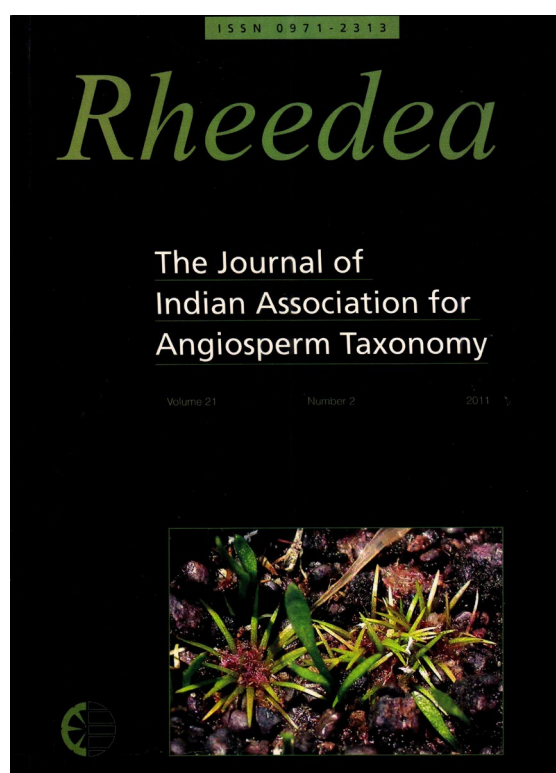




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Hydatellaceae: A historical review of systematics and ecology

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Abstract

This paper presents an overview of the history of taxonomic and evolutionary studies of species currently assigned to the family Hydatellaceae, including a comparison of the ecology of species from India, Australia and New Zealand. We review previous ideas on the relationships of Hydatellaceae with the monocot family Centrolepidaceae and their current placement within the early-divergent angiosperm order Nymphaeales. An earlier hypothesis is discussed regarding the putative close relationships between Hydatellaceae and the Lower Cretaceous fossil genus *Archaeofructus*. We hope that this review will stimulate field botanists in various countries for new records of these highly unusual and interesting plants.

Keywords: *Archaeofructus*, Australia, Basal Angiosperms, Ecology, Evolution, *Hydatella*, India, Morphology, New Zealand, Nymphaeales, Phylogeny, *Trithuria*

Introduction

During the past two decades, a molecular revolution in phylogenetics has radically changed earlier, morphology-based views on the classification of the flowering plants. The extent of the molecular changes is not identical at different hierarchical levels. Many traditionally accepted angiosperm families, such as Leguminosae (Fabaceae), Gramineae (Poaceae), Orchidaceae, Compositae (Asteraceae) have survived with almost the same circumscription as initially proposed on the basis of morphology. In contrast, many views on infra- and supra-familial relationships have changed dramatically. Some currently accepted angiosperm orders (APG III, 2009) represent entirely novel assemblages of families, including the eudicot order Malphigiales and the monocot order Pandanales. The highest level relationships in angiosperms also represent an area of stability. The classical concept of subclass Magnoliidae (e.g., Takhtajan, 1987) as a paraphyletic group that gave rise to both monocots and higher dicots is strongly supported by molecular phylogenetic data. It is a secondary issue that magnoliids (*sensu* APG III, 2009) are now commonly treated in a narrower sense than Magnoliidae of Takhtajan (1987), following adoption of the cladistic concept of monophyly and clarification of exact

phylogenetic relationships among basal angiosperm families.

In general, the view of monocots as a well-defined monophyletic unit derived from within the paraphyletic group of basal dicots (Magnoliidae *sensu* Takhtajan, 1987) is one of the morphology-based theories that are most readily supported by molecular data. Extensive molecular phylogenetic studies have allowed only one refinement to the classical circumscription of monocots, with a total complement of *ca* 65000 species and 3000 genera (Takhtajan, 2009). Specifically, the family Hydatellaceae (twelve species in a single genus: Sokoloff *et al.*, 2008b) has been transferred from monocots to the early-divergent angiosperms (Saarela *et al.*, 2007).

Since Hydatellaceae represent the single exception in an otherwise relatively harmonious congruence between the traditional and molecular circumscription of the monocot clade, the structural diversity of this remarkable family is of considerable interest. Hydatellaceae are small and inconspicuous plants. They received little attention from botanists prior to their taxonomic reassignment to the basal angiosperms. Many new data on Hydatellaceae have been accumulated during the past five years.

In the present paper, we review our current knowledge on this species-poor but interesting family.

History of classification

Historically, the first species currently assigned to Hydatellaceae was discovered by Ferdinand von Mueller in SE Australia (Victoria) and by Ronald Campbell Gunn in Tasmania. Mueller (cit. after Hooker, 1858) proposed naming the plant *Juncella tasmanica* and placed it in affinity with *Centrolepis*, but he never published a formal description for his new genus. Hooker (1858) named the plant *Trithuria submersa*, providing a full description and a high-quality colour illustration of the plant (Fig. 1, left). He described the reproductive structures of *Trithuria* as inflorescences (capitula) composed of minute unistaminate male and unisepalate female flowers enclosed in an involucre. Hooker refused to accept Mueller's name because the plant is not confined to Tasmania and has no affinity with or resemblance to *Juncus*. The name *Trithuria* is derived from Greek roots and can be translated as 'three-windowed', which nicely reflects the dehiscence of the single-seeded fruits by three membranous valves separating from narrow ribs. Subsequently, Hieronymus (1888) published a description for *Juncella* and accepted this name rather than *Trithuria* (as did some other authors), but *Trithuria* clearly has nomenclatural priority.

In 'Flora Australiensis', Bentham (1878: 199) described the flowers of *Trithuria* as "probably hermaphrodite, with one stamen and one ovary each, but the stamens and ovaries so closely packed as to appear irregularly mixed". He recorded *T. submersa* from Southeast Australia and Tasmania and described another species, *T. occidentalis*, based on a collection made by James Drummond near Swan

River Colony, at the place where Perth is now located. Swan River Colony was the first British settlement in Western Australia (WA), and Drummond emigrated there with his family in the year of its foundation (1829), though we do not know exactly the year that he collected *Trithuria*. Ironically, *T. occidentalis*, which is the first-discovered and the first-described Western Australian species of Hydatellaceae, is also the rarest of the WA species in this family. Despite extensive floristic works in subsequent years, *T. occidentalis* was not found anywhere outside the closest neighbourhoods of Perth, where it deserves protection as an endangered plant. Bentham (1878) distinguished *T. occidentalis* from *T. submersa* in the shape of the involucre bracts and fruits and considered these two species to be closely related to each other. Subsequently, these differences were regarded to be of limited taxonomic value, and *T. occidentalis* was placed in synonymy with *T. submersa* (Cooke, 1987).

Rodway (1898¹) described *Trithuria filamentosa* from Tasmania and Cheeseman (1906a) discovered another species, *T. inconspicua* in New Zealand. These two are the only perennial species in the group, and they differ from *T. submersa* in possessing indehiscent fruits.

Diels (1904, in Diels & Pritzel, 1904 – 1905) described another genus, *Hydatella*, with two species (subsequently united into one: Sokoloff *et al.* 2008b) from SW Western Australia (fig. 1, right).

¹ Interestingly, Rodway (1898: 47) provided the following note on the genus *Trithuria*: "Like the order to which it belongs, it is probably the remnant of an ancient stock that flourished in the past ages". Although he operated in a different taxonomic context, we can still accept this quotation under the current taxonomic view.



Fig. 1. Left: Illustration of *Trithuria submersa* published with the first description of the species, reproduced here from Hooker (1858, pl. 138). Image courtesy of the Biodiversity Heritage Library, <http://www.biodiversitylibrary.org>. Right: Illustration of *Hydatella australis* published with the first description of the species, reproduced in a slightly modified form from Diels & Pritzel (1904 – 1905: fig. 7).

Diels listed unisexual stamen and pistil capitulae, a greater number of 'styles' (i.e., stigmatic hairs) and a lesser number (2) of involucre bracts surrounding the capitulate. Diels apparently did not know about *T. filamentosa*, while Cheeseman (1906a) did not know about this description of *Hydatella*. Further research highlighted differences in fruit morphology between the two genera (dehiscent in *Trithuria* vs. indehiscent in *Hydatella*) and supported transference of *T. filamentosa* and *T. inconspicua* to *Hydatella* (Cheeseman, 1906b; Morris & Curtis, 1974; Hamann et al., 1979). In addition, Hamann et al. (1979) reported considerable differences in seed structure between the two genera.

During last years of the 19th century and the first years of 20th century, extensive plant collections were made by Alexander Morrison (1849 – 1913) and William Vincent Fitzgerald (1867 – 1929). These collections, containing several unpublished plant species, were deposited and accessible at Herbaria of several institutions, including those of Kew, London, Edinburgh, Berlin and Perth. The Austrian-born Kew botanist Otto Stapf (1857 – 1933) conducted a detailed study of *Trithuria* samples collected in Western Australia by Morrison and Fitzgerald. In April 1903, Stapf drew high-quality pencil sketches of his dissections, which remain in the Kew Herbarium. Stapf was probably the first to discover that all plants of *T. occidentalis* are entirely female (and thus fundamentally different from the bisexual *T. submersa*). Also, Stapf proposed recognition of two new species from the same area as *T. occidentalis*. For *Trithuria macranthera*, only male plants were known. *Trithuria bibracteata* was distinguished from *T. submersa* by sessile inflorescences and involucres of two bracts. These two species were formally described 80 years later by Cooke (1983) who changed the name *T. macranthera* to *Hydatella dioica*. According to Cooke (1983, 1987), the main diagnostic features of *Hydatella* are unisexual inflorescences (capitula) and fruits without three prominent ribs. No female material was available for *H. dioica* and fruit morphology was not accessible, but as inflorescences (and even entire plants) were unisexual, Cooke placed the species in *Hydatella*.

Cooke (1981) described the first tropical member of the group, *Trithuria lanterna* from northern Australia. The first collections of this plant were made as far back as 1948 by Specht, but remained incorrectly identified until Cooke's study. In habit, *T. lanterna* appeared to be similar to *T. bibracteata* but differed in apparently indehiscent fruits (Cooke, 1987), though subsequent research demonstrated a special kind of fruit dehiscence in *T. lanterna* (Rudall et al., 2007; Sokoloff et al., 2008b).

Yadav & Janarthanam (1994, 1995) discovered a new species of *Trithuria* (*T. konkanensis*) in the Western Ghats region of India. This represented an unexpected discovery, because *Trithuria* and *Hydatella* were traditionally considered to be confined to Australia and New Zealand. Morphologically, *T. konkanensis* is closest to the tropical Australian *T. lanterna* (Sokoloff et al., 2010b).

Sokoloff et al. (2008b) demonstrated that plants traditionally known as *Trithuria occidentalis* and *Hydatella dioica* represent female and male individuals of the same biological species. This idea was already suggested by an unsigned annotation on a sheet in the Kew herbarium (the annotation probably dates from the 1970s), but it has apparently not been published elsewhere. Sokoloff et al. (2008b) showed that seeds of *T. occidentalis* can be precisely distinguished from those of all other species of *Trithuria* and *Hydatella*. They found two individuals of *H. dioica* (male plants) still remaining in organic association with the seed coat of the seeds that gave rise to them. The seed coat has sculpturing that is typical of *T. occidentalis*. Together with other morphological observations, this supported a broad concept of *Trithuria* to include all species previously placed in *Hydatella*. Earlier, Hutchinson (1959) proposed combining *Hydatella* with *Trithuria* under the illegitimate name *Juncella*.

Sokoloff et al. (2008b) described four new Australian species of *Trithuria*, of which three are dioecious. The newly described dioecious species *T. austinensis* is known from several localities in SW Western Australia; chronologically the first collection known to us was made by Greg Keighery in 1989. Male plants of *T. austinensis* are extremely similar to *T. occidentalis* (i.e., *H. dioica*). Therefore, it was initially hypothesised that the plants currently described as *T. austinensis* belong to *H. dioica*. When organic connection between seed coat and male plants was examined, it became obvious that the two dioecious species with very similar male plants and very different female plants both occur in SW Western Australia.

A similar pair of dioecious species, *T. cookeana* and *T. polybracteata*, was described from tropical Northern Australia (Sokoloff et al., 2008b). Each of them is so far known by one collection (Northern Territory, Maningrida, I.D. Cowie 5934 and Western Australia, North Kimberley, J.H. Willis s.n.). Both collections were annotated by D.A. Cooke as *Trithuria polybracteata*, but this name was not published. Male plants of the two species are very similar, but fruit morphology is highly different. The fourth new species (*T. cowieana*), also from tropical northern Australia,

has bisexual reproductive units and fruits resembling those in *T. cookeana*. It is named in honour of Ian D. Cowie who made many significant collections of Hydatellaceae in Northern Territory.

In total, 12 species of *Trithuria* are currently recognized, of which 8 are endemic to mainland Australia, one each to Tasmania, New Zealand and India; one species (*T. submersa*) occurs in both Tasmania and mainland Australia.

