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Seeds and indehiscent fruit of Anarthriaceae and Australian Restionaceae (Poales): a gallery of micromorphology

Barbara G. Briggs and Carolyn L. Connelly

Australian Institute of Botanical Science, Royal Botanic Gardens and Domain Trust,
Sydney, Australia 2000
Author for correspondence: barbara.briggs@botanicgardens.nsw.gov.au

Abstract

The diaspores of Anarthriaceae and Australian Restionaceae are seeds or small nuts and are illustrated by scanning electron microscopy or multi-focus microscopy. Their morphology is considered in relation to a previously published phylogeny based on plastid genes. Loculicidal trilocular capsular fruits are the basal condition in the restiid clade, but indehiscent fruits have evolved many times. In the Australasian members, indehiscent fruits are found in Anarthriaceae (*Hopkinsia*); Restionaceae: Centrolepidoideae (*Aphelia*); Sporadanthoideae (*Calorophus*); Leptocarpoideae (*Empodisma*, *Winifredia* and the whole of the *Leptocarpus* and *Desmocladus* clades). Seeds of dehiscent fruits show a diversity of surface ornamentation with distinctive surface patterns characterising genera such as *Lyginia*, *Chordifex* and *Loxocarya*. Pericarps are membranous in subfam. Centrolepidoideae, but in the *Leptocarpus* clade range from hyaline in much of *Leptocarpus*, to hard and woody in *Alexgeorgea* and *Hypolaena.* Pericarps are parenchymatous in most of the *Desmocladus* clade, but woody in *Catacolea*. Indehiscent fruits are mostly shed with tepals and floral bracts attached or, in *Baloskion* and some *Lepidobolus* species, also with the subtending glume. Seed weights were not comprehensively sampled but vary from 0.08 mg in *Centrolepis* to >600 mg in *Alexgeorgea*, with most in the range 0.3–3 mg [dry weight]. The smaller weights are mostly either in perennials from habitats with more reliable rainfall or in ephemeral annuals that avoid drought by their brief growing season, but the association between seed type and habitat has not been investigated. We see no convincing evidence to link the fossil taxon *Restiocarpum* and the *Milfordia* pollen that occurs with it in Eocene–Oligocene sediments of Queensland to Restionaceae.

Introduction

With leaves mostly reduced to sheaths and small wind-pollinated flowers, Anarthriaceae and Restionaceae seem to offer limited informative morphological characters to assist in characterising taxa. Culm anatomy offers a wealth of features, with major differences especially in the epidermis, chlorenchyma and presence of silica bodies (Cutler 1969, Linder 2000, Linder *et al.* 1998, Meney and Pate 1999b, Pate and Delfs 1999). Another source of distinctive features is the surface ornamentation of seeds, as we illustrate here for Anarthriaceae and for the Australian subfamilies of Restionaceae: Centrolepidoideae, Sporadanthoideae and Leptocarpoideae. The remaining subfamily, the African Restionoideae, was studied by Linder (1984) who found 'a great range in the surface micro-morphology of the seeds'.

A phylogeny of the restiid clade of Poales (Fig. 1, derived from Briggs *et al.* 2014) provides a framework for this study and shows the clades that we refer to here. That phylogeny is based on analyses of several chloroplast genes and has led to some relatively recent changes in the generic classification (Briggs 2014a, b, Briggs *et al.* 2020a, b, 2020–2021). Anarthriaceae is recognised here at family rank as the sister group to the Restionaceae (Briggs *et al.* 2014). The latest Angiosperm Phylogeny Group classification, APG IV (2016), took a different view, including Anarthriaceae in Restionaceae. Hochbach *et al.* (2018) gave no phylogenetic support for or against including the *Anarthria* clade in Restionaceae but Givnish *et al.* (2018) advocated recognising Anarthriaceae sister to Restionaceae.

Materials and methods

This study proceeded intermittently over a considerable time, so the technology conveniently available to us changed over time. Most of the study used SEM with the following procedure: whole mature seeds were extracted from dried herbarium sheets. Seeds were readily extracted from fruit with membranous or parenchymatous pericarp, but with more difficulty from fruits with a woody pericarp. Standard SEM pin stub mounts, 12.7 mm surface diameter (product number G040 ProSciTech, Thuringowa, Qld. Australia), were used and self-adhesive sticky tabs (P/N IA022 ProSciTech) applied to the surface of the stub. The paper backing was peeled off before seeds were placed onto the adhesive tape. Prepared mounted stubs were coated in an EmiTech K550X sputter coater, using an energised gold target in an argon atmosphere. Default settings were used with a coating time of 3 minutes resulting in a gold layer approximately 21 nm (210 Angstroms) thick. Seeds were examined using a Cambridge S360 SEM with a backscattered electron detector. Photographs were taken on film and thumbnail positive prints of the images scanned with a Microtek ScanMaker 9800XL. Some images were from earlier work by Prabha Gupta or others using an ISI 40 SEM and scanned prints are shown here. Other SEMs were imaged for us by Sue Lindsay, Microscopy Unit Manager at Macquarie University. Colour photos are from a Leica M125 multi-focus stereo dissector and Leica DFC295 camera.

Voucher specimens are held in the NSW herbarium except where otherwise indicated. The species illustrated, authorities, vouchers and source of the images are listed in Table 1. Full collection details are available at the Atlas of Living Australia (www.ala.org.au). Photographs of seeds of some taxa have previously been published (Briggs and Johnson 1999, 2004, 2012); some of these are repeated to give a more comprehensive coverage here. The sequence in which the images are placed (in Figs 2–13) and the taxa discussed largely follows the order in which the branches arise in the cladogram (Fig. 1), but with multi-focus images (Figs 12 and 13) separate from SEM images.

The mass of some seeds and fruits, dissected from dry voucher specimens, was determined using a Mettler Toledo ME204 balance sensitive to 0.1 mg. Where a number of seeds or fruits were available these were weighed together to give an average weight. Standard deviations for the measurements were not determined because few seeds were available for most species and therefore only general comparisons were sought.

Most of the scanning electron microscopy was done by one of us (CC), with the other (BB) responsible for collecting many of the specimens, multi-focus photography and assembling the manuscript. We did not investigate the chemical composition of the surface structures nor generally the underlying cellular structure where it was obscured by surface features.

Table 1. Taxa studied for seeds or fruit, voucher specimens, relevant figures, and source of images.

Taxon	Voucher	NSW accession[1]	Figs	Image[2]
Alexgeorgea nitens (Nees) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 6759	406919	12a, b	BB
Anarthria barbata R.Br.	B.G. Briggs 9602b	716658	–	–
Anarthria dioica (Steud.) C.I.Fomichev	B.G. Briggs 7654	406590	2c, d	CC
Anarthria humilis Nees	P.G. Wilson 5414	101312	2e, f	CC
Anarthria polyphylla Nees	B.G. Briggs 8510	212695	2g, h	CC
Anarthria prolifera R.Br.	R. Melville 4435	406671	2i, j	CC
Anarthria scabra R.Br.	K. Hill 4554	279690	2a	CC
Anarthria scabra	R. Melville 4416	406560	2b	CC
Aphelia cyperoides R.Br	S.W.L. Jacobs 6932	293103	3e, f	SL
Apodasmia brownii (Hook.f.) B.G.Briggs & L.A.S.Johnson	A.C. Beauglehole 1999	96033	6m, n, o	SL
Apodasmia ceramophila B.G.Briggs & L.A.S.Johnson	K. Meney 912	382910	7a	SL
Baloskion gracile (R.Br.) B.G.Briggs & L.A.S.Johnson	O.D. Evans s.n.	54119	10g, h	PG

Taxon	**Voucher**	**NSW accession[1]**	**Figs**	**Image[2]**
Baloskion pallens (R.Br.) B.G.Briggs & L.A.S.Johnson	L.A.S. Johnson 8656	367690	10e, f	CC
Baloskion stenocoleum (L.A.S.Johnson & O.D.Evans) B.G.Briggs & L.A.S.Johnson	O.D. Evans s.n.	61054	10i	CC
Baloskion tenuiculme (S.T.Blake) B.G.Briggs & L.A.S.Johnson	L.A.S. Johnson s.n.	55370	10j, k	PG
Baloskion tetraphyllum (Labill.) B.G.Briggs & L.A.S.Johnson ssp. *meiostachyum* L.A.S.Johnson & O.D.Evans	E.F. Constable s.n.	48995	10 l	PG
Baloskion tetraphyllum (Labill.) B.G.Briggs & L.A.S.Johnson ssp. *tetraphyllum*	D.A & D.V. Ratkowsky 1213	368012	10m, n	PG
Baloskion tetraphyllum (Labill.) B.G.Briggs & L.A.S.Johnson ssp. *tetraphyllum*	D.A & D.V. Ratkowsky 1213	368012	10o	SL
Calorophus elongatus Labill.	B.G. Briggs 7062	252353	12c	BB
Calorophus erostris (C.B.Clarke) L.A.S.Johnson& B.G.Briggs	B.G. Briggs 9107	264692	6d	SL
Calorophus erostris	B.G. Briggs 7020	1003819	12d	BB
Catacolea enodis B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7729	391577	11a, b, c	CC
Centrolepis fascicularis Labill.	P.H. Raven 25926	655460	3c, d	SL
Chaetanthus aristatus (R.Br.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 812	94746	12f	BB
Chaetanthus tenellus (Nees) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 589	95201	12g	BB
Chordifex abortivus (Nees) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8702	233041	9f, g	CC
Chordifex amblycoleus (F.Muell.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7575	413911	8m, n	PG
Chordifex capillaceus B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7662	395790	9e	PG
Chordifex chaunocoleus (F.Muell) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8636	232591	9j, k	CC
Chordifex dimorphus (R.Br.) B.G.Briggs & L.A.S.Johnson	E.F. Constable s.n.	48845	9a, b	CC
Chordifex fastigiatus (R.Br.) B.G.Briggs & L.A.S.Johnson	R.H. Cambage 413	47822	9c, d	CC
Chordifex isomorphus (K.W.Dixon & Meney) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7648a	413549	8k, l	PG
Chordifex jacksonii B.G.Briggs & L.A.S.Johnson	S. Pignatti s.n.	876732	8g, h	CC
Chordifex laxus (R.Br.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 664a	96216	8o	PG
Chordifex microcodon B.G.Briggs & L.A.S.Johnson	B.G. Briggs 852	95101	8i, j	CC
Chordifex sinuosus B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7445	446290	9h, i	JE
Coleocarya gracilis S.T.Blake	S.T. Blake 13177	48420	11d	CC
Coleocarya gracilis	D.F. Blaxell 139	380560	11e	CC
Cytogonidium leptocarpoides (Benth.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 525	94300	9n, o	CC
Dapsilanthus elatior (R.Br.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7299	362444	7b	CC
Desmocladus castaneus B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8475b	212594	11j, k	CC
Desmocladus confertospicatus (Steud.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8704	233048	11i	CC
Desmocladus elongatus B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7483	256891	11 l	PG
Desmocladus elongatus	B.G. Briggs 7489	252388	13e	BB
Desmocladus eyreanus B.G.Briggs & L.A.S.Johnson	S.W.L. Jacobs 7046	281816	11f	CC
Desmocladus laxiflorus (Steud.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 6606	391585	11g, h	CC
Desmocladus myriocladus (Gilg) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7781	256967	11m	CC
Desmocladus parthenicus B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8607	233339	11n, o	SL
Desmocladus quiricanus B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7920	209348	13f	BB
Dielsia stenostachya (W.Fitzg.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 9030	1099056	9 l, m	CC
Empodisma gracillimum (F.Muell). L.A.S.Johnson & D.F.Cutler	B.G. Briggs 10079	870968	12e	BB
Eurychorda complanata (R.Br.) B.G.Briggs & L.A.S.Johnson	A.B. Rose 18	391889	6e, f	CC
Gaimardia setcea Hook.f.	B.G. Briggs 9515	494431	3a, b	SL
Hopkinsia anoectocolea (F.Muell.) D.F.Cutler	B.G. Briggs 6407A	406888	2o	JP
Hopkinsia anoectocolea	B.G. Briggs 7624	299309	2n	CC
Hypolaena caespitosa B.G.Briggs & L.A.S.Johnson	B.G. Briggs 6731	265266	6i	CC
Hypolaena exsulca R.Br.	B.G. Briggs 8581	233287	6 l	CC
Hypolaena grandiuscula F.Muell.	B.G. Briggs 8444b	213095	6g	CC
Hypolaena humilis (Gilg) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7832	265375	6h	CC
Hypolaena pubescens (R.Br.) Nees	K. Meney s.n.	254915	6j	CC

