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X-rays and virtual taphonomy resolve the first *Cissus* (Vitaceae) macrofossils from Africa as early diverging members of the genus.

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1 **X-rays and virtual taphonomy resolve the first *Cissus* (Vitaceae) macrofossils**
2 **from Africa as early diverging members of the genus¹**

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20 **Running Head**

21 First fossil seeds of *Cissus* (Vitaceae) from Africa

22 **Footnotes**

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ABSTRACT

- *Premise of the study:* Fossilized seeds similar to *Cissus* (Vitaceae) have been recognized from the Miocene of Kenya, though some were previously assigned to the Menispermaceae. We undertake a comparative survey of extant African *Cissus* seeds to identify the fossils and consider their implications for the evolution and biogeography of *Cissus* and for African early Miocene paleoenvironments.
- *Methods:* Micro-computed tomography (μ CT) and synchrotron-based X-ray tomographic microscopy (SRXTM) were used to study seed morphology and anatomy. Virtual taphonomy, using SRXTM datasets, produced digital fossils to elucidate seed taphonomy. Phylogenetic relationships within *Cissus* were reconstructed using existing and newly produced DNA sequences for African species. Paleobiology and paleoecology were inferred from African nearest living relatives.
- *Key results:* The fossils are assigned to four new *Cissus* species, related to four modern clades. The fossil plants are interpreted as climbers inhabiting a mosaic of riverine woodland and forest to more open habitats. Virtual taphonomy explains how complex mineral infill processes concealed key seed features, causing the previous taxonomic misidentification. Newly sampled African species, with seeds most similar to the fossils, belong to four clades within core *Cissus*, two of which are early diverging.
- *Conclusions:* Virtual taphonomy, combined with X-ray imaging, has enabled recognition of the first fossil *Cissus* and Vitaceae from Africa. Early divergent members of the core *Cissus* clade were present in Africa by at least the early Miocene, with an African origin suggested for the *Cissus sciaphila* clade. The

71 fossils provide supporting evidence for mosaic paleoenvironments inhabited by
72 early Miocene hominoids.

73

74 **Key words**

75 *Cissus*; Hiwegi Formation; liana; *Menispermicarpum*; microCT; Miocene;

76 paleoecology; seeds; SRXTM; virtual taphonomy.

78 The volcanic and clastic sediments of the Hiwegi Formation on Rusinga Island, Lake
79 Victoria, Kenya have yielded a rich early Miocene flora and fauna with well over one
80 hundred recorded species, dated to ca. 18–20 Ma (Drake et al., 1988; Andrews et al.,
81 2009; Peppe et al., 2011). The floral assemblage contains fossilized fruits, seeds,
82 twigs, wood, bark, and leaves (Chesters, 1957; Collinson et al., 2009; Maxbauer et
83 al., 2013; Michel et al., 2014), and the faunal assemblage comprises numerous fossil
84 mammals (e.g., Whitworth, 1958; Pickford, 1981; Butler, 1984; Werdelin, 2011),
85 reptiles (e.g., Clos, 1995; Conrad et al., 2013), birds (e.g., Harrison, 1980; Rich &
86 Walker, 1983) and invertebrates (e.g., Leakey, 1952; Verdcourt, 1963; Thackray,
87 1994; Pickford, 1995). The fauna also contains several genera of early hominoids
88 (e.g., Le Gros Clark and Leakey, 1951; Andrews and Simons, 1977; Walker and
89 Teaford, 1988; Walker et al., 1993; Harrison, 2002; McNulty et al., 2007; Harrison
90 and Andrews, 2009; Pickford et al., 2009), including *Ekembo* (previously *Proconsul*,
91 see McNulty et al., 2015), which mark the transition between Paleogene arboreal
92 primates, thought to inhabit tropical forests (Andrews, 1992; Janis, 1993), and
93 Neogene bipedal hominids, often associated with open savanna grassland
94 (Robinson, 1963; Reed, 1997; Pickford, 2002). Study of the Hiwegi Formation flora is
95 essential to understand the paleoenvironments in which these transitional hominoids
96 evolved.

97 The fruit and seed flora was partly described by Chesters (1957) from surface-
98 picked collections, but these lacked a sedimentological and stratigraphic context.
99 This prompted in situ excavations at the new site of R117 (Collinson et al., 2009),
100 where over 360 fruits and seeds were collected, including several specimens
101 tentatively assigned to 'cf. *Cissus* sp. 1 nov.' (Vitaceae). During that study, three

102 other morphotypes with similarity to seeds of extant *Cissus* L. species were
103 recognized among the collections originally studied by Chesters (1957, 1958). If
104 these four fossil records of *Cissus* can be verified, they would constitute the first
105 records of the Vitaceae in the flora, the earliest reported record of Vitaceae from the
106 African continent, and could provide evidence for arid- or rainforest-adapted taxa in
107 the African Miocene vegetation (De Santo et al., 1987; Verdcourt, 1993; Lombardi,
108 2000; Manchester et al., 2012a).

109 Recent molecular phylogenetic analyses of the genus *Cissus* (Liu et al., 2013;
110 Rodrigues et al., 2014) showed that modern species could be assigned to several
111 distinct clades. All African species fell within the 'core *Cissus*' clade, but within that
112 were distributed in more than seven distinct clades, two of which also included Asian
113 species (Liu et al., 2013). Many African species were missing from these
114 phylogenies, including those with external seed morphology most similar to the
115 putative *Cissus* fossils. If the fossils are *Cissus*, molecular study of these neglected
116 modern species will be essential to place them in their phylogenetic context.

117 This paper therefore aims to: (i) confirm or refute the identification of Hiwegi
118 Formation fossils to *Cissus* and, if confirmed, identify the clades to which the fossil
119 species are likely related by comparing external and internal seed morphology of the
120 fossils to extant African species; (ii) place the nearest living relatives of the fossils
121 into the existing phylogenetic framework; and (iii) evaluate the paleoenvironmental
122 and biogeographic significance of these fossils.

