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A new heterocarpidic fruit type for the Myrtaceae, with dehiscent and indehiscent loculi, in two genera from Western Australia

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Abstract

Rye, B.L. and Trudgen, M.E. A new heterocarpidic fruit type for the Myrtaceae, with dehiscent and indehiscent loculi, in two genera from Western Australia. *Nuytsia* 15(3): 485–493 (2005). A form of heterocarpidy with dehiscent and indehiscent loculi present in the same fruit is described from species in two genera of Myrtaceae occurring in the south-west of Western Australia. This extreme development of heterocarpidy results in a very unusual fruit type, one that has not previously been described for the Myrtaceae. It is also apparently rare in the angiosperms, although smaller differences between carpels (mostly in their size and the number of seeds) are not uncommon. In *Astus* Trudgen & Rye and the *Baeckea robusta* F. Muell. complex, two types of ovary loculi develop, with one type dehiscent by a suture on the floral disc and the other type lower in the ovary and indehiscent. The occurrence of this heterocarpidic fruit type in two fairly different genera is considered to be a convergent development rather than indicating a particularly close relationship. The heterocarpidic fruit in these groups is described and illustrated, and its adaptive and taxonomic significance discussed.

Introduction

A very unusual fruit type, which has both dehiscent and indehiscent carpels, is reported from two genera of Myrtaceae occurring in the south-west of Western Australia. This fruit type is an extreme example of heterocarpidy – the differential development of loculi within the same ovary. It occurs in the new genus *Astus* Trudgen & Rye (Trudgen & Rye 2005) and also in the *Baeckea robusta* F. Muell. species complex, and its occurrence in these genera is the first record of such a fruit for the Myrtaceae.

The heterocarpidic fruit described from *Astus* and *Baeckea robusta* and its allies is a remarkable phenomenon that demonstrates a significant plasticity in the fruit of at least some Myrtaceae. The development and survival of this fruit type in two groups raises significant questions with respect to the comparative advantages of fully dehiscent, fully indehiscent and heterocarpidic fruits in Australian Myrtaceae. The heterocarpidic fruit type probably has advantages for seed dispersal and survival and also has implications for the understanding of the importance of fruit types in classification within the Myrtaceae.

In Niedenzu's (1893) classification, the family Myrtaceae is divided into the fleshy-fruited subfamily Myrtoideae and the dry-fruited subfamily Leptospermoideae, with the latter subfamily subdivided into the tribe Leptospermeae with a capsular fruit and the tribe Chamelaucieae with a nut. While the fleshy-

fruited taxa are pantropical, the dry-fruited ones (with the exception of the subtribe *Metrosiderinae*) are primarily distributed in Australasia and predominantly occur in temperate and arid climates. In contrast to this correlation between climatic zones and the distributions of the subfamilies, the tribes *Chamelaucieae* and *Leptospermeae* have similar distributions, even having about the same proportion of species occurring in the arid zone (Rye & James 1992).

Separation of the tribe *Chamelaucieae* purely on the basis of its having a nut has long been considered problematical. In fact Bentham (1867: 5) noted that some members of one of the subtribes of the *Chamelaucieae* “pass so gradually into the *Leptospermeae*, as only to be distinguishable from *Baeckea* by the examination of the ovary”. Briggs & Johnson (1984) combined the *Chamelaucieae* with the subtribe *Baeckeiniae* of the *Leptospermeae* to form an informal *Chamelaucium* alliance, which they considered to include a number of separate lineages in which capsular groups have given rise to taxa with nuts. For example, the unilocular genus *Malleostemon* J.W. Green shows a much closer similarity in its morphology, particularly in its anther type, to some of the multilocular genera, such as *Babingtonia* Lindl. and *Scholtzia* Schauer, than it does to other unilocular genera of the alliance. Molecular analyses of DNA samples (Lam *et al.* 2002) provide independent evidence that *Malleostemon* is closely related to *Babingtonia* and *Scholtzia*. A broader (compared to Bentham) circumscription of the tribe *Chamelaucieae* has recently been formally published (Wilson *et al.* 2005), with limits the same as that of the *Chamelaucium* alliance of Briggs & Johnson.

As outlined above, the major divisions of the *Myrtaceae* have traditionally been based on fruit type. Consequently, the heterocarpidic fruit described here is of particular interest as it is another example of the ability of groups in the *Myrtaceae* to change their fruit loculi from dehiscent to indehiscent, adding to our understanding of the evolution of fruits in this family. It is possible that the change to an indehiscent fruit from a fully dehiscent capsule in some other groups of the *Myrtaceae* has involved an intermediate stage where there was a heterocarpidic fruit similar to that described here.