Inferring the closest extant relatives of Hydatellaceae

Until the 1970s, *Trithuria* (and *Hydatella*) were placed in the monocot family Centrolepidaceae (e.g., Bentham, 1878; Hieronymus, 1888; Gilg-Benedict, 1930). Some members of *Trithuria* and *Centrolepis* are indeed very similar to each other in habit and ecology (Fig. 2). These are tiny annuals growing in temporarily wet localities in Australia, with a rosette of filiform basal leaves and stalked or sessile reproductive structures surrounded by scale-like phyllomes. Species of *Trithuria* and *Centrolepis* often grow in close proximity, and as they are such minute plants they can be easily mistaken for each other by collectors in the field. For example, the type specimen of the tropical northern Australian species *Trithuria lanterna* (Cooke, 1981) was initially identified and labelled as *Centrolepis pusilla*, and the type specimen of *C. racemosa* (Sokoloff *et al.*, 2009c) was initially identified and labelled as *Trithuria lanterna*.

By the 1970s, it became clear that apart from habitual similarity, species of *Trithuria* (incl. *Hydatella*) and *Centrolepis* have almost nothing in common in their structure and development, not only in embryological characters (Hamann, 1975), but also in vegetative anatomy (Cutler, 1969) and pollen morphology (Bortenschlager *et al.*, 1966). Hamann (1976) therefore segregated *Trithuria* and *Hydatella* as a distinct family Hydatellaceae.

Characters distinguishing Hydatellaceae from Centrolepidaceae *s. str.* are listed below, following Hamann (1976) and Dahlgren *et al.* (1985: 32–33), with corrections and additions based on recent research. Cataphylls are frequently present in Centrolepidaceae (e.g., Cooke, 1992) but absent from Hydatellaceae (Sokoloff *et al.*, 2009a). Leaves and bracts are pilose in many species of Centrolepidaceae, but always glabrous in Hydatellaceae, though remarkable dense hairs occur on the stem surface (Rudall *et al.*, 2007). Vessels are present in the xylem of Centrolepidaceae but are apparently absent in Hydatellaceae (Carlquist

& Schneider, 2009). Stomata are paracytic, of the grass type, in Centrolepidaceae and anomocytic in Hydatellaceae. Inflorescences of Centrolepidaceae are simple or (more commonly) compound spikelets, with bracts on the primary axis subtending either lateral flowers or lateral spikelets (Sokoloff *et al.*, 2010a). In contrast, the involucrel phyllomes surrounding the reproductive units of Hydatellaceae apparently do not subtend lateral structures (Rudall *et al.*, 2009b; Sokoloff *et al.*, 2010b). Anthers are versatile, bisporangiate and monotheal in Centrolepidaceae and basifixed, tetrasporangiate and dithecal in Hydatellaceae. Pollen grains are ulcerate in Centrolepidaceae and monosulcate in Hydatellaceae. The carpel possesses a plicate region in Centrolepidaceae (Sokoloff *et al.*, 2009b) but not in Hydatellaceae (Rudall *et al.*, 2007). Carpels are usually united into a syncarpous gynoecium in Centrolepidaceae (except in *Aphelia*: Sokoloff *et al.*, 2009b) but never so in Hydatellaceae (Rudall *et al.*, 2007). Stigmatic hairs are very long, unbranched and multicellular in Hydatellaceae, but much shorter and often branched in Centrolepidaceae. Ovules are anatropous in Hydatellaceae and orthotropous in Centrolepidaceae. The female gametophyte is of the Polygonum-type in Centrolepidaceae and of the Schisandra-type in Hydatellaceae (Friedman, 2008; Rudall *et al.*, 2008). Endosperm development is *ab initio* nuclear and the endosperm becomes multicellular and functions as a nutritive tissue in Centrolepidaceae. In Hydatellaceae, the first nuclear division in the endosperm is followed by cell-wall formation (Rudall *et al.*, 2009a), and the endosperm is few-celled. In contrast to Centrolepidaceae, the endosperm is usually exposed on seed germination in Hydatellaceae (Sokoloff *et al.*, 2008a; Rudall *et al.*, 2009a). Abundant perisperm is present in Hydatellaceae but absent in Centrolepidaceae, and differences in nucellus structure of ovules are also observed. Seeds are exotestal in Hydatellaceae but endotegmic in Centrolepidaceae. A seed operculum formed by the inner part of the tegmen is present in Hydatellaceae but absent in Centrolepidaceae. In dehiscent fruits, each derivate of a carpel opens by a dorsal longitudinal slit in Centrolepidaceae and by three slits in Hydatellaceae. The cotyledon of Centrolepidaceae has a phaneromer (the proximal part of the cotyledonary hyperphyll that raises the seed well above the soil surface, representing the first assimilating organ of the seedling), which is absent in Hydatellaceae (Tillich, 2007; Tillich *et al.*, 2007; Sokoloff *et al.*, 2008a; Rudall *et al.*, 2009a).



Fig. 2. Habit similarity between species of *Trithuria* and *Centrolepis* in Northern Territory, Australia. a. *Trithuria cowieana* (about 1.3 km S of Finnis River crossing on Wangi Road, 37.4 km south of Cox Peninsula Road, SE of Darwin, 12°58'34" N, 130°45'30" E, 4 May 2007, Macfarlane et al. 4217, MW); b. *T. lanterna* (45.8 km E of Mary River, SE of Wildman River west branch, 12°49'26" N, 132°1'21" E, 8 May 2008, Macfarlane et al. 4262, MW); c. *Centrolepis banksii* (Pioneer Drive, Humpty Doo, 12°33'10" N, 131°8'19" E, 6 May 2008, Macfarlane et al. 4256, MW); d. *C. curta* (8 km N of Mary River on Kakadu Highway, 13°33'56" S, 132°15'49" E, 11 May 2008, Macfarlane et al. 4305, MW).

This impressive list of differences between the two groups shows that Hydatellaceae should not only be regarded as a family distinct from Centrolepidaceae but even cannot be regarded as a phylogenetically closely related lineage (e.g., a sister group).

Most morphological characters (e.g. the peculiar monothechal anthers) agree with the hypoth-

esis that Centrolepidaceae *s. str.* are most closely related to the graminid families, especially Restionaceae (Hamann, 1976; Dahlgren et al., 1985). Molecular phylogenetic data also support placement of Centrolepidaceae in the graminid clade, closest to (or even embedded within) Restionaceae (Briggs et al., 2000, 2010; Bremer, 2002; Michelangeli et al., 2003; Chase et al., 2006; Briggs & Linder, 2009).

Hamann (1976) and Dahlgren *et al.* (1985) emphasised the fact that the combination of characters found in Hydatellaceae is unique among monocotyledons, so that none of the extant monocot groups can be considered a close relative of Hydatellaceae. As noted by Dahlgren *et al.* (1985: 399), the family is “so different from other monocotyledons that its inclusion even in any superorder will be most strained”. Although Hydatellaceae, like Centrolepidaceae, are highly reduced in many respects, not all key morphological features can be viewed as derived character states. For example, the anomocytic type of stomata is widely viewed as more primitive than the paracytic graminid type that is characteristic of grasses, Centrolepidaceae, Restionaceae and other allied families. Tetrasporangiate anthers and monosulcate pollen are more primitive than the bisporangiate anthers and ulcerate pollen of Centrolepidaceae and Restionaceae.

Cronquist (1981) classified Hydatellaceae in its own order, Hydatellales. He noted that the presence of the opercular swelling of the seed coat suggests a possible relationship with the order Commelinales. Takhtajan (1987) accepted a superorder Hydatellanae that he considered to be sister to Commelinanae (comprising Commelinales, Restionales and Poales). At that time, the order Commelinales included a different set of families (such as Mayacaceae, Xyridaceae, Rapateaceae, Eriocaulaceae – all now in Poales) from the classification of APG (1998, 2009). In a later version of his system, Takhtajan (1997) restricted Commelinanae to include only Commelinaceae, Mayacaceae, Xyridaceae, Rapateaceae and Eriocaulaceae and viewed Hydatellanae as a relative of Commelinanae based on the shared presence of operculate seeds.

The morphological cladistic analysis of Stevenson & Loconte (1995) suggested close relationships between Acoraceae, Hydatellaceae and Typhaceae. Common features of these families include the occurrence of a perisperm, anthers with a connective protrusion and apical placentation. However, the dermal non-starchy perisperm of *Acorus* is not homologous with the subdermal, starchy perisperm that characterises Hydatellaceae (Rudall & Furness, 1997).

Early molecular (Bremer, 2002; Davis *et al.*, 2004) and combined molecular–morphological (Stevenson *et al.*, 2000) phylogenetic analyses of monocots suggested a close relationship between Hydatellaceae, *Mayaca* (Mayacaceae) and *Xyris* (Xyridaceae) as members of the highly expanded order Poales. As pointed out by Davis *et al.* (2004),

this placement agreed with the idea of Cronquist (1981) on the significance of shared presence of the seed operculum in these families. Commelinaceae, which is not placed in Poales by molecular data, has a different type of operculum formed by the outer rather than inner integument (Davis *et al.*, 2004). The Angiosperm Phylogeny Group (APG, 2003) placed Hydatellaceae in Poales. However, Bremer (2002) noted difficulties with the molecular data of Hydatellaceae (and Mayacaceae), citing possible long-branch attraction, and Davis *et al.* (2004) were able to obtain sequence data only from *rbcL* in Hydatellaceae, which represented only one of their two molecular markers.

Saarela *et al.* (2007), in the course of producing a multigene molecular phylogeny from all families of Poales, revealed robust and unequivocal placement of Hydatellaceae not with Poales, nor even with monocots, but as sister to the early-divergent angiosperm families Nymphaeaceae and Cabombaceae. This conclusion was further supported by subsequent molecular studies (Graham & Iles, 2009; Qiu *et al.*, 2010; Moore *et al.*, 2011; Soltis *et al.*, 2011), so that evidence is currently available from plastid, mitochondrial and nuclear genomes. Saarela *et al.* (2007) re-examined patterns of variation along the previously published *rbcL* sequence from Hydatellaceae (*T. submersa*) as part of a large-scale phylogenetic survey of grasses and relatives, and discovered that it was probably a PCR-based artefact representing a fusion product between a grass and a moss sequence. Saarela *et al.* (2007) also conducted a morphological cladistic analysis that supported placement of Hydatellaceae as sister to Cabombaceae plus Nymphaeaceae. They demonstrated that the most important characters distinguishing Hydatellaceae from Centrolepidaceae (and from other monocots) are in fact shared with Cabombaceae and Nymphaeaceae, such as anomocytic stomata, boat-shaped pollen, entirely ascidiate carpels, a four-nucleate embryo sac, palisade exotesta (seeds exotestal), seed operculum formed by cell enlargement in the inner integument and the occurrence of perisperm. In fact, many other features of morphology-based phylogenetic trees for basal angiosperms are much less congruent (or incongruent) with the molecular phylogeny than the placement of Hydatellaceae as sister to Cabombaceae and Nymphaeaceae (see also Endress & Doyle, 2009; Doyle & Endress, 2000, 2011). The current placement of Hydatellaceae probably provides one of best examples of congruence between molecular and morphological data.

Why did morphologists not discover that Hydatellaceae are closest to water lilies prior to the

molecular studies? On the one hand, tradition dictated that they restrict their search to monocot taxa, even though cotyledon number was not closely investigated in Hydatellaceae until the work of Tillich *et al.* (2007). On the other hand, the four-nucleate structure of female gametophyte was only recently discovered in water lilies (Winter & Shamrov, 1991a, b).

Tillich *et al.* (2007) provided the first detailed descriptions of seedling morphology in Hydatellaceae. They found that, in addition to the overall seedling morphology, cotyledon structure is typical for the monocotyledons. As noted by Tillich *et al.* (2007; see also Saarela *et al.*, 2007), a second character of the family that is typical of monocots was the supposed presence of protein-accumulating sieve-tube plastids of the P2c subtype (Behnke, 2000). This plastid type with triangular crystalloid protein bodies is found throughout the monocotyledons, with the sole exception of *Pistia*, which has starch-accumulating (S-type) plastids (Behnke, 1995) that are typical of early-divergent angiosperms and gymnosperms. Outside the monocots, P2c plastids are known only in some Aristolochiaceae. According to Tillich *et al.* (2007), the combined occurrence of a single cotyledon with typical monocotyledonous structure and P2c plastids is known only in monocotyledons; they considered it difficult to accept that this combination of two derived characters should have evolved independently, both in the monocotyledons and a family sister to Nymphaeales close to the angiosperm stem group. Therefore, Tillich *et al.* (2007) questioned the placement of Hydatellaceae proposed by Saarela *et al.* (2007). However, Tratt *et al.* (2009) subsequently re-investigated the sieve-element plastids of Hydatellaceae and found that they are exclusively of the S-type, as in Nymphaeales and most other basal angiosperms. The previous record of P2c subtype of sieve-element plastids was probably due to use of mislabeled material (possibly of Centrolepidaceae).