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MATERIALS AND METHODS

Specimens studied—The fossil fruits and seeds from the Hiwegi Formation are composed of carbonate minerals, which derive from highly alkaline ash erupted from the nephelinite-carbonatite Kisingiri volcano during the Miocene (Bestland et al., 1995; Harris and Van Couvering, 1995), and which replaced biological structures (Collinson et al., 2009). The specimens were collected from the Hiwegi Formation (for wider stratigraphic context see Drake et al., 1988; Collinson et al., 2009) by surface picking and in situ excavation and are stored in collections at the Natural History Museum, London (NHMUK, numbers prefixed V) and the National Museums of Kenya, Nairobi (KNM). Three fossil seed morphotypes in NHMUK, which Chesters (1957, 1958) had placed in the Menispermaceae (due to their bisymmetry, horseshoe-shaped curvature, and sculptured margins), were noted by Collinson to have strikingly similar exterior seed coat morphology to modern African *Cissus* species, as illustrated in African floras (e.g., Dewit and Willems, 1960; Descoings, 1967, 1972; Verdcourt, 1993). Collinson et al. (2009) also listed several specimens from the R117 site assigned to 'cf. *Cissus* sp. 1 nov.' (Vitaceae) based on similarity to modern *Cissus* seeds. All these fossils were re-examined during the current study.

Fifteen modern species of African *Cissus* and three species of African *Cyphostemma* (Planch.) Alston, which have comparable seed ornamentation to the putative *Cissus* fossils, were sampled from loose fruits on herbarium sheets in the Royal Botanic Gardens, Kew Herbarium (K) to study seed anatomy. The most visibly mature and undamaged specimens were selected. Additionally, fruits of *Cissus dasyantha* were obtained from the herbarium at the Botanic Garden Meise, Belgium (BR). Herbarium sheet information for the species sampled is provided in Appendix S1 (see Supplemental Data with the online version of this article).

148 **Macrophotography and VP-SEM**—Photographs of the specimens described
149 by Chesters (1957, 1958) were provided by the NHMUK Photographic Unit. The
150 smaller specimens, assigned to ‘cf. *Cissus* sp. 1 nov.’ by Collinson et al. (2009), were
151 examined uncoated under a Leo 1455 vapour pressure scanning electron
152 microscope (VPSEM) at the Imaging and Analysis Centre, NHMUK. Specimens were
153 placed loose onto a sheet of black paper in a small tray, moved into appropriate
154 orientation and turned over using a fine (size 00000) artist's brush. A small amount of
155 Blu-Tack® (Bostik, Paris, France) was used, when unavoidable, to orient specimens
156 for apical and basal views. Images were obtained using the back scatter detector
157 (BSD), a chamber pressure of 14–15 Pa, current of 20 kV, spot size 500 and working
158 distance 38–39 mm. Images were adjusted uniformly for contrast and brightness
159 using Adobe Photoshop CS2 or CS6.

160 **Synchrotron-based X-ray tomographic microscopy (SRXTM)**—The
161 traditional method of boiling and scrubbing modern fruits to study their seeds is
162 problematic. Depending on tissue toughness, seed features may not be revealed in a
163 repeatable or comparable manner across different species or genera. Cutting or
164 histological sectioning to study internal anatomy also has limitations: it is destructive,
165 may introduce artefacts (tears, gaps), and multiple planes of section through the
166 same specimen cannot be acquired. X-ray imaging solves these problems because
167 multiple planes of section through a single specimen can be easily and non-
168 destructively obtained (e.g., Smith et al., 2009). Modern *Cissus* and *Cyphostemma*
169 fruits were scanned using SRXTM, as this technique provides the necessary quality
170 of resolution to enable distinction of cellular details in the fruit wall and seed coat
171 layers for systematic study and for virtual taphonomy (Smith et al., 2009; Collinson et
172 al., 2013). The SRXTM was performed on the TOMCAT beamline at the Swiss Light

173 Source, Paul Scherrer Institut, Villigen, Switzerland (Stampanoni et al., 2006).
174 Specimens were mounted onto brass pin stubs using polyvinyl acetate glue and were
175 scanned during one session of beamtime in July 2014. X-rays transmitted by the
176 specimens were converted into visible light by a 300 μm -thick Ce-doped LAG
177 scintillator screen. A microscope objective of 1.25 \times or 2 \times (depending on fruit size)
178 magnified the projection data, which were then digitized by a high-resolution scientific
179 CMOS camera (PCO.edge; PCO GmbH, Kelheim, Germany), giving a resultant voxel
180 size of 3 to 5 μm . The energy was set at 17.5 keV and the exposure time per
181 projection was 50 ms. For each scan a total of 1501 projections (2560 \times 2160 pixels
182 with PCO.edge camera) were acquired over 180°. Reconstruction algorithms were
183 then used to combine the projections and obtain a three-dimensional volume,
184 reconstruction was performed on a dedicated Linux PC cluster using a highly
185 optimized routine based on the Fourier transform method and a gridding procedure
186 (Marone et al., 2010; Marone & Stampanoni, 2012). Multiple stacked scans were
187 used if the specimens did not completely fit within the field of view. 3D datasets were
188 visualized, and images and videos were captured, in Avizo 8.1 (FEI Visualization
189 Science Group, Bordeaux, France). Images were adjusted uniformly for contrast and
190 brightness using Adobe Photoshop CS2 or CS6. Videos of digital SRXTM
191 tomograms in transverse section (DTS) through fruits of each of these modern
192 species are available from the Dryad Digital Repository
193 (<http://dx.doi.org/10.5061/dryad.g9r36>).

194 ***Micro-computed tomography (μCT)***—Externally visible ventral infolds are a
195 characteristic feature of *Cissus* seeds (Chen and Manchester, 2011), but are not
196 evident in the fossils (Fig. 1). Information on internal structure of the fossils (including
197 holotypes) is required to test whether these characteristic ventral infolds are: (a)

