Lancewoods and five-fingers: hybridisation, conservation, and the ice-age[1]

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In our talk, we shared what we had learnt about *Pseudopanax* from our field experiences and research projects of the last several years. *Pseudopanax*, at least as we circumscribe it (Perrie & Shepherd 2009), comprises 12 species, and is endemic to New Zealand (i.e., all of the species occur only within the New Zealand Botanical Region).

Some *Pseudopanax* species are well-known, but others are much less so. Even some of the common taxa can be challenging to identify accurately. Consequently, we began our talk by discussing each of the species: how to recognise them and good places to see them. We then covered the hybridisation that occurs in *Pseudopanax*, and finished by presenting results from our research into the patterns of genetic variation that occur in *P. lessonii* (coastal five-finger, houpara) and *P. ferox* (fierce lancewood).

CATALOGUE OF *PSEUDOPANAX* SPECIES

Three groups can be recognised on the basis of morphology: the stipulate five-fingers (*P. arboreus* group), the exstipulate five-fingers (*P. lessonii* group), and the lancewoods (*P. crassifolius* group). Genetic evidence supports the distinctiveness of the stipulate five-fingers. Indeed, some place these species in a separate genus, *Neopanax* (e.g., Frodin & Govaerts 2004). We, however, see no compelling reason for doing so, based on the uncertainty that continues to surround their relationship to the other species of *Pseudopanax* and other genera (see Perrie & Shepherd 2009). Despite their very different morphology, genetic evidence for the distinctiveness of the exstipulate five-fingers and the lancewoods is lacking, and they appear to be closely related (Perrie & Shepherd 2009).

The lancewoods have simple leaves (i.e., the leaves are not compound with multiple leaflets) and, except for *P. chathamicus*, are strongly heteroblastic, having longer, narrower leaves and generally unbranched stems as juveniles.

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Both groups of five-fingers have multifoliolate leaves (i.e., compound leaves with multiple leaflets). However, they differ in that the leaves of the *P. arboreus* group are stipulate (Fig. 1). That is, the base of the petiole (leaf stalk) sheathes or clasps partially around the stem from which it arises. Such sheathing is absent in the *P. lessonii* group; hence, they are exstipulate (i.e., without stipules). (The lancewoods are also exstipulate.)

Figure 1. Left: Stipulate-leaved *Pseudopanax arboreus*, with the petioles (leaf stalks) sheathing the stem. Right: Exstipulate-leaved *P. lessonii*, with the petioles not sheathing the stem.

Only the indigenous distributions are here discussed and mapped, except where explicitly stated. The distribution maps were compiled using specimen data from the AK (Auckland War Memorial Museum), CHR (Landcare Research, Lincoln), and WELT (Museum of New Zealand Te Papa Tongarewa) herbaria. We have not verified the identity of most of these specimens.

The following features are what we presently use to identify *Pseudopanax* specimens, based on what we have read, been told, and seen in herbaria and out in the field. We welcome corrections and additions.

THE STIPULATE FIVE-FINGERS (*P. ARBOREUS* GROUP)

***P. arboreus* (Murray) Philipson (Fig. 2)** **Five-finger, whauwhaupaku**
Recognised by the leaflets having distinct stalks (i.e., there are distinct petiolules), the green colour of the stalks of the leaves and leaflets (petioles and petiolules), and the usual presence of prominent teeth on the leaflet margins.

Common in many lowland areas of forest and scrub in the North Island and parts of the northern South Island.

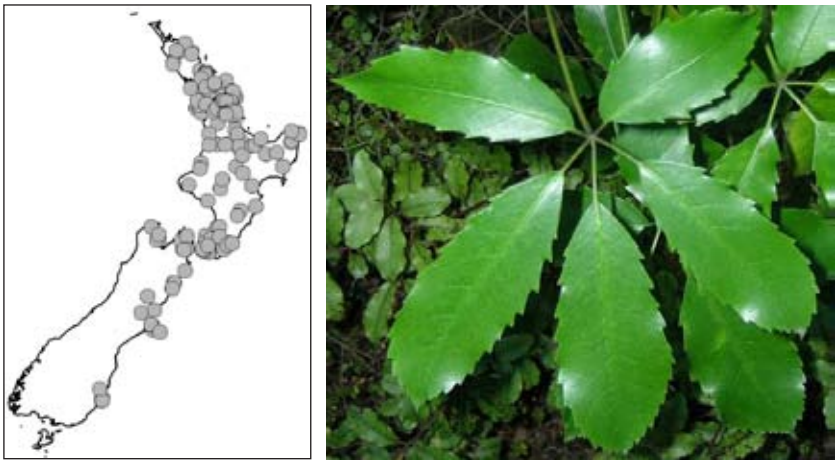

Figure 2. *Pseudopanax arboreus*.

