MICROMORPHOLOG OF THE SEED ENVELOPE OF *EPHEDRA* L. (GNETALES) AND ITS RELEVANCE FOR THE TIMING OF EVOLUTIONAR EVENTS

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Micromorphology of the seed envelope of Ephedra (Gnetales) is known to be variable, but variation patterns have never been systematically documented. We test the usefulness of this feature for species determination and subclade delimitation in Ephedra and investigate the relationship of this character to infrageneric evolutionary patterns. Most species have a basically smooth seed envelope, which in some species appears slightly striate or reticulate due to convex or depressed outer periclinal cell walls. Ephedra rhytidosperma from China and Ephedra torreyana

species recognition. Furthermore, parallel evolution of similar micromorphological patterns in unrelated subclades of Ephedra is evident and cannot be explained by similar seed dispersal mechanisms. The Asian species with transverse lamellae or papillae on the seed are dispersed by frugivores whereas similar American species are anemochoric. Transverse ridges occur in several Early Cretaceous fossil seeds with affinity to Ephedra. However, our results indicate that the resemblance between these fossils and extant taxa with similar features is superficial and convergent. In line with other recent studies, we find that Cretaceous ephedroids are extinct stem relatives to the extant clade.

Keywords: Early Cretaceous, Ephedra, fossils, Gnetales,to the extanta558-335smc71talessexplingc71t54.7electr-306TBT1-337.2scopy

~50 species inhabiting dry,

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Clade, specimen ID	Species	Locality	Voucher	Seed shape in longitudinal section; apex shape	General epidermal pattern	Sculpt size (mm)	Cell length (mm)	Periclinal cell walls	ITS[a]
Mediterranean:									
UAF	E. foeminea Forssk.	Italy	1526: 1983 (PE seed bank)[b]	Elliptic; acute	Smooth	...	80–200	Variable	...
130	E. foeminea Forssk.	Greece	Rydin 130 (Z)[b]	Narrowly elliptic; acute	Smooth	...	120–200	Convex	GU968546
152	E. foeminea Forssk.	Dalmatia	Freitag 19.807 (KAS)[c]	Elliptic; acute	Smooth	...	100–180	Convex	GU968551
159	E. foeminea Forssk.	Greece	Fries C-7619 (S)[c]	Narrowly elliptic; acute	Smooth	...	100–180	Convex	...
UAF	E. alata Decne.	Algeria	Cosson s.n. (MO)[b]	Ovate; acuminate	Smooth (partly weakly transversely lamellar)	...	Unclear	Flat	...