Thus, current overall evidence robustly places Hydatellaceae with Nymphaeaceae and Cabombaceae in the order Nymphaeales (Rudall *et al.*, 2007; APG III, 2009). This poses the question of possible parallel evolution of seedling morphology between monocots and Hydatellaceae. The bilobed cotyledonary sheath found in seedlings of *Trithuria submersa* and other extra-tropical Australian species could be interpreted either as a homologue of two united cotyledons (Sokoloff *et al.*, 2008a), or alternatively as a single cotyledon (Tillich *et al.*, 2007).

Hydatellaceae and the fossil record

Saarela *et al.* (2007) first suggested the possibility of a close relationship between Hydatellaceae and the Lower Cretaceous fossil genus *Archaeofructus* (initially interpreted as Jurassic and thus reportedly the oldest known angiosperm: Sun *et al.*, 1998). This fossil genus (Sun *et al.*, 1998, 2001, 2002; Ji *et al.*, 2004), so far known as three species from China, comprises herbaceous aquatics (some in whole-plant preservation) with finely dissected alternate leaves attached along a shoot with long internodes and terminal elongate reproductive structures bearing stamens proximally and carpels distally. Carpels are solitary or in pairs, while stamens are typically in groups of 2 or 3. At the boundary between the male and female zones, bisexual clusters (e.g., one stamen plus two carpels) are reportedly present (Ji *et al.*, 2004), though Friis *et al.* (2011) noted that these are not clearly visible on published illustrations.

The reproductive structures of *Archaeofructus* were interpreted as flowers or preflowers (Sun *et al.*, 2002), thus supporting multiaxial theories of flower origin (see Rudall & Bateman, 2010) or as an inflorescence (raceme) of reduced perianthless unisexual flowers lacking subtending bracts (Friis *et al.*, 2003). Sun *et al.* (1998, 2001), using cladistic analysis, suggested a placement of *Archaeofructus* as sister to a large clade that includes all extant angiosperms. Friis *et al.* (2003) and Endress (2005) noted that several key morphological characters of *Archaeofructus* are difficult to interpret because of the poor structural preservation of the fossil. In particular, it is uncertain whether the bodies described as boat-shaped (monosulcate) pollen grains could represent an artefact of preservation and whether the initial interpretation of carpels as plicate and fruits as follicles can be supported by direct observations. Friis *et al.* (2003) suggested that *Archaeofructus* could be a crown-group angiosperm, possibly related to Ranunculales. This alternative interpretation assumes that pollen morphology is unknown in this fossil (see also Ji *et al.*, 2004). Friis *et al.* (2011) also noted that though an angiosperm relationship for *Archaeofructus* is likely, its angiospermous affinity has not been fully explored, and suggested possible alternative relationships with some extinct gymnosperms, such as *Caytonia*, *Dirhopalostachys* and *Schweitzeria*.

Doyle (2008) and Endress & Doyle (2009) tested the hypothesis of a close relationship between *Archaeofructus* and Hydatellaceae using cladistic analyses (see also Doyle & Endress, 2010). Since

some characters cannot be unambiguously scored from *Archaeofructus*, different possible interpretations were explored, such as (pre)floral and inflorescence interpretation of its reproductive structures. Doyle (2008) performed a cladistic analysis of extant and fossil seed plants, with limited sampling of derived angiosperm groups. He found good support for placement of *Archaeofructus* with Hydatellaceae or at least with Nymphaeales. Endress & Doyle (2009) included a much broader set of angiosperms, but did not include gymnosperms. They used two constrained tree topologies, one based on their previous combined molecular and morphological phylogenetic analysis and another based on recent phylogenetic studies exploring complete plastid genomes. Adding data on *Archaeofructus*, they explored its position in the constrained backbone trees. Endress & Doyle (2009) found that placement of *Archaeofructus* depends on assumptions about its morphology (especially on accepting the view that it had monosulcate pollen) and on the backbone tree topology. They concluded that placement of *Archaeofructus* as sister to Hydatellaceae is highly plausible, though some analyses allowed other possibilities, such as in basal eudicots and as sister to *Ceratophyllum*. The Hydatellaceae plus *Archaeofructus* clade was sister to Cabombaceae plus Nymphaeaceae.

Sister-group relationships between Hydatellaceae and *Archaeofructus* were revealed when reproductive structures in both groups were interpreted as inflorescences of perianthless unisexual flowers lacking subtending bracts. Unequivocal synapomorphies of the two groups are the loss of flower-subtending bracts and loss of perianth (Endress & Doyle, 2009). As pointed out by Endress and Doyle (2009), their results would suggest that Hydatellaceae could represent what became of one member of the *Archaeofructus* group after 125 myr of further reduction in an aquatic habitat.

At first glance, inflorescence morphology (if these structures are interpreted as inflorescences) is very different between Hydatellaceae and *Archaeofructus*. In *Archaeofructus*, the distal part of the inflorescence is female, whereas it is male in the bisexual reproductive structures of Hydatellaceae. However, in the framework of the inflorescence interpretation, this apparent difference could be viewed as an aberration caused by comparing incompatible structures. The inflorescence of *Archaeofructus* is a spike (i.e., a raceme in the broad sense). The reproductive units of Hydatellaceae could be interpreted as thyrses (Hieronymus, 1888; Rudall *et al.*, 2007; Endress, 2010). A thyrses differs from a raceme in that lateral cymes are present instead of lateral

flowers. In the bisexual reproductive units of Hydatellaceae, the lateral cymes could be all bisexual or (as interpreted by Rudall *et al.*, 2007, fig. 5D) the lower proximal cymes are bisexual while the distal ones are female. In the bisexual lateral cymes, the first flower is always male and flowers of subsequent orders are female. These subsequent flowers are physically inserted at the periphery of the entire reproductive unit, causing an impression of distal stamen and proximal carpel positions. The morphologically correct way of comparing sex allocation in inflorescence models of *Archaeofructus* and *Trithuria* is considering only first-order flowers in the putative lateral cymes of *Trithuria*. When we consider the putative thyrses illustrated in Rudall *et al.* (2007, fig. 5D), it has the same relative arrangement of male and female flowers as in *Archaeofructus*. However, the problem is that several other lines of evidence do not support interpretation of reproductive units in Hydatellaceae as thyrses, and they might represent peculiar uniaxial structures such as possible flower homologues in which the integrity of developmental processes was secondarily lost during the course of evolution (Rudall *et al.*, 2009b; Sokoloff *et al.*, 2010b).

Endress & Doyle (2009) distinguished (as cladistic character states) between two major inflorescence types, i.e. those with a terminal flower, such as panicles, thyrsoids and botryoids, and those without a terminal flower, such as racemes (in a broad sense) and thyrses. They argued that thyrses and racemes are closely related, and, for example, *Hedyosmum* (Chloranthaceae) has thyrses of female flowers and spikes of male flowers (see also Endress, 1987). In a rather similar case in the monocot *Dioscorea* (Dioscoreaceae), the female flowers are often in spikes and the male flowers are in thyrses (Remizowa *et al.*, 2010). In groups such as lilioid monocots, racemose inflorescences with bracteoles are closely related to thyrses because the occurrence of the next-order flower in the bracteole axil is a labile feature (Remizowa *et al.*, 2011). The evolutionary origin of a thyrses from a raceme is possible, but the presence of bracteole(s) – i.e. prophyll(s) on floral pedicels – represents a key condition for such a transition. In the inflorescence interpretation of *Archaeofructus*, not only the prophylls but even the flower-subtending bracts are reduced. Adopting the occurrence of cryptic bracteoles as well as cryptic bracts in *Archaeofructus* is a strong assumption, but the same applies to male inflorescences of *Hedyosmum* if these are interpreted as inflorescences potentially homologous to female thyrses (rather than as flower-like or strobilar structures: Leroy, 1983). In the coding of Endress & Doyle (2009), Hydatellaceae and *Archae-*

fructus possess the same major inflorescence type (raceme or thyrse).

In our view, the character coding of inflorescences in Endress & Doyle (2009) is probably optimal, but character-based interpretation of such complex issues as inflorescences will be always problematic. Transitions are possible not only between thyrses and racemes but also between racemes and botryoids (e.g. Sokoloff *et al.*, 2006; Bull-Hereñu & Claßen-Bockhoff, 2011) and between racemes and solitary terminal flowers (Sokoloff *et al.*, 2006; Lock *et al.*, 2010). Within the inflorescence interpretation of reproductive units in Hydatellaceae, the absence of a terminal flower is extremely difficult to prove, because of the absence of flower-subtending bracts (Sokoloff *et al.*, 2010b).

There are several differences between *Archaeofructus* and Hydatellaceae that can be hardly explained by reductions in the lineage leading to extant *Trithuria*. These include the presence of an involucre of phyllomes surrounding the reproductive units and different stamen morphology.

Recent data show that the involucre phyllomes of the reproductive units in Hydatellaceae do not subtend any lateral structures (Rudall *et al.*, 2009b; Sokoloff *et al.*, 2010b). If pseudanthial interpretations are accepted for reproductive units in both Hydatellaceae and Ceratophyllaceae (Endress & Doyle, 2009), then the two families share the absence of flower-subtending bracts plus the presence of an involucre of phyllomes that normally do not subtend flowers. This represents a specialised type of inflorescence; we know of no other basal angiosperms that possess this feature. The presence of an involucre is a potential parsimony-informative character that could be added to the data matrix used by Endress & Doyle (2009).

Stamens of Hydatellaceae possess long filaments that remain attached to the plant when anthers are shed after anthesis. Long filaments are not recorded in *Archaeofructus*, and its stamens shed completely after anthesis, as in *Ceratophyllum*. It is unknown whether pollination in *Archaeofructus* was achieved by water (Friis *et al.*, 2003, 2006) or wind (Sun *et al.*, 2002, see also Ji *et al.*, 2004). The absence of well-preserved pollen in *Archaeofructus* (Ji *et al.*, 2004) could suggest that the exine was poorly developed, as in many extant plants with underwater pollination, including *Ceratophyllum*. In Hydatellaceae, underwater pollination is not documented and appears unlikely (Taylor *et al.*, 2010).

In summary, more data are needed for precise phylogenetic placement of *Archaeofructus*. Finding

better preserved fossils will be crucial for resolving the issue.

Regarding other fossils, Hofmann & Zetter (2010) suggested that the dispersed fossil pollen of *Monosulcites riparius* from Cretaceous sediments in Siberia could be assigned to Hydatellaceae based on close comparison with surface morphology of extant species (Remizowa *et al.*, 2008). It is noteworthy that Siberia is located far from the extant distribution area of Hydatellaceae. Although there is considerably external similarity between *Monosulcites riparius* and pollen of extant *Trithuria*, attributing the dispersed fossil pollen to Hydatellaceae will remain tentative until associated macro- or mesofossils are discovered. Convergent similarity of pollen grains in unrelated lineages is well-known. For example, Remizowa *et al.* (2008) documented rare atypical grains for two species of *Trithuria* in which part of the surface possessed sculpturing typical of Hydatellaceae and part resembled *Gymnotheca* (Saururaceae, Piperales). The occurrence of such mosaics demonstrates that minor changes in regulation of developmental programs can cause major phenotypic effects in pollen morphology.

A problematic Late Cretaceous fossil is *Mosacaulis spinifer* (van der Ham *et al.*, 2011). This fossil is interpreted as an aquatic marine (pseudo)herbaceous plant with axes bearing densely-spaced, semi-amplexicaul leaves arranged in low spirals, with reproductive structures (sporangia?, prophylls associated with flowering axes?) attached to the adaxial sides of the leaf-bases (van der Ham *et al.*, 2011). *Mosacaulis* is a fossil of unknown affinity (probably a lycopsid, but possibly an angiosperm), but the authors mention its resemblance to shoots of Nymphaeales, especially Hydatellaceae.

Ecology of Hydatellaceae

According to the available data, the distribution of Hydatellaceae is disjunctive, and different species grow in quite different climatic conditions. The following distribution areas can be recognized, from northwest to southeast: (1) Western Ghats in India (*T. konkanensis*), (2) tropical northern Australia, from the Kimberley region in Western Australia to the northern part of Queensland (*T. lanterna*, *T. polybracteata*, *T. cookeana*, *T. cowieana*), (3) the southwestern part of Western Australia (*T. submersa*, *T. bibracteata*, *T. occidentalis*, *T. australis*, *T. austinensis*), (4) the southeastern part of South Australia, southernmost New South Wales and part of Victoria (*T. submersa*), (5) Tasmania (*T. submersa*, *T. filamentosa*), (6) the northern part of North Island, New Zealand (*T. inconspicua*), (7) the southern part of South Island, New Zealand (*T. inconspicua*). Areas 1–2 are tropical,

while areas 3–7 are subtropical to temperate. Phylogenetic data suggest deep divergence between the tropical and subtropical/temperate group of *Trithuria* (Iles *et al.*, 2011; Iles *et al.*, in press).

It is possible that the apparent disjunctions at least partly represent an artefact reflecting incomplete knowledge of the distribution of these tiny plants, which can easily be overlooked in the field. Indeed, the occurrence of *Trithuria* in India was only discovered in the 1990s (Yadav & Janarthanam, 1994) and the first findings in the South Island of New Zealand were made in the 1990s (see Wells *et al.*, 1998). We cannot exclude further records of Hydatellaceae in other areas of the world with appropriate climatic conditions, for example from African savannas or the Cape region of South Africa. On the other hand, we believe that current knowledge on the distribution of Hydatellaceae within Australia provides a general idea of the real situation, because generations of Australian field botanists have known about and collected these curious plants.