Fruit types found in the *Leptospermoideae*

The most common fruit type found in the *Leptospermoideae** is a crustaceous to woody capsule with loculicidal dehiscence of its 2–5, or more, loculi. The other common type is a unilocular indehiscent fruit that is usually one-seeded and which is appropriately described as a nut (Roth 1977: 244; Rye & James 1992) even when more than one-seeded. However, in a small proportion of the species and genera of *Leptospermoideae* the fruit is intermediate between these two fruit types, in that it is multilocular and indehiscent. This type of fruit is found, for example, in all members of *Enekbatus* Trudgen & Rye ms. and *Scholtzia*.

Another fruit type found in the *Leptospermoideae* that is intermediate between the capsule and the nut, is the heterocarpidic fruit described in this paper from species in two genera. This fruit type is much rarer in the *Myrtaceae* and is currently known from only eight species. It is especially interesting since there seem to be very few records of such fruits in the literature, although lesser differentiation between loculi (e.g. reduction in ovule number) is relatively common (Roth 1977). The only published indication of this fruit type in south-western Australian *Myrtaceae* was the observation made by Rye (1987) that one loculus was situated at a somewhat lower level than the other two loculi in the ovary of *Baeckea robusta* F. Muell.

*No longer recognised in the recent classification of Wilson *et al.* (2005), subfamily *Leptospermoideae* is not a natural group but is used here for convenience to refer to the dry-fruited *Myrtaceae* as a whole.

Terminology

Roth (1977) and Spjut (1994) have both carried out extensive reviews of fruit types, with Roth emphasising the anatomy of angiosperm fruits and Spjut attempting to provide a systematic means for recognising fruit types and a strict terminology for them. Roth (pp. 591, 598) very briefly discusses heterocarpidy, which she describes as a “different development of the carpels composing the coenocarpous gynoecium” that is usually expressed in carpel reduction or reduction in the number of seeds, frequently with one or several underdeveloped carpels either being sterile or having a reduced number of seeds. Roth attributes the term to Stopp (1962), whose work included a description of this phenomenon in the South African genus *Rogeria* (Pedaliaceae). In *Rogeria bigibbosa* and *R. adenophylla* “the abaxially situated carpel is favoured in its development and contains more seeds than the reduced one, the latter being indehiscent, while the favoured carpel dehisces” (Roth 1977: 598). This is the only example Roth gives that resembles the fruit type described here for the Myrtaceae in having a combination of dehiscent and indehiscent fertile loculi.

In Spjut’s (1994) extensive classification of fruits, a very large number of specific terms are described in detail, many of them based on the mode of dehiscence. However, his key has no provision for fruit types that have both dehiscent and indehiscent loculi, and he does not mention heterocarpidy, nor refer to the genus *Rogeria*. In fact, he does not have specific terms for any of the dry fruit types that have evolved from the Myrtaceous capsule, i.e. the multilocular indehiscent fruit, the unilocular indehiscent fruit referred to here as a nut, and the partly indehiscent capsule.

We suggest that the fruit type of *Astus* species and of members of the *Baeckea robusta* complex is best described as an extreme case of heterocarpidy that results in a fruit with dual functions. It functions partly as a capsule and partly as an indehiscent fruit. As far as we can ascertain, there is no accepted name for such a fruit, although it can be described as a *heterocarpidic capsule with one or sometimes two indehiscent loculi*, or more simply as a *partly indehiscent capsule*. For convenience, we will use the latter phrase in this paper.

We do not propose a new term here for the partly indehiscent capsule. It would be better for this to be done in a critical review of terminology for all fruit types in the Myrtaceae. Such a study should pay particular attention to the large variation in the capsule, and ideally would involve sufficient anatomical work to define the varying roles of different tissues in each of the fruit types.

Morphology of the partly indehiscent capsule

Roth (1977: 591) has observed that heterocarpidy “is widespread in the plant kingdom, especially in flowers with dorsiventral symmetry”. An interesting aspect of the development of the partly indehiscent capsule in the Myrtaceae, is that this extreme form of heterocarpidy has evolved in a family that predominantly has radially symmetric flowers. While the corolla, calyx and stamens are radially symmetric in the heterocarpidic species, the ovary can be either bilaterally symmetric (when there are two indehiscent loculi and two dehiscent loculi) or asymmetric (when there is one indehiscent and two dehiscent loculi). In either case, the axis of symmetry of the ovary does not seem to be strictly aligned either dorsiventrally or at right angles to the stem.