Taxon	**Voucher**	**NSW accession**[1]	**Figs**	**Image**[2]
Hypolaena viridis B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8359a	264041	6k	CC
Lepidobolus preissianus Nees	B.G. Briggs 6762B	299723	13a	BB
Lepidobolus preissianus	B.G. Briggs 7494	299467	13b	BB
Leptocarpus decipiens B.G.Briggs	B.G. Briggs 6737	299926	12k	BB
Leptocarpus denmarkicus (Suesseng.) B.G.Briggs	B.G. Briggs 880a	94918	12n, o	BB
Leptocarpus laxus (R.Br.) B.G.Briggs	B.G. Briggs 8675	232887	7g, h	CC
Leptocarpus scariosus (R.Br.) B.G.Briggs	B.G. Briggs 9977	784604	12 l, m	BB
Leptocarpus tenax (Labill.) R.Br	B.G. Briggs 10187	1004152	12h, i	BB
Leptocarpus thysananthus B.G.Briggs	B.G. Briggs 8698	232976	7c, d	CC
Leptocarpus thysananthus	M. Koch 2662	48036	12j	BB
Leptocarpus trisepalus (Nees) B.G.Briggs	B.G. Briggs 9060	261649	7e, f	CC
Lepyrodia anarthria F.Muell.	S. Krauss 98	210730	5g, h	CC
Lepyrodia cryptica B.G.Briggs & L.A.S.Johnson	E.F. Constable s.n.	60933	5k	CC
Lepyrodia curvescens B.G.Briggs & L.A.S.Johnson	B.G. Briggs 9018	261933	4 l, m	CC
Lepyrodia drummondiana Steud.	B.G. Briggs 7651	262351	4n, o	CC
Lepyrodia extensa B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7616	262328	6a, b	CC
Lepyrodia flexuosa (Benth.) L.A.S.Johnson & O.D.Evans	A.C. Beauglehole 22238	96075	4c	CC
Lepyrodia fortunata B.G.Briggs & L.A.S.Johnson	B. Conn 3438	226467	5a, b	CC
Lepyrodia glauca (Nees) F.Muell.	B.G. Briggs 6689	262469	4a, b	CC
Lepyrodia heleocharoides Gilg	B.G. Briggs 8355	212349	4d, e	CC
Lepyrodia hermaphrodita R.Br.	B.G. Briggs 7612	262392	6c	CC
Lepyrodia imitans B.G.Briggs & L.A.S.Johnson	S.T. Blake 1314	58317	5 l, m	CC
Lepyrodia leptocaulis L.A.S.Johnson & O.D.Evans	S.T. Blake 23673	567590	5i, j	CC
Lepyrodia monoica F.Muell.	S. Krauss 187	216922	5e, f	CC
Lepyrodia muelleri Benth.	L.A.S. Johnson s.n.	76095	4h, i	CC
Lepyrodia muirii F.Muell.	B.G. Briggs 591a	84835	4f, g	CC
Lepyrodia porterae B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8364	212362	5c, d	CC
Lepyrodia riparia B.G.Briggs & L.A.S.Johnson	B.G. Briggs 6783	260244	5e, f	PG
Lepyrodia scariosa R.Br.	B.G. Briggs 9270	280269	5n, o	CC
Lepyrodia valliculae J.M.Black	J.B. Cleland	AD968071188	4j, k	CC
Loxocarya cinerea R.Br.	B.G. Briggs 8459	212550	7m, n	CC
Loxocarya gigas B.G.Briggs & L.A.S.Johnson	B.G. Briggs 7742	259507	7o	PG
Loxocarya magna Meney & K.W.Dixon	B.G. Briggs 8668	232863	7k	CC
Loxocarya magna	B.G. Briggs 6503	259467	7 l	JP
Loxocarya striata (F.Muell) B.G.Briggs & L.A.S.Johnson subsp. *implexa* Keighery	B.G. Briggs 6666	399270	7i, j	CC
Lyginia barbata R.Br.	B.G. Briggs 9602b	716658	–	–
Lyginia excelsa B.G.Briggs & L.A.S.Johnson	B.G. Briggs 9320	391337	–	–
Lyginia imberbis R.Br.	B.G. Briggs 6671	298859	2m	CC
Lyginia imberbis	B.G. Briggs 7624	299309	2k, l	PG
Melanostachya ustulatus (F.Muell. ex Ewart & Sharman) B.G.Briggs & L.A.S.Johnson	S.W. Jackson	78862	10c, d	CC
Platychorda applanata (Spreng.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 567	94739	8e, f	PG
Sporadanthus caudatus (L.A.S.Johnson & O.D.Evans) B.G.Briggs & L.A.S.Johnson	D.J. McGillivray 2363	94592	3m	CC
Sporadanthus gracilis (R.Br.) B.G.Briggs & L.A.S.Johnson	E. McBarron 8704	65816	3i	JE
Sporadanthus rivularis B.G.Briggs & L.A.S.Johnson	B.G. Briggs 665	95036	3g, h	JE
Sporadanthus strictus (R.Br.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 6548	364397	3j, k, l	CC
Sporadanthus tasmanicus (Hook.f.) B.G.Briggs & L.A.S.Johnson	J.H. Willis s.n.	MEL501865	3n, o	PG
Tremulina cracens B.G.Briggs & L.A.S.Johnson	B.G. Briggs 6931b	413553	8a, b	CC
Tremulina tremula (R.Br.) B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8321	212284	8c, d	CC
Tyrbastes glaucescens B.G.Briggs & L.A.S.Johnson	B.G. Briggs 8349	212330	10a, b	CC

[1] Vouchers are placed in the NSW Herbarium unless another herbarium acronym is given.

[2] Images are by one of us (CC) or (BB), or by PG = Prabha Gupta, SL = Sue Lindsay, JE = Joy Everett or JP = Jocelyn Powell.

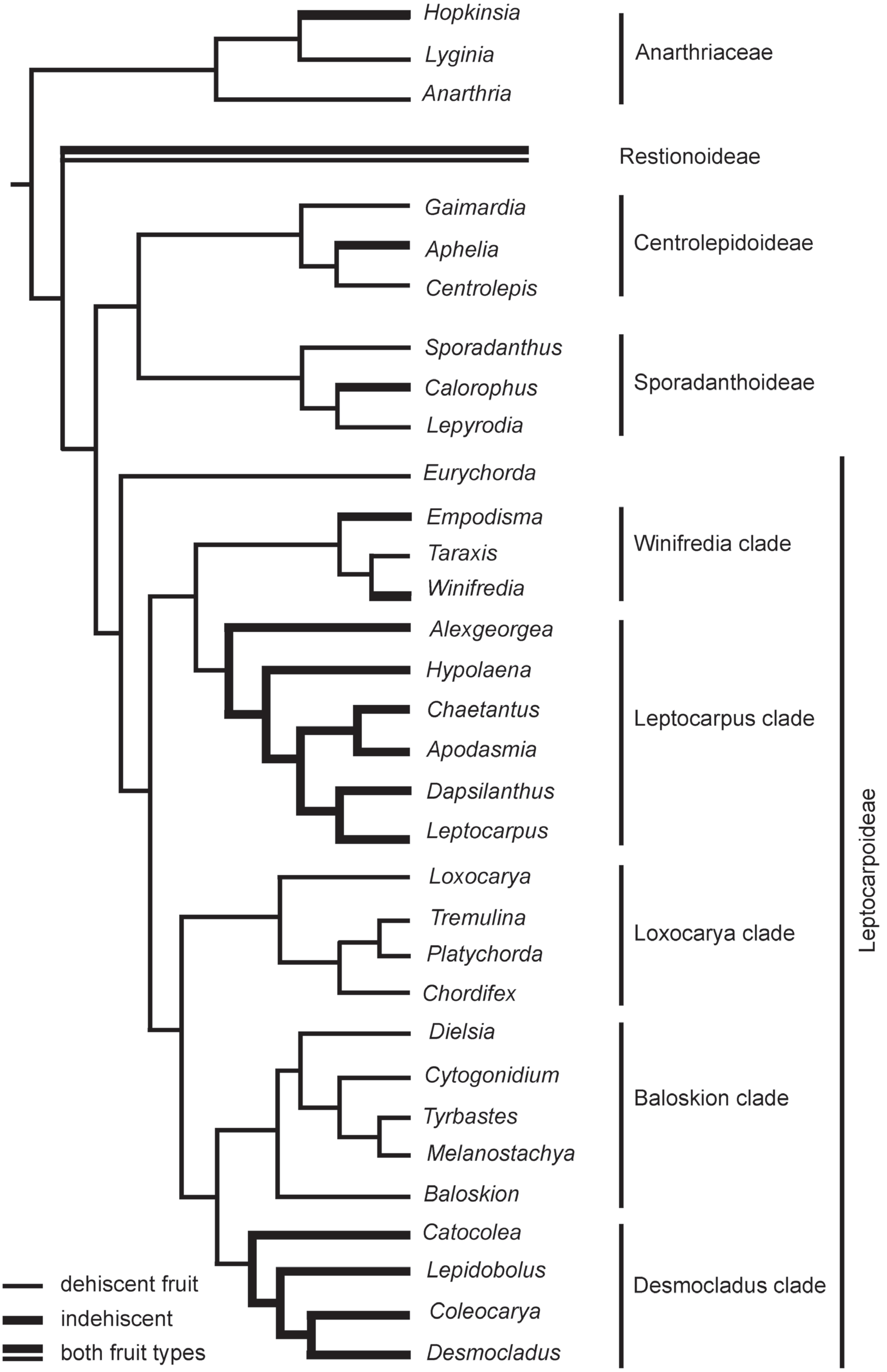

Fig. 1. Cladogram of Anarthriaceae and Restionaceae (the restiid clade of Poales) based on Bayesian analysis of chloroplast data (following Briggs *et. al.* 2014).

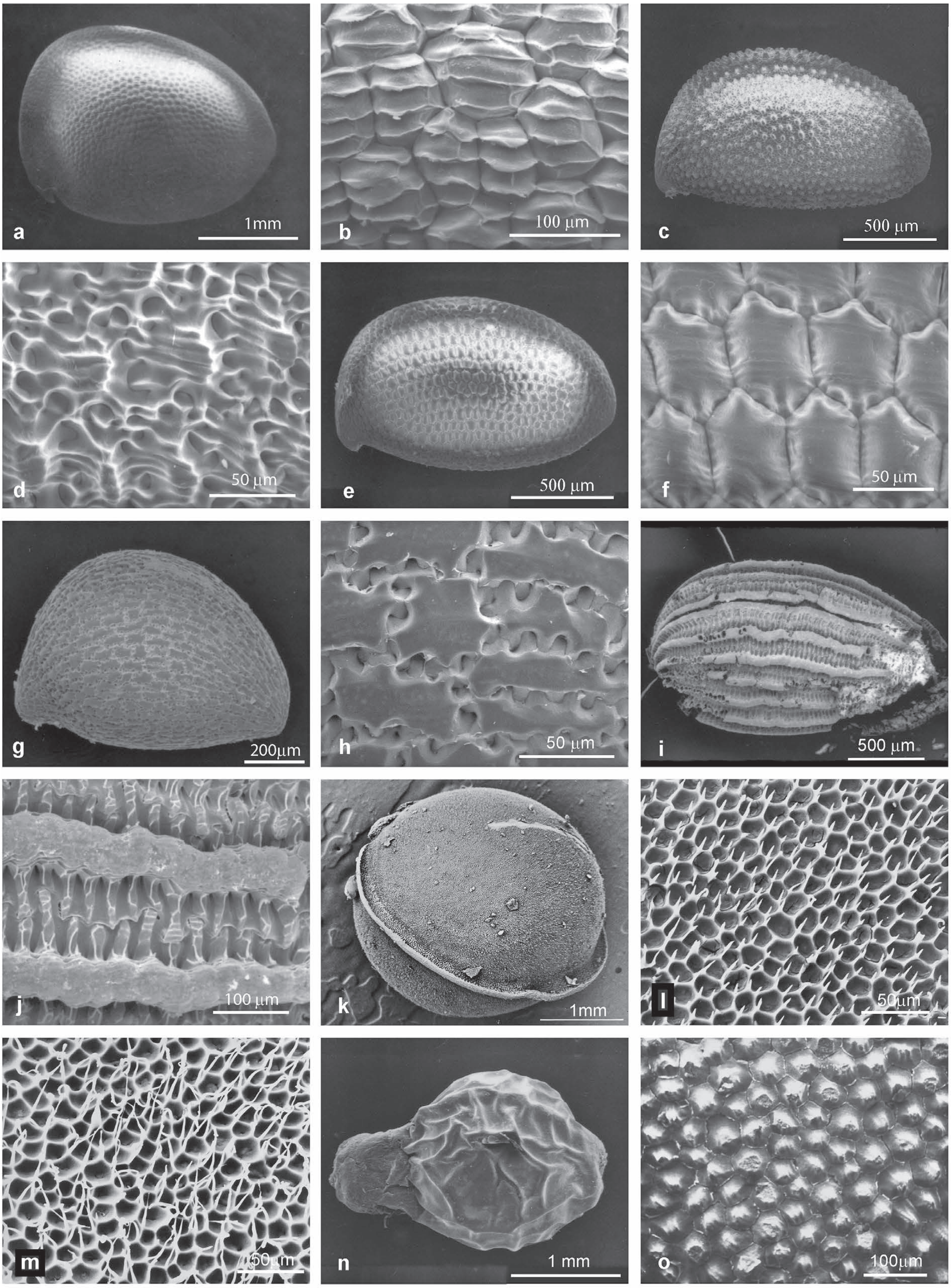

Fig. 2. Seed morphology of Anarthriaceae. Figs 2–13 show SEM images of seeds and seed surface detail unless otherwise noted. The sequence largely follows the order in which the branches arise in Fig. 1, but with multi-focus images (Figs 12, 13) separate from SEM images. Voucher specimens are listed in Table 1 and further details may be found in the *Atlas of Living Australia* (www.ala.org.au). a, b: *Anarthria scabra*. c, d: *A. dioica*. e, f: *A. humilis*. g, h: *A. polyphylla*. i, j: *A. prolifera*. k, l, m: *Lyginia imberbis*. n, o: *Hopkinsia anoectocolea*, fruit, seed surface.