At least at first glance, the uneven distribution of Hydatellaceae in Australia can be explained by local differences in humidity. This is particularly obvious in the western and central part of Australia, where Hydatellaceae are absent from dry areas between tropical monsoon northern Australia and the winter-wet southwest of Western Australia. The absence of any records of Hydatellaceae along most of the Pacific coast of Australia (between about 39° S in Victoria and about 20° S in Queensland) cannot be explained by the aridity of these coastal areas. It is highly unlikely that *Trithuria* has been overlooked here, because the Pacific coast of New South Wales is one of the botanically best explored areas in Australia. It seems that the mainland Australian species of *Trithuria* – which are all annuals – require a regular alternation of prominent dry and wet seasons.

Ecology of *Trithuria konkanensis* in India

Trithuria konkanensis S.R. Yadav & Janarth. was discovered and described from India in 1994 (Yadav & Janarthanam, 1994, 1995). It is a member of a typical herbaceous monsoon plant community (Fig. 3b) on accumulated gravely sandy soils (Fig. 3a, d, f) on lateritic plateaus from sea level to 600 meters in altitude. This is a special kind of habitat harbouring idiosyncratic species, most of which are endemic and restricted to these kinds of habitats (Joshi & Janarthanam, 2004). *Trithuria konkanensis* is found growing in coastal regions of Western India from Ratnagiri (Maharashtra) in the

north to Mangalore (Karnataka) in the south (Fig. 3c). A typical monsoon plant community of accumulated gravely sandy soils on lateritic plateaus (rocks) includes *Cyperus pumila*, *Dimeria hohenackeri*, *D. ornithopoda*, *D. woodrowii*, *Drosera indica*, *Xyris indica*, *Eriocaulon eurypeplon*, *E. minutum*, *E. stellulatum*, *E. xeranthemum*, *Glyphochloa acuminata*, *G. santapau*, *Hedyotis* spp., *Indigofera dalzellii*, *Ischaemum indicum*, *Lindernia oppositifolia*, *Murdannia* spp., *Ophioglossum graminifolium*, *O. nudicaule*, *Rhynchospora wightiana*, *Rotala densiflora*, *Salomoniaciliata*, *Smithia salsuginea*, *S. sensitiva*, *Utricularia albocaerulea*, *U. caerulea*, *U. minutissima*, *U. polygaloides*, *U. praterita*, *U. reticulata*, *Zornia diphylla* and *Z. gibbosa*. Other interesting members of ponds and ditches on lateritic plateaus are *Oryza rufipogon*, *Wiesneria triandra*, *Rotala densiflora*, *Eriocaulon cuspidatum*. *Trithuria konkanensis* also grows in sandy soil along the sea (Fig. 3e).

Seeds of *T. konkanensis* (Fig. 3k) germinate sometime in June and plants show vegetative growth during the period of heavy rainfall (500–600 cm per annum) from July to the end of August. The species shows peak flowering during September (Fig. 3d, e, f). By early October, the habitats dry, and seeds remain embedded in the soil until the subsequent monsoon. The soil remains flooded or saturated with water and the sky cloudy from the end of June to September. The plants remain submerged during rainy days but as the rain recedes the water gets drained off exposing the plants. The monsoon retreats by the end of September and the sky remains clear for some part of the day, when the plants receive sunlight and start flowering. Depending upon the soil moisture, plants of *T. konkanensis* continue to flower until November. With exposure to heat and light, the plants accumulate red pigments in their body (Fig. 3d, e). The seeds mature during September and October and with the drying of the ground remain embedded in the soil until the following June. There is no noticeable mechanism for seed dispersal except for shifting of soil by water currents or human activities. The plants possess a rosette habit (Fig. 3f), producing several inflorescences in the centre at ground level. The inflorescence consists of a central stamen surrounded by several pistils (Fig. 3h, i). Pistils produce 3–5 uniseriate stigmatic hairs (Fig. 3h, i) on which pollens germinate (Fig. 3j). The stigmatic hairs form a cluster. Cytoplasmic streaming in the cells of the uniseriate stigmatic hairs is of special interest, indicating an active metabolism in the hairs. Although red stigmatic hairs are attractive, insects have never been observed visiting stigmas.

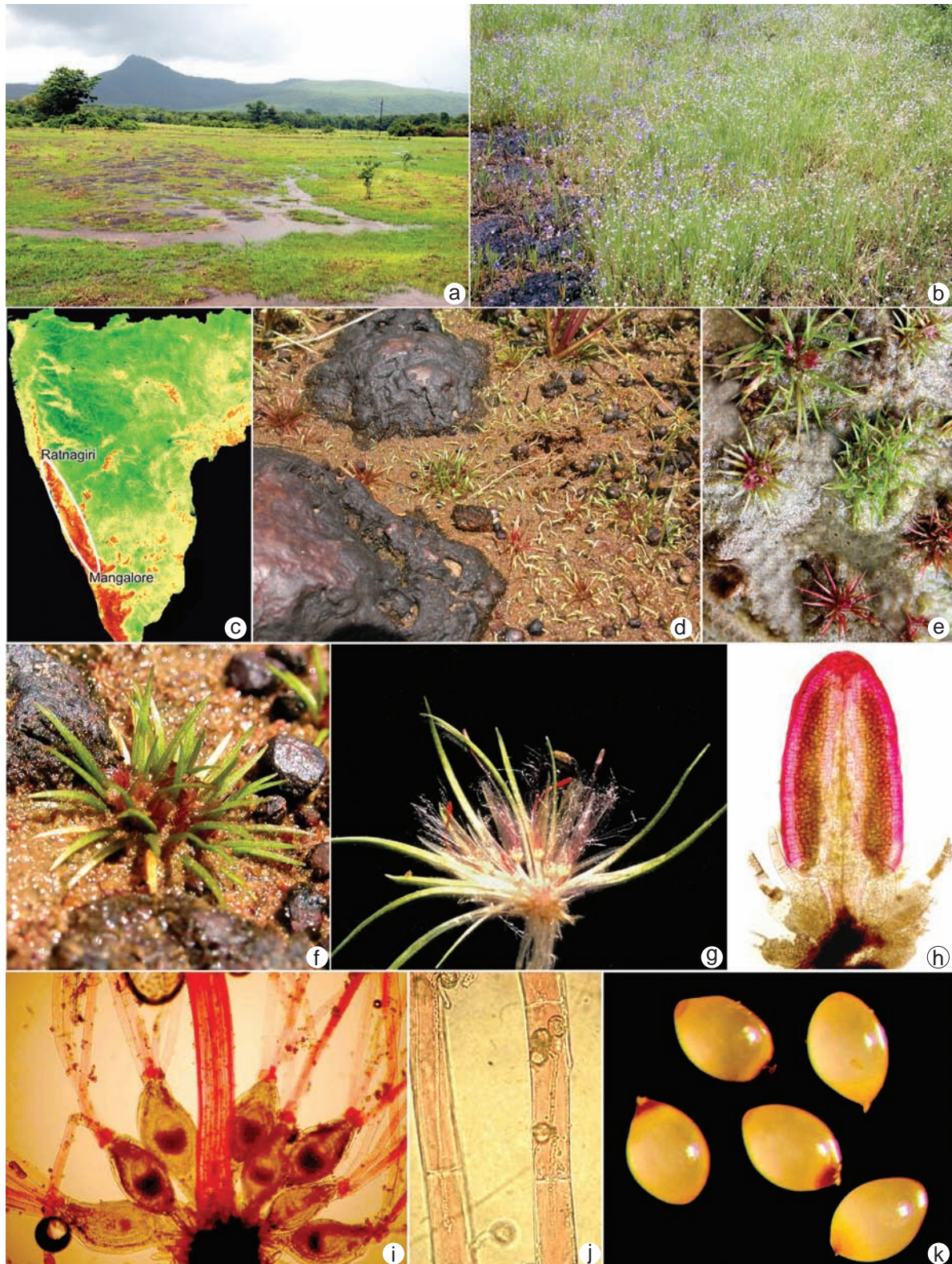


Fig. 3. *Trithuria konkanensis* S.R. Yadav & Janarth.: a. Habitat – A plateau along Western Ghats; b. Herbaceous community in the habitat; c. Distribution; d & e. Habitat close-up (d. Lateritic; e. Sandy); f. Rosette habit; g. Leaves (few) removed to show the reproductive structures; h. & i. Stamen surrounded by several pistils with 3 – 5 uniseriate pigmented stigmatic hairs (h – young); j. Germination of pollen on uniseriate stigmatic hairs; k. Seeds.

Trithuria konkanensis closely resembles *T. lanterna*, a species from tropical northern Australia in its morphology and ecology (Sokoloff *et al.*, 2010b). Plants of both species are self-pollinated, though (as they grow in close vicinity to each other) cross-pollination could also be expected. The stigmatic hairs are produced in succession and thus the pistils remain receptive for quite a long period ensuring fertilization.

Ecology of *Trithuria* in tropical northern Australia

Within Northern Territory, we possess field observations only for the Darwin region. Two species are recorded here (*T. lanterna* and *T. cowieana*), and the absence of two other tropical Australian species appears not to be biased by poor investigation of the region. So far, *T. cowieana* appears to be endemic to the Darwin region, where it is less frequent than *T. lanterna* (which has a range extending from Kimberley to northern Queensland). The time of seed germination is unknown, but it must occur during the wet season under high temperatures. The plants grow at habitats covered by water during the wet season. They flower during the short period at the beginning of the dry season when the water has disappeared but the habitat is still wet. They quickly set seed and dry out completely, as other herbs in these habitats, such as species of *Utricularia*. Both species are probably self-pollinated within their bisexual reproductive units. Reproductive units of *T. lanterna* (Fig. 4, 5) are sessile or very short-stalked. They are situated at ground level or largely submerged in the substrate, along with the leaf bases. In the latter case, only the stigmatic hairs and anthers are exerted above ground level. The significance of their exposure is not clear, as plants are probably self-pollinated. Wind clearly cannot transport pollen, but the possible significance of water transport could be explored. *Trithuria cowieana* (Fig. 6) has both stalked and sessile reproductive units in the same plants. In our material, reproductive units on elongate stalks were always fruiting, while sessile units were both anthetic and pre-anthetic (Rudall *et al.*, 2009a). It is therefore likely that units are self-pollinated at ground-level and then exposed on elongating stalks to facilitate fruit dispersal.

Habitats of *Trithuria* spp. are diverse in the Darwin region, and we were unable to find clear species-specificity. They were not found along the banks of rivers and streams. Rather, they seem to prefer flat, temporarily inundated areas, temporary pools and shores of billabongs. The sub-

strate can be sand or closer to clay and *T. lanterna* sometimes occurs on very shallow sand deposits above sandstone. In the wet season, these likely represent small pools on sandstone (e.g.: Johnson 4597: "in 7 cm water with *Nymphoides*, on top of sandstone escarpment"). Depending on the local situation, communities can be either species-poor (in a few cases, apparently just *T. lanterna*) or species-rich. Both original observations and herbarium labels (also from Queensland) suggest that *T. lanterna* frequently occurs in open shrubland with *Grevillea pteridifolia* and grasses, often also with Restionaceae (Fig. 7). In this community, very small plants of *T. lanterna* grow between tall herbs. Figure 8 shows a grassland locality (Wangi Road, near Finnis River crossing, seasonally shallowly flooded area near river) where *T. cowieana* was found on the sand of the road track while *T. lanterna* was growing nearby between tall grasses (*Eriachne*) and plants such as *Eriocaulon* and *Xyris*. Seasonal swamps with *Melaleuca* also can be inhabited by *Trithuria*.

Trithuria lanterna and *T. cowieana* can grow in disturbed places such as vehicle tracks or communities with pig disturbance, though these places are commonly side by side with undisturbed vegetation where *Trithuria* is also abundant. For example, in a population examined near Jabiru (12°44'14" S, 132°46'2" E), *T. lanterna* was found in a drainage line near the roadside but the very expansive population extended into a wetland with scattered trees of *Eucalyptus*, *Pandanus*, *Melaleuca* and *Acacia* and with tall grasses; plants of *T. lanterna* were concentrated towards the margin of the wetland.