198 genuinely absent, which would exclude affinity with Vitaceae; (b) present but
199 externally obscured by a seed coat layer, which would indicate affinity with
200 *Cyphostemma* (Chen and Manchester, 2011); or, (c) obscured as a consequence of
201 taphonomic processes, such as mineral infilling during fossilization, which would
202 support identification to *Cissus*. For holotypes and rare fossils this information must
203 be obtained non-destructively. Therefore, three fossil specimens (V33753, V68501,
204 V68506) from collections studied by Chesters (1957, 1958) stored in NHMUK and
205 two specimens (R117.1981.314, R117.1981.476) from the R117 site, identified by
206 Collinson et al. (2009) as 'cf. *Cissus* sp. 1 nov.', housed in KNM were scanned by
207 μ CT using a Nikon Metrology HMX ST 225 at the Imaging and Analysis Centre,
208 NHMUK. Specimens were stabilised by inserting them into blocks of OASIS® Floral
209 Foam (Smithers-Oasis Company, Kent, Ohio, USA) within in a plastic tube.
210 Specimens were wrapped for protection in cling film: a thin film of PVC (polyvinyl
211 chloride) or LDPE (low density polyethylene). A voltage of 200 kV was used with a
212 current of 180 μ A, a tungsten reflection target, a 0.5 or 0.25 mm copper filter and an
213 exposure time of 708 ms; this resulted in a voxel size of 12 μ m. Four modern *Cissus*
214 fruits scanned by SRXTM (one *C. dinklagei*, one *C. populnea*, two *C. integrifolia*)
215 were also scanned using μ CT. This duplicative scanning aimed to ensure that μ CT
216 scans of the fossils could be interpreted in the context of directly comparable scans
217 of modern seeds (a comparison of imaging methods is provided in Appendix S2, see
218 Supplemental Data with the online version of this article). A voltage of 125 kV was
219 used with a current of 200 μ A, a molybdenum reflection target, no filter and an
220 exposure time of 708 ms; this resulted in a voxel size of 8 to 15 μ m. μ CT datasets
221 were reconstructed using CT Pro (Nikon Metrology, Tring, UK) and were visualized in

222 Avizo 8.1. Images and videos were obtained as for SRXTM datasets. Videos are
223 available from the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.g9r36>).

224 **Virtual taphonomy**—The technique of ‘virtual taphonomy’, developed by
225 Smith et al. (2009), solves the problem of potential variability in tissue removal with
226 traditional boiling or scrubbing methods in seed preparation. Virtual taphonomy uses
227 X-ray datasets to digitally remove specific tissue or cell layers from modern fruits or
228 seeds, thereby creating digital fossils, the surfaces of which can be directly compared
229 to real fossils to determine which layers are preserved. Digital seed infills can also be
230 produced using this technique, mimicking the mineral infill of fruits and seeds that
231 can occur during fossilization (Smith et al., 2009; Collinson et al., 2013). For modern
232 *Cissus populnea* Guill. & M.Brandt, a digital infill of the space inside the inner seed
233 coat (the endotesta) was produced (a ‘virtual fossil’), to mimic mineral infill during
234 fossilization. The ventral infolds were then digitally infilled to mimic processes that
235 might have led to mineral obscuring the ventral infolds during fossilization.

236 **Molecular phylogeny**—Phylogenetic relationships within *Cissus* and the
237 placement of species assigned to this genus within Vitaceae were assessed using
238 available sequence data from the plastid genome (*trnL* intron, *trnLF* spacer, *atpB*-
239 *rbcL* spacer, *trnC*-*petN* spacer and *rps16* intron), as well as newly produced
240 sequences of *trnLF* and *rps16* for eight African *Cissus* species with seeds most
241 similar to the putative *Cissus* fossils, which were not represented in previous
242 molecular phylogenetic studies (see Appendix 1). Sequence data obtained from
243 public repositories comprise 91 *Cissus* species and 92 species from other genera of
244 Vitaceae (see Appendix 2).

245 Total genomic DNA was extracted using a standard CTAB-based protocol
246 (Doyle and Doyle, 1987) and purified using a combined caesium chloride/ethidium

247 bromide gradient and dialysis procedure. The *trnL* intron/*trnL*-*F* spacer and the *rps16*
248 intron were amplified using the primers designed by Taberlet et al. (1991) and Shaw
249 et al. (2005), respectively. Further details regarding the polymerase chain reactions,
250 amplification procedures, PCR product purifications, and cycle sequencing reactions
251 are provided in Appendix S3, see Supplemental Data with the online version of this
252 article.

253 Matrices (including sequences obtained from public repositories and those
254 produced for the present study) were aligned using MUSCLE (Edgar, 2004) in
255 Geneious; alignments are available from TreeBASE (<https://treebase.org>; study ID
256 18491). A phylogenetic analysis was performed on a combined matrix using the
257 maximum likelihood criterion as implemented in the programme RAxML v8.1.24
258 (Stamatakis, 2014) using the rapid bootstrap algorithm with 1000 replicates and a
259 search for the best-scoring tree. Divergence time estimates were obtained using the
260 Bayesian inference approach implemented in the package BEAST v.1.8.2
261 (Drummond and Rambaut, 2007). All analyses were run on the Cipres Science
262 Gateway portal (www.phylo.org). Further details of the phylogenetic analyses are
263 provided in Appendix S3, see Supplemental Data with the online version of this
264 article.

265 Calibration was performed using three fossils. The first is the oldest known
266 fossil securely identified to the Vitaceae family (*Indovitis*) from the latest
267 Cretaceous/earliest Paleogene Deccan traps of India (ca. 66Ma, based on
268 radiometric dating and biostratigraphy; Manchester et al., 2013) and was used as
269 calibration on the crown node of subfamily Vitoideae (calibration A), comprising all
270 genera of Vitaceae except the genus *Leea*, which is assigned to subfamily
271 Leeoideae. A lognormal distribution was used, which allows the age to vary (given

272 the uncertainty in fossil age estimation and given that a fossil's age is considered a
273 minimum age for a given group), with an offset value of 65 and a standard deviation
274 of 1.0. The second calibration point comes from fossil seeds assigned to
275 *Ampelocissus parvisemina* Chen & Manchester from the late Paleocene of North
276 America at the Beicegel Creek locality of the Sentinel Butte Formation, Fort Union
277 Group, North Dakota (Chen and Manchester, 2007), considered by Zetter et al.
278 (2011) to be late Paleocene (61.7–56.8 Ma) in age based on molluscan and
279 mammalian (Kihm and Hartman, 1991; Hartman and Kihm, 1995) biostratigraphy and
280 pollen zonation (Nichols and Ott, 1978). It was assigned to the stem node of the
281 clade comprising genera *Ampelocissus* Planch., *Nothocissus* (Miq.) Latiff,
282 *Parthenocissus* Planch., *Pterisanthes* Blume, *Vitis* L., and *Yua* C.L. Li, following Nei
283 et al. (2012) and Liu et al. (2016) (calibration B). As for the previous calibration, a
284 lognormal distribution was used, with an offset value of 55.8 and a standard deviation
285 of 1.0. The third calibration point is the oldest fossil unequivocally assigned to genus
286 *Cissus*, from the Belén flora (North Coastal Peru) of the Oligocene, with a maximum
287 age of 30–28.5 Ma based on diatom biostratigraphy (Manchester et al., 2012a). This
288 fossil has features shared with species from Morphotype 1 and the *Cissus integrifolia*
289 clade (see below); it was therefore assigned to the stem node of this group
290 (calibration C) with a lognormal distribution with an offset value of 27.5 and a
291 standard deviation of 1.0.