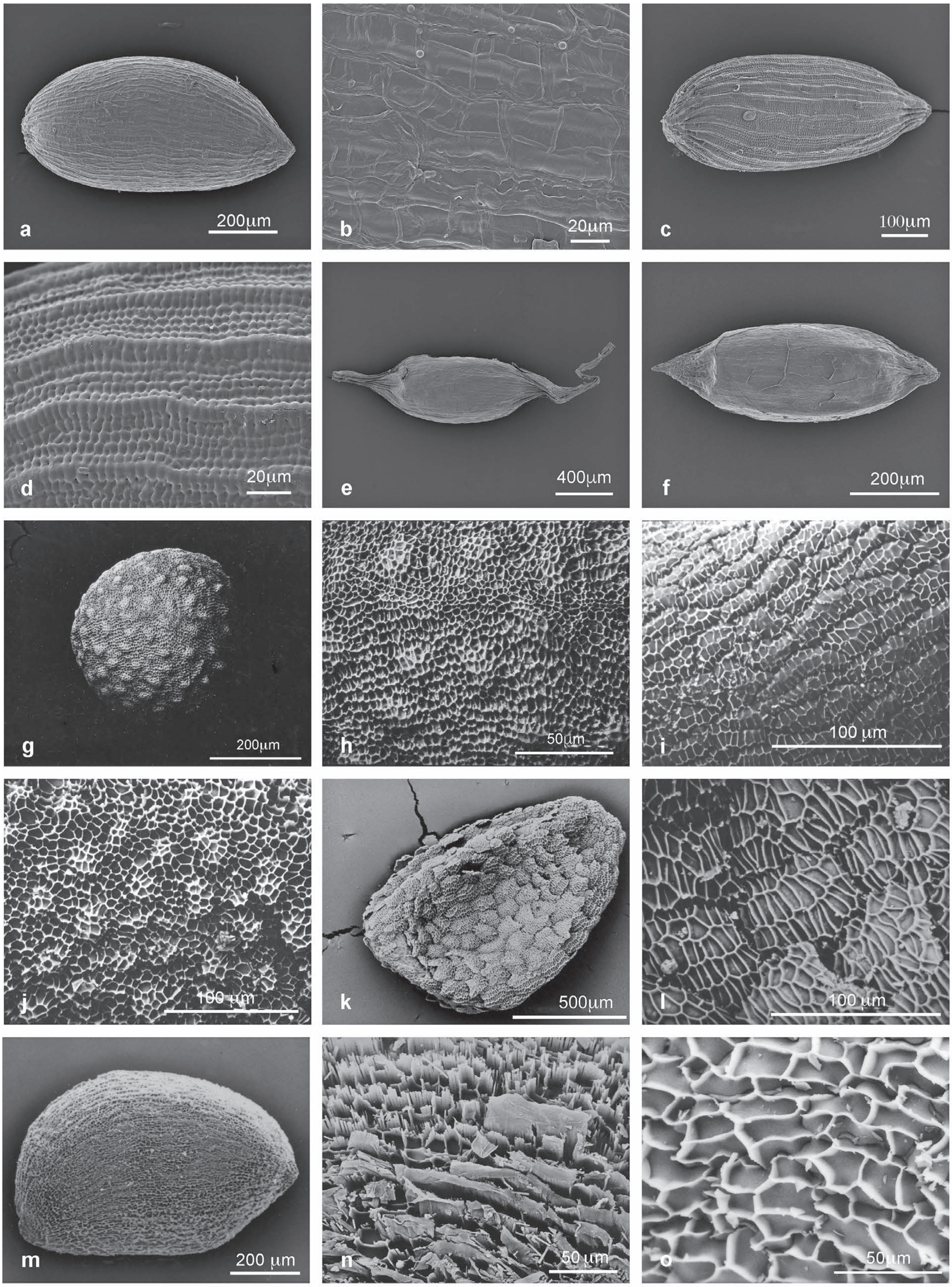

Fig. 3. Seed morphology of Restionaceae, subfamilies Centrolepidoideae and Sporadanthoideae. a, b: *Gaimardia setacea*. c, d: *Centrolepis fascicularis*. e, f: *Aphelia cyperoides* fruit (formed from one of several carpels) and seed. g, h: *Sporadanthus rivularis*. i: *S. gracilis*. j: *S. caudatus*. k, l: *S. tasmanicus*. m, n: *Lepyrodia glauca*. o: *L. flexuosa*.

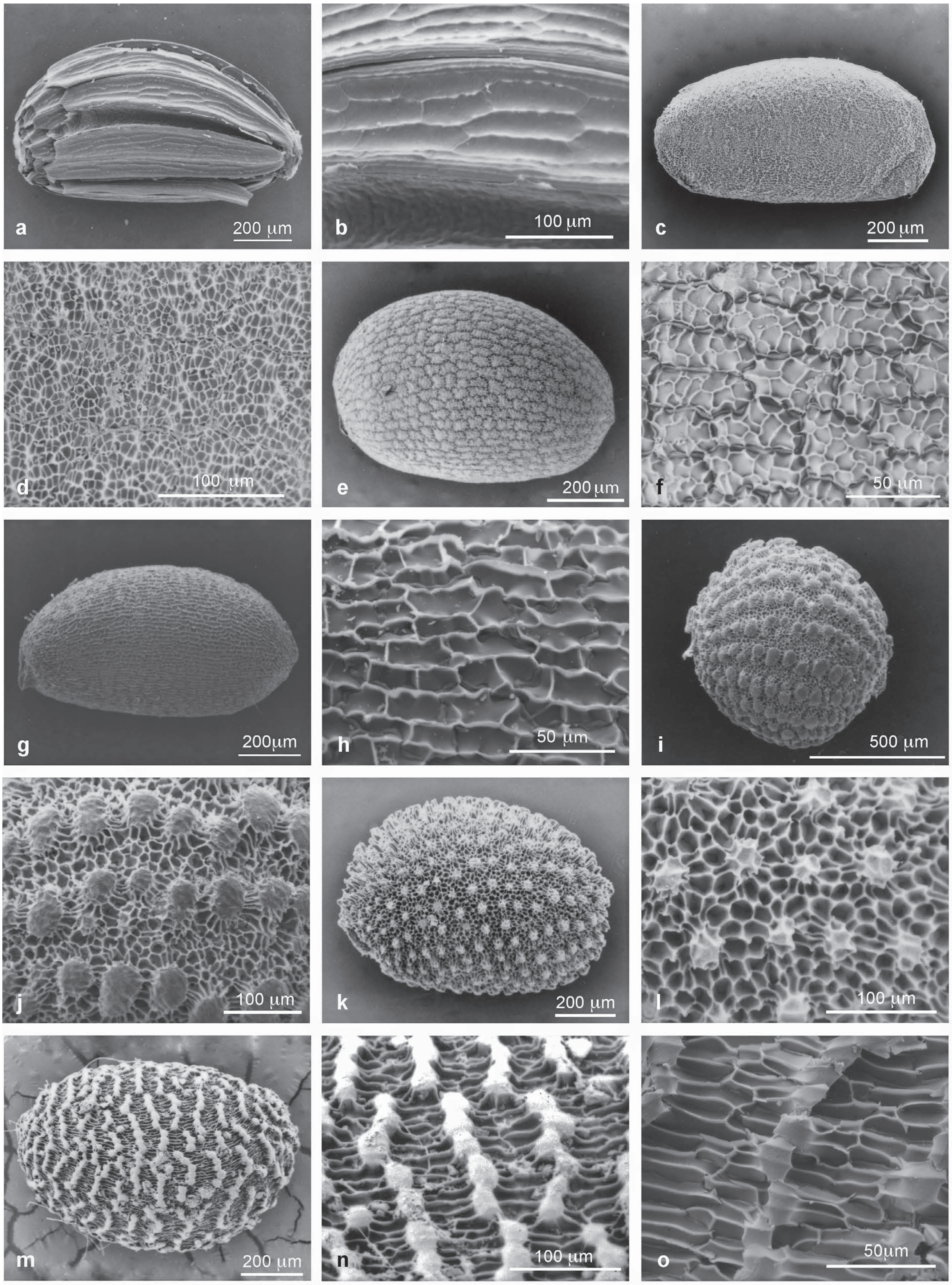

Fig. 4. Seed morphology of Restionaceae, subfamily Sporadanthoideae: *Lepyrodia*. a, b: *L. heleocharoides*. c, d: *L. muirii*. e, f: *L. muelleri*. g, h: *L. valliculae*. i, j: *L. curvescens*. k, l: *L. drummondiana*. m, n, o: *L. monoica*.

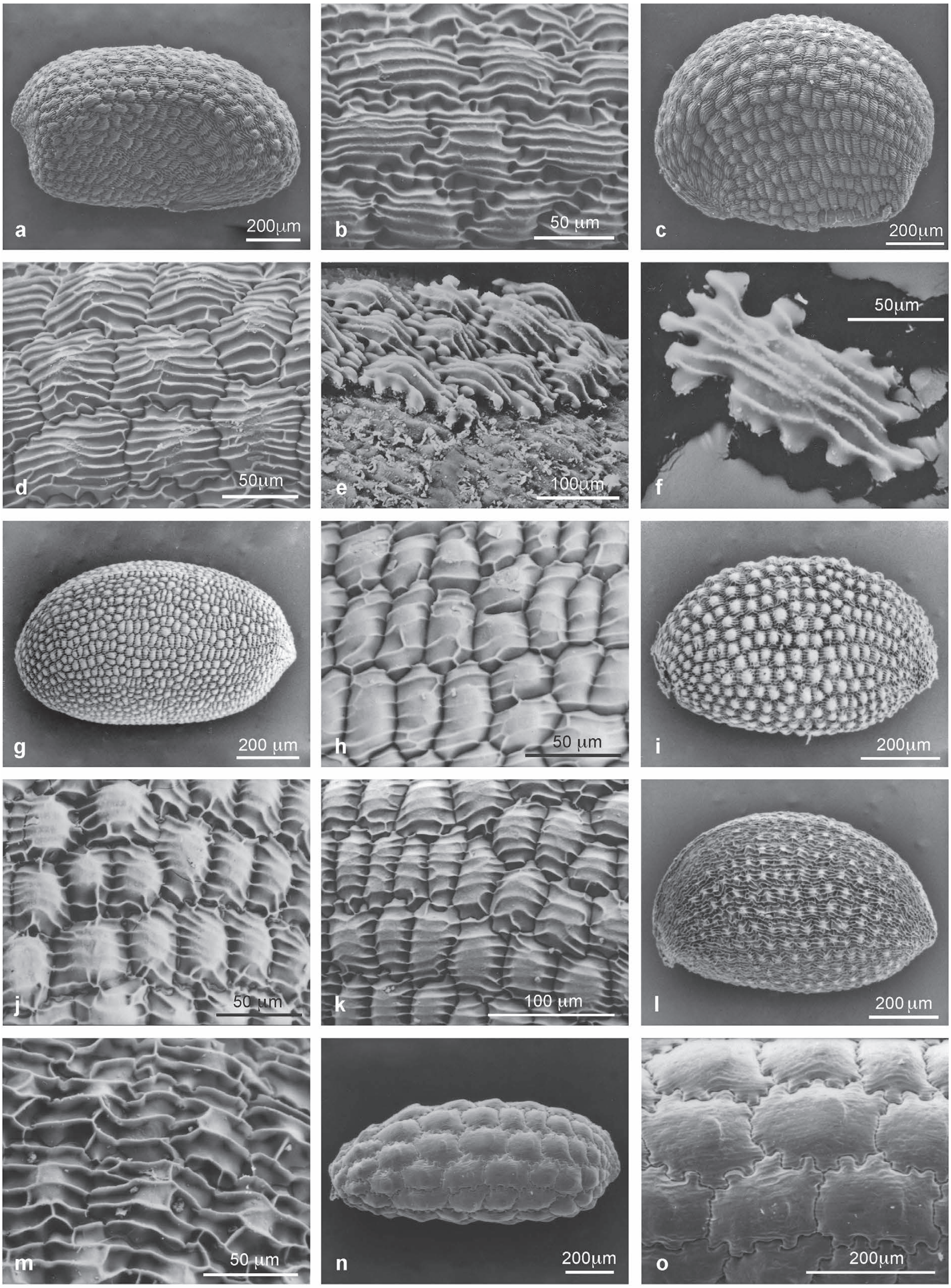

Fig. 5. Seed morphology of *Lepyrodia*: a, b: *L. fortunata.* c, d: *L. porterae*. e, f: *L. riparia,* surface layer partially removed, single surface cell. g, h: *L. anarthria*. i, j: *L. leptocaulis.* k: *L. cryptica*. l, m: *L. imitans*. n, o: *L. scariosa*.