***P. kermadecensis* (W.R.B.Oliv.) Philipson (Fig. 3) Kermadec five-finger**
Very similar and closely related to *P. arboreus*. The teeth on the leaflet margins are much reduced compared with what is typical for *P. arboreus* (see Sykes 1993 for other differentiating characters).

Confined to the Kermadec Islands, where it is the only *Pseudopanax* species.

Figure 3. *Pseudopanax kermadecensis*. Photo: Peter de Lange.

***P. laetus* (Kirk) Philipson (Fig. 4)**

Recognised by the red colour of the petioles and petiolules (stalks of the leaves and leaflets). The leaves and leaflets are generally bigger than in *P. arboreus*, and there are fewer teeth on the leaflet margins.

Easily seen in the Kauaeranga Valley near Thames and alongside the Kawhia Road (State Highway 31) near Te Rauamoa (Kawhia).

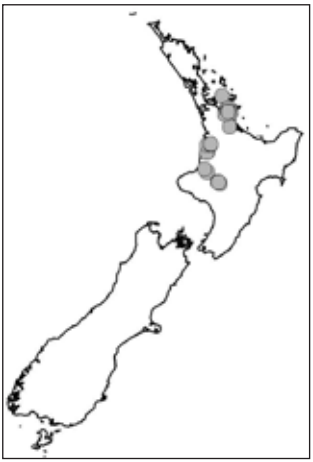

Figure 4. *Pseudopanax laetus*.

***P. colensoi* (Hook.f.) Philipson (Fig. 5)** **Mountain five-finger**

Morphologically variable. Differs from *P. arboreus* by having the petiolules (leaflet stalks) very short or absent. Wardle (1968) recognised three varieties. Although the extremes are distinctive, the morphological and geographic boundaries between them are unclear.

Var. *colensoi* (Fig. 5)

Typically five leaflets, with short petiolules.

Occurs in the North Island, and northern South Island, at least as far south as Banks Peninsula. Easily viewed at many North Island mountains (although it may be uncommon in the axial ranges) and higher parts of Banks Peninsula.

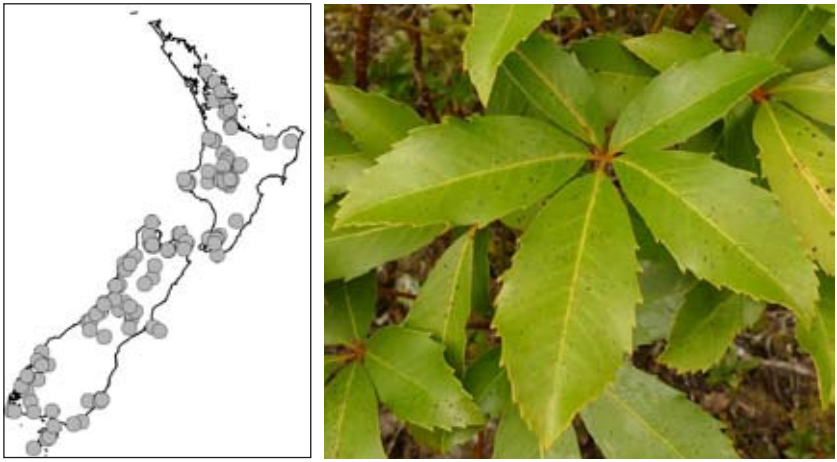

Figure 5. Left: Distribution of *Pseudopanax colensoi* (all three varieties). Right: *P. colensoi* var. *colensoi*.

Var. *ternatus* Wardle (Fig. 6)

Typically three, broad leaflets, with the lower two more or less perpendicular to the middle leaflet. No petiolules.

South Island. Prominent on the West Coast, lowland Otago, and the Catlins. Belying the common name of the species, mountain five-finger, it reaches the coast in many southern localities.

Var. *fiordensis* Wardle (Fig. 6)

Typically five leaflets, with no petiolules.

Fiordland, coastal Southland, and Stewart Island. The most accessible locality we know of is Bluff Hill.

Figure 6. Left: *Pseudopanax colensoi* var. *ternatus*. Right: *P. colensoi* var. *fiordensis*.

***P. macintyrei* (Cheeseman) Wardle (Fig. 7)**

Typically three leaflets, narrower than *P. colensoi* var. *ternatus*. The middle leaflet can have a short petiolule. (We do not know this species very well.)

Generally associated with (and possibly restricted to) calcareous sites.

Relatively common amongst scrub on Takaka Hill (e.g., Bobs and Hawkes Lookouts), and near the Buller River around Murchison. Seen at Fenian Track in the Oparara Basin during the 2009 Wellington Botanical Society summer trip (Rewi Elliot pers. comm.).

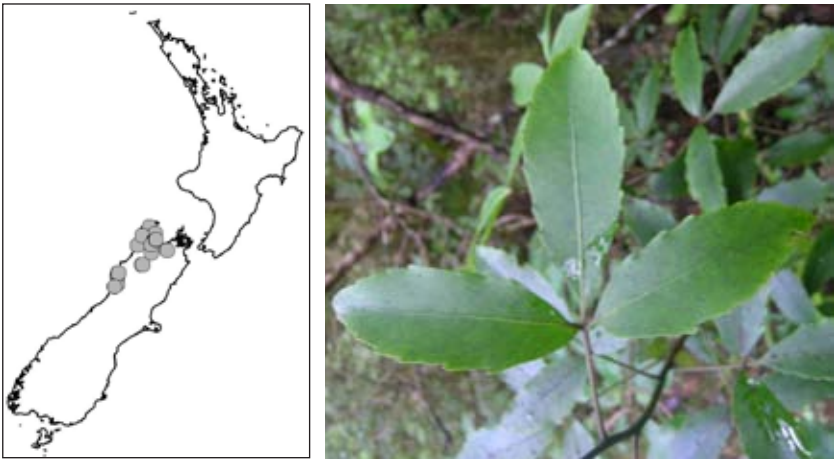

Figure 7. *Pseudopanax macintyrei*.

THE EXSTIPULATE FIVE-FINGERS (*P. LESSONII* GROUP)

***P. lessonii* (DC.) K.Koch (Fig. 8)** **Coastal five-finger, houpara**

Typically five leaflets, all broad and without petiolules. The apical three are generally larger; those at the base are smaller and project backwards. Some plants on the Aupouri Peninsula (Northland) only have three leaflets.

Common in many coastal places around the northern North Island. Does not naturally extend inland by more than a few kilometres (and usually much less). The southern boundary of the indigenous distribution is unclear. In the west it is at least Manukau Harbour (and perhaps Raglan). In the east it is at least East Cape.

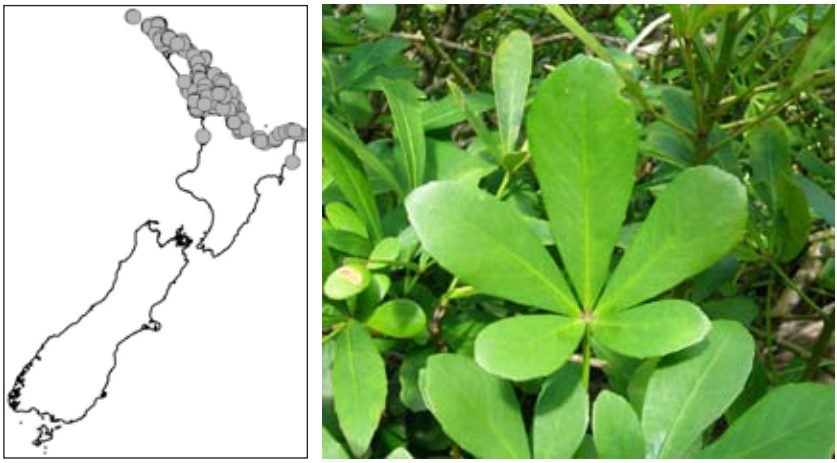

Figure 8. *Pseudopanax lessonii*.

***P. gilliesii* Kirk (Fig. 9)**

Has successive whorls of leaves with three leaflets and leaves with a single leaflet, these representing the start and finish, respectively, of each year's growth.

Easily seen on the walking track from Totara North's (Whangaroa Harbour) Campbell Road to Pekapeka Bay's Lane Cove.

Figure 9. *Pseudopanax gilliesii*.

***P. discolor* (Kirk) Harms (Fig. 10)**

Easily separated from the other *Pseudopanax* species by its bronze to yellow-green leaves. In our (limited, southern Coromandel) experience of wild plants, the bronze colouration is rather insipid. At least some of the strongly bronzed plants in cultivation appear to be *P. discolor* × *P. lessonii*.

Accessible at several southern Coromandel sites, often associated with kauri; e.g., Waiomu Kauri Grove, Kauaeranga Valley, alongside the Kopu-Hikuai Road, as well as walking tracks (e.g., Devcich Kauri, Piraunui Track) from that road.

Figure 10. *Pseudopanax discolor*.

THE LANCEWOODS (*P. CRASSIFOLIUS* GROUP)

***P. crassifolius* (Sol. ex A.Cunn.) K.Koch (Fig. 11) Lancewood, horoeka**
Heteroblastic: the juvenile has long, narrow, brown to dark-brown, and deflexed (pointing downwards) leaves, and the stem is generally unbranched; the adult has shorter, broader, green leaves, and is much branched. The juvenile leaves are less toothed than in *P. ferox*, and the teeth project laterally (although the teeth can be recurved at their apex). The teeth on juvenile leaves can be marked with orange, green, or white splotches, or not at all. The leaves of both juveniles and adults are never multifoliolate; that is, they never have two or more leaflets. (The leaves are almost always simple. However, some plants from situations where they are very unlikely to be hybrids exhibit a joint, or articulation, between the petiole and lamina; these might be regarded as unifoliolate. Consequently, presence of a petiole joint does not prove that an individual is not *P. crassifolius*, but it is very atypical.)

Abundant throughout mainland New Zealand.

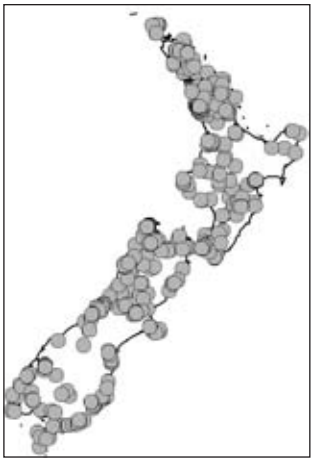

Figure 11. *Pseudopanax crassifolius*.

***P. chathamicus* Kirk (Fig. 12)** **Chatham lancewood, hoho**

Similar and closely related to *P. crassifolius*, but a juvenile phase is much less evident (i.e., it is barely heteroblastic).

Confined to the Chatham Islands, where it is the only *Pseudopanax* species.

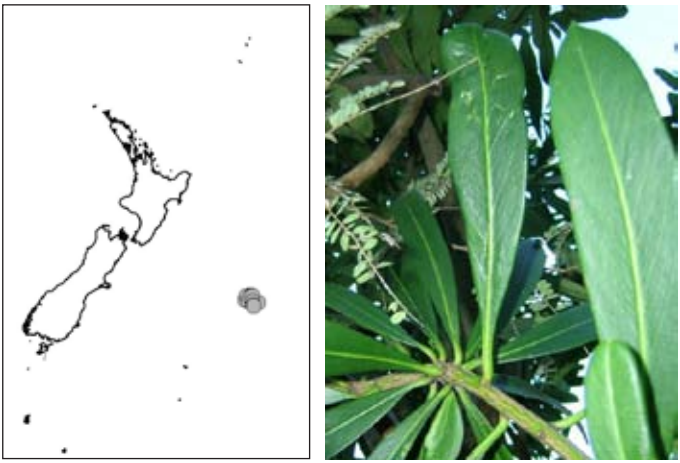

Figure 12. *Pseudopanax chathamicus*.

***P. ferox* Kirk (Fig. 13)** **Fierce lancewood**

Similar to *P. crassifolius*, but the teeth of the juvenile leaves are bigger, usually have prominent white splotches, and 'bubble' upwards, with this three-dimensionality of the teeth being especially pronounced at the leaf apex. The adult leaves of *P. ferox* are more rectangular (shorter, narrower, with parallel sides, and a blunt apex), smaller, and greyer than those of *P. crassifolius*.

Widespread, but populations are often small and/or inaccessible. Perhaps the most publically accessible place to see abundant *P. ferox* is from the walking track (principally the southern end) through Forest Hill Scenic Reserve near Invercargill. The Taieri River track and Waipori Picnic area near Dunedin are alternatives.

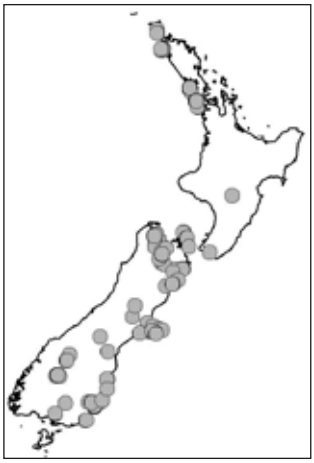

Figure 13. *Pseudopanax ferox*.

***P. linearis* (Hook.f.) K.Koch (Fig. 14)** **Mountain lancewood**

Similar to *P. crassifolius*, but the leaves are smaller at all stages, the juvenile leaves are not strongly deflexed, and it is much shorter (both in terms of juvenile to adult transition, and total height, which is only c.2–3m).

Easily accessible from the Arthur's Pass area, including the track to the Devils Punchbowl Falls. Other places include the Heaphy Track, Denniston Plateau, and Key Summit (Fiordland).

Figure 14. *Pseudopanax linearis*.

HYBRIDISATION IN *PSEUDOPANAX*

Hybridisation adds further to the morphological diversity of *Pseudopanax*; indeed, it was this beguiling morphological complexity that initially attracted us to the genus (Fig. 15). We believe that most of the hybridisation in *Pseudopanax* occurs between *P. crassifolius* and *P. lessonii*. These hybrids appear to be fertile and viable. They seem to breed with one another, or backcross to individuals of either of the parental species. Our unpublished genetic analyses indicate that there is a genetic continuum from 'pure' *P. crassifolius*, through hybrids that have mostly *P. crassifolius* DNA, approximate 50:50 mixtures, mostly *P. lessonii* DNA, to 'pure' *P. lessonii*. Interestingly, most hybrids appear to be 'later-generation' (i.e., not first generation hybrids), and, even though hybrids are frequently numerically abundant, the gene-pools of the two parental species are still readily distinguishable (see Perrie & Shepherd 2009).

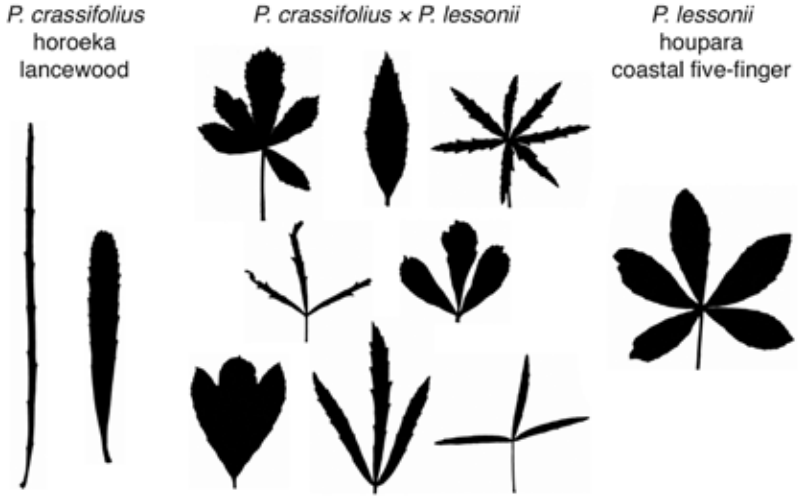

Figure 15. Hybridisation between *Pseudopanax crassifolius* and *P. lessonii*.

Pseudopanax crassifolius × *P. lessonii* hybrids and *P. lessonii* are both popular in cultivation. They self-propagate in many places (including Wellington) beyond their indigenous distributions. In such instances, these taxa are regarded by at least some (including ourselves) as weeds; indeed, they can be quite invasive. It is unknown whether the weedy hybrids are the offspring of cultivated hybrids or result from *de novo* hybridisation between cultivated and/or weedy *P. lessonii* and indigenous and/or cultivated *P. crassifolius*. There is, nevertheless, at least some potential for non-local genes from introduced, non-local *P. lessonii* or hybrids to 'genetically pollute' indigenous populations of *P. crassifolius*.

It is relatively straightforward to identify most *Pseudopanax crassifolius* × *P. lessonii* hybrids, at least with practice. Both of the parental species are relatively morphologically uniform. *Pseudopanax crassifolius* never has leaves with two or more leaflets. If an individual has leaves that look like those of *P. crassifolius* but even only a single leaf has two or more leaflets, then it is actually a hybrid. If an individual has single-leafleted leaves, but they have a prominent joint between the petiole and lamina, then they are likely, but not definitely, a hybrid (see under *P. crassifolius* above); this suspicion is heightened if the petiole is more than a couple of centimetres long. *Pseudopanax lessonii* usually has five leaflets, which are broad (the apical three often close to touching) and with the basal two directed backwards. All of the remainder – the morphological 'intermediates' (some are more just odd than intermediate) – are hybrids.

It is easiest to identify *Pseudopanax crassifolius* × *P. lessonii* hybrids as juveniles. This is because hybrids usually become more like the parental species as they mature (they usually become more like *P. crassifolius*, but we know of one population where the transition was to a very close resemblance of *P. lessonii*). For this reason, when identifying adults look for reversion shoots (i.e., where adults produce juvenile leaves, often in response to damage); the juvenile leaves on a reversion shoot may clearly mark an individual as a hybrid even when its adult leaves closely resemble one of the parental species.

Some other hybrid combinations do, or probably do, occur. On the basis of morphology, we believe that *P. discolor* × *P. lessonii* (commonly cultivated), *P. ferox* × *P. lessonii* (very rare), and *P. crassifolius* × *P. ferox* (very rare) exist. We intend using genetic analyses to test the hypotheses that these combinations occur. Additionally, it would not be surprising if *P. gilliesii* × *P. lessonii*, *P. arboreus* × *P. colensoi*, and *P. colensoi* × *P. macintyrei* occurred.

Although we have seen it suggested many times, we ourselves have not seen any evidence for *P. arboreus* × *P. crassifolius*. After all, *P. arboreus* and *P. crassifolius* frequently co-occur (e.g., Tararua and Ruahine Ranges) but do not produce morphological intermediates. We have found that 'odd' looking plants (i.e., hybrids) are only present where *P. crassifolius* and *P. lessonii* meet, be this in the wild or gardens. Further, if *P. arboreus* was a parent, we would expect the hybrid to have petiolules (leaflet stalks), but we know of no such specimens. We suspect that claims for *P. arboreus* × *P. crassifolius* are based on misidentifications of *P. crassifolius* × *P. lessonii*. This difference in propensity for hybridisation between these three widespread and common species is probably because *P. crassifolius* and *P. lessonii* are much more closely related to one another than either are to *P. arboreus* (Perrie & Shepherd 2009).

GENETIC VARIATION IN *PSEUDOPANAX LESSONII* AND *P. FEROX*

Aside from carrying out genetic analyses of the hybridisation between *Pseudopanax crassifolius* and *P. lessonii*, we have also been studying the patterns of genetic variation that occur within *P. lessonii* (coastal five-finger, houpara) and *P. ferox* (fierce lancewood). We are interested in *P. lessonii* because it has been suggested that plants from Northland's Surville Cliffs are a distinct taxon. These plants generally have leaves with three (rather than five) leaflets, and are low-growing, producing several main stems from ground level rather than a principal trunk. For *P. ferox*, it is its discontinuous distribution that intrigues us. We are testing whether there are genetic subgroups within *P. ferox*, how genetically isolated the different populations are, and where populations survived during the colder glacial periods of the ice-age.

Although we presented preliminary results on these research projects during our talk, we have yet to publish the majority of them in the peer-reviewed scientific literature. Hopefully we will be able to do so within the next few years, at which point we will be able to make the results more widely available.

ACKNOWLEDGEMENTS

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