Data on ecology of the two dioecious species, *T. cookeana* and *T. polybracteata* are available only from labels of their type specimens. *Trithuria cookeana*: Northern Territory, 24 km SE of Maningrida, 12°07' S, 134°26' E, with *Utricularia* on damp sand at edge of drying swamp, *Melaleuca viridifolia* over story, 22 Aug. 1995, I.D. Cowie 5934 (DNA, AD). *Trithuria polybracteata*: Western Australia, North Kimberley, Vansittart Bay, Pauline Bay Area, west side of mangrove inlet, 1.5 km N from camp at mouth of freshwater creek, 14°12'30" S, 126°22' E, in spring with *Utricularia*, 26 May 1984, J.H. Willis s.n. (MEL). Both species have stalked male and female reproductive units, and stalk elongation most likely takes place before pollination. Self-pollination is not possible in dioecious species, and as pollen tubes are found on stigmatic hairs, at least in *T. polybracteata* (Prychid *et al.*, 2011) plants must be wind-pollinated, as in the SW Australian species *T. austinensis* (Taylor *et al.*, 2010). Both *T. cookeana* and *T. polybracteata* were collected at fruiting stage, but

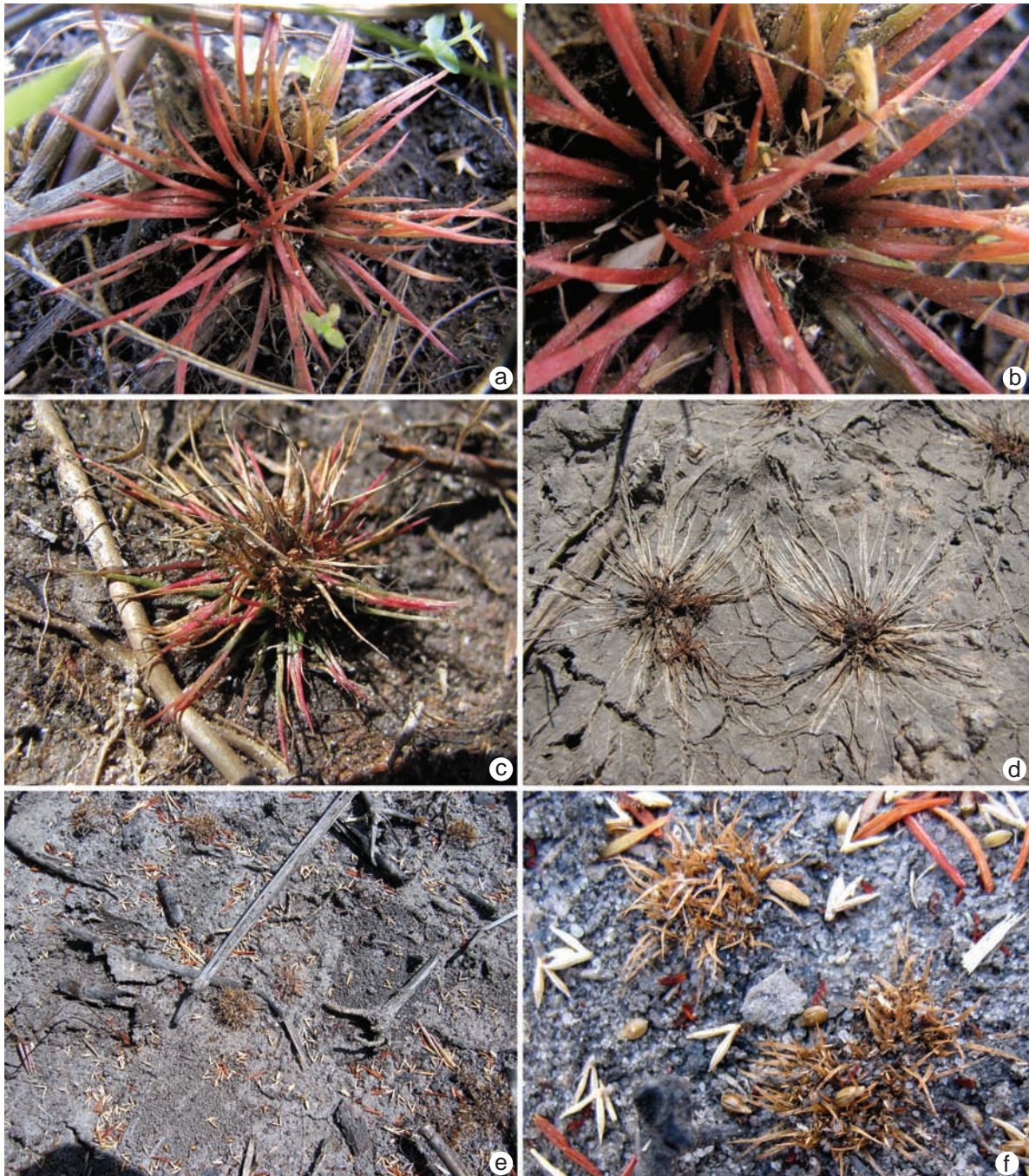


Fig. 4. *Trithuria lanterna* in Northern Territory, Australia. a & b. Plant at anthesis (8 km E of Adelaide River crossing on Arnhem Highway, 12°41'52" N, 131°23'50" E, 7 May 2008, *Macfarlane et al.* 4258, MW); c. Plant from another locality, less submerged into substrate (45.8 km E of Mary River, SE of Wildman River west branch, 12°49'26" N, 132°1'21" E, 8 May 2008, *Macfarlane et al.* 4262, MW); d. Dried plants with fruits on grey sandy clay (dried mud), old vehicle track (Howard Springs area, 6.5 km N of Howard river along Gunn Point Road, E of Darwin, 12°26'10" N, 131°8'5" E, 5 May 2008, *Macfarlane et al.* 4237, MW); e & f. Dried plants with fruits on sand above sandstone near Cahills crossing over East Alligator River, Kakadu National Park, 12°26'0" S, 132°58'13" E, 9 May 2008, *Macfarlane et al.* 4275, MW).



Fig. 5a – f. *Trithuria lanterna* and its locality near Humpty Doo in Darwin Region, Northern Territory, Australia. Images taken on 6 May 2008 at the same locality showing situation at different magnifications.

the intriguing fact is that *T. cookeana* was collected in late August, and the plants appear less dried out than those of the late May collection of *T. polybracteata*. Most specimens of the more common northern species *T. lanterna* and *T. cowieana* are collected in April to May, and some are collected in March and June, but we know of no collections made in July or August. Apparently, *T. cookeana* grows in a large swamp that dries out by August. The label of

T. polybracteata allows us to speculate that the plant might be more salinity-tolerant, like another dioecious species, *T. austinensis* (see below).

Ecology of *Trithuria* in south-western Western Australia

The five species of *Trithuria* currently recognised in southwestern Australia are all winter annuals

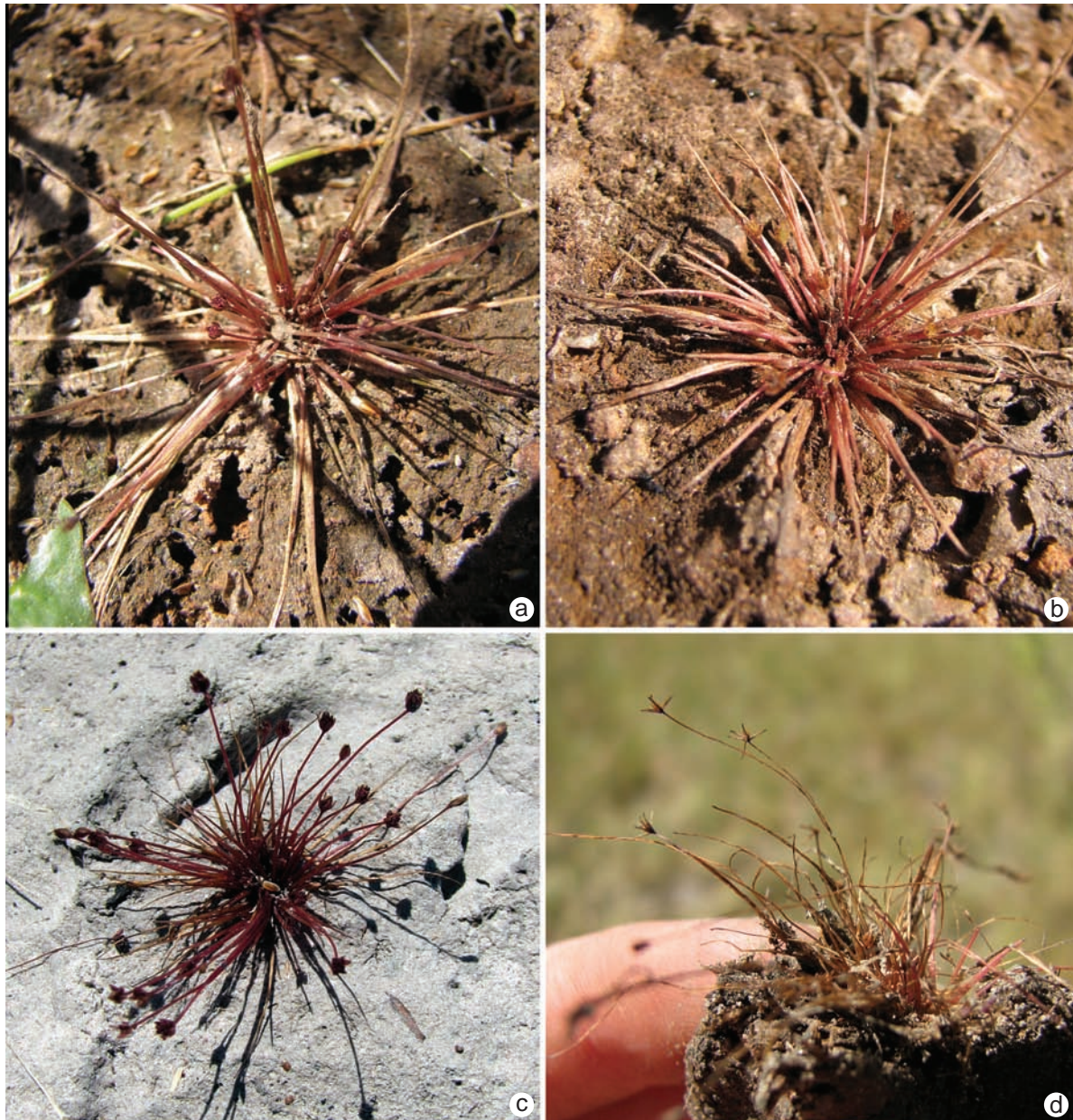


Fig. 6. *Trithuria cowieana* in Darwin Region, Northern Territory. a – c. Images taken on 4 May 2008 (c. 1.3 km S of Finnis River crossing on Wangi Road, 37.4 km south of Cox Peninsula Road, SE of Darwin, 12°58'34" N, 130°45'30" E, *Macfarlane et al.* 4217, MW); d. Image taken on 8 May 2008 (45.8 km E of Mary River, SE of Wildman River west branch, 12°49'26" N, 132°1'21" E, *Macfarlane et al.* 4261, MW).

that occur in the Mediterranean climate region. The most common habitat is in clay-rich mud, often clay-bottomed seasonal wetlands, but also in ephemeral pools on granite outcrops. Plants may be in fully exposed sites or in the shade of trees or sedges. They germinate early in the winter as the dried-out habitats become sufficiently wet, grow vegetatively during winter, initiate inflorescences in spring, which may proceed to full development prior to the plants becoming exposed as the water recedes through evaporation. Three species,

Trithuria bibracteata (Fig. 9d, e), *T. occidentalis* and *T. submersa*, tend to grow in shallow water that submerges the plants for a relatively short period during winter, or they may even be exposed and grow only in saturated mud. The remaining two species, *T. austinensis* (Fig. 9a – c) and *T. australis* (Fig. 9f), grow in deeper water and are fully submerged for a long period over winter. Algal blooms or flocculent mud may obscure the plants for part of the growing period, but this does not seem to be deleterious. The plants may be submerged in up to



Fig. 7. One of the typical habitats of *Trithuria lanterna*, open bushland with *Grevillea pteridifolia* and grasses. Image taken on 10 May 2008 in the Darwin Region, Northern Territory, Australia (near Jabiru).

50 cm of water during the vegetative period, but all the species appear to behave like *T. submersa*, whose anthers dehisce only after exposure (Taylor *et al.*, 2010).

To date, there is little quantitative information on the growing period of any of the species except for the work of Taylor *et al.* (2010) on *T. submersa*, but observations indicate that the growth cycle is highly dependent on the presence, quantity and duration of water. The plants fail to germinate in very dry seasons and may fail to complete their life cycle if the wet period is too brief. Physical water parameters, including depth, temperature and dissolved salts, were studied by R.J. Hearn (unpublished, partly summarised by Macfarlane & Hearn, 2011) in several lakes or swamps where *T. austinensis* particularly grows, but the data do not extend to the phenological state of *Trithuria* spp. *Trithuria* species often grow in diverse herbaceous communities of the sort described by Pignatti & Pignatti (1994). Up to three (and even four) species frequently grow in the same site, sometimes inter-

mingled, especially *T. bibracteata* and *T. submersa*, with *T. australis* or *T. austinensis* nearby in deeper water. However, *T. occidentalis* and *T. austinensis* apparently do not co-occur in the same sites.