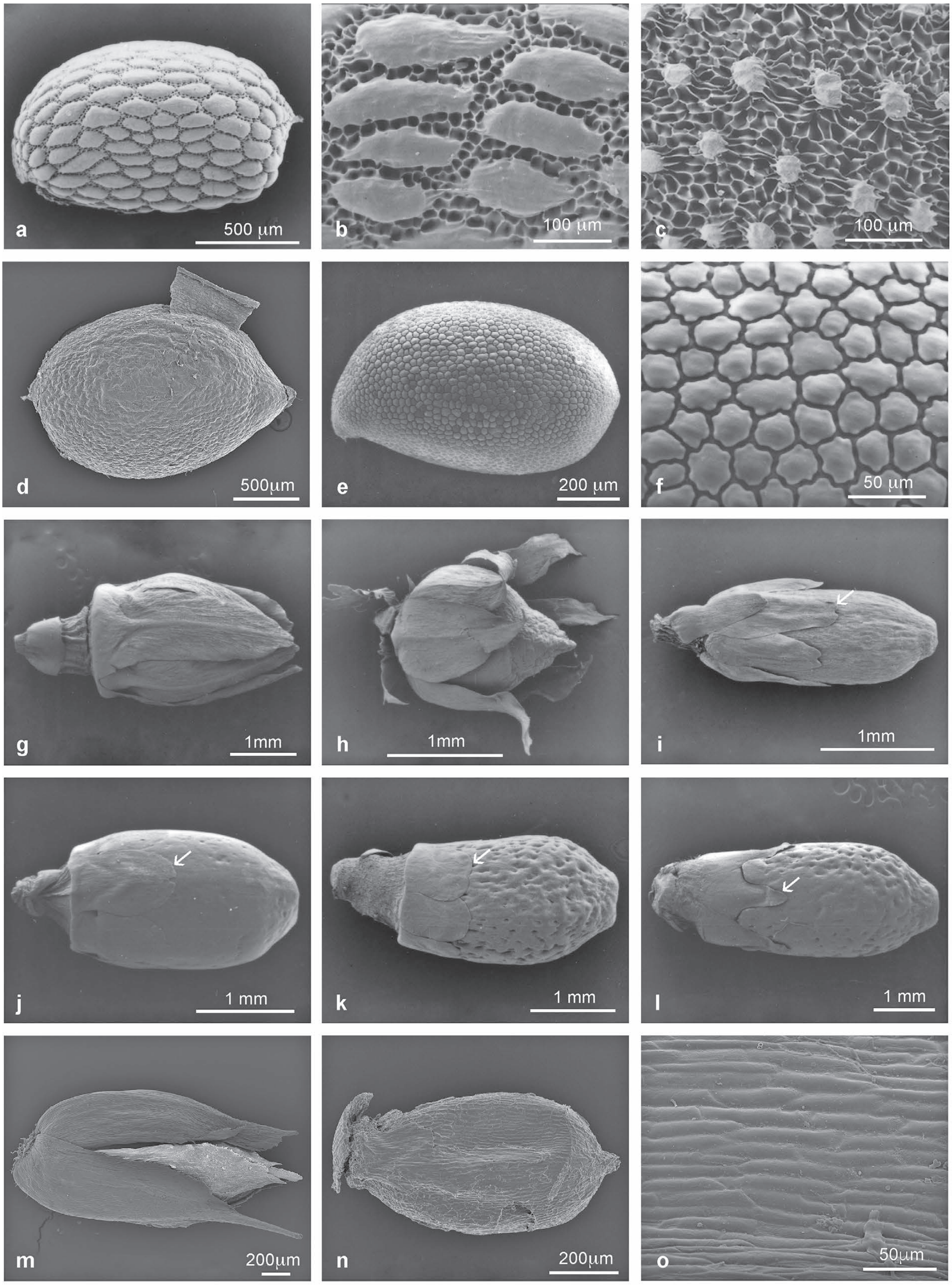

Fig. 6. Seeds and fruit of *Lepyrodia*, *Calorophus*, *Eurychorda, Hypolaena* (fruit with attached tepals and stipe, arrows mark the edge of the appressed tepals) and *Apodasmia*: a, b: *Lepyrodia extensa*. c: *L. hermaphrodita*. d: *Calorophus erostris*, (damaged at upper right). e, f: *Eurychorda complanata*. g: *Hypolaena grandiuscula* enclosed by tepals. h: *H. humilis*. i: *H. caespitosa*. j: *H. pubescens*. k: *H. viridis*. l: *H. exsulca*. m, n, o: *Apodasmia brownii* fruit with tepals and bracts, seed, seed detail.

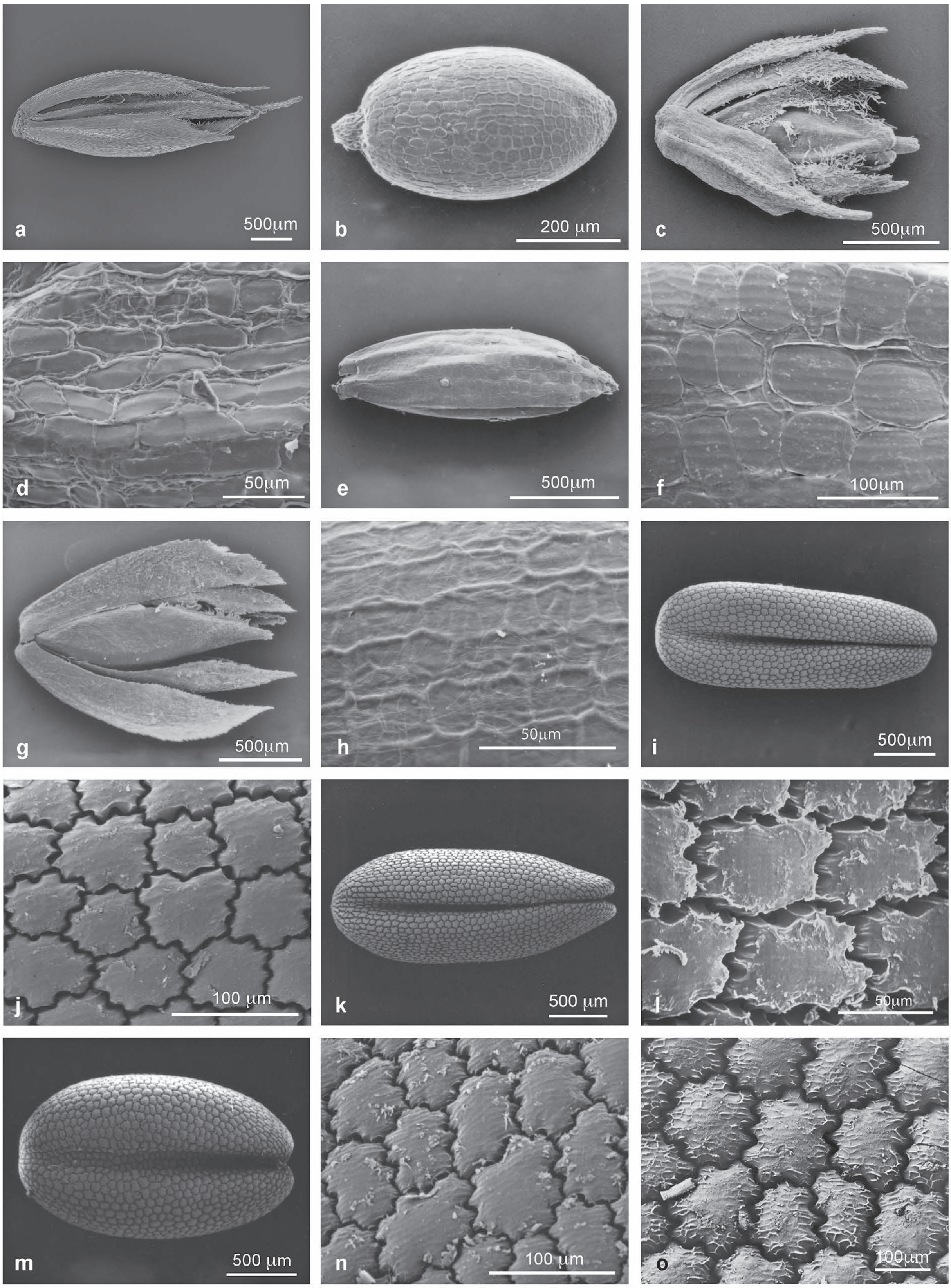

Fig. 7. Seed and fruit of *Leptocarpus* and *Loxocarya* clades: a: *Apodasmia ceramophila* fruit with bracts and tepals. b: *Dapsilanthus elatior*. c, d: *Leptocarpus thysananthus*, fruit with bracts and tepals, seed detail. e, f: *Leptocarpus trisepalus*, seed, seed detail. g, h: *Leptocarpus laxus*, fruit with tepals, seed. i, j: *Loxocarya striata* ssp. *implexa*. k, l: *Loxocarya magna*. m, n: *Loxocarya cinerea*. o: *Loxocarya gigas*.

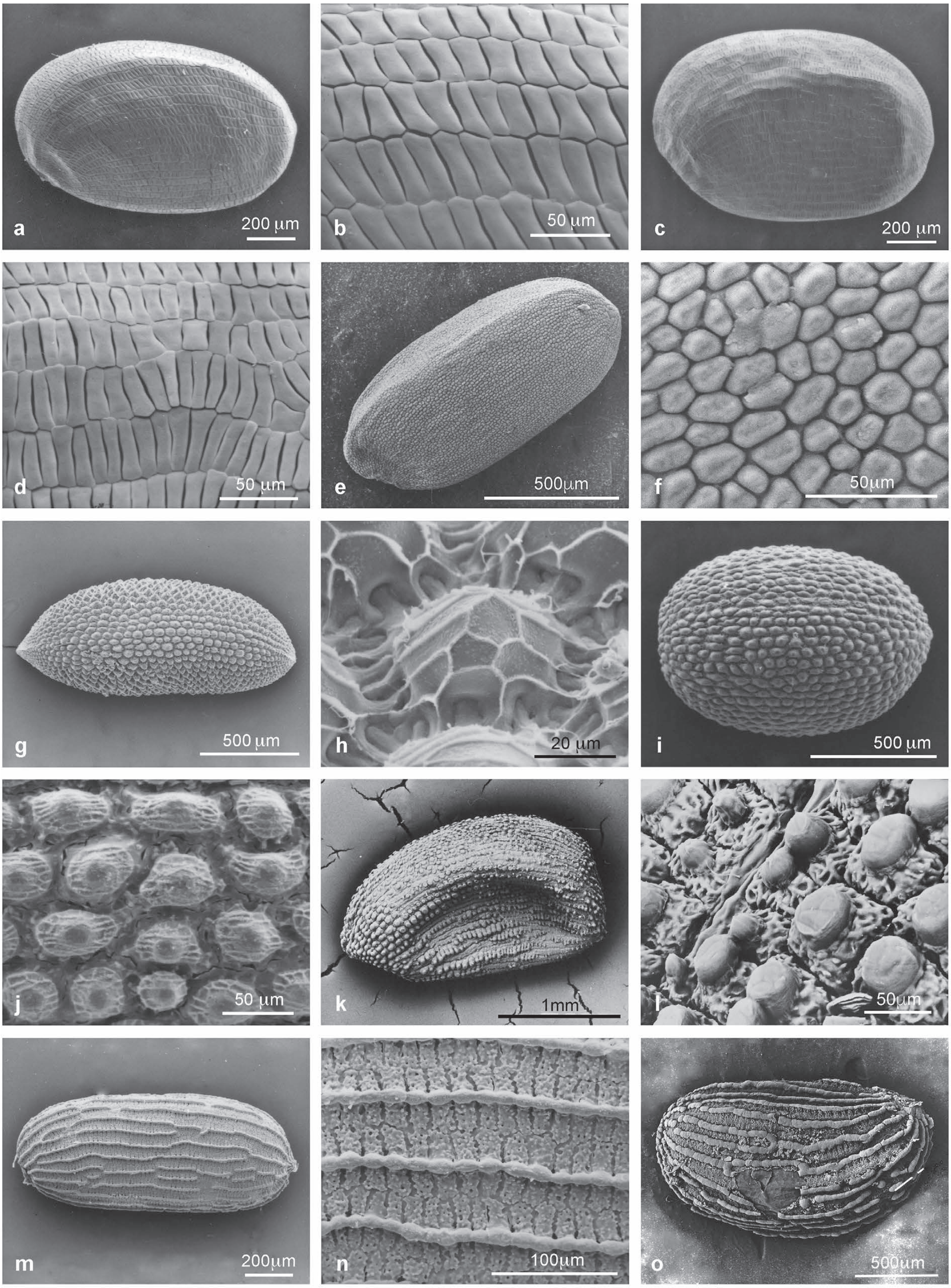

Fig. 8. Seeds of the *Loxocarya* clade: a, b: *Tremulina cracens*. c, d: *T. tremula*. e, f: *Platychorda applanata*. g, h: *Chordifex jacksonii*. i, j: *C. microcodon*. k, l: *C. isomorphus*. m, n: *C. amblycoleus*. o: *C. laxus*.