128	E. alata Decne.	Algeria	Anderberg 481 (S)[c]	Ovate; acuminate	Smooth (partly weakly transversely lamellar)	100–300	100–180	Flat or convex	...
147	E. alata Decne.	Algeria	Cosson C-311 (S)[b]	Ovate; acuminate	Smooth (partly weakly transversely lamellar)	~300	Unclear	Flat	...
082	E. altissima Desf.	Tunisia	Botan SU 18 (S)[c]	Elliptic; acute	Smooth	...	40–150	Convex	AY755773
132	E. altissima Desf.	Morocco	Freitag 35.001 (KAS)[b]	Ovate; acute	Smooth	...	150–200	Convex	...
080	E. aphylla Forssk.	Libya	Anderberg 853 (S)[c]	Elliptic; acute	Smooth	...	30–60	Convex	AY755771
124	E. aphylla Forssk.	Palestine	Kramer 4727 (Z)[c]	Narrowly elliptic; acute	Smooth	...	100–200	Convex	GU968544
154	E. aphylla Forssk.	Israel	Amdursky 402 (S)[c]	Ovate; acute	Smooth	...	150–300	Variable	GU968552
101	E. fragilis Desf.	Morocco	Jonsell 5412 (UPS)[c]	Narrowly oblong; acute	Smooth	...	50–100	Variable	FJ958014
109	E. fragilis Desf.	Morocco	Denk s.n. (S)[c]	Narrowly elliptic; acute	Smooth	...	70–140	Convex	FJ958019
120	E. fragilis Desf.	Hispaniola	Freitag 328–40 (Z)[c]	Narrowly elliptic; acute	Smooth	...	50–150	Convex	...
162	E. major Host ssp. major	Spain	Ipse 71/677E (Z)[c]	Narrowly oblong; acute	Smooth	...	120–220	Convex	GU968553
166	E. major Host ssp. major	Algeria	Hofmann 013–1971 (Z)[c]	Narrowly oblong; acute	Smooth	...	120–150	Convex	GU968557
167	E. major Host ssp. major	Algeria	Juillet 94 (Z)[c]	Narrowly oblong; acute	Smooth	...	80–180	Convex	GU968558
Clade A:									
146	E. ciliata Fisch. et C.A. Mey.	Morocco	Balls B2487 (S)[c]	Ovate; acute	Smooth	...	70–180	Variable	GU968548
153	E. ciliata Fisch. et C.A. Mey.	Turkmenistan	Androssov 3367 (S)[c]	Elliptic; acute	Smooth	...	80–200	Flat or depressed	...
096	E. foliata Boiss. et C.A. Mey.	Somalia	Thulin 10745 (UPS)[c]	Elliptic; acute	Smooth	...	80–180	Flat or convex	FJ958010
North America:									
ASU	E. antisyphilitica Berl. ex C.A. Mey.	Texas	Ickert-Bond 900 (ASU)[b]	Elliptic; obtuse	Smooth	...	110–140	Depressed	AY599148
UAF	E. aspera Engelm. ex S. Watson	Arizona	Rose 40086 (MO)[b]	Ovate; acute	Smooth	...	50–100	Depressed	...
ASU	E. aspera Engelm. ex S. Watson	Texas	Correll 23971 (NY)[b]	Ovate; acute	Indistinctly coarse	...	Unclear	Convex	...
UAF	E. aspera Engelm. ex S. Watson	California	Faulkner 545 (UCR)[b]	Ovate; acute	Indistinctly coarse	...	200–280	Convex	...