Trithuria austinensis is apparently more salinity tolerant than the other species. This species is quite characteristic (though not restricted) to an unusual plant community of hypo-saline seasonal lakes (Fig. 9a, b) (Macfarlane & Hearn, 2011). The community is composed of a small number of species, and not all of them are present in every locality. Apart from *T. austinensis*, these are the angiosperms *Ruppia polycarpa*, *Lepilaena cylindrocarpa* and *Triglochin mucronata* (all members of the monocot order Alismatales that includes most salt-tolerant angiosperm aquatics), two species of the aquatic liverworts *Riella* and a charophyte alga *Lamprothamnium heraldii* (Macfarlane & Hearn, 2011). The small number of species suggests that only a few plant groups have developed a capacity to grow in the demanding physiological and seasonal conditions of the lakes (Macfarlane & Hearn, 2011). Early in the season, the plants grow



Fig. 8. Habitat of *Trithuria lanterna* (on rough vehicle track in and around wheel track depressions, and scattered in native vegetation, either among bases of grasses, etc. or localised in small hollows caused by animal footprints or uprooting of tree bases by wind) and *T. cowieana* (hundreds of plants seen; abundant along a rough vehicle track in and around wheel track depressions, common in roadside drain, uncommon in undisturbed vegetation). Open grassland with sedges and a variety of other herbaceous plants including species of *Xyris*, *Eriocaulon*, *Utricularia*, *Drosera* and *Sowerbaea*, occasional trees and magnetic termite mounds, and also at wetland margins in very open woodland over grassland with trees of *Melaleuca*, *Eucalyptus*, *Corymbia*, *Grevillea*, *Pandanus* and *Livistona* palms. Darwin region, Northern Territory, Australia (Wangi Road, Near Finnis River crossing), images taken on 4 May 2008.

in cold water (5–10°C) with low salinity, but once the temperature increases up to c. 30°C later in the season and water disappears, salinity increases rapidly. *Trithuria austinensis* also grows in other kinds of sites which suggests that it is tolerant of a range of water conditions as well as of varying shade levels from none to considerable. At some sites, still in water, it grows under sparse to rather dense tree cover of the species *Eucalyptus rudis*, *Casuarina obesa* or *Melaleuca cuticularis* in different places, in a herbaceous understorey or in openings within dense sedgeland of *Meeboldina* sp. (Restionaceae), *Chorizandra enodis* or *Baumea vaginalis* (both Cyperaceae).

It is apparent from the density of plants and the potentially large number of seeds per plant that there is a large soil seed bank of *Trithuria*. Therefore, it is not unlikely that the frequent occurrences of *T. bibracteata* and *T. submersa* in roadside drains, and of *T. bibracteata* and *T. austinensis* in granite outcrop pools results from water birds transporting seeds in mud. Tuckett *et al.* (2010a) compared the longevity of seeds of Hydatellaceae (*T. submersa*, *T. austinensis*) with other temporary wetland aquatics from the South-west Australian Floristic Region under standard experimental storage conditions. They found that seeds of Hydatellaceae species are longer-lived than the other temporary wetland aquatic species tested. In another paper, Tuckett *et al.* (2010b) investigated details of seed germination in the southwest of Australia. They found that seed viability was high (82 – 91%). Temperatures at which maximum germination occurred were 5, 10 and 15°C for *T. submersa*, *T. austinensis* and

T. bibracteata, respectively, and all species required light for germination or germinated better in light than darkness. The time taken to achieve 50% of maximum germination for seeds on water agar was variable between species, but all seeds took ≥ 35 d. Seeds of all species were desiccation-tolerant, and drying of seeds increased maximum germination percentage (Tuckett *et al.*, 2010b). Low temperatures are essential for seed germination of temperate/subtropical Hydatellaceae, reflecting an adaptation for their germination in the cold and wet season.

Ecology of *Trithuria* in the southeast of Australia and Tasmania

The ecology of *T. submersa* in the southeast of Australia appears to be similar to that of the same species in SW Western Australia. It grows as a winter annual in the mud of stream margins, seasonal swamps and pools, where it flowers in September to November (Conran, 2011) or November to December (Conn, 1993).

In Tasmania, the annual *T. submersa* and perennial *T. filamentosa* have different and only slightly overlapping distribution areas (see map in fig. 14 of Sokoloff *et al.*, 2008b). The distribution difference correlates with climatic conditions: 24 of 25 analysed localities of *T. filamentosa* belong to the western part of Tasmania with annual rainfall above 1200 mm. All ten analysed localities of *T. submersa* from Tasmania belong to the central and northern parts of the island, with annual rainfall below 1000 mm. *Trithuria*

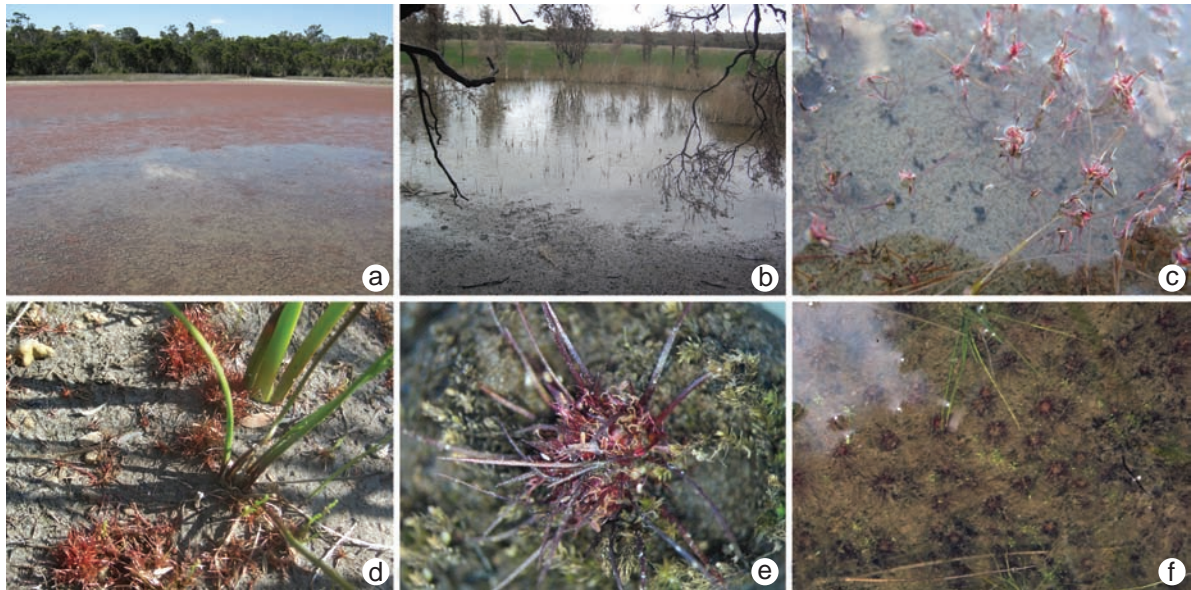


Fig. 9. *Trithuria* species in southwest Western Australia. a & b. Habitats of *T. austinensis*. a. Lake "Branchinella"; b. Tolkerlup swamp; c. Flowering of submerged plants of *T. austinensis* with exposed reproductive units (Tolkerlup Swamp, Unicup Nature Reserve, about 64 km ESE of Manjimup, 26 Oct. 2006, *Macfarlane & Tuckett TDM 3988*, PERTH); d & e. *T. bibraceata* (15.1 km N of Manjimup, 24 Oct. 2006, *Macfarlane 3903*); f. *T. australis* (4 km S of Tone Bridge settlement along Wingebellup Road, about 50 km E of Manjimup, 15 Dec. 1999, *Macfarlane & Hearn TDM 3357*, PERTH).

submersa apparently prefers areas with higher mean daily maximum temperatures in summer than *T. filamentosa*. According to Duretto (2011), *T. submersa* is localized but sometimes abundant in marshes, roadside soaks or on the margins of lakes and lagoons, flowering and/or fruiting in September to January. *Trithuria filamentosa* is localized and uncommon on the Central Plateau and Mount Field, where it is usually found submerged in shallows of alpine lakes and tarns; in the south-west it is also often found on stream margins and in swamps (Cooke, 1987; Duretto, 2011). Flowering and fruiting of *T. filamentosa* is reported for December to April (Duretto, 2011). Abnormal pollen morphology found in *T. filamentosa* suggests the possible occurrence of apomixis, as in another perennial species, *T. inconspicua*. The two perennial species are morphologically and ecologically close to each other.

Ecology of *Trithuria inconspicua* in New Zealand

The perennial species *T. inconspicua* grows in permanent lakes of the northern part of North Island (Northland) and the extreme south of South Island of New Zealand (Edgar, 1966; Pledge, 1974; Wells *et al.*, 1998). The strong predominance of plants lacking stamens, abundant fruit set and abnormal

pollen morphology in plants that produce male reproductive units are indirect (but strong) arguments suggesting apomictic reproduction in *T. inconspicua* (Hamann, 1975; Remizowa *et al.*, 2008; Rudall *et al.*, 2008).

In Northland, *T. inconspicua* grows in lakes situated behind the coastal sand dunes along the western coast of the island (Cheeseman, 1906b). It was initially collected in 1902 growing in sand on the shore of Lake Ngatu, submerged except in a dry season (see Edgar, 1966). Subsequent discoveries in other lakes of Northland showed that plants (which are about an inch high) can grow and flower completely submerged in four inches of water (Edgar, 1966). Pledge (1974) reported *T. inconspicua* growing at a depth of 1.15 m, which was the limit of visibility from the surface.

Pledge (1974) reported the apparent disappearance of the species from two of the five previously recorded sites in Northland. He speculated that the apparent disappearance from these localities could be because the land around these lakes has undergone a change of usage from raising sheep to cattle since the original discovery in the 1950s. Tanner (1992) investigated in detail the cattle-grazing effects on lake margin vegetation in dune lakes of Northland. He concluded that sites with light to moderate grazing pressure were associated with more open inshore sedge zones (and reduced

litter accumulation) showing an increased diversity and abundance of short shallow-water species including the endangered *T. inconspicua*. The ecosystems of dune lakes in Northland are critically sensitive to biological invasions. *Trithuria inconspicua* is reported as apparently extinct in Lake Waingata (with invasive *Elodea canadensis*), though seed bank studies have demonstrated the presence of its seeds there (Champion *et al.*, 1993, cit. after Rowe & Champion, 1994). In 1993, *T. inconspicua* was known to be present in ten lakes in Northland and it was regarded as locally common in only six (Champion *et al.*, 1993, cit. after Wells *et al.*, 1998).

In South Island, the species was first discovered in 1993 during an investigation of submerged vegetation of lakes in Fiordland National Park, Southland, where it was found in five lakes (Wells *et al.*, 1998). In spite of the strong geographical gap between northern and southern populations of *T. inconspicua* (more than 1000 km), no obvious morphological characters were found to distinguish between the northern and southern plants (Sokoloff *et al.*, 2008b). Male reproductive units are so far not known for southern plants, but this may be due to differences in sampling and the lack of special attempts to find plants with stamens. The relative abundance of *T. inconspicua* in different lakes varies. It was found in 20% of profiles in Lake Hauroko and in 8% of profiles in Lake Te Anau, but it was very rare in Lake Manapouri and apparently absent from Lake Monowai (Wells *et al.*, 1998). The authors speculated that the 2.8 m rise in water level in 1926 would have drowned most suitable habitats for *T. inconspicua* at that time (Wells *et al.*, 1998). In Southland, *T. inconspicua* grows in notably cooler water and coarser sediments than in Northland; its depth range in Southland lakes is 0.3 – 2.0 m (Wells *et al.*, 1998).

Wells *et al.* (1998) suggested that the species is unlikely to be present in the Central Otago lakes in a region of South Island adjacent to Southland, which raises a question of the historical biogeography of *T. inconspicua*. Johnson & Rogers (2003) indicated the rare occurrence of *T. inconspicua* in ephemeral wetlands in the Otago region, but the record should actually apply to Fiordland lake shores (P.N. Johnson, Dec. 2011, pers. comm.). So far, *T. inconspicua* is only documented for Southland in South Island.

The species endemic to New Zealand is threatened in the country (de Lange *et al.*, 2004). However, there are reports that *T. inconspicua* is fairly abundant, at least in some lakes, and both Edgar (1966) and Pledge (1974) were able to examine hundreds of individuals during a search for the rare male

inflorescences. According to Wells *et al.* (1998), the discovery of southern populations of the species means that it should no longer be considered endangered.

Outlook

Following the discovery that Hydatellaceae belongs to a basal angiosperm lineage (Saarela *et al.*, 2007), our knowledge of many aspects of the taxonomy, comparative and evolutionary morphology and ecology of the family has increased exponentially. Nevertheless, several important issues remain to be studied. In particular, we believe that the geographical range and taxonomic diversity of Hydatellaceae might be currently underestimated. We hope that this review will stimulate field botanists in various countries for new records of these highly unusual and interesting plants.

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Literature Cited

- APG (Angiosperm Phylogeny Group), 1998.** An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* **85**: 531 – 553.
- APG (Angiosperm Phylogeny Group), 2003.** An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *J. Linn. Soc., Bot.* **141**: 399 – 436.
- APG (Angiosperm Phylogeny Group), 2009.** An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *J. Linn. Soc., Bot.* **161**: 105 – 121.
- Behnke, H.-D. 1995.** P-type plastids and the systematics of the Arales (sensu Cronquist 1988) with S-type plastids in *Pistia*. *Pl. Syst. Evol.* **195**: 87 – 119.
- Behnke, H.-D. 2000.** Forms and sizes of sieve-element plastids and evolution of the monocotyledons. In: Wilson, K.L. & D.A. Morrison (Ed.), *Monocots. Systematics and Evolution*. Melbourne. pp. 163 – 188.