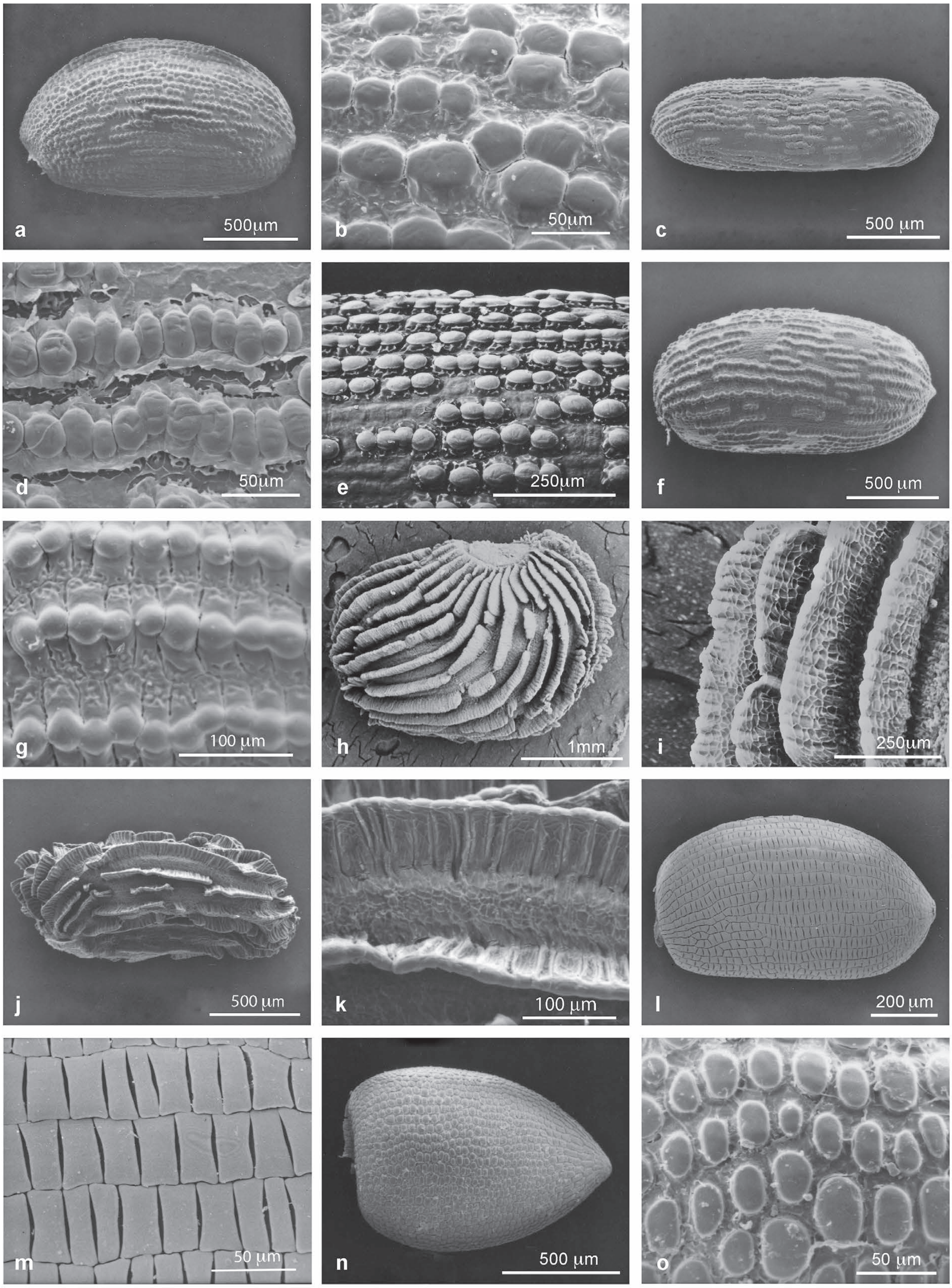

Fig. 9. Seeds of the *Loxocarya* and *Baloskion* clades. a, b: *Chordifex dimorphus*. c, d: *C. fastigiatus*. e: *C. capillaceus*. f, g: *C. abortivus*. h, i: *C. sinuosus*. j, k: *C. chaunocoleus*. l, m: *Dielsia stenostachya*. n, o: *Cytogonidium leptocarpoides*.

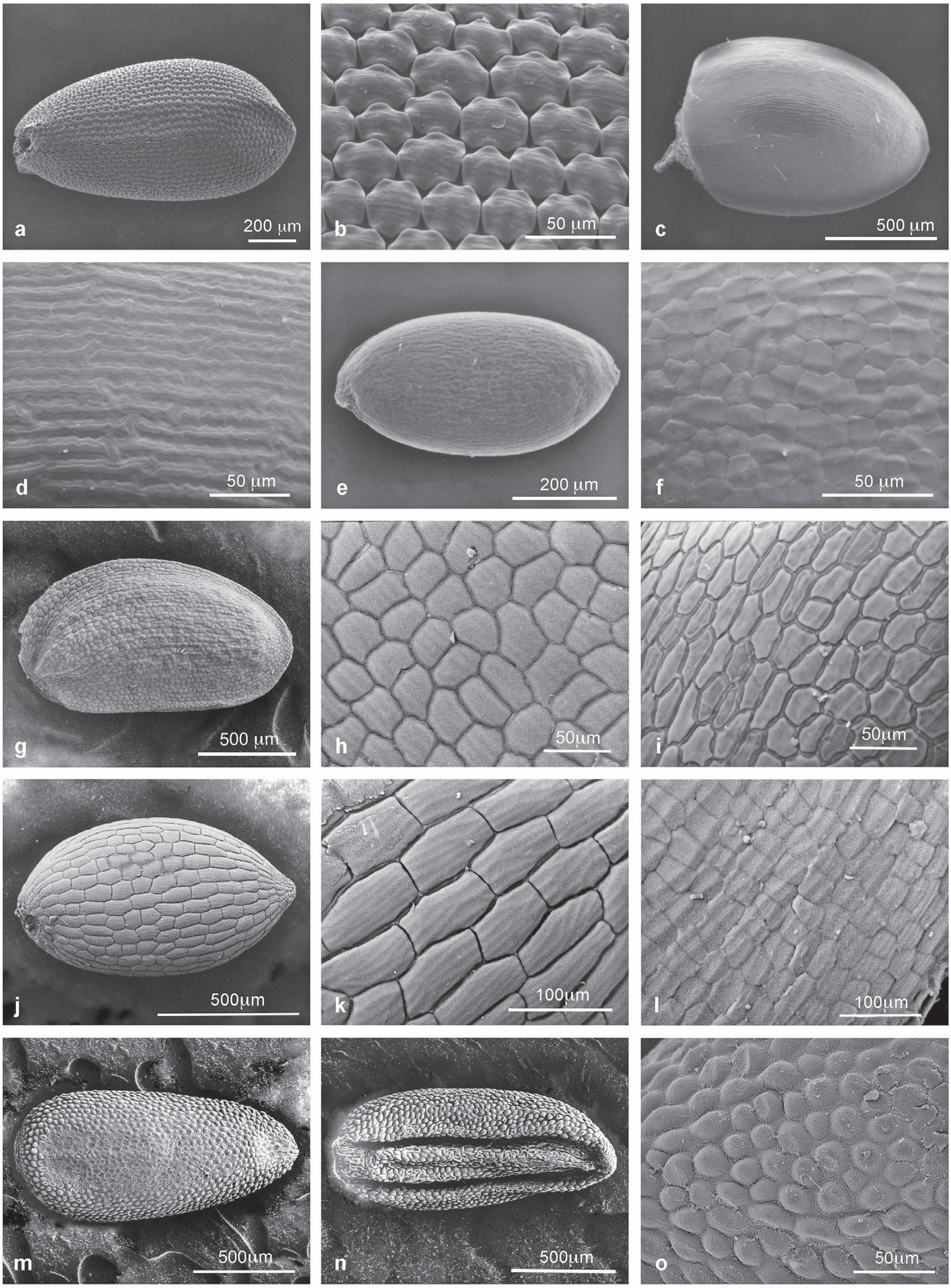

Fig. 10. Seeds of the *Baloskion* clade. a, b: *Tyrbastes glaucescens*. c, d: *Melanostachya ustulata*. e, f: *Baloskion pallens*. g, h: *B. gracile*. i: *B. stenocoleum*. j, k: *B. tenuiculme*. l: *B. tetraphyllum* ssp. *meiostachyum*. m, n, o: *B. tetraphyllum* ssp. *tetraphyllum*.

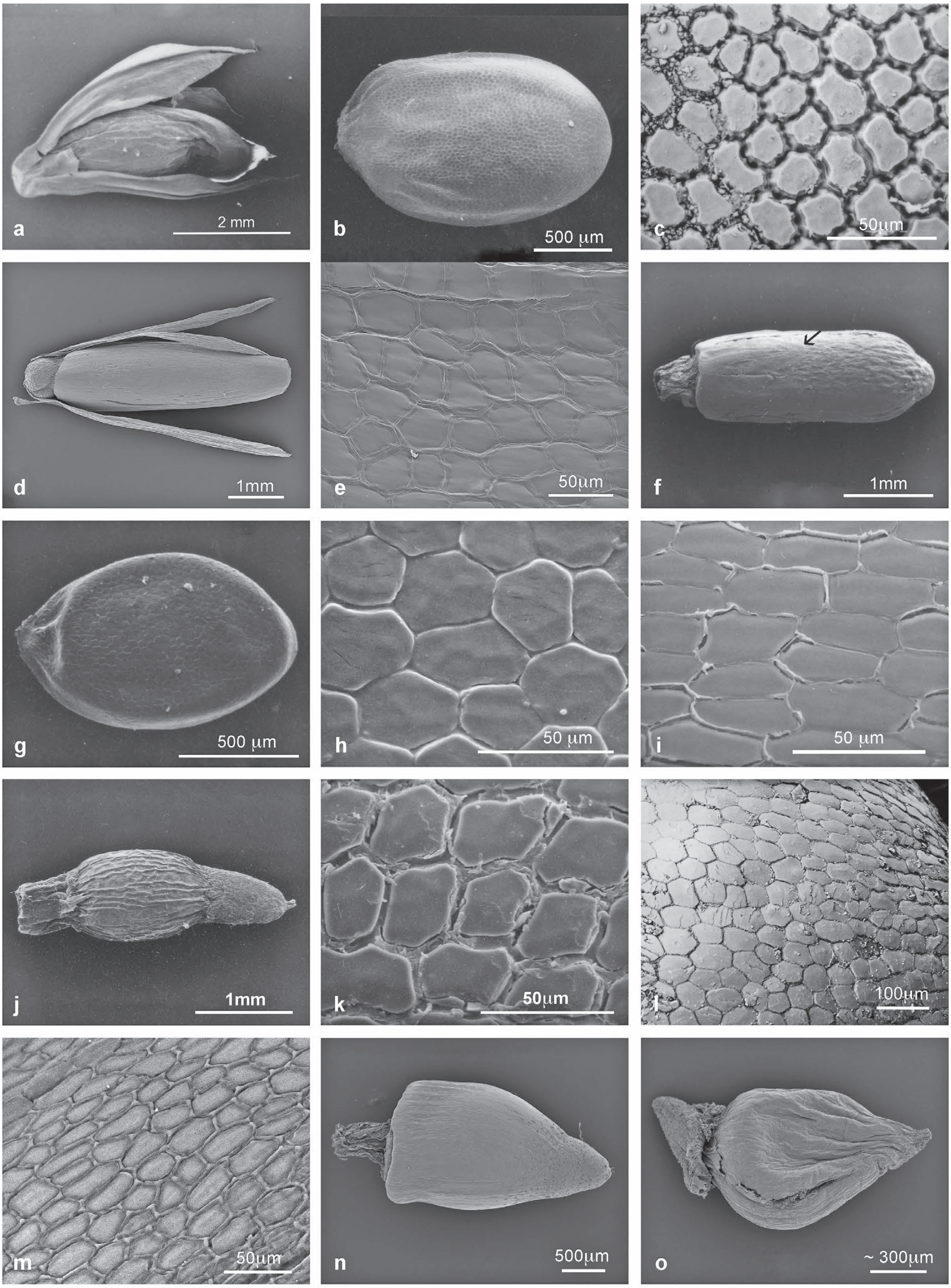

Fig. 11. Fruit and seeds of the *Desmocladus* clade. a, b, c: *Catacolea enodis*, fruit with bracts seed, seed detail. d, e: *Coleocarya gracilis,* fruit with tepals, seed detail. f: *Desmocladus eyreanus*, fruit with tepals, arrow marks the edge of an appressed tepal. g, h: *D. laxiflorus*. i: *D. confertospicatus*. j, k: *D. castaneus,* fruit, seed detail. l: *D. elongatus*, seed detail. m: *D. myriocladus*. n, o: *D. parthenicus*, fruit tightly encased in surrounding rigid bract, fruit removed from bract.