The partly indehiscent capsules (illustrated in Figure 1 and compared in Table 1) found in *Astus* and the *Baeckea robusta* complex are very similar in morphology, although those of the latter group are larger

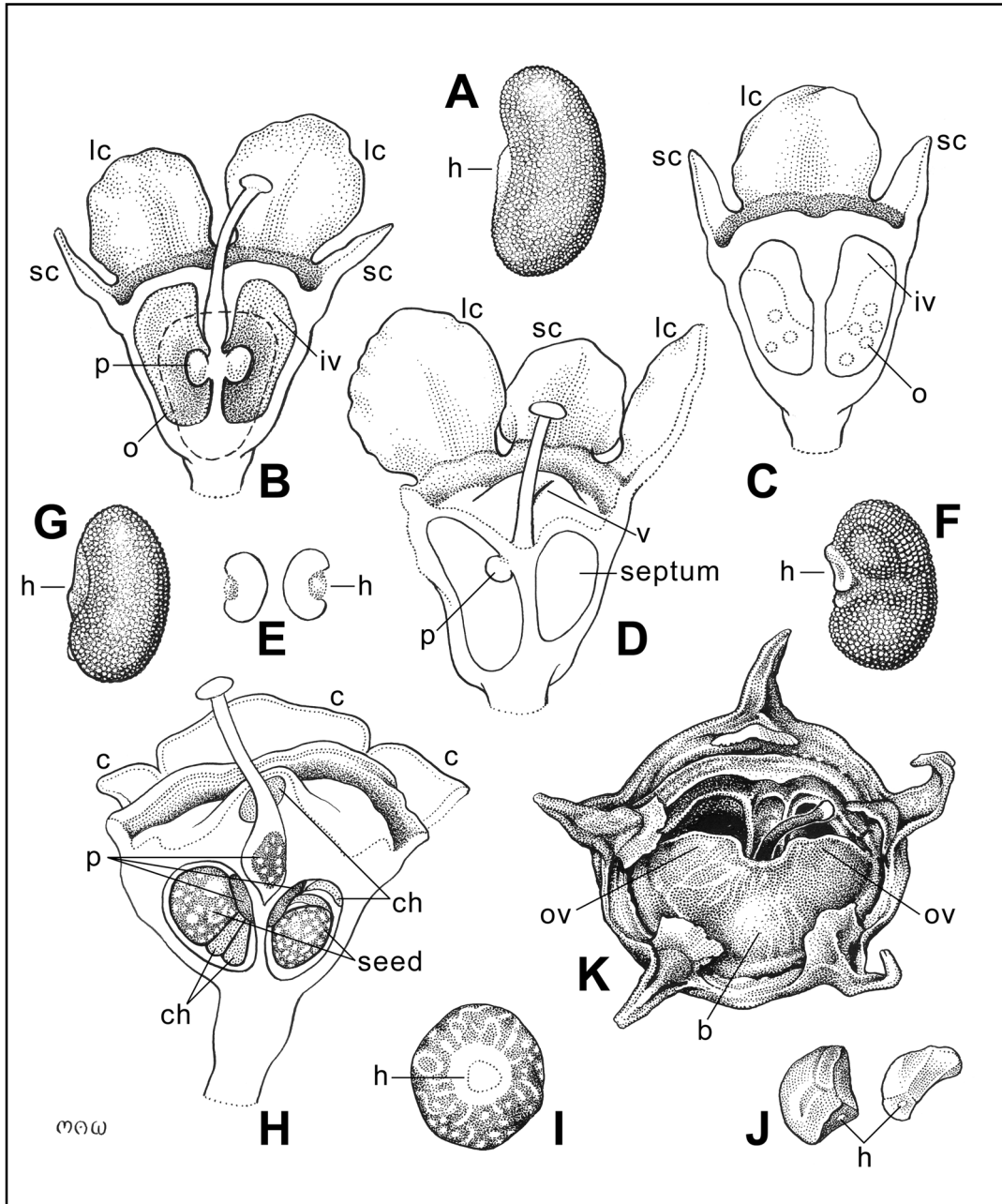


Figure 1. A – *Astus duomilius* seed; B–E. *Astus subroseus*. B,C – two halves of a fruit longitudinally divided along its two valves, the seeds and chaff removed, with the dotted area in B showing the location of the hidden indehiscent locusus; D – fruit divided longitudinally at right angles to the valves, the indehiscent locusus on the left and the septum dividing the two dehiscent loculi on the right, E – chaff; F – *Astus tetragonus* seed; G – *Astus wittweri* seed; H–J. *Baeckea* sp. Mingenew. H – longitudinal section of fruit at right angles to the valves, with an additional section through inner end of the valve of a dehiscent locusus, I – seed, J – chaff; K – *Baeckea blackallii* dehiscent fruit from top view, with arrow showing the location of the hidden indehiscent locusus. All figures magnified at between $\times 15$ and $\times 20$. Drawn from G.J. Keighery & N. Gibson 5005 (A), M.E. Trudgen 22079 & B.L. Rye (B–E), R. Meissner LB164 (F), E Wittwer W1898 (G), G.G. Smith Dec. 1957 (H–J) and A.C. Burns 125 (K).

Key: b – bulge of indehiscent locusus; ch – chaff; h – hilum; p – placenta; o – oil gland; c – calyx lobe, lc – large calyx lobe, sc – small calyx lobe; v – valve, iv – inside of valve, ov – opened valve.

and have more numerous seeds and chaff. In both these plant groups, there are two upper loculi, which show as sutures on the floral disc in the flower. As the fruit matures these loculi become more prominent, with the sutures on ridges, and eventually dehisce. There are also either one or two indehiscent loculi situated somewhat lower in the ovary. The two types of loculi are not superposed, and in fact have a considerable vertical overlap. Transverse sections across the middle of the ovary cut through the lower part of the dehiscent loculi, but through the upper part of the indehiscent loculus or loculi. The dehiscent loculi have a prominent valve that is raised above the level of the remainder of the disc of the fruit, and are broadest along the width of their valve. In contrast, the indehiscent loculi are fully immersed, as they are not or are scarcely raised on the disc, lack a