- Bentham, G. 1878.** *Flora of Australia*. Vol. 7. L. Reeve & Co. Ltd., London.
- Bortenschlager, S., Erdtman, G. & J. Pragłowski 1966.** Pollenmorphologische Notizen über einige Blütenpflanzen incertae sedis. *Bot. Not.* **119**: 160 – 168.
- Bremer, K. 2002.** Gondwanan evolution of the grass alliance of families (Poales). *Evolution* **56**: 1374 – 1387.
- Briggs, B.G. & H.P. Linder 2009.** A new subfamilial and tribal classification of Restionaceae (Poales). *Telopea* **12**: 333 – 345.
- Briggs, B.G., Marchant, A.D., Gilmore, S. & C.L. Porter 2000.** A molecular phylogeny of Restionaceae and allies. In: Wilson, K.L. & D.A. Morrison (Ed.), *Monocots: Systematics and Evolution*. CSIRO Publishing, Collingwood. pp. 661 – 671.
- Briggs, B.G., Marchant, A.D. & A.J. Perkins 2010.** Phylogeny and features in Restionaceae, Centrolepidaceae and Anarthriaceae (Restiid Clade of Poales). In: Seberg, O., Petersen, G., Barfod, A. & J.I. Davis (Ed.), *Diversity, Phylogeny, and Evolution in the Monocotyledons*. Aarhus University Press, Aarhus. pp. 357 – 388.
- Bull-Hereñu, K. & R. Claßen-Bockhoff 2011.** Ontogenetic course and spatial constraints in the appearance and disappearance of the terminal flower in inflorescences. *Int. J. Pl. Sci.* **172**: 471 – 498.
- Carlquist, S. & Schneider, E.L. 2009.** Do tracheid microstructure and the presence of minute crystals link Nymphaeaceae, Cabombaceae and Hydatellaceae? *J. Linn. Soc., Bot.* **159**: 572 – 582.
- Chase, M.W., Fay, M.F., Devey, D.S., Maurin, O., Rønsted, N., Davies, J., Pillon, Y., Petersen, G., Seberg, O., Tamura, M.N., Asmussen, C.B., Hilu, K., Borsch, T., Davis, J.I., Stevenson, D.W., Pires, J.C., Givnish, T.J., Sytsma, K.J., Mcpherson, M.M., Graham, S.W. & H.S. Rai 2006.** Multi-gene analyses of monocot relationships: a summary. *Aliso* **22**: 63 – 75.
- Cheeseman, T.F. 1906a.** *Manual of the New Zealand Flora*. Government Printer, Wellington.
- Cheeseman, T.F. 1906b.** Notice on the occurrence of *Hydatella*, a genus new to the New Zealand flora. *Trans. New Zeal. Inst.* **39**: 433 – 434.
- Conn, B.J. 1993.** Hydatellaceae. In: Harden, G.J. (Ed.), *Flora of New South Wales*. Vol. 4. New South Wales University Press, NSW Australia. pp. 265 – 266.
- Conran, J.C. 2011.** Hydatellaceae. In: Kellermann, J. (Ed.), *Flora of South Australia* (ed. 5). 3 pp. (State Herbarium of South Australia: Adelaide). www.flora.sa.gov.au/ed5.
- Cooke, D.A. 1981.** New species of *Schoenus* (Cyperaceae) and *Trithuria* (Hydatellaceae). *Muelleria* **4**: 299 – 303.
- Cooke, D.A. 1983.** Two Western Australian Hydatellaceae. *Muelleria* **5**: 123 – 125.
- Cooke, D.A. 1987.** Hydatellaceae. In: George, A.S. (Ed.), *Flora of Australia*. Vol. 45. Hydatellaceae to Liliaceae. Australian Government Publishing Service, Canberra. pp. 1 – 5.
- Cooke, D.A. 1992.** A taxonomic revision of *Centrolepis* (Centrolepidaceae) in Australia. *J. Adelaide Bot. Gard.* **15**: 1 – 63.
- Cronquist, A. 1981.** *An integrated system of classification of flowering plants*. Columbia University Press, New York.
- Cutler, D.F. 1969.** *Anatomy of the Monocotyledons. IV. Juncales*. Oxford University Press, Oxford.
- Dahlgren, R.M.T., Clifford, H.T. & P.F. Yeo 1985.** *The Families of the Monocotyledons*. Springer, Berlin.
- Davis, J.I., Stevenson, D.W., Petersen, G., Seberg, O., Campbell, L.M., Freudenstein, J.V., Goldman, D.H., Hardy, C.R., Michelangeli, F.A., Simmons, M.P., Specht, C.D., Vergara-Silva, F. & M. Gandolfo 2004.** A phylogeny of the monocots, as inferred from *rbcL* and *atpA* sequence variation, and a comparison of methods for calculating jackknife and bootstrap values. *Syst. Bot.* **29**: 467 – 510.
- Diels, L. & Pritzel, E. 1904 – 1905.** *Fragmenta Phytographiae Australiae occidentalis. Beiträge zur Kenntnis der Pflanzen Westaustraliens, ihrer Verbreitung und ihrer Lebens-Verhältnisse*. *Bot. Jahrb. Syst.* **35**: 55 – 662.
- Doyle, J.A. 2008.** Integrating molecular phylogenetic and paleobotanical evidence on origin of the flower. *Int. J. Pl. Sci.* **169**: 816 – 843.
- Doyle, J.A. & Endress, P.K. 2000.** Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. *Int. J. Pl. Sci.* **161**(Suppl.): S121 – S153.
- Doyle, J.A. & P.K. Endress 2010.** Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: Magnoliidae and Eudicots. *J. Syst. Evol.* **48**: 1 – 35.

- Doyle, J.A. & P.K. Endress 2011. Tracing the evolutionary diversification of the flower in basal angiosperms. In: Wanntorp, L. & L.R. de Craene (Ed.), *Flowers on the Tree of Life*. Cambridge University Press, Cambridge. pp. 88 – 119
- Duretto, M.F. 2011. 1. Hydatellaceae, 2011: 1. In: Duretto, M.F. (Ed.), *Flora of Tasmania*. Online. 4 pp. Tasmanian Herbarium, Tasmanian Museum & Art Gallery, Hobart. www.tmag.tas.gov.au/floratasmania
- Edgar, E. 1966. The male flowers of *Hydatella inconspicua* (Cheesem.) Cheesem. (Centrolepidaceae). *New Zealand J. Bot.* 4: 153 – 158.
- Endress, P.K. 1987. The Chloranthaceae: Reproductive structures and phylogenetic position. *Bot. Jahrb. Syst.* 109: 153 – 226.
- Endress, P.K. 2005. Carpels of *Brasenia* (Cabombaceae) are completely ascidiate despite a long stigmatic crest. *Ann. Bot.* 96: 209 – 215.
- Endress, P.K. 2010. Disentangling confusions in inflorescence morphology: Patterns and diversity of reproductive shoot ramification in angiosperms. *J. Syst. Evol.* 48: 225 – 239.
- Endress, P.K. & J.A. Doyle 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. *Amer. J. Bot.* 96: 22 – 66.
- Friedman, W.E. 2008. Hydatellaceae are water lilies with gymnospermous tendencies. *Nature* 453: 94 – 97.
- Friis, E.M., Crane, P.R. & K.R. Pedersen 2011. *Early Flowers and Angiosperm Evolution*. Cambridge University Press, Cambridge.
- Friis, E.M., Doyle, J.A., Endress, P.K. & Q. Leng 2003. *Archaeofructus* – Angiosperm precursor or specialized early angiosperm? *Trends Pl. Sci.* 8: 369 – 373.
- Friis, E.M., Pedersen, K.R. & P.R. Crane 2006. Cretaceous angiosperm flowers: innovation and evolution in plant reproduction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 232: 251 – 293.
- Gilg-Benedict, C. 1930. Centrolepidaceae. In: Engler, H.G.A. & K.A.E. Prantl (Ed.), *Die Natürlichen Pflanzenfamilien*. Vol. 15a. W. Engelmann, Leipzig. pp. 27 – 33.
- Graham, S.W. & Iles, W.J.D. 2009. Different gymnosperm outgroups have (mostly) congruent signal regarding the root of flowering plant phylogeny. *Amer. J. Bot.* 96: 216 – 227.
- van der Ham, R.W.J.M., van Konijnenburg-van Cittert, J.H.A., Kieft, B.N. & A.W. Sachs 2011. *Mosacaulis spinifer* gen. et sp. nov.: An enigmatic Maastrichtian plant. *Rev. Palaeobot. Palynol.* 168: 51 – 67.
- Hamann, U. 1975. Neue Untersuchungen zur Embryologie und Systematik der Centrolepidaceae. *Bot. Jahrb. Syst.* 96: 154 – 191.
- Hamann, U. 1976. Hydatellaceae – A new family of Monocotyledoneae. *New Zeal. J. Bot.* 14: 193 – 196.
- Hamann, U., Kaplan, K. & T. Rübsamen 1979. Über die Samenschalenstruktur der Hydatellaceae (Monocotyledoneae) und die systematische Stellung von *Hydatella filamentosa*. *Bot. Jahrb. Syst.* 100: 555 – 563.
- Hieronymus, G. 1888. Centrolepidaceae. In: Engler, H.G.A. & K. Prantl (Ed.), *Die Natürlichen Pflanzenfamilien*. Bd. II, 4. W. Engelmann, Leipzig. pp. 11 – 16.
- Hofmann, C.C. & R. Zetter 2010. Upper Cretaceous sulcate pollen from the Timerdyakh Formation, Vilui Basin (Siberia). *Grana* 49: 170 – 193.
- Hooker, J.D. 1858. *Flora Tasmaniae*. Vol. 2. L. Reeve & Co. Ltd., London. pp. 78 – 79.
- Hutchinson, J. 1959. *The Families of Flowering Plants*. Second Edition. Clarendon Press, Oxford.
- Iles, W.J.D., Rudall, P.J., Sokoloff, D.D., Remizowa, M.V., Lee, C., Barker, M.S., Rieseberg, L.H. & S.W. Graham 2011. Phylogenetics and Evolution of Hydatellaceae. In: *Int. Bot. Congr.* Abstract book. Melbourne. p. 8
- Iles, W.J.D., Rudall, P.J., Sokoloff, D.D., Remizowa, M.V., Macfarlane, T.D., Logacheva, M.D. & S.W. Graham. Molecular phylogenetics of Hydatellaceae (Nymphaeales): sexual-system homoplasy and a new sectional classification. *Amer. J. Bot.* (in press).
- Ji, Q., Li, H., Bowe, L.M., Liu, Y. & D.W. Taylor 2004. Early Cretaceous *Archaeofructus eoflora* sp. nov. with bisexual flowers from Beipiao, western Liaoning, China. *Acta Geol. Sin.* 78: 883 – 896.
- Johnson, P. & G. Rogers 2003. *Ephemeral wetlands and their turfs in New Zealand*. *Science for Conservation* 230. New Zealand Department of Conservation, Wellington.
- Joshi, V.C. & M.K. Janarthanam 2004. The diversity of life-form type, habitat preference and phenology of the endemics in the Goa region of the Western Ghats, India. *J. Biogeogr.* 31: 1227 – 1237.