292 ***Extant Cissus seed morphological information***—In addition to the
293 sixteen SRXTM datasets of African *Cissus* seeds most similar to the Hiwegi
294 Formation fossils, published seed illustrations and descriptions were sourced, where
295 available, for all African *Cissus* species included in the molecular phylogeny (Table 1
296 and Appendix S4, see Supplemental Data with the online version of this article).

297 Together these data were used to determine the modern species with seeds most
298 similar to those of the fossils and to place these nearest living relatives into the
299 existing phylogenetic framework.

300 **Ecological and biogeographic information**—Data on the habit, habitat
301 and biogeographic distributions of extant *Cissus* species were gathered for extant
302 species in clades containing similar seed morphotypes to the fossils (Table 2).
303 Georeferenced occurrence data from illustrated herbarium sheets were obtained
304 from the Global Biodiversity Information Facility (GBIF, 2013) and floras, and other
305 herbarium sheets were also used. Herbarium sheet sources are given in Appendix
306 S5, see Supplemental Data with the online version of this article.

307

308 SYSTEMATICS

309 Definitions of lateral, ventral, dorsal, apical and basal views and seed height, width
310 and dorsiventral dimension are given in Appendix S6 (see Supplemental Data with
311 the online version of this article).

312

313 **Family**—Vitaceae Juss. 1789.

314 **Genus**—*Cissus* L. 1753.

315 **Species**—*Cissus crenulata* (Chesters) Adams, Collinson, S.Y. Smith &
316 Bamford comb. nov.

317 **Basionym**—*Menispermicarpum crenulatum* Chesters 1957 (pl. 19, figs. 19,
318 20).

319 **Emended diagnosis**—Seed bilaterally symmetrical, 19 mm in dorsiventral
320 dimension, laterally flattened, sub-oval to D-shaped in lateral view, narrowly elliptical
321 and 7 mm wide in apical and basal views, and elliptical in ventral view. Center of

322 lateral face crossed by four pronounced, long ridges radiating from adjacent to the
323 ventral infolds; longest ridge almost as long as seed; curved ridge, 2–3 mm from
324 dorsal and basal margins of lateral faces, delineates faceted marginal area;
325 prominent median ridge (rib perichalaza) extends from beneath ventral infolds,
326 around base, over dorsal margin, and almost full length of apical margin as far as
327 ventral infolds. Upper portion of ventral surface concave, forming acute angle with
328 long axis of seed; pair of very deep, narrow ventral infolds present.

329 **Holotype**—Seed—V33753 (Fig. 1A–D; μ CT DTS video available from the
330 Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.g9r36>).

331 **Excluded specimens**—KNMP-RU7787 (8 specimens with field number
332 60*52, formerly P. B. 8, designated as paratypes of *Menispermicarpum crenulatum*
333 by Chesters, 1957).

334 **Type locality**—Rusinga Island, Lake Victoria, Kenya.

335 **Geological horizon and age**—Hiwegi Formation, early Miocene.

336 **Repository**—Natural History Museum, London, U.K.

337 **Description**—The seed is bilaterally symmetrical around a prominent median
338 perichalazal rib (Fig. 1B, C), laterally flattened with a height/width ratio of 1.7 (Fig.
339 1A, B), sub-oval to D-shaped in lateral view (Fig. 1A), 19 mm in the dorsiventral
340 dimension and 11 mm in height, narrowly elliptical and 7 mm wide in apical (Fig. 1B)
341 and basal (Fig. 1C) views, and elliptical in ventral view (Fig. 1D). The seed apex is
342 rounded, with no indication of an apical notch or chalazal grooves (Fig. 1A-C), and
343 the seed narrows to the ventral margin (Fig. 1A-C). The seed ornamentation is most
344 clearly visible on one lateral face (Fig. 1A). A curved ridge, 2–3 mm from the basal
345 and dorsal margins of the lateral faces, delineates a faceted outer margin with facets
346 spaced at 2.5 to 4.5 mm (Fig. 1A). There are short ridges (ca. 2 mm long), roughly

347 perpendicular to the long curved ridge, within the outer margin, which define the
348 facets (Fig. 1A). There are at least four ridges crossing the center of the lateral face,
349 with one long (10 mm) ridge perpendicular to the ventral surface, and three curved
350 ridges, which radiate away from the ventral surface towards the basal margin,
351 abutting the curved ridge (Fig. 1A). The reverse lateral face is partly obscured by
352 mineral encrustation in the holotype (the only specimen), making the ornamentation
353 less clear. Nevertheless, there are clearly at least three ridges crossing the center of
354 the face radiating from the ventral surface, with one longer and more pronounced
355 than the others. In lateral view, the upper portion of the ventral surface is nearly
356 straight for three-quarters of its length but the basal-most part is indented, forming an
357 angle of ca. 65° with the long axis of the seed (Fig. 1A). The seed narrows into a
358 rounded point on the ventral surface, possibly equivalent to the beak in typical
359 Vitaceae (see fig. 1 in Chen and Manchester, 2011). The lateral flattening, near-
360 straight ventral surface and sub-oval, or near elliptical, outline give the seed a very
361 different shape from typical Vitaceae genera (e.g. Chen and Manchester, 2011).
362 Externally the ventral infolds are only tentatively identifiable from a pink mineral infill
363 from the apical and ventral views (Fig. 1B, D). However, in μ CT digital transverse
364 section (DTS), a pair of very deep (4.5 mm) and narrow (0.5 mm) ventral infolds are
365 clearly delineated by a very thin gap (black in Fig. 2C) between the inferred outer
366 surface of the endotesta and the mineral infill of the infolds (outlined in solid yellow in
367 Fig. 2D).