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Clade, specimen ID	Species	Locality	Voucher	Seed shape in longitudinal section; apex shape	General epidermal pattern	Sculpt size (mm)	Cell length (mm)	Periclinal cell walls	ITS[a]
253	E. trifurca Torrey ex S. Watson	Arizona	Goodding 2268 (S)[b]	Lanceolate; acuminate	Smooth	...	150–320	Convex	...
254	E. trifurca Torrey ex S. Watson	Arizona	Nelson & Nelson 1290 (S)[b]	Lanceolate; acuminate	Smooth	...	170–240	Convex	...
ASU	E. viridis Coville	California	Parish 2975 (NY)[b]	Oblong-ovate; acute	Smooth	...	190–280	Convex	...
091	E. viridis Coville	Utah	Holmgren et al. 1826 (UPS)[c]	Ovate; acute	Smooth	...	25–60	Convex	FJ958005
South America:									
ASU	E. americana Humb. et Bonpl. ex Willd.	Ecuador	Juncosa 2257 (NY)[b]	Elliptic; acute	Smooth	...	190–400	Depressed	...
127	E. americana Humb. et Bonpl. ex Willd.	Argentina	Novara 8219 (S)[c]	Elliptic; acute	Smooth	...	120–300	Convex	GU968545
UAF	E. boelkei Roeg.	Argentina	Ickert-Bond 1252 (ASU)[b]	Ovate; acute	Smooth	...	100–250	Convex	AY599175
ASU	E. breana Phil.	Chile	Ickert-Bond 1233 (ASU)[b]	Elliptic; rounded	Smooth	...	140–240	Depressed	...
025	E. chilensis K. Presl	n.a.	Chase 10140 (K)[c]	Elliptic; acute	Smooth	...	40–80	Convex	AY755744
ASU	E. chilensis K. Presl.	Argentina	Jostasato 4333 (NY, ARIZ)[b]	Elliptic; acute	Smooth	...	120–220	Convex	...
075	E. chilensis K. Presl.	Chile	Forbes 49.0542 (UC)[c]	Elliptic; acute	Smooth	...	30–100	Convex	AY755767
123	E. chilensis K. Presl.	Chile	Gay 400 (Z)[c]	Elliptic; acute	Smooth	...	40–140	Convex	GU968543
UAF	E. multiflora Phil. ex Stapf	Chile	Ickert-Bond 1211 (ASU)[b]	Ovate; acuminate	Transversely wavy	120–480	120–470	Flat	AY599173
UAF	E. multiflora Phil. ex Stapf	Chile	Ickert-Bond 1231 (ASU)[b]	Ovate; acuminate	Transversely wavy	100–500	100–500	Flat	...
UAF	E. ochreata Miers	Argentina	Ickert-Bond 1253 (ASU)[b]						