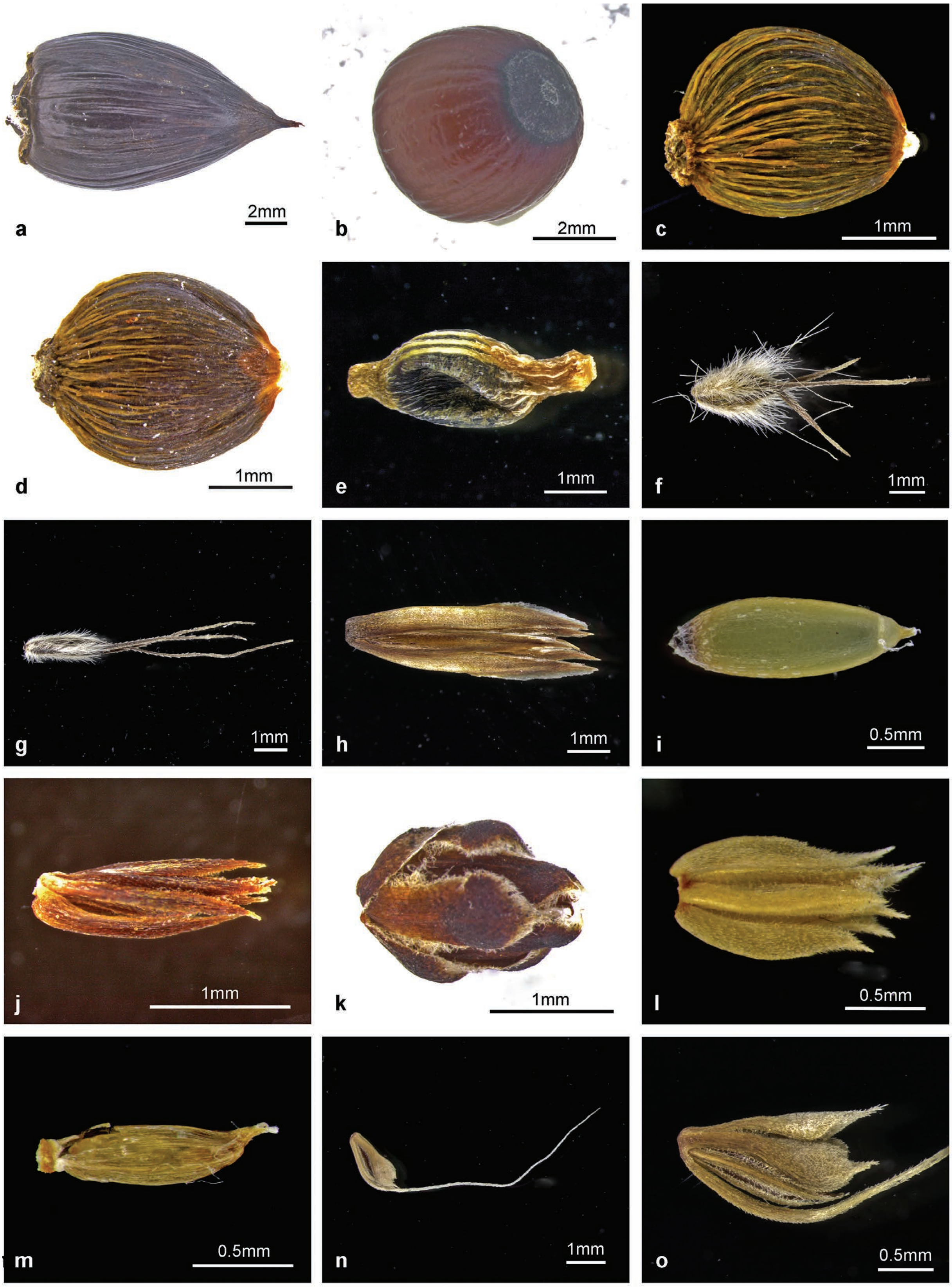

Fig.12. Multi-focus images of fruits, mostly surrounded by bracts and tepals, as dispersed. a, b: *Alexgeorgea nitens* fruit, seed. c: *Calorophus elongatus,* fruit with attached tepals. d: *C. erostris,* fruit. e: *Empodisma gracillimum*, fruit. f: *Chaetanthus aristatus,* fruit surrounded by awned tepals. g: *C. tenellus,* fruit surrounded by awned tepals. h, i: *Leptocarpus tenax,* fruit surrounded by tepals, fruit. j: *L. thysananthus,* fruit surrounded by bract and tepals. k: *L. decipiens,* fruit surrounded by bracts and tepals. l, m: *L. scariosus,* fruit surrounded by bracts and tepals, fruit. n, o: *Leptocarpus denmarkicus,* fruit surrounded by bracts and tepals, one bract expanded into a long awn, two outer tepals spathulate.

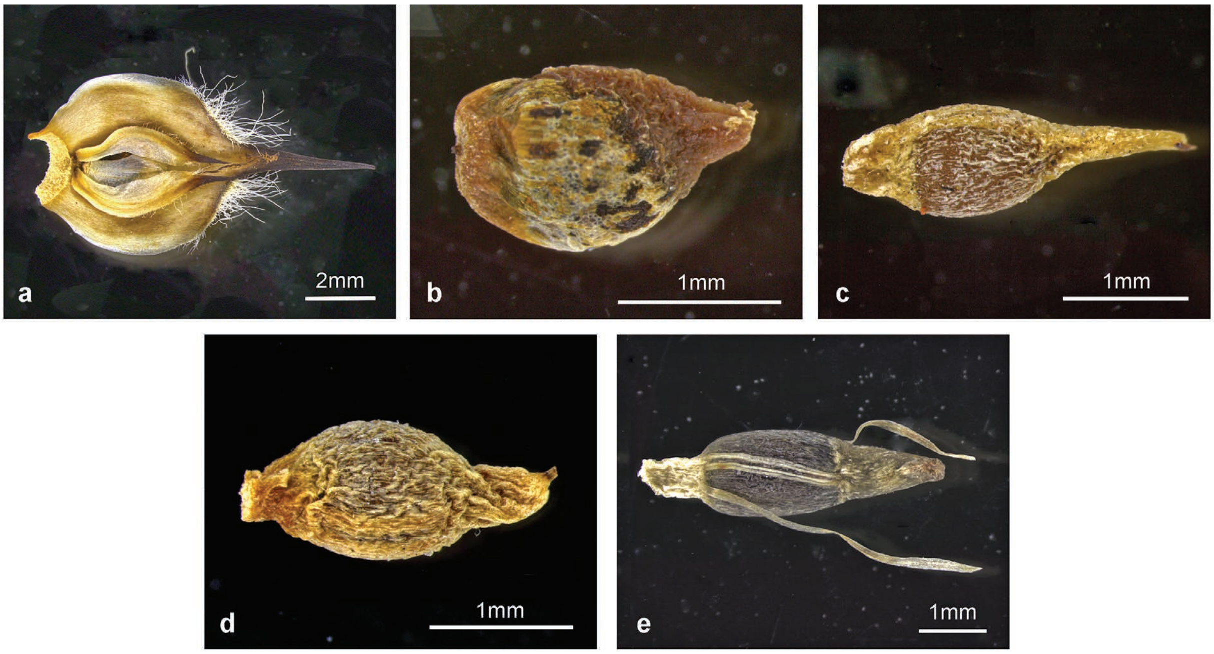

Fig. 13. Multi-focus images of fruits, mostly surrounded by bracts and tepals, as dispersed. a, b: *Lepidobolus preissianus*, fruit attached to glume with tepals, fruit. c: *Desmocladus myriocladus*, fruit. d: *D. quiricanus*, fruit. e: *D. elongatus*, fruit with tepals, showing lateral lines and stout stylar beak.

Results

Diaspore type and ornamentation

Anarthriaceae

The three genera, *Anarthria* (Figs 2a–j), *Lyginia* (Figs 2k–m) and *Hopkinsia* (Figs 2n–o) have very different seeds and fruit. Until recently, six species were recognised in *Anarthria* (e.g. Briggs *et al.* 2020a), but *A. gracilis*, as formerly recognised, has been shown to be a complex of three species (Fomichev *et al.* 2021). *Anarthria dioica* (Figs 2c, d) is newly recognised by Fomichev *et al.* (2021). Seeds of *Anarthria* have a brittle white outer layer of cells and a pattern of relatively large cells in longitudinal rows. The rows are indistinct in *A. dioica* and *A. scabra*, distinct in *A. humilis* but very prominent in *A. prolifera*. Cells are polygonal in *A. humilis* with some minor lobing but intricately lobed in *A. polyphylla*. In *A. prolifera* the cells meet in the 'valley' between the ridges and each cell has a convex central portion forming part of a ridge and narrow elongated 'wings' with heavily thickened radial walls forming the slopes of a 'valley' between the ridges. Longitudinal sculpturing overlays the cells, distinct in *A. scabra*, faint in *A. humilis* but complex and irregular in *A. dioica*.

The three species of *Lyginia* all have similar seeds of a very distinctive type: almost spherical, with a brittle white outer layer, and with a hyaline flange encircling the seed in the median vertical plane and the surface marked by small concavities—each the surface of a cell—with short fragile spicules arising at the angles of the cells (Figs 2k–m). Sections of seeds show a palisade-like outer layer of narrow thick-walled cells, much taller than wide, with the outer surface concave. *L. imberbis* showed considerable variation in the length of the spicules, short in Fig. 2l but longer in Fig. 2m. In examples studied of *L. excelsa* the projections were uniformly short, similar to Fig. 2l, but in *L. barbata* the straight, filiform projections perpendicular to the seed surface were up to four times longer than the width of the surface cells.

Hopkinsia has small nut fruits (Fig. 2n, o), shed with the attached stout pedicel which may act as an elaiosome. A pale lateral line marks the carpel margins and the style bases persist as three small apical peaks. The inner layer of the perianth is woody but the outer layer is fleshy, although fairly thin, and red when young, aging to brown (Meney *et al.* 1999c). If the red colour and fleshy consistency suggests that some dispersal agent is attracted to the fruits while still on the plant, this would be unique in the restiid clade. The seed surface shows convex polygonal cells overlain by longitudinal striations, presenting more relief than is usual in indehiscent fruits.

Restionaceae subfamily Centrolepidoideae

We have included only a token sampling of the centrolepid clade, which deserves further study. Examples of *Gaimardia*, *Aphelia* and *Centrolepis* (Figs 3a–f), have small, ovoid seeds, smooth or marked by longitudinal ridges. *Aphelia* is indehiscent whereas the other genera have loculicidal capsules (Cooke 1998, Sokoloff *et al.* 2015) with the carpels of *Aphelia* and *Centrolepis* separated on an elongated receptacle. In *Aphelia cyperoides* the seed is visible through the membranous pericarp which is readily opened along the suture line. *Aphelia* and *Centrolepis* have the smallest and lightest seeds reported in the Restionaceae, with a mass of 0.08–0.2 mg (Table 2).

Table 2. Seed and fruit dry weight of some species of Anarthriaceae and Restionaceae. Genera are listed mostly in the order in which the branches arise in the cladogram Fig. 1.

Taxon	Voucher NSW accession or reference	Number of items averaged	Seed or fruit weight (mg)	Description
Anarthriaceae				
Anarthria scabra	279690	5	4.6	seed
Hopkinsia anoectocolea	391550	7	3.6	fruit + stipe
Lyginia imberbis	–	10	3.02	seed
Lyginia imberbis	279735	1	1.9	seed
Restionaceae				
Centrolepidoideae				
Gaimardia setacea	494431	3	0.3	seed
Aphelia cyperoides	293103	8	0.2	seed
Centrolepis fascicularis	655460	16	0.08	seed
Sporadanthoideae				
Sporadanthus rivularis	870999	6	0.37	seed
Calorophus elongatus	264835	1	4.2	fruit
Calorophus erostris	264692	6	5.7	fruit
Lepyrodia macra	–	11	0.31	seed
Lepyrodia scariosa	280324	9	0.23	seed
Leptocarpoideae				
Alexgeorgea ganopoda	Meney *et al.* (1990)	–	605	seed
Alexgeorgea nitens	Meney *et al.* (1990)	–	190	seed
Alexgeorgea nitens	1100291	1	265	fruit
Alexgeorgea subterranea	Meney *et al.* (1990)	–	162	seed
Alexgeorgea subterranea	1100294	9	256	fruit
Hypolaena caespitosa	232897	10	2.27	fruit + stipe & tepals
Hypolaena exsulca	233287	6	4.7	fruit + stipe & tepals
Hypolaena exsulca	232625	5	4.5	fruit + stipe & tepals
Hypolaena robusta	233255	1	10.2	fruit + stipe & tepals
Leptocarpus denmarkicus	409883	12	0.025	fruit
Leptocarpus laxus	232887	55	0.224	fruit + tepals
Leptocarpus trisepalus	261649	31	1.07	fruit + tepals & bracts
Loxocarya gigas	233295	20	12.54	seed
Loxocarya magna	232863	15	3.35	seed
Loxocarya striata ssp. *striata*	233343	38	2.71	seed
Loxocarya striata ssp. *implexa*	399270	7	2.27	seed
Chordifex abortivus	233041	6	0.52	seed
Chordifex chaunocoleus	232591	7	0.27	seed
Chordifex stenandrus	233330	75	0.114	seed
Tyrbastes glaucescens	261643	13	0.36	seed
Lepidobolus chaetocephalus	233333	7	0.19	fruit
Lepidobolus preissianus ssp. *preissianus*	299471	5	2.96	fruit
Coleocarya gracilis	052329	14	3.72	fruit + tepals
Desmocladus lateriticus	209307	10	0.8	fruit

Restionaceae subfamily Sporadanthoideae

Seed shape in *Sporadanthus* ranges from spherical to cylindrical with cells arranged in longitudinal rows in the species with cylindrical seeds. All have a network of narrow ridges overlaying the cells (Figs 3g–l), a tertiary sculpture in the terminology of Barthlott (1981). The prominent ridges in *S. strictus* appear to be similar to those of *Anarthria prolifera* in that the cells extend from 'valley' to 'valley' with a convex central portion of the cell forming a segment of a ridge. de Lange *et al.* (1999) described the surfaces of the New Zealand *Sporadanthus traversii* seeds as having bi-reticulate surface with rectangular to rectangular-polygonal primary ridges and prominent secondary ridges, while in *S. ferrugineus* the secondary pattern is obscure to weak and irregular.