368 **Comments**—Seeds of modern *Cissus integrifolia* (Baker) Planch. are very
369 similar to the holotype of *C. crenulata*, being narrow, laterally flattened and sub-oval
370 in lateral view with a line of bisymmetry passing through a median longitudinal rib
371 perichalaza and having a similar seed coat ornamentation. However, the greater

372 number of ridges across the lateral faces and different orientation of the ventral
373 surface relative to the long axis of the seed in *Cissus integrifolia* support the
374 recognition of a separate species. Chesters (1957) listed P. B. 8 as a paratype of
375 *Menispermicarpum crenulatum*. Currently the number KNMP-RU7787 (P. B. 8)
376 includes eight specimens, which have here been transferred to *Cissus andrewsii* sp.
377 nov. (see below). Therefore, *Cissus crenulata* is represented only by a single
378 specimen.

379

380 **Species**—*Cissus andrewsii* Adams, Collinson, S.Y. Smith, & Bamford sp. nov.

381 **Etymology**—The species epithet “*andrewsii*” is named in honor of Dr. Peter
382 Andrews, in recognition of his extensive work on the Kenyan Miocene and the
383 invaluable support he provided, which enabled one of us (Collinson) to undertake
384 fieldwork on Rusinga and Mfangano Islands in 1980-1981.

385 **Diagnosis**—Seeds bilaterally symmetrical, 16–19 mm in dorsiventral
386 dimension, laterally flattened, sub-oval in lateral view, narrowly elliptical and 5–8 mm
387 wide in apical and basal views, elliptical in ventral view. Centers of lateral faces
388 ornamented by 4–5 short ridges in radial pattern; curved ridge 1–2.5 mm from
389 margins of lateral faces extends around most of seed and delineates faceted to
390 reticulate marginal area; prominent median ridge (rib perichalaza) extends from base
391 of ventral surface, around base, over dorsal surface, and almost full length of apical
392 surface. Upper portion of ventral surface forms acute angle with long axis of the
393 seed. Pair of deep, wide ventral infolds present.

394 **Holotype hic designatus**—Seed—V68501 (Fig. 1E–H; μ CT DTS video
395 available from the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.g9r36>).

396 **Type locality**—Rusinga Island, Lake Victoria, Kenya.

397 **Paratypes**—V68500 (Fig. 1I–J); V68502 (Fig. 1K–L); KNMP-RU7787 (8
398 specimens with field number 60*52, formerly P. B. 8, previously listed as paratypes of
399 *Menispermicarpum crenulatum* by Chesters, 1957; re-examined for this study by
400 Bamford).

401 **Geological horizon and age**—Hiwegi Formation, early Miocene.

402 **Repository**—Natural History Museum, London, U.K. (holotype and paratype
403 specimens with prefix V); National Museums of Kenya, Nairobi, Kenya (other
404 paratypes).

405 **Description**—Seeds are bisymmetrical around a prominent median
406 perichalazal rib (Fig. 1H, J) and vary from 16 to 19 mm in dorsiventral dimension, 11
407 to 15 mm in height and 5 to 8 mm in width (Fig. 1E–L). Seeds are laterally flattened
408 with height/width ratios of 1.9–2.4 and are narrow in apical and basal views (Fig. 1G,
409 H, J, L). The seed apex is rounded, with no indication of an apical notch or chalazal
410 grooves (Fig. 1E–G), and narrows to the ventral margin (Fig. 1F, G). The ventral
411 surface is slightly rounded, not straight (Fig. 1F, K). The lateral surfaces have a
412 curved ridge, delimiting a sculptured outer margin, which extends from approximately
413 half way along the apical margin, around the dorsal margin, and fully along the basal
414 margin (Fig. 1F). The sculptured marginal band is faceted, facets spaced at 2 to 3.5
415 mm, and ridged with ridges sometimes fusing to form a reticulum (Fig. 1F, I, K). The
416 central areas of the lateral faces are ornamented by four to five short (2–3 mm)
417 ridges in a radial arrangement (Fig. 1F). Where undamaged, the upper portion of the
418 ventral surface forms an angle of 52 to 55 degrees with the long axis of the seed
419 (Fig. 1F, K). The ventral infolds are not visible on the outside of the seed (Fig. 1E, G,
420 L) but by using μ CT, deep (2.5 mm), broad (0.6 mm) ventral infolds can be identified
421 in V68501 (Fig. 2F) by differences in X-ray attenuation (grey level) due to variation in

422 mineral density and mineral texture in the infold infills. There is a very clear gap
423 (black in Fig. 2E) demarcating the inferred original position of the endotesta outer
424 surface in the areas away from the infolds, where endotesta would have been
425 originally thicker based on observations in modern seeds. Some additional outer
426 mineral (possibly representing exotesta or fruit wall remnants) is also present in the
427 holotype (Fig. 2E).

428 **Comments**—In her unpublished thesis, Chesters (1958) assigned the
429 specimen shown in Fig. 1E-H (V68501) to *Menispermicarpum crenulatum*, here
430 revised to *Cissus crenulata*, but there are clear differences between *C. crenulata* and
431 V68501, supporting assignment of this specimen, and other similar specimens, to a
432 new species. Although there is now only a single specimen of *Cissus crenulata*
433 (making it impossible to assess intraspecific variation), there are eleven specimens of
434 *C. andrewsii*, all with consistent morphology distinct from that of the single specimen
435 of *C. crenulata*. In *Cissus andrewsii* the central portion of the lateral faces is crossed
436 by short ridges in a radial pattern, unlike *C. crenulata*, and the lateral faces have a
437 greater number of short transverse ridges in the outer margins, some of which fuse to
438 form a reticulum. In addition, the curved ridge, delineating the sculptured margin from
439 the central flat area, extends further down the ventral surface and the ventral margin
440 is curved not straight. *Cissus andrewsii* is therefore more similar to seeds of modern
441 *Cissus dasyantha* Gilg & M.Brandt than *C. integrifolia*, but is sufficiently different from
442 these extant species to warrant assignment to a new species, and differs in several
443 ways from the fossil *C. crenulata*.

444

445 **Species**—*Cissus rusingensis* Adams, Collinson, S.Y. Smith, & Bamford sp.
446 nov.

447 **Synonymy**—‘cf. *Cissus* sp. 1 nov.’ in Collinson et al. (2009).

448 **Etymology**—The epithet “*rusingensis*” refers to the type locality on Rusinga
449 Island from which the specimens were collected during in situ excavations.

