessile or sessile, 2. in the style and stigma becoming shorter, 3. in inflorescences and inflorescences getting longer.

Leafed inflorescences are known in the Salicaceae family in the genus Salix, too. They occur in primitive forms, almost, in all ligneous willows from the group Pleiandrae, and in old high-mountain oreophytes (Szafer 1959). In this group the inflorescences are placed on rather well developed short shoots, while in younger forms they are short and have only small leaves, and forms youngest in evolution have leafless catkins, sessile, apparently growing out of the main shoot. A similar course of evolution is met in the poplar. It can be seen in the schematic drawing above (Fig. 4).

As we can see P. ilicifolia should be treated as a species historically old, having a very original structure. There is no doubt whatever it is the most primitive species in the Balsamiflua subgenus, yet we must be rather careful to accept the whole Populus genus as such. The disappearance of the terminal bud in the Balsamiflua subgenus and the sympodial ramification of shoots are a secondary feature which appeared when the poplar met a dry climate, just as the sympodial characteristic

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**Fig. 4.** Diagram of structure of inflorescences in Populus: a — sect. Tsavo, b — sect. Turanga, c — sect. Tacamahaca.
in willows was caused by their adaptation to the conditions of a cool climate. Of all living willows, nowadays, the oldest historically are the tropical and subtropical species, yet their characteristic is their strictly monopodial structure (Szafer 1959). Taking the monopodial feature as a primitive feature, we must thus question the primitivity of the *Balsamiflua* subgenus. We must, however, state that the direction of changes found in the structure of inflorescences in this subgenus is an important factor of the evolution of the whole *Populus* genus, an evolution in which *P. ilicifolia* is a very valuable evidence that could change the view as to the original country of the poplar; it may be that one of the centres of the formation of the *Populus* genus was just east Africa.

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Populus ilicifolia (Engler) Rouleau


Populus ilicifolia (Engler) Rouleau i jej stanowisko systematyczne

Streszczenie


Te dwie sekcje można doskonale oddzielić od pozostałych sekcji rodzaju Populus, a to na podstawie: zaniku pączka szczycowego i związanego z tym sympodialnego rozgałęzienia pędów, budowy i kształtu liści oraz powcinanego głęboko i odpadającego okwiatu. W związku z tym wyróżniono dwa podrodzaje: 1. Balsaminflora (Griff.) Browicz, do którego należy sekcja Tsavo i Turanga oraz 2. Populus z czterema sekcjami.

U P. ilicifolia kwiatostany żeńskie opatrzono są normalnie wykształconymi liśćmi (1—3), które utrzymują się również na owocostanach, same zaś owocostany nie odpadają po dojściu owoców (torebki). Kwiaty żeńskie są nieliczne (do 10), osadzone na długich szypułkach (7 mm), dzięki czemu kwiatostan ma łupną budowę. Taki typ kwiatostanu przypomina bardziej grono lub podbaldach, niż typową dla topoli kotkę. Drugą osobliwością cechą P. ilicifolia jest znamienie z wydłużonymi i rozgałęzionymi klapami. Koniec tych rozgałęzień są jeszcze raz, wtórnie klapowane. U gatunków z sekcji Turanga kwiatostany są bezlistne, lub też niekiedy opatrzone silnie zredukowanymi i wcześniej odpadającymi liśćmi; również i owocostany odpadają po dojściu. Różnice zaznaczają się także w budowie znamienia, które jest krótsze, nerkowato wycięte i nie klapowane.

Taką budowę kwiatów i kwiatostanów żeńskich P. ilicifolia należy uznać za bardziej pierwotną, a tą topólę za najstarszy filogenetycznie gatunek w podrodzaju Balsaminflora. Zmiany w budowie kwiatostanów zachodzące w rodzaju Populus znane są również w drugim rodzaju rodziny Salicaceae, Salix.