125	*E. equisetina* Bunge	Turkmenistan	Sintensis 666 (S)[c]	Narrowly ovate; acute	Smooth	...	80–200	Convex	...
142	*E. equisetina* Bunge	Russian Altai	Freitag 05.2008 (KAS)[c]	Ovate; acute	Smooth	...	100–200	Convex	...
234	*E. equisetina* Bunge	Turkmenistan	Lipsky 2610 (S)[c]	Ovate; acute	Smooth	...	40–100	Convex	GU968572
249	*E. equisetina* Bunge	Turkestan	Moldengauer 22 (S)[c]	Ovate; acute	Smooth	...	75–200	Convex	...
250	*E. equisetina* Bunge	Turkmenistan	Lipsky 3653 (S)[b]	Ovate; acute	Smooth	...	100–180	Convex	...
251	*E. equisetina* Bunge	Turkmenistan	Lipsky 2587 (S)[c]	Ovate; acute	Smooth	...	100–200	Convex	...
252	*E. equisetina* Bunge	Kopet Dag Mountain	Lipsky 2124 (S)[c]	Ovate; acute	Papillate	4–10	70–150	Convex	...
148	*E. gerardiana* Wall. ex Florin	Almora, India	Parker 2099 (S)[c]	Oblong; acute	Smooth	...	50–150	Depressed	...
UAF	*E. major* Host	Morocco	Lewalle 9642 (MO)[b]	Oblong; acute	Papillate	4–8	40–100	Flat; papillate	...
163	*E. major* Host	Spain	Montserrat 319171 (Z)[c]	Elliptic; acute	Papillate	4–10	100–130	Convex; papillate	GU968554
164	*E. major* Host	Transcaucasia	Grossheim s.n. (Z)[c]	Elliptic; acute	Papillate	2–8	90–150	Convex; papillate	GU968555
165	*E. major* Host	Herzegovina	Baenitz s.n. (Z)[c]	Elliptic; acute	Papillate	2–8	100–175	Convex; papillate; with apical warty projections	GU968556
169	*E. major* Host	France	Zogg & Gassner 8388 (Z)[c]	Elliptic; acute	Papillate	2–8	120–180	Convex; papillate	GU968559
156	*E. pachyclada* Boiss.	Hissar, Turkestan	Regel s.n. (S)[c]	Elliptic; rounded	Smooth (at mid-length with weak transverse lamellae)	10–35	Unclear	Flat or convex; papillate; with apical warty projections	...
UAF	*E. rhytidosperma* Pachom.	Mount Helan, China	Yang 20060620 (PE)[b]	Obovate-elliptic; acute	Transversely lamellar	100–500	Unclear	Convex	...
138	*E. saxatilis* (Stapf) Royle ex Florin	n.a.	Cult. 1947–2603 (K)[c]	Oblong; obtuse	Smooth	...	50–130	Flat or convex	...
144	*E. saxatilis* (Stapf) Royle ex Florin	Nepal	Freitag 098–38–74–84 (KAS)[c]	Oblong; obtuse	Smooth	...	100–200	Flat or convex	...
Asia M:									
140	*E. distachya* L.	n.a.	Cult. 46126.000 (K)[c]	Elliptic; acute	Smooth	...	15–40	Convex	...
143	*E. sarcocarpa* Aitch. et Hemsl.	Iran	Freitag 13.988 (KAS)[c]	Ovate; acute	Smooth	...	100–170	Flat	...
UAF	*E. strobilacea* Bunge	Asia Media	Collector unknown (PE seed bank no. 0679: 1961)[b]	Lanceolate; narrowly acute	Smooth	...	40–100	Depressed	...
150	*E. strobilacea* Bunge	Turkmenistan	Androssov 1900 (S)[c]	Lanceolate; narrowly acute	Smooth	...	100–240	Flat or convex	GU968549
111	*E. transitoria* Riedl	Saudi Arabia	Collenette 9095 B (E)[c]	Narrowly oblong; acute	Smooth	...	70–130	Flat	FJ958021
Asia N:									
173	*E. fedtschenkoae* Paulsen	Xinjiang, China	Zhu Taiyan 650764 (N)[c]						