450 **Diagnosis**—Seeds bilaterally symmetrical, 7–8 mm in dorsiventral dimension,
451 slightly laterally flattened, sub-rounded to pyriform in lateral view, broadly elliptical in
452 apical, basal and ventral views. Lateral faces ornamented by ridges and reticula with
453 7–11 wide muri radiating to margins and enclosing lumina in central area; prominent
454 median ridge (rib perichalaza) extends from ventral margin, around base, over dorsal
455 surface, and almost full length of the apex. Upper portion of ventral surface forms
456 acute angle with long axis of the seed. Pair of deep, very wide ventral infolds present.

457 **Holotype hic designatus**—Seed—R117.1981.314 (Fig. 1M–O; μ CT DTS
458 video available from the Dryad Digital Repository,
459 <http://dx.doi.org/10.5061/dryad.g9r36>).

460 **Type locality**—R117 site (see Collinson et al., 2009), Rusinga Island, Lake
461 Victoria, Kenya.

462 **Paratypes**—Seeds—KNMP-RU9647 (field number R117.1981.422);
463 R117.1981.476 (Fig. 1P–R; μ CT DTS video available from the Dryad Digital
464 Repository, <http://dx.doi.org/10.5061/dryad.g9r36>); R117.1981.604 (Fig. 1S–U);
465 R117.1981.605 (Fig. 1V–X).

466 **Geological horizon and age**—Grit Member, Hiwegi Formation, early
467 Miocene.

468 **Repository**—National Museums of Kenya, Nairobi, Kenya (KNM).

469 **Description**—Seeds are bisymmetrical around a prominent median
470 perichalazal rib (Fig. 1N–O, Q–R, T–U, W–X) and they vary from 7 to 8 mm in
471 dorsiventral dimension, 5 to 6 mm in height, and 3 to 4 mm in width (Fig. 1M–X). The

472 seeds are laterally flattened with a height/width ratio varying between 1.5 and 1.8 and
473 are broadly elliptical in apical and basal views (Fig. 1N, O, Q, R, T, U, W, X). The
474 seeds have a rounded apex (Fig. 1M, P, S, V) but are variable in their lateral shape
475 (Fig. 1M, P). The perichalazal rib extends around less of the specimen in
476 R117.1981.476 (Fig. 1P) and R117.1981.604 (Fig. 1S), resulting in a reduced lateral
477 width higher up the seed, a longer ventral projection and a more pyriform shape. By
478 contrast, the holotype (Fig. 1M) and R117.1981.605 (Fig. 1V) are both sub-rounded
479 with only small ventral projections. The lateral surfaces have a reticulate
480 ornamentation with one or two centrally positioned lumina (Fig. 1M, P, S, V) and 7 to
481 11 muri or ridges ranging in width from 0.2 to 0.6 mm (e.g., Fig. 1M). Some ridges
482 radiate to the edges of the specimen and join up with the strong perichalazal rib
483 producing marginal lumina (Fig. 1O, X). Others terminate before reaching the margin
484 without forming a reticulum (bottom right in Fig. 1S; top left in Fig. 1V), resulting in a
485 radiating pattern of marginal ridges and unenclosed marginal depressions. The upper
486 portion of the ventral surface forms an angle of 35 to 55 degrees with the long axis of
487 the seed (Fig. 1M, P, S, V). The ventral infolds, although not externally visible (Fig.
488 1N, Q, T, W), are readily identifiable in the holotype by differences in contrast and
489 mineral density in μ CT scans (Fig. 2G). A distinct pale area (highlighted yellow in Fig.
490 2H) marks the position of the embryo cavity, while the deep (1.5 mm) and very broad
491 (0.75 mm) ventral infolds are infilled with mineral with lower X-ray attenuation and
492 hence darker grey colour (Fig. 2H).

493 **Comments**—*Cissus rusingensis* is distinctive in lacking a distinct curved ridge
494 delineating a marginal region and in having muri in the central area of the lateral
495 faces forming a reticulum. This species is very similar to seeds of modern *Cissus*
496 *lebrunii* Dewit, but *C. rusingensis* has fewer muri and at most two (rather than three)

497 centrally positioned lumina.

498

499 **Species**—*Cissus psilata* Adams, Collinson, S.Y. Smith, & Bamford sp. nov.

500 **Etymology**—The epithet “*psilata*” derives from the ancient Greek adjective

501 “*psilós*”, meaning “bare” or “smooth”, and refers to the lack of seed coat

502 ornamentation on the smooth surface of the lateral faces.

503 **Diagnosis**—Seed bilaterally symmetrical, 7.5 mm in dorsiventral dimension,

504 sub-rounded in lateral view, broadly elliptical in apical, basal, and ventral views. Seed

505 smooth, lacks external ornamentation (psilate), except for prominent median ridge

506 (rib perichalaza) that extends all around dorsal surface, over apex, and almost full

507 length of ventral surface. Base of ventral surface concave, forming acute angle with

508 long axis of seed. Pair of very short, narrow ventral infolds present.

509 **Holotype hic designatus**—Seed—V68506 (Fig. 1Y-BB; μ CT DTS video

510 available from the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.g9r36>).

511 **Type locality**—Rusinga Island, Lake Victoria, Kenya.

512 **Geological horizon and age**—Hiwegi Formation, early Miocene.

513 **Repository**—Natural History Museum, London, UK.

514 **Description**—Seed inferred to be originally bilaterally symmetrical around a

515 prominent median perichalazal rib, although the single specimen is slightly deformed

516 (Fig. 1Z, AA), probably due to abnormal development in life or distortion during

517 fossilization. The seed is sub-rounded in lateral view (Fig. 1Y), 7.5 mm in dorsiventral

518 dimension and 6 mm in height, and broadly elliptical in apical and basal (Fig. 1Z, AA)

519 views, 4.5 mm in width. The seed is not laterally flattened and has an inflated

520 morphology with a height/width ratio of 1.3. The perichalazal rib is ca. 0.3–0.45 mm

521 thick around the dorsal and basal margins (Fig. 1Y, Z) but thicker at the seed base

522 (ca. 0.8 mm), forming a strong point (Fig. 1Y, AA), equivalent to the beak in typical
523 Vitaceae (see fig. 1 in Chen and Manchester, 2011). The lateral surfaces are smooth
524 (Fig. 1Y). The upper portion of the ventral surface forms an angle of 45 degrees with
525 the long axis of the seed (Fig. 1Y). The ventral infolds are not visible on the outside
526 of the seed (Fig. 1Z, BB). μ CT scans of the holotype (Fig. 2I) show very little internal
527 information compared to the other fossils, except for two very short (less than 0.5
528 mm) grooves at the base of the ventral surface (Fig. 2J), which correspond to the
529 position of the ventral infolds characteristic of *Cissus*.