- de Lange, P.J., Norton, D.A., Heenan, P.B., Courtney, S.P., Molloy, B.P.J., Ogle, C.C., Rance, B.D., Johnson, P.N. & R. Hitchmough 2004.** Threatened and uncommon plants of New Zealand. *New Zeal. J. Bot.* **42**: 45 – 76.
- Leroy, J.-F. 1983.** The origin of Angiosperms: An unrecognized ancestral dicotyledon, *Hedyosmum* (Chloranthales), with a strobiloid flower is living today. *Taxon* **32**: 169 – 175.
- Lock, I.E., Sokoloff, D.D. & M.V. Remizowa 2011.** Morphogenetic lability of the *Ruppia maritima* (Ruppiaceae, Alismatales) reproductive organs: from two lateral flowers to a terminal flower. *Russ. J. Dev. Biol.* **42**: 247 – 260.
- Macfarlane, T.D. & R.W. Hearn 2011.** An interesting plant community of hypo-saline seasonal lakes in the Muir-Unicup catchment, Western Australia. Australasian Plant Conservation: *J. Austral. Network Pl. Conserv.* **19**(3): 27 – 29.
- Michelangeli, F.A., Davis, J.I. & D.W. Stevenson 2003.** Phylogenetic relationships among Poaceae and related families as inferred from morphology, inversions in the plastid genome, and sequence data from the mitochondrial and plastid genomes. *Amer. J. Bot.* **90**: 93 – 106.
- Moore, M.J., Hassan, N., Gitzendanner, M.A., Bruenn, R.A., Croley, M., Vandeventer, A., Horn, J.W., Dhingra, A., Brockington, S.F., Latvis, M., Ramdial, J. Alexandre, R., Piedrahita, A., Xi, Z., Davis, C.C., Soltis, P.S. & D.E. Soltis 2011.** Phylogenetic analysis of the plastid inverted repeat for 244 species: insights into deeper-level angiosperm relationships from a long, slowly evolving sequence region. *Int. J. Pl. Sci.* **172**: 541 – 558.
- Morris, D.I. & W.M. Curtis 1974.** Recent additions to the Tasmanian Flora and some notes on nomenclature. *Rec. Queen Victoria Mus. (Tasmania)* **50**: 1 – 5.
- Pignatti, E. & S. Pignatti 1994.** Centrolepidi-Hydrocotyletea alatae, a new class of ephemeral communities in Western Australia. *J. Veg. Sci.* **5**: 55 – 62.
- Pledge, D.H. 1974.** Some observations on *Hydatella inconspicua* (Cheesem.) Cheesem. (Centrolepidaceae). *New Zeal. J. Bot.* **12**: 559 – 561.
- Prychid, C.J., Sokoloff, D.D., Remizowa, M.V., Tuckett, R.E., Yadav, S.R. & P.J. Rudall 2011.** Unique stigmatic hairs and pollen-tube growth within the stigmatic cell wall in the early-divergent angiosperm family Hydatellaceae. *Ann. Bot.* **108**: 599 – 608.
- Qiu, Y.-L., Li, L., Wang, B., Xue, J.-Y., Hendry, T.A., Li, R.-Q., Brown, J.W., Liu, Y., Hudson, G.T. & Z.-D. Chen 2010.** Angiosperm phylogeny inferred from sequences of four mitochondrial genes. *J. Syst. Evol.* **48**: 391 – 425.
- Remizowa, M.V., Choob, V.V., Lock, I.E., Sokoloff, D.D., & P.J. Rudall 2011.** Racemose inflorescences in monocots: Diversity, development and evolution. In: *XVIII Int. Bot. Congr. Melbourne*. pp. 204 – 205.
- Remizowa, M.V., Sokoloff, D.D. & K. Kondo 2010.** Early flower and inflorescence development in *Dioscorea tokoro* Makino (Dioscoreales): shoot chirality, handedness of cincinni and common tepal-stamen primordia. *Wulfenia* **17**: 77 – 97.
- Remizowa, M.V., Sokoloff, D.D., Macfarlane, T.D., Yadav, S.R., Prychid, C.J. & P.J. Rudall 2008.** Comparative pollen morphology in the early-divergent angiosperm family Hydatellaceae reveals variation at the infraspecific level. *Grana* **47**: 81 – 100.
- Rodway, L. 1898.** On *Trithuria filamentosa*. *Pap. Proc. Roy. Soc. Tasmania* **1897**: 47 – 48.
- Rowe, D.K. & P.D. Champion 1994.** Biomanipulation of plants and fish to restore Lake Parkinson: a case study and its implications. In: Collier, K.J. (Ed.), *Restoration of Aquatic Habitats. Selected papers from the second day of the New Zealand Limnological Society 1993 Ann. Confer.* New Zealand Department of Conservation. pp. 53 – 65.
- Rudall, P.J. & C.A. Furness 1997.** Systematics of *Acorus*: Ovule and anther. *Int. J. Pl. Sci.* **158**: 640 – 651.
- Rudall, P.J. & R.M. Bateman 2010.** Defining the limits of flowers: the challenge of distinguishing between the evolutionary products of simple versus compound strobili. *Philos. Trans. Roy. Soc. B* **365**: 397 – 409.
- Rudall, P.J., Remizowa, M.V., Prenner, G., Prychid, C.J., Tuckett, R.E. & D.D. Sokoloff 2009a.** Nonflowers near the base of extant angiosperms? Spatiotemporal arrangement of organs in reproductive units of Hydatellaceae and its bearing on the origin of the flower. *Amer. J. Bot.* **96**: 67 – 82.
- Rudall, P.J., Remizowa, M.V., Beer, A.S., Bradshaw, E., Stevenson, D.W., Macfarlane, T.D., Tuckett, R.E., Yadav, S.R. & D.D. Sokoloff 2008.** Comparative ovule and megagametophyte

- development in Hydatellaceae and water lilies reveal a mosaic of features among the earliest angiosperms. *Ann. Bot.* **101**: 941 – 956.
- Rudall, P.J., Eldridge, T., Tratt, J., Ramsay, M.M., Tuckett, R.E., Smith, S.Y., Collinson, M.E., Remizowa, M.V. & D.D. Sokoloff 2009b. Seed fertilization, development, and germination in Hydatellaceae (Nymphaeales): implications for endosperm evolution in early angiosperms. *Amer. J. Bot.* **96**: 1581 – 1593.
- Rudall, P.J., Sokoloff, D.D., Remizowa, M.V., Conran, J.G., Davis, J.I., Macfarlane, T.D. & D.W. Stevenson 2007. Morphology of Hydatellaceae, an anomalous aquatic family recently recognized as an early-divergent angiosperm lineage. *Amer. J. Bot.* **94**: 1073 – 1092.
- Saarela, J.M., Rai, H.S., Doyle, J.A., Endress, P.K., Mathews, S., Marchant, A.D., Briggs B.G. & S.W. Graham 2007. Hydatellaceae identified as a new branch near the base of the angiosperm phylogenetic tree. *Nature* **446**: 312 – 315.
- Sokoloff, D.D., Remizowa, M.V., Briggs, B.G. & P.J. Rudall 2009a. Shoot architecture and branching pattern in perennial Hydatellaceae (Nymphaeales). *Int. J. Pl. Sci.* **170**: 869 – 884.
- Sokoloff, D.D., Remizowa, M.V., Linder, H.P., Macfarlane, T.D. & P.J. Rudall 2010a. Arrangement of reproductive units in *Centrolepis* (Poales: Centrolepidaceae): Cincinnus or spikelet? In: Seberg, O., Petersen, G., Barfod, A. & J.I. Davis (Ed.), *Diversity, Phylogeny, and Evolution in the Monocotyledons*. Aarhus University Press, Aarhus. pp. 425 – 436.
- Sokoloff, D.D., Remizowa, M.V., Linder, H.P. & P.J. Rudall 2009b. Morphology and development of the gynoecium in Centrolepidaceae: the most remarkable range of variation in Poales. *Amer. J. Bot.* **96**: 1925 – 1940.
- Sokoloff, D.D., Remizowa, M.V., Macfarlane, T.D. & P.J. Rudall 2008b. Classification of the early-divergent angiosperm family Hydatellaceae: One genus instead of two, four new species and sexual dimorphism in dioecious taxa. *Taxon* **57**: 179 – 200.
- Sokoloff, D.D., Remizowa, M.V., Macfarlane, T.D., Tuckett, R.E., Ramsay, M.M., Beer, A.S., Yadav, S.R. & P.J. Rudall 2008a. Seedling diversity in Hydatellaceae: implications for the evolution of angiosperm cotyledons. *Ann. Bot.* **101**: 153 – 164.
- Sokoloff, D.D., Remizowa, M.V. & P.J. Rudall 2009c. A new species of *Centrolepis* (Centrolepidaceae: Poales) from Northern Australia, with remarkable inflorescence architecture. *Bot. Zh.* **94**: 92 – 100.
- Sokoloff, D.D., Remizowa, M.V., Yadav, S.R. & P.J. Rudall 2010b. Development of reproductive structures in the sole Indian species of Hydatellaceae, *Trithuria konkanensis*, and its morphological differences from Australian taxa. *Austral. Syst. Bot.* **23**: 217 – 228.
- Sokoloff, D.D., Rudall, P.J. & M.V. Remizowa 2006. Flower-like terminal structures in racemose inflorescences: a tool in morphogenetic and evolutionary research. *J. Exp. Bot.* **57**: 3517 – 3530.
- Soltis, D.E., Smith, S.A., Cellinese, N., Wurdack, K.J., Tank, D.C., Brockington, S.F., Refulio-Rodriguez, N.F., Walker, J.B., Moore, M.J., Carlswald, B.S., Bell, C.D., Latvis, M., Crawley, S., Black, C., Diouf, D., Xi, Z., Rushworth, C.A., Gitzendanner, M.A., Sytsma, K.J., Qiu, Y.-L., Hilu, K.W., Davis, C.C., Sanderson, M.J., Beaman, R.S., Olmstead, R.G., Judd, W.S., Donoghue, M.J. & P.S. Soltis 2011. Angiosperm Phylogeny: 17 genes, 640 taxa. *Amer. J. Bot.* **98**: 704 – 730.
- Stevenson, D.V., Davis, J.I., Freudenstein, J.V., Hardy, C.R., Simmons, M.P. & C.D. Specht 2000. A phylogenetic analysis of monocotyledons based on morphological and molecular character sets, with comments on the placement of *Acorus* and Hydatellaceae. In: Wilson, K.L. & D.A. Morrison (Ed.), *Monocots: Systematics and Evolution*. CSIRO, Collingwood. pp. 17 – 24.
- Stevenson, D.W. & H. Loconte 1995. Cladistic analysis of monocot families. In: Rudall, P.J., Cribb, P.J., Cutler, D.F. & C.J. Humphries (Ed.), *Monocotyledons: Systematics and Evolution*. Royal Botanic Gardens, Kew. pp. 543 – 578.
- Sun, G., Dilcher, D.L., Zheng, S. & Z. Zhou 1998. In search of the first flower: A Jurassic angiosperm, *Archaeofructus*, from northeast China. *Science* **282**: 1692 – 1695.
- Sun, G., Ji, Q., Dilcher, D.L., Zheng, S., Nixon, K.C. & X. Wang 2002. Archaeofructaceae, a new basal angiosperm family. *Science* **296**: 899 – 904.
- Sun, G., Zheng, S., Dilcher, D.L., Wang, Y. & S. Mei 2001. *Early Angiosperms and their associated plants from western Liaoning, China*. Scientific and Technological Education Publishing House, Shanghai.
- Takhtajan, A. 1987. *Systema Magnoliophytorum*. Nauka, Leningrad.

- Takhtajan, A. 2009.** *Flowering Plants*. Second Edition. Springer, New York.
- Tanner, C.C. 1992.** A review of cattle grazing effects on lake margin vegetation with observations from dune lakes in Northland, New Zealand. *New Zeal. Nat. Sci.* **19**: 1 – 14.
- Taylor, M.L., Macfarlane, T.D. & J.H. Williams 2010.** Reproductive ecology of the basal angiosperm *Trithuria submersa* (Hydatellaceae). *Ann. Bot.* **106**: 909 – 920.
- Tillich, H.-J. 2007.** Seedling diversity and the homologies of seedling organs in the order Poales (Monocotyledons). *Ann. Bot.* **100**: 1413 – 1429.
- Tillich, H.-J., Tuckett, R. & E. Facher 2007.** Do Hydatellaceae belong to the monocotyledons or basal angiosperms? Evidence from seedling morphology. *Willdenowia* **37**: 399 – 406.
- Tratt, J., Prychid, C.J., Behnke, H.-D. & P.J. Rudall 2009.** Starch-accumulating (S-type) sieve-element plastids in Hydatellaceae: implications for plastid evolution in flowering plants. *Protoplasma* **237**: 19 – 26.
- Tuckett, R.E., Merritt, D.J., Hay, F.R., Hopper, S.D. & K.W. Dixon 2010a.** Comparative longevity and low-temperature storage of seeds of Hydatellaceae and temporary pool species of south-west Australia. *Austral. J. Bot.* **58**: 327 – 334.
- Tuckett, R.E., Merritt, D.J., Rudall, P.J., Hay, F., Hopper, S.D., Baskin, C.C., Baskin, J.M., Tratt, J. & K.W. Dixon 2010b.** A new type of specialized morphophysiological dormancy and seed storage behaviour in Hydatellaceae, an early-divergent angiosperm family. *Ann. Bot.* **105**: 1053 – 1061.
- Wells, R.D.S., Clayton, J.S. & M.D. Winton de 1998.** Submerged vegetation of Lakes Te Anau, Manapouri, Monowai, Hauroko, and Poteriteri, Fiordland, New Zealand. *New Zeal. J. Mar. Freshwater Res.* **32**: 621 – 638.
- Winter, A.N. & I.I. Shamrov 1991a.** The development of the ovule and embryo sac in *Nuphar lutea* (Nymphaeaceae). *Bot. Zh.* **76**: 378 – 390.
- Winter, A.N. & I.I. Shamrov 1991b.** Megasporogenesis and embryo sac development in representatives of the genera *Nymphaea* and *Victoria* (Nymphaeaceae). *Bot. Zh.* **76**: 1716 – 1728.
- Yadav, S.R. & M.K. Janarthanam 1994.** Hydatellaceae: A new family to Indian Flora with a new species. *Rheedea* **4**: 17 – 20.
- Yadav, S.R. & M.K. Janarthanam 1995.** *Trithuria konkanensis* (Hydatellaceae), eine neue Art aus Indien. *Aqua-Planta* **3**: 91 – 97.

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