suture, and differ in shape to fit the available space within the fruit. For example in *Astus subroseus* Trudgen & Rye, the single indehiscent loculus has a broad flat summit when viewed from the centre of the fruit (Figure 1B) but is compressed dorsiventrally (with respect to the floral axis) with the base broadest and tapering to the summit when sectioned longitudinally (Figure 1D).

Where there is only one indehiscent loculus, as in *Astus* and also commonly in the *Baeckea robusta* complex, the fruit develops a somewhat lop-sided appearance, especially from the top. In this situation, the two dehiscent loculi have their sutures aligned on a ridge across the disc and the indehiscent loculus sometimes bulges slightly on one side of this ridge (Figure 1K). The indehiscent loculus does not have a suture and has fewer ovules than the dehiscent loculi. However, in one member of the *B. robusta* complex, *Baeckea* sp. Mingenew (*M.E. Trudgen* 12029), there are often two indehiscent loculi, as illustrated in Figure 1H, resulting in a bilaterally symmetric fruit. Three placentas are visible in that figure, two of them for the indehiscent loculi being in side view and positioned slightly lower than the other placenta, which is for one of the dehiscent loculi and is visible from the front. A fourth placenta, for the other dehiscent loculus, is hidden from view. The placenta that is visible from the front view shows the attachment points for eight seeds and chaff.

Seeds developed in the partly indehiscent capsule

Within the Chamelaucieae, many, but not all, of the taxa that have indehiscent fruits have seeds with a very soft testa, while those genera with dehiscent fruits invariably have seeds with a crustaceous testa. Given this, it might be expected that the seeds developing in the indehiscent and dehiscent loculi in *Astus* and the *Baeckea robusta* complex would differ in morphology; however this is not the case.

Many indehiscent-fruited taxa in the Chamelaucieae have only one seed develop even though most of them have more than one ovule in the loculus. Reduced seed number is also found in the indehiscent loculi of the fruit in the two species groups discussed in this paper (see Table 1). In both groups there is usually only one seed in an indehiscent loculus, while in dehiscent loculi the number of seeds produced is more variable, ranging up to four.