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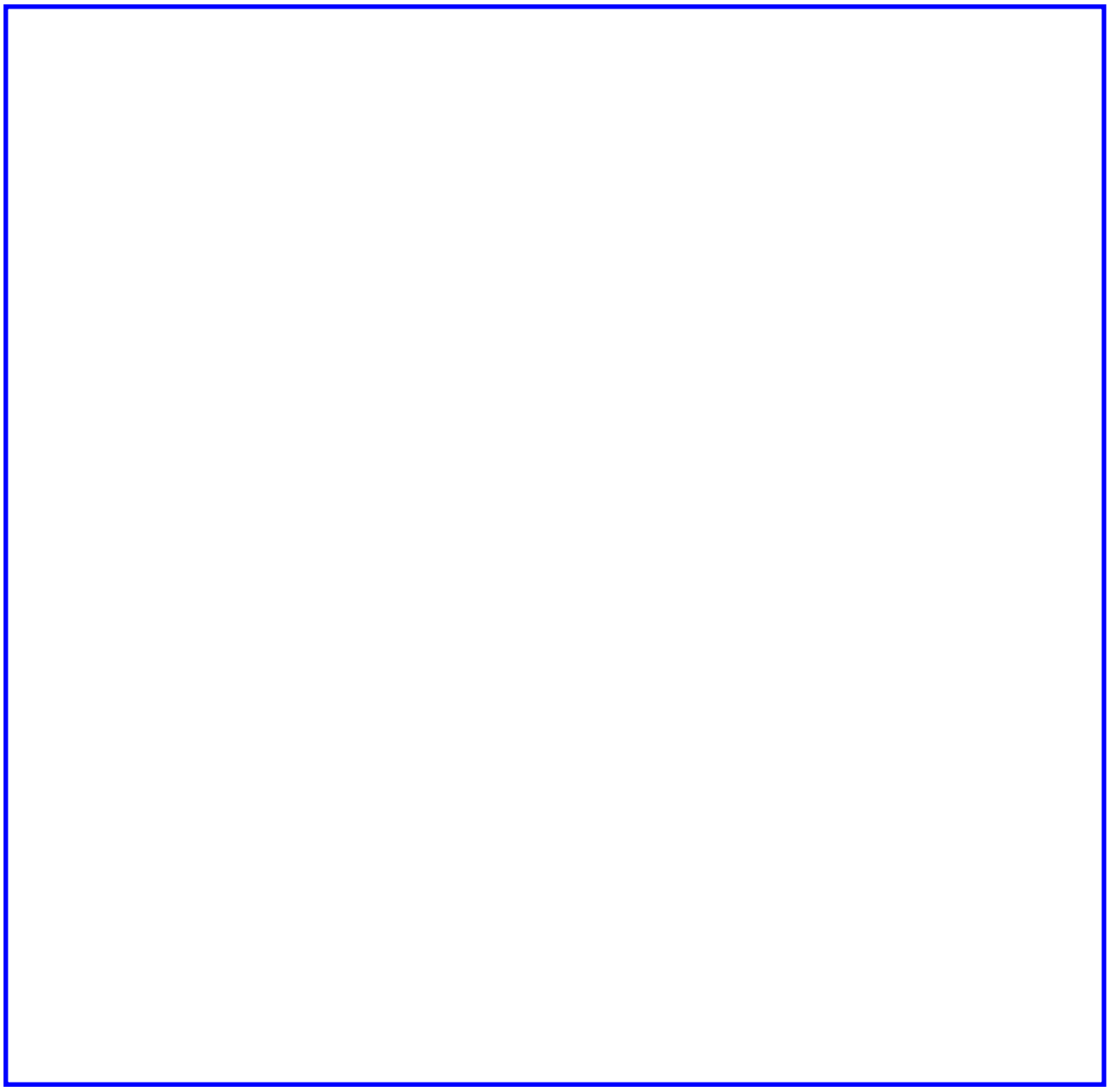
Clade, specimen ID	Species	Locality	Voucher	Seed shape in longitudinal section; apex shape	General epidermal pattern	Sculpt size (mm)	Cell length (mm)	Periclinal cell walls	ITS[a]
174	E. lomatolepis Schrenk	Pakistan	Bosshard et al. 803.24 (Z)[c]	Elliptic; acute	Smooth	...	70–190	Flat or depressed	GU968562
UAF	E. regeliana Florin	Xinjiang, China	K.C. Kuan 1067 (PE)[b]	Narrow elliptic; acute	Smooth	...	50–100	Flat or depressed	...
UAF	E. sinica Stapf	Hebei, China	Unknown coll. s.n. (herb. no. 00015747, PE)[b]	Ovate; acute	Smooth	...	40–150	Flat	...
UAF	E. sinica Stapf	Inner Mongolia, China	Chu 20060801 (PE)[b]	Ovate; acute	Smooth	...	70–150	Flat	...
151	E. sinica Stapf	Inner Mongolia, China	Eriksson 05–9020 (S)[c]	Ovate; acute	Smooth	...	Unclear	Depressed	GU968550