Lepyrodia seeds (Figs 3m–o, 4, 5, 6a–c) are highly diverse with *L. glauca, L. flexuosa, L. muelleri* and *L. valliculae* having an intricate network of narrow plates overlying the cells, reminiscent of the surfaces of *Sporadanthus* seeds. This appears to be a plesiomorphic condition for *Lepyrodia*. In most species the epidermal cells are arranged in more or less prominent longitudinal files. In *L. curvescens* (Fig. 4i, j) and *L. hermaphrodita* (Fig. 6c) the seeds are colliculate with the convexities each centred on a cell and with a network of superficial ridges spreading radially from the centre of the cell. In many species (Fig. 5a–m) the cells are overlain by prominent longitudinal ridges, but longitudinal striations are scarcely expressed in *L. scariosa*. A longitudinal pattern not involving convex cells is even more prominent in *L. heleocharoides* (Figs 4a, b) in which the cell structure is obscured. *L. scariosa* (Fig. 5n, o) is notable for its very large-cell pattern. Specimens of *L. scariosa* can be difficult to distinguish from *L. cryptica* (Fig. 5k), *L. imitans* (Fig. 5l, m) and *L. verruculosa* unless the seed surface morphology, or the corresponding pattern imprinted on the inner surface of the capsule, can be seen, so this is an important feature for identifying female plants. The similarity of seeds in *L. curvescens* (Fig. 4i, j) and *L. drummondiana* (Fig. 4k, l) accords with their close relationship in the phylogeny of Briggs *et al.* (2014), but other groupings in the phylogeny such as *L. glauca* sister to *L. heleocharoides* or (*L anarthria* (*L. muelleri* + *L scariosa*)) are not shown in seed features. The DNA phylogeny showed poor resolution within *Lepyrodia*, with few branches supported in both the Bayesian and PAUP analyses, so did not clearly suggest relationships within the genus.

Calorophus (Figs 6d, 12c, d) has three separate styles but only a single loculus and develops small indehiscent nuts with a woody pericarp, almost spherical but less convex adaxially where there is an indistinct furrow, opposite an indistinct ridge abaxially. The fruit surface is longitudinally furrowed and the seed surface consists of slightly convex polygonal cells.

Restionaceae subfamily Leptocarpoideae

Analyses of DNA chloroplast data (Briggs *et al.* 2000, 2010, 2014) show *Eurychorda complanata*, the sole species of its genus, sister to the remainder of Leptocarpoideae. It has 2-locular capsules and smooth seeds with thick-walled cells separated at the surface by deep clefts (Fig. 6e, f).

Unfortunately, we have not studied seeds of the *Winifredia* clade. It comprises the monotypic genera *Winifredia* (*W. sola*) and *Taraxis* (*T. grossa*) with *Empodisma* (three species). Meney *et al.* (1999c) described *Winifredia* as having small indehiscent nut fruits and *Taraxis* as having capsular fruit. In the absence of observations of our own, we accept those descriptions but note that, except for *Taraxis*, the whole branch of the tree (Fig. 1) that includes both the *Winifredia* and *Leptocarpus* clades is characterised by indehiscent fruit. Both *Winifredia* and *Taraxis* retain three style branches (rarely only two in *Taraxis*) but female flowers of *Taraxis* are often galled and fruits are very rarely produced. The ovary of *Taraxis* is 'unilocular, laterally thickened on two edges' (Briggs and Johnson 1998). No fruits of *Winifredia* were seen in the NSW and HO herbaria; the gynoecium has a single loculus and ovule. Both Australian species of *Empodisma*, *E. minus* and *E. gracillimum*, have globular, pale or dark brown, glossy fruit, c. 1.5 mm diam., with a thin pericarp (Fig. 12e) and a pale abaxial longitudinal line, but—although *E. minus* is very widespread and often abundant—we have not seen mature seed. Wagstaff and Clarkson (2012) note that few specimens they examined had mature fruits but described fruits of *E. minus* and *E. gracillimum* as ovoid 1-seeded nuts and illustrated them showing a pronounced lateral ridge.

All of the *Leptocarpus* clade have indehiscent fruit and most are dispersed with perianth and bracts attached. *Alexgeorgea* (Figs 12a, b) and *Hypolaena* (Figs 6g–l), the two basal branches, have nuts with a woody pericarp. In most of *Hypolaena* the tepals are closely appressed and the pedicel stout. *Alexgeorgea* is highly unusual in having female flowers borne on short branches arising from the rhizomes, with the base of the flower and surrounding bracts below ground level, only the tips of erect scarious bracts (cataphylls) and tepals and the 3-branched style emerging. The female spikelets mostly develop a single flower but sometimes two flowers are observed within the same group of enclosing cataphylls (E.M. Sandiford pers comm.). The nuts (9–11 mm diam.) are much larger and more massive than any other Restionaceae and exceed in mass the largest fruits of the African Restionaceae, such as *Cannomois grandis* (Table 2, Caddick and Linder 2002). The rhizomes are long and slender and field observations suggest that plants form patches to 15 m across (Briggs *et al.*

2020b). Rhizome growth alone may distribute seeds well away from the site of germination of the parent plant. *Chaetanthus*, *Apodasmia, Dapsilanthus* and *Leptocarpus* (Figs 7a–h, 12f–o) have a thin membranous or papery pericarp. In some species the attached tepals are inflated (*L. trisepalus*, Fig. 7e, f) or wing-like, or are expanded into awns and covered with long hairs (*Chaetanthus* Fig. 12f, g). Fruits of *L. denmarkicus* (Fig. 12n, o) are shed with two bracts elongated into awns, one of them much longer than the other. In all these indehiscent fruits, the seed surfaces are smooth, mostly with large surface cells (Fig. 7b, d). *Apodasmia brownii* has longitudinally elongated cells (Fig. 6o) while *Dapsilanthus elatior* has large isodiametric cells (Fig. 7b). *Apodasmia* and *Dapsilanthus* have proved their ability to disperse. *Apodasmia* has one species in each of south-western Australia, south-eastern Australia, New Zealand and Chile. *Dapsilanthus*, with four species, occurs in northern Australia and southeast Asia as far north as Hainan Island.

***Loxocarya* clade:** *Loxocarya* has capsular fruits with both the two carpels mostly developing in *L. albipes*, *L. gigas* and *L. striata*, but only a single carpel developing in *L. cinerea* and *L. magna*. The seeds (Fig. 7i–o) are narrow ellipsoid, compressed, much broader in the axial plane than laterally, with a deep abaxial furrow (deeper towards the micropylar end). The pericarp is rigid and extends apically above the loculus, so that the upper third of the capsule is formed of thick pericarp, distal to the loculus and seed. All species show a distinctive seed surface pattern with lobed cells, separated from the adjoining cells by deep narrow crypts. The inner wall of the ovary is marked with a pattern of narrow ridges matching these crypts. The surface cells of the testa are shallow, broader than deep, with a very thick outer wall.

As in most members of the *Loxocarya* clade, the capsules of *Tremulina* are two-locular. The seeds (Fig. 8a–d) have longitudinal lines of flat angular cells, elongated transversely to the lines. They are surprisingly similar to those of *Dielsia* (Fig. 9l, m) in the *Baloskion* clade. The capsules of *Platychorda* are trilocular and the seeds ellipsoid with an irregular pattern of small convex cells (Fig. 8e, f). Mapping synapomorphies onto a Bayesian consensus cladogram Briggs *et al.* (2014) identified the three-locular capsule as a reversal of an earlier reduction of the number of developed carpels, rather than a plesiomorphic condition.

Chordifex (Figs 8g–o, 9a–k) is characterised by longitudinal lines of convex cells, in some species fused into continuous ridges and in some species exaggerated into sharp blade-like ridges. There is a fine network of intricate narrow ridges between the convexities, or between the ridges, or over the whole surface including the ridges, as in *C. chaunocoleus* (Fig. 9j, k). In the sharp ridges of *C. chaunocoleus*, the ridges are one cell wide, each cell four to six times as high as wide, thick walled with a narrow lumen. In the species with longitudinal ridges, the cells meet in the 'valley' between the ridges and each cell has a convex central portion forming part of a ridge and narrow elongated 'wings' forming part of the slope of a 'valley' between the ridges.

The similarities in seed morphology mostly accord with the groupings in the DNA phylogeny (Briggs *et al.* 2014), for example (among the species represented in the phylogeny) *C. jacksonii* is sister to *C. microcodon* and *C. sinuosus* groups with *C. chaunocoleus*. Before we had DNA data, seed morphology suggested that the eastern Australian species, *C. dimorphus*, *C. fastigiatus*, *C. hookeri* and *C. monocephalus*, might be referred to *Chordifex*, despite a prominent difference from western species of that genus in culm anatomy: the lack of pillar cells (Cutler 1969) in the chlorenchyma. These four eastern species form a clade in the DNA phylogeny suggesting a shared loss of pillar cells, while retaining the longitudinal lines of convex cells characteristic of *Chordifex* seeds.

***Baloskion* clade:** *Baloskion* (Fig. 10e–o) has late-dehiscent capsules that are attached to the subtending glume and dispersed with the glume. The pericarp is thin and papery and, in most members, the seeds are smooth, lacking surface relief, as in *B. pallens*, *B. gracile*, *B. stenocoleum*, *B. tenuiculme* and *B. tetraphyllum* subsp. *meiostachyum*. Surprisingly, the seeds of *B. tetraphyllum* subsp. *tetraphyllum* differ in showing deep longitudinal furrows and convex cells isodiametric in surface view (Fig. 10m–o), unlike the flat cells of *B. tetraphyllum* subsp. *meiostachyum* (Fig. 10l). Our only specimen of subsp. *tetraphyllum* with mature fruits (and numerous seeds) is from Tasmania and we have not been able to check the seed features elsewhere in the range of the species. The other members of the *Baloskion* clade are four monotypic genera, *Dielsia*, *Cytogonidium*, *Tyrbastes* and *Melanostachya* (Figs 9 l–o, 10a–d). In seed morphology they form a disparate assemblage. The rounded convex surface cells of *Cytogonidium* (Fig. 9n, o) are very different from the elongated cells with sinuous walls and low sinuous ridges in *Melanostachya* (Fig. 10c, d) or the lobed cells separated by small deep crypts of *Tyrbastes glaucescens* (Fig. 10a, b). The rows of smooth rectangular cells in *Dielsia* are reminiscent of those in *Tremulina* and very different from other members of the *Baloskion* clade. Most, but not all, populations of *Cytogonidium* are apomictic, producing abundant seed in the absence of male plants.

***Desmocladus* clade:** All members of the *Desmocladus* clade (Figs 11, 13) share the same gynoecial structure. A single carpel develops into a shortly stipitate 1-locular ovary with a single style that is unbranched, often stout and mostly stigmatic. The fruit is indehiscent, a nut, mostly with two pale lateral longitudinal lines marking the carpel margins on the more convex abaxial side and, opposite these, a narrow ridge mostly in line with the stylar beak. The fruit is shed with a persistent short stipe and tepals if present. The pericarp is hard and bony in *Coleocarya* but is readily split along the adaxial – abaxial plane into two husks. In most species of *Lepidobolus* and *Desmocladus,* and in *Catacolea,* the pericarp is parenchymatous, but in others it is thin and almost membranous (e.g. *L. densus*, *D. laxiflorus* and *D. nodatus*) but it is hard and bony in *D. elongatus* and *D. confertospicatus*. In *D. elongatus,* Fig. 13e shows two pale lateral lines in the ovary region, each of which is double; these appear to represent the carpel margins. On the opposite side of the fruit, which is slightly less convex, is a narrow pale double lateral line.

In the parthenogenetic species in which male plants are unknown, *D. parthenicus* (Fig. 11n–o) and *D. diacolpicus*, the fruit is shed closely enwrapped by a rigid glume. The glume is striate with pale lines (veins) and so closely enwraps the fruit that only its striate nature shows that the diaspore does not consist of the nut alone. The illustration of the 'fruit' of *D. parthenicus* by Pate and Meney (1999 Fig. 1.7B) shows the nut enwrapped by the innermost glume. Both male and female plants are known in *D. glomeratus*, but the fruit is closely enwrapped by the striate innermost glume as in the parthenogenetic species. The nut of *D. glomeratus* is ovoid, c. 1.8 mm long, dark brown with pale lateral lines at the carpel margins, shed enclosed in the innermost glume, with a short (0.7–1 mm) stipe below that glume and also a short stipe between the ovary and glume. The DNA phylogeny placed *D. glomeratus* sister to *D. parthenicus* but the rare *D. diacolpicus* was not sequenced.

Fruit size in the clade varies from 1.5 mm long in *Desmocladus nodatus* to 4–6.3 mm long in *Coleocarya gracilis*. Most have a conical stylar beak persistent on the fruit and in some species (Figs 11j, 13e) the beak is broad, often differentiated in surface texture from the remainder of the fruit, and forms a quarter or more of the fruit. Possibly this development of the fruit above the loculus and seed acts as an elaiosome, attractive to ants as dispersal agents. The seeds are smooth with subangular cells arranged in lines or in an irregular pattern (Fig. 11k–m).

Seed or diaspore mass

Weights for some of the largest and smallest seeds, and for a variety of other Australian restiid seeds and fruits, are given in Table 2. All species of *Alexgeorgea* have large seeds with *A. nitens* at 265 mg and *A. subterranea* at 256 mg. Seeds of other Restionaceae are mostly within the range 0.3 mg to 3 mg, with some fruits (e. g. *Leptocarpus* spp.) lighter than the seeds of other species.

Discussion

Seed morphology proved of limited usefulness in phylogenetic studies of African Restionaceae (Linder 1984). Features of seed shape and ornamentation were described and illustrated by Linder who designated thirteen seed morphology groups among 137 species with dehiscent fruits but was unable 'to establish any polarity for the various characters found in the African taxa'. More recently, Linder and Hardy (2010) included the character of fruit dehiscence but no seed morphology features among the 20 diagnostic or distinctive morphological characters that they used to characterise genera and subgenera of Restioneae. Within Restionoideae they found five separate developments of indehiscent fruits, whereas we noted one development of indehiscent fruits in Anarthriaceae and six in Australian Restionaceae (Fig. 1).