Systematic and geographic occurrence of the partly indehiscent capsule

At least eight species of the Myrtaceae have a partly indehiscent capsule. Four of these species belong to the new genus *Astus*, which is described in an accompanying paper (Trudgen & Rye 2005). *Astus* is distributed along the south coast of Western Australia and extends inland to the central wheatbelt and goldfields. The members of the other species group, the *Baeckea robusta* complex, are distributed along the west coast of Western Australia between Kalbarri and Perth. Their generic

placement has yet to be fully determined, but the complex certainly does not belong to *Baeckea s. str.*, a well-defined genus occurring in eastern Australia and extending north to southern China. The *Baeckea robusta* complex is closer to *Babingtonia* Lindl. and *Scholtzia* Schauer than to *Baeckea s. str.*

Table 1. Comparison of the fruits and seeds of *Astus* and the *Baeckea robusta* complex.

Character	<i>Astus</i>	<i>Baeckea robusta</i> complex
Fruit		
length (mm)	1.7–2.5	2.5–3
width (mm)	1.4–2.2	2.5–3.5
Dehiscent loculi		
position	high	high
number per ovary	2	2
ovule number	2–7	6–14
usual seed number	0–3	1–4
Indehiscent loculi		
position	low	low
number per ovary	1	1 or 2
ovule number	1–4	3–8
usual seed number	1	1
Seed		
shape	broadly reniform	somewhat faceted
length (mm)	1–1.6	1.2–1.4
surface	shallowly colliculate	smooth
Chaff		
shape	broadly reniform	strongly faceted
degree of compression	marked	slight to moderate
texture	soft	hard
colour	often 2-toned, partly translucent	uniformly brown, opaque

Notes: The width of the fruit does not include the width of the limb (i.e. the free part of the hypanthium). The sample size for seed set in *Astus* species was small owing to the small number of fruiting collections available. The position of the loculus is described as *high* when its top has a raised suture from the centre of the flower and the bottom is above the lowest part of the ovary. It is described as *low* when its top only partly touches the disc (and does not have a suture) and the bottom is at the lowest part of the ovary.

Rye (1987) noted that northern populations of *Baeckea robusta* s. lat. had more numerous stamens than the remainder, and it is now clear that these are part of a complex of species. True *Baeckea robusta* (illustrated in Blackall & Grieve 1980: 82) is known from Kalbarri National Park and adjacent pastoral stations south to near Binnu, and has prominently horned calyx lobes, 15–18 stamens mostly concentrated close to the petal claws, and rather broad filaments. The southern taxon, known informally as *Baeckea* sp. Mingenew (*M.E. Trudgen* 12029), is illustrated in Rye (1987: Figure 142). This taxon is very variable and may need to be divided into several species or infra-specific taxa. It extends from near Northampton to Perth and has ridged, but not horned, calyx lobes, 9–14 stamens with 1–4 opposite each calyx lobe, and narrower filaments.

A third member of the *Baeckea robusta* complex is currently known as *B. blackallii* Trudgen ms. This species occurs on sandplain, extending from Tamala Station south-east to Indarra Springs Nature Reserve. Trudgen noted, on a determinavit dated 14 Aug. 1990, that a fruit on the specimen *A.C. Burns* 125 had two dehiscent loculi and one indehiscent loculus. All fruits of this species examined in the current study were of this kind. *Baeckea blackallii* is readily distinguished from *B. robusta* and *B. sp.* Mingenew by its non-rugose hypanthium, which is dotted with obvious oil glands and irregularly longitudinally ridged. Its horned calyx lobes also have a distinct petaline rim, and it has more numerous stamens, with 19–23 per flower. It has up to 14 ovules in each of the dehiscent loculi of its ovary, compared with a maximum of 11 ovules in *B. robusta* and *B. sp.* Mingenew, although it has just as few as or fewer ovules than the other two taxa in its indehiscent loculus.

No other species are known to exclusively produce the partly indehiscent capsule and no other species appear to belong to the *Baeckea robusta* complex; certainly none has been found to have the same seed type with its smooth mottled testa. However, there is one other species that appears to belong in the same genus that produces partly indehiscent capsules in greater frequency than fully dehiscent fruits. This species, *Baeckea* sp. Billeranga Hills (*M.E. Trudgen* 2706), produces both types of fruits on the same branches.

Convergent development of the partly indehiscent capsule in *Astus* and *Baeckea*

Astus and the *Baeckea robusta* complex have evidently developed the same partly indehiscent type of fruit quite independently, as they are not closely related. The degree of separation of these two species groups is indicated by significant differences in their stamens and seeds. *Astus* belongs to the reniform-seeded group with dorsifixed, versatile anthers and a free connective gland (Trudgen & Rye 2005); such stamens are considered the more primitive type in the family. In the *Baeckea robusta* complex the seeds are not reniform and are somewhat faceted, and the highly modified stamens place the complex in what Niedenzu (1893) treated as *Baeckea* subg. *Hystero-baeckea* Nied. The stamens in this part of the Chamelaucieae have the anthers broadly dorsifixed and not versatile and the connective gland fused to the filament and/or anther cells.