[a] The internal transcribed spacer of the nuclear ribosomal DNA (ITS) is available for some of the vouchers and has been included in phylogenetic analyses in published studies (Ickert-Bond and Wojciechowski 2004; Rydin et al. 2004, 2010; Rydin and Korall 2009). n.a. = information not available.

[b] Material = mature seeds.

[c] Material in pollination stage of development.

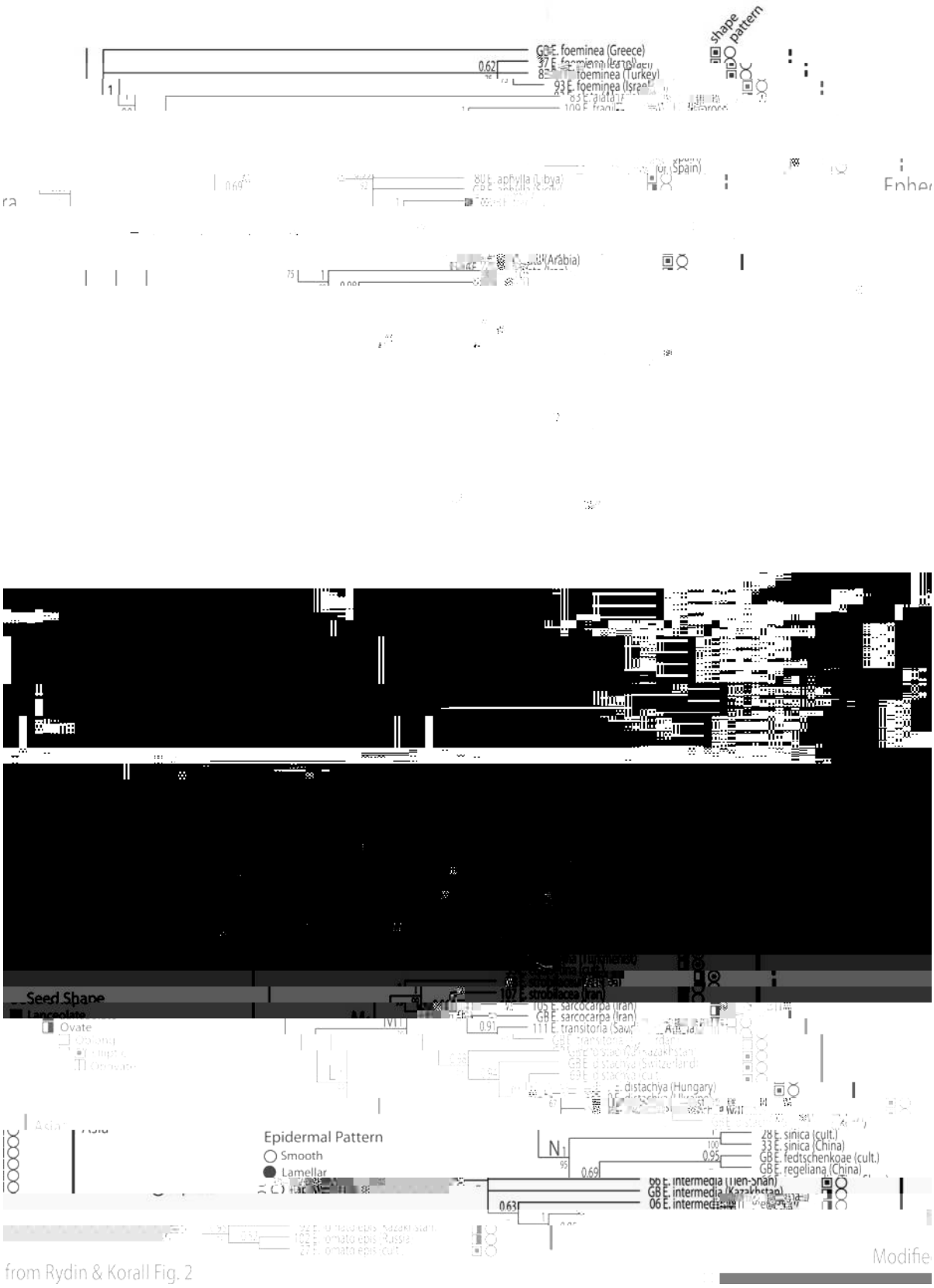
F . 1 Seed shapes in longitudinal outline (A–D) and surface patterns of the seed envelope (E–L



specimens of E. equisetina lack papillae altogether and have smooth seed envelopes (not shown). Seeds of E. equisetina from Mount Helan, China, have transverse lamellae similar to those in E. rhytidosperma and E. torreyana but with papillae on the lamellae (fig. 1K).

The specimens of E. pachyclada and E. lomatolepis and one specimen of E. major (table 1) have wartlike projections on the surface (fig. 1L). In E. pachyclada and E. major, they are present only in the apical region of the seed envelope. In E. lomatolepis, they are rare but may occur over the entire seed surface. Each projection is ~10–40 mm across. Some overarch cell boundaries, and some appear to have collapsed.

In several unrelated species (e.g., E. alata,



from Rydin & Korall Fig. 2

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to plants; James A. Doyle and an anonymous reviewer for valuable comments on the text; and John Benedict, Monte Garroutte, Zachary Meyers, and Yong Yang for technical assistance. This work was supported by grants from the Swedish Research Council to C. Rydin and a National Science Foundation grant (Collaborative Research: Gymnosperms on the Tree of Life: Resolving the Phylogeny of Seed Plants, NSF-0629657) to S. M. Ickert-Bond.

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