530 **Comments**—In her unpublished thesis, Chesters (1958) suggested that
531 V68506 could be assigned to the genus *Menispermicarpum* as a new, but never
532 published, species. However, the fossil morphology differs from endocarps of
533 Menispermaceae. It is almost identical to seeds of modern *Cissus petiolata* Hook.f.,
534 differing in the greater extent of the rib perichalaza on the dorsal surface. In modern
535 *Cissus petiolata* seeds, the ventral infolds are very shallow and short which, in
536 combination with mineralization effects, can explain the very limited evidence for this
537 diagnostic feature in V68506 (Fig. 2J).

538

539

RESULTS

540 **Identification of fossils to genus *Cissus***—The lack of cellular and tissue
541 detail in the fossils (Fig. 2C-J), and the complexities of mineralization during
542 fossilization, make it difficult to judge if the external morphology of a fossil represents
543 the external morphology of a living equivalent. The SRXTM videos of modern *Cissus*
544 seeds (available from the Dryad Digital Repository,
545 <http://dx.doi.org/10.5061/dryad.g9r36>) show that the inner and outer surfaces of the
546 endotesta are parallel to one another and hence a mineral infill of the endotesta will

547 have a very similar external morphology to a mineral replacement of the endotesta
548 itself. Therefore, it is justifiable to compare the external surface of the Hiwegi
549 Formation fossils with that of modern seeds for purposes of identification. These
550 comparisons show that several modern African *Cissus* species have seeds with
551 almost identical shape and ornamentation to the Hiwegi Formation fossil seeds (see
552 *Phylogenetic context of seed morphotypes*). However, the ventral infolds that
553 characterize modern *Cissus* seeds are not visible on the fossils. The taphonomy of
554 the fossils may explain the absence of these key features.

555 A novel approach in virtual taphonomy was used to produce a digital infill of
556 the endotesta of a modern *Cissus* seed (Fig. 3A). This showed all the characters
557 typical of *Cissus* seeds (i.e., a long linear chalaza, 'perichalaza'; a thickened ridge of
558 seed coat along the perichalaza 'perichalazal rib'; deep, narrow, linear ventral
559 infolds). Digital infilling of the ventral infolds produced a digital fossil comparable to
560 the real Hiwegi Formation fossils (Fig. 3B). This virtual taphonomy suggests a two-
561 stage fossilization process with an initial infilling of the endotesta (and perhaps some
562 mineral replacement of organic tissues) followed by a later stage of infilling of the
563 ventral infolds. μ CT imaging supports this hypothesis as mineral-infilled ventral
564 infolds can be recognized (Fig. 2C-J) in digital sections through the fossils (albeit
565 more clearly in some specimens than others).

566 The only other modern genus including seeds similar to *Cissus* is
567 *Cyphostemma*, some seeds of which may be laterally flattened and have somewhat
568 similar ornamentation. Unlike *Cissus* (Fig. 4A) the ventral infolds on extant
569 *Cyphostemma* seeds are externally concealed by extra layers of endotestal sclereids
570 (Chen and Manchester, 2011; Fig. 4B). If the fossils were originally *Cyphostemma*
571 seeds with the endotesta infilled by mineral during initial stages of fossilization, then

572 the spaces enclosed by the endotesta over the ventral infolds would have been
573 infilled at the same time as the main area within the endotesta. However, μ CT
574 images of the fossils show mineral infills of the ventral infolds that are distinct from
575 other mineral infill within the endotesta (Fig. 2C-H) indicating infill during a later stage
576 of fossilization.

577 The combined data show that four African fossil seed morphotypes conform to
578 the genus *Cissus* in all characters that can be determined from the fossils. The
579 complex taphonomy and concealment of key features diagnostic of the genus explain
580 the original taxonomic misidentification to the Menispermaceae.

581 ***Phylogenetic relationships within Cissus***—In our maximum likelihood
582 analysis, species of *Cissus* are found in three distinct groups (Fig. 5; Appendix S7,
583 see Supplemental Data with the online version of this article): the *Cissus striata* clade
584 (81%/0.94 [hereafter, bootstrap support/Bayesian posterior probabilities]), the *Cissus*
585 *trianae* clade (<50%/0.25), and the core *Cissus* clade (60%/1.0), as previously
586 identified by Rodrigues et al. (2014). Within the core *Cissus* clade in our analysis, the
587 early-diverging lineages comprise only African species (Fig. 5). The African species
588 *Cissus barbeyana*, *C. sagittifera* and *C. floribunda* form a clade (the *Cissus*
589 *barbeyana* clade; 100%/1.0) sister to the remainder of the core *Cissus* clade, in
590 which the *Cissus integrifolia* clade (*C. integrifolia* + *C. populnea*; 100%/1.0) is sister
591 to two main clades that comprise the rest of the species in genus *Cissus*. In the first
592 of these two main clades (100%/1.0) only eight of 35 species in our analysis are not
593 African; whilst only seven of the 49 species in the second clade are African (Fig. 5).
594 The topologies and support values obtained with the maximum likelihood (Fig. 5) and
595 Bayesian analyses (Appendix S8, S9, and S10, see Supplemental Data with the
596 online version of this article) do not present well-supported topological discrepancies.

597 The divergence time analyses estimated that the core *Cissus* clade diverged 57.9 Ma
598 (highest posterior density (HPD) 55.9–64.0 Ma; 95% HPD intervals of age estimates
599 are provided in Appendix S11, see Supplemental Data with the online version of this
600 article), in the late Paleocene (Appendix S8, see Supplemental Data with the online
601 version of this article), and started to diversify 41.5 Ma (HPD 31.6–51.0 Ma), in the
602 late middle Eocene (Appendix S9, see Supplemental Data with the online version of
603 this article).

604 ***Phylogenetic context of seed morphotypes***—Seeds of four distinct *Cissus*
605 species are now recognized from the early Miocene Hiwegi Formation. Given that
606 claims of Vitaceae pollen from the Oligocene of Cameroon remain unconfirmed
607 (Salard-Cheboldaef, 1978, 1981; Muller, 1981), these seeds represent the first
608 confirmed fossil record of Vitaceae and of the genus *Cissus* in Africa. The four fossil
609 species represent distinct morphotypes, which are also found in seeds of extant
610 species (Table 1), as revealed by SRXTM imaging of modern fruits and by a
611 literature survey of published seed descriptions. The phylogenetic position of these
612 extant species provides a phylogenetic context for the early Miocene fossils.

613 ***Morphotype 1***—*Cissus crenulata* (Fig. 1A-E) has laterally flattened, sub-oval
614 seeds with a faceted marginal area, several long radiating lateral ridges and two
615 marginal ridges. The extant species *Cissus integrifolia* (Fig. 6D, 7A) and *C. populnea*
616 (Fig. 2A, 6E) share this distinctive morphotype (Table 1). These two species are
617 recovered in our phylogenetic analyses with strong support (100% BS) as a distinct
618 clade, the *Cissus integrifolia* clade, which is one of the two earliest-diverging clades
619 in core *Cissus* (Fig. 5). It is, therefore, likely that *Cissus crenulata* was a member of
620 the early diverging *Cissus integrifolia* clade.

621 ***Morphotype 2***—*Cissus andrewsii* has seeds that are laterally flattened and

622 have a ridged and faceted marginal area where ridges sometimes fuse to form a
623 reticulum, two prominent marginal ridges, and short radiating lateral ridges. The
624 extant species *Cissus barbeyana* (Fig. 6B) and *C. dasyantha* (Fig. 7B and fig. 13J in
625 Dewit and Willems, 1960) are most similar to *C. andrewsii*, in that they are slightly
626 laterally flattened (H:W ratio of 1.3-1.5) with a similarly ridged and faceted marginal
627 reticulum, two marginal ridges and short radiating lateral ridges (Table 1). Although
628 the sampled specimen of *Cissus dasyantha* failed to amplify material for phylogenetic
629 analysis, *C. barbeyana* was found in the basal clade of core *Cissus*, the *Cissus*
630 *barbeyana* clade, with *C. floribunda* and *C. sagittifera* (Fig. 5). Seeds of *Cissus*
631 *floribunda* (Fig. 6A) and *C. sagittifera* (fig. 14 in Descoings, 1967) also possess the
632 Morphotype 2 characters, (except that *C. sagittifera* lacks the ridged and faceted
633 marginal area). This suggests that Morphotype 2 is characteristic of the basal *Cissus*
634 *barbeyana* clade and that *C. andrewsii* can be placed in this clade. Future work
635 determining if *Cissus dasyantha* is in the *C. barbeyana* clade would test this
636 hypothesis.

637 *Morphotype 3*—*Cissus rusingensis* has slightly laterally flattened seeds and
638 ridges forming a complete to incomplete reticulum across the lateral faces. Extant
639 species sharing these features (Table 1) include: *Cissus lebrunii* (fig. 13K in Dewit
640 and Willems, 1960), *C. oreophila* (pl. 39, fig. 11 in Descoings, 1972), *C. sciaphila*
641 (Fig. 6H), *C. smithiana* (Fig. 6G) and *C. tiliifolia* (Fig. 7C and Verdcourt, 1993).
642 *Cissus sciaphila* and *C. tiliifolia* are found together in the *C. sciaphila* clade (*C.*
643 *lebrunii* did not amplify), with five other African species (*C. aphyllantha*, *C. polyantha*,
644 *C. quarrei*, *C. rhodotricha*, *C. smithiana*) and the Asian/Australasian species, *C.*
645 *adnata* and *C. rostrata* (Fig. 5). Seed descriptions suggest these species share most,
646 if not all, of the external morphological features of Morphotype 3 (Appendix S4, see

647 Supplemental Data with the online version of this article). *Cissus polyantha* seeds are
648 very variable in surface ornamentation from smooth to extensively ridged (pl. 36, figs.
649 11-12 in Descoings, 1972; fig. 13H in Dewit and Willems, 1960), also seen in our
650 sampling of two specimens (Appendix S1, see Supplemental Data with the online
651 version of this article). However, one illustration of a ridged specimen (fig. 13H in
652 Dewit and Willems, 1960) falls into Morphotype 3. Morphotype 3 is characteristic of
653 almost all of the species belonging to the *Cissus sciaphila* clade (and occurs in at
654 least one collection of *C. polyantha*). This suggests that *Cissus rusingensis* was an
655 early Miocene member of this clade. *Cissus auricoma* has seeds of Morphotype 3 but
656 is a member of the *C. microdonta*-*C. auricoma* clade (Fig. 5). This being the only
657 species in that clade with Morphotype 3 seeds suggests parallel evolution of seed
658 morphology in this case, although further sampling of both DNA and seed
659 morphology would be needed to confirm this.

660 *Morphotype 4*—Seeds of *Cissus psilata* are sub-rounded with smooth lateral
661 faces almost indistinguishable to seeds of extant *C. petiolata* (Table 1; Fig. 6M, 7D). *Cissus*
662 *petiolata* is found in a clade with seven solely African species (Fig. 5): *C. aralioides*,
663 *C. oliveri*, *C. polita*, *C. rondoensis*, *C. rotundifolia*, *C. sylvicola*, *C. welwitschii*. Of
664 these, *Cissus aralioides* (Fig. 6L), *C. rotundifolia*, *C. sylvicola* and *C. welwitschii* have
665 Morphotype 4 seeds (Appendix S4, see Supplemental Data with the online version of
666 this article). *Cissus oliveri*, with coarsely pitted seeds and very strong radial and
667 lateral ribs (Verdcourt, 1993), and *C. rondoensis*, with seeds bearing two to three,
668 faint transverse ridges (Verdcourt, 1993), lack the smooth seed coat typical of
669 Morphotype 4. These two species occupy contrasting habitats to the rest of the clade
670 (Table 2), so contrasting seed morphology may reflect different environmental
671 pressures.

672 Extant species in the *Cissus pseudoguereana*-*C. albiporcata* clade, for which
673 seed descriptions were available, also share seed Morphotype 4: *C. faucicola* and *C.*
674 *quadrangularis* have smooth seeds (Appendix S