Development, dehiscence and dispersal: The distribution of fruit types in the restiid clade of Poales shows trilocular loculicidal dehiscent capsules as the basic condition. From this there have been increase of carpel number in the Centrolepidoideae (Sokoloff *et al.* 2009) but reduction to bilocular capsules in *Eurychorda* and in the *Loxocarya* and *Baloskion* clades (with a reversal to trilocular in *Platychorda*; Briggs *et al.* 2014), as well as many reductions to one or two developed carpels in the Restionoideae. Reductions to a single developed carpel and indehiscent nut fruit (Fig. 1) are *Empodisma*, *Winifredia,* and the whole of the *Leptocarpus* and *Desmocladus* clades in Leptocarpoideae and in other subfamilies *Aphelia* (Centrolepidoideae) and *Calorophus* (Sporadanthoideae), as well as *Hopkinsia* (Anarthriaceae). Although *Aphelia* is indehiscent (Cooke 1998), it has a membranous pericarp, as in other members of its subfamily, and the carpel margins are readily separable in dried and soaked fruits. From detailed morphological studies, Fomichev *et al.* (2019) concluded that 'Our data suggest that the gynoecium of *Hopkinsia* is unicarpellate (monomerous), as in *Aphelia* (centrolepid clade) whereas gynoecia of some monothecal restiids [such as *Alexgeorgea*] are pseudomonomerous. Thus, we provide further support for the idea that gynoecia with a single fertile ovule probably appeared several times, potentially via different morphological pathways in the evolution of wind-pollinated Poales'.

Linder (1992) investigated which carpel is developed in clades where a single fertile carpel develops, finding some flexibility in whether carpel 2 (the right abaxial) or carpel 3 (left abaxial) develops. In *Apodasmia similis* (referred to as *Leptocarpus similis*) Kircher (1986) showed that carpel 1 (adaxial) or 2 are fertile.

From flowering to seed maturation takes about 10–12 months in many Australian species but ranges from two to three months in *Leptocarpus scoparius* to 15–21 months in *Alexgeorgea* species (Meney *et al.* 1999c). In nut-fruited African species it is reported to take 18 months in *Hypodiscus aristatus* but seven months in *Willdenowia incurvata* (Newton *et al.* 2002).

It is widely found that seeds of indehiscent fruits are not ornamented (although *Hopkinsia* is an exception), so it may be assumed that surface ornamentation has adaptive value in seed disseminules. Likely it may facilitate myrmechory and many restiid species are ant-dispersed in the Cape region and in southwest Australia (Rundel *et al.* 2018). Restiid seeds are often found collected at ant colony sites (Meney *et al.* 1999a, R. Dunn pers. comm.). The pedicel of nut fruit acts as an elaiosome in myrmechorous species in Africa (Bond and Singsby 1983) and probably similarly in *Hopkinsia*, *Desmocladus* and *Hypolaena*.

Studying African species, Caddick and Linder (2002) found that diaspore size is positively correlated with seedling size in the first 4 months of growth and with seedling survival over summer drought following the first growing season. In the Australian Restionaceae there is a great difference in seed mass, with seeds of *Alexgeorgea* more than 10^3 times the mass of the smallest seeds and most species with seed weights in the range 0.3 to 3 mg. Among the smallest seeds are those of the centrolepid clade, mostly ephemeral annuals that avoid drought by their brief growing season.

Fire is an important aspect of the habitats of these species (Pate *et al.* 1999), and many genera include both obligate seeder and resprouter taxa (Meney *et al.* 1997, 1999a, b). Such fire responses have been a feature of African Restionaceae since the Cretaceous (He *et al.* 2016; Litsios *et al.* 2014). Meney *et al.* (1997, 1999a) compared the reproductive potential of a range of Western Australian obligate seeder and resprouter species of Anarthriaceae and Restionaceae, finding that the germinable seed output in some species might be scarcely able to compensate for natural senescence or catastrophic loss of parent populations. Species that regenerate by seed after fire often have more prolific seed set than resprouters and germination in many species is stimulated by fire or smoke.

Indehiscent fruits are mostly shed with tepals and pedicel attached and these act as wings or bear awns or hairs that may aid dispersal. In some *Lepidobolus* species the glumes fall with the fruit held in the glume keel (Fig. 13a). Fruits of *Baloskion* are late-dehiscent capsules dispersed with the fruit and floral parts attached to a glume—which acts as a wing—but retain two loculi and two styles. This condition was illustrated for *Baloskion tetraphyllum* in the protologue of *Restio tetraphyllus* (Labillardière 1806: tab. 227). The seeds are mostly smooth but *B. tetraphyllum* subsp. *tetraphyllum* show some ornamentation (Fig. 10m–o).

Diaspore mass: Caddick and Linder (2002) contrasted the alternative strategies for reproduction and dispersal in African Restionaceae with large and small diaspores. Only obligate seeder species were included in their study, since resprouting species are less evolutionarily constrained by diaspore characteristics. They found a negative correlation between diaspore size and diaspore number, indicating a trade-off between these variables in the allocation of reproductive resources. They also found that large woody nuts produced in small numbers have well-protected diaspores with large resources to develop large seedlings that survive summer drought. The alternative strategy of small seeds or soft nutlets produced in large numbers are poorly protected diaspores with small resources that develop small seedlings and have high mortality during summer drought. The majority of Australian Restionaceae occur in the south of Western Australia on low-nutrient soils in seasonally moist or wet sites (winter wet, summer dry) in a mediterranean climate of summer drought similar to that experienced by the South African species. We did not investigate the way in which seed features are related to habitat in the Australian taxa, but field observations suggested that a similar relationship exists. For example, the larger-fruited *Hypolaena* and *Desmocladus* are mostly in drier habitats than *Leptocarpus,* although the larger-seeded *Anarthria* and *Loxocarya* are not in notably drier sites than the smaller-seeded *Chordifex*. The species of the genus with the largest fruits, *Alexgeorgea*, range from sub-arid (*A. subterranean*) to seasonally waterlogged sites in a more mesic region (*A. ganopoda*) and the large fruit size is presumably associated with their development below ground, rather than with climatic factors. Such development may be an extreme adaptation to avoid fire and predation. The seeds of *Alexgeorgea ganopoda*, at 0.605 g (Meney *et al.* 1990), the largest in Restionaceae, have over 1000 times the mass of the smallest seeds we report in *Centrolepis fascicularis,* with most species within the range 0.3–3 mg. The smallest seeds are in perennials in regions with relatively reliable rainfall, such as some *Leptocarpus* species, or ephemeral annuals that avoid drought by their brief growing season, as in most *Centrolepis* and *Aphelia* species. The largest fruit among African species reported by Caddick and Linder (2002) is *Cannomois grandis* at 0.303 g. Our sampling was not comprehensive and the findings (Table 2) are subject to error since often few seeds or fruits were available and it was not feasible to test for seed maturity although, in nut fruited species, 'early hardening of the ovary wall gives the impression that seed is mature' (Newton *et al.* 2002).

Seed surface patterns: The surface features illustrated here do not show patterns that are indicative of the relationships shown in the DNA-based phylogeny. No features have been hypothesised as plesiomorphic states. The basal branches of the restiid clade have diverse seed surface features: longitudinal lines of more or less convex cells in *Anarthria*, small cells with a concave surface and spicules at the cell corners in *Lyginia*, convex polygonal cells in *Hopkinsia*, a prominent intricate network of narrow ridges over the cells (tertiary structure) in *Sporadanthus* and some of *Lepyrodia*, longitudinal ridges in some of the centrolepid clade.

Some genera have distinctive seed features, such as *Chordifex* with longitudinal lines of convex cells, sometimes fused into ridges or *Loxocarya* with a longitudinal furrow and a distinctive surface cell shape and deep clefts between the cells. A very distinctive surface pattern, rows of cells that are flat, parallelogram-shaped and elongated transversely to the row, is shared by *Dielsia* and *Tremulina* whose relationships suggest that this is not a synapomorphy.

Fossil fruits referred to Restionaceae: Dettmann and Clifford (2000) assigned small, indehiscent unilocular fruits with a single pendulous orthotropous seed that has a structured micropylar cap from late Eocene or early Oligocene sediments of central eastern Queensland to the fossil genus *Restiocarpum*, describing five species of *Restiocarpum* from those sediments. The generic description noted 'the fruits are assumed to be indehiscent as there is no indication of dehiscence structures on their walls, which are usually preserved intact' and 'Fruit wall single-layered … Seed wall single-layered except about the micropyle, where a multicellular cone is developed' and that the ellipsoidal to ovoid fruit tapers apically 'to a stigma of one to three styluli'. The apical region of the fruit is well preserved in specimens they examined of four of the species of *Restiocarpum* and the styluli are slight rounded projections, described as 40 µm long in *R. verrucatum* and 110 µm long in *R. latericum*.

Smith *et al.* (2010) accepted *Restiocarpum* as probably belonging to Restionaceae, in the absence of suggestions that they belong to another family. They noted that 'More work is needed to document detailed anatomical and morphological features of monocots, especially for reproductive material that can provide a suite of morphological characters'. All modern Restionaceae have well-developed styles and this would appear to be an obstacle to matching *Restiocarpum* with Restionaceae. Styles in the family include: the three separate styles of *Sporadanthus* and *Calorophus* arising at distal corners of the fruit apex; in Centrolepidoideae the long slender styles of individual carpels of *Aphelia* and *Centrolepis* or the long but partially fused styles of *Gaimardia* (Sokoloff *et. al.* 2015); the long styles of the *Leptocarpus* clade, mostly fused for about half their length with three long stigmatic branches; and the stout, almost wholly stigmatic styles of the *Desmocladus* clade. But nowhere in the restiid clade are there gynoecia and fruit with extremely short styles and minute styluli. Particularly in *R. tesselatum* (Dettmann & Clifford 2000, Plate VI, figs 1 and 2) the very short, rounded protuberances appear well preserved and are impossible to interpret as broken styles, very different from the elongated styles of all modern Restionaceae and Anarthriaceae. Apart from the major difference in the stylar region, only *Leptocarpus*, *Apodasmia*, *Chaetanthus, Dapsilanthus* and the centrolepid clade have pericarps as thin and membranous as *Restiocarpum*. Similarities to Restionaceae in other features mentioned by Dettmann and Clifford are not convincing to us in matching the fossil fruits to any living taxa or clades.

Dettmann and Clifford (2000) noted the presence of *Milfordia* pollen in the same deposits as *Restiocarpum* and that the source community of the deposits had similarities to 'restiad swamps of present day Wallum (swamp heathland) vegetation which is extensively developed along the Queensland coast'. *Milfordia* pollen was widely identified with modern Restionaceae (e.g. Ladd 1977, Krutzsch 1989) and described from a great range of sites, including ones in Europe and north America, far outside the present or likely range of Restionaceae, an almost exclusively southern hemisphere family. Linder (1987) and Linder *et al.* (1998) concluded that there are no diagnostic features linking the *Milfordia* pollen-type (graminoid pollen) to Restionaceae. Instead, this fossil pollen type could equally belong in Flagellariaceae (which does currently occur in northern Australia), Joinvilleaceae (currently southeast Asia and the Pacific islands) or Anarthriaceae (currently southwest Australia only). *Restiocarpum* fruits show no notable similarities to fruits of Flagellariaceae (3-locular drupes), Joinvilleaceae (1–3-seeded drupes) or Anarthriaceae (3-locular capsules or small 1-seeded nuts with a woody pericarp and stout style). Four major types have been recognised in modern restiid pollen (Linder and Ferguson 1985), with the graminoid type in Anarthriaceae and the Australian restioid and centrolepidoid types present in living Australian Restionaceae (as recognised here). Pollen similar to that of modern Australian Restionaceae occurs in Oligocene deposits from southeast Australia (Martin 1973) and from the Miocene onwards in New Zealand (Conran *et al.* 2015). We see no adequate evidence to link *Restiocarpum*, or the *Milfordia* pollen that occurs with it, to Restionaceae.

The circumscription of Restionaceae: Restionaceae s.str. or Restionaceae s. lat.? To recognise Anarthriaceae? Centrolepidoideae or Centrolepidaceae?

There are currently varied opinions on whether to recognise Anarthriaceae separate from Restionaceae (Briggs *et al.* 2014, Givnish *et al.* 2018) or to include the *Anarthria* clade in Restionaceae (APG IV 2016, Fomichev *et* *al.* 2019), and whether the centrolepid clade should be included in Restionaceae as Centrolepidoideae (Briggs *et al.* 2014) or treated as Centrolepidaceae (Sokoloff *et al.* 2015). As noted above, Anarthriaceae as recognised here are extraordinarily diverse in their seed and fruit types: *Hopkinsia* having woody indehiscent fruits with a fleshy outer pericarp layer; *Lyginia* having dehiscent capsules and seeds with a unique circular flange and surface ornamentation of spicules at the corners of surface cells. *Anarthria* also has dehiscent capsules and seeds with a pattern of longitudinal lines of cells and a secondary pattern of striations that is different in detail from the ornamentation of seeds of any genus of Restionaceae, but not outside the range of variation within Restionaceae. The seeds of the centrolepid genera, *Gaimardia*, *Aphelia* and *Centrolepis*, range from smooth to longitudinally furrowed and are mostly smaller than those of other restiid genera. We consider that, not surprisingly, seed morphology does not contribute to determining an appropriate circumscription of Restionaceae.

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