The differences between *Astus* and the *Baeckea robusta* complex in their seed types are listed in Table 1 and illustrated in Figure 1. They are perhaps most obvious in the chaff pieces, which are compressed-reniform in *Astus* and strongly faceted in the *Baeckea robusta* complex. The seeds of both groups are more rounded than the chaff pieces so that the basic type, whether reniform or faceted, is not as readily appreciated as in some other species. The seeds of *Astus* are uniformly coloured, minutely colliculate and not very shiny, whereas those of the *Baeckea robusta* complex are mottled, smooth and very shiny. *Baeckea* sp. Billeranga Hills has seeds similar to those of *Astus* in being uniformly coloured and minutely colliculate, but differing in their distinctly faceted shape.

Adaptive significance of the partly indehiscent capsule

The partly indehiscent capsule of *Astus* and the *Baeckea robusta* species complex combines the advantages of the capsule of genera such as *Rinzia* Schauer and *Hypocalymma* (Endl.) Endl., and those of the indehiscent fruit of genera such as *Micromyrtus* Benth. and *Scholtzia*. Having two diaspore types produced from one heterocarpic fruit presumably:

- increases the protection of the seed retained in the indehiscent loculus from predation of various types,
- increases the variation in response to germination events, and
- increases the variation in dispersal mechanisms.

It seems likely that seeds distributed within the fruit would be less vulnerable to predation than the seeds shed directly into the environment, through a combination of disguise, physical protection and chemical protection. Being enclosed in a non-edible fruit would disguise the seed, making it less obvious as a food source. If the capsule were recognised as being a food source, the inedible casing would still have to be penetrated before the seed could be consumed. This could prevent some organisms, such as small ants, from utilising the seed. Finally, the essential oils in the oil glands of the hypanthium and disc might have a significant effect in inhibiting insect predation and reducing attack by bacteria and fungi.

Enclosure of the seeds probably results in a significant delay in the onset of germination and more variation in when it occurs, so that germination occurs over a longer time period. This effect has been documented in a number of genera of Myrtaceae by Rye & James (1992). Enclosed seeds are apparently not able to imbibe water until the fruit casing has been worn down or broached by exposure to prolonged or more intense rainfall, or by other environmental factors. For example, germination rates in *Thryptomene calycina* (Lindl.) Stapf were found (Beardsell *et al.* 1993) to be very high for seeds enclosed in indehiscent fruits that had been naturally weathered for two years. In contrast, seed germination failed completely for freshly harvested fruits. This phenomenon greatly reduces the risk of simultaneous failure of all or a large proportion of the seeds in one germination event.

The two types of diaspores produced by the partly indehiscent capsule have marked differences in their size, shape and density that would be likely to affect their dispersal. The larger size, more irregular shape and lower density of the diaspore with the enclosed seed probably increase its chances of being transported away from the parent plant. There is also, possibly, an interaction between the delayed germination of enclosed seeds and dispersal. Seeds dispersed within in the fruit would have a much longer time to be moved by a sequence of events, such as heavy rainfall or strong winds, before they germinate.

Collectively, these factors amount to a potentially very significant increase in the chance of seed survival and dispersal through having two kinds of diaspores, and could be expected to lead to increased recruitment over a wider area. The partly indehiscent capsule, seemingly an oddity due to its rarity, therefore appears to confer significant adaptive advantages over a fully dehiscent capsule. These advantages closely parallel the advantages of heterocarpy (having two or more fruit types develop from separate flowers on the same plant).

These apparent advantages do raise the question as to why the partly indehiscent capsule is much less common than either the fully dehiscent or the fully indehiscent multilocular fruit types in the Myrtaceae. The most plausible explanation for its not having arisen frequently is the complexity of this

fruit type, which requires substantial changes from the fully dehiscent capsule, including the loculi not being so integrated in the fruit. Such changes may be much less likely than having all the loculi become indehiscent as in *Scholtzia* and *Enekbatus*. If the main advantage is the better protection of seeds, the latter fruit type may simply be an easier way to get most of the advantage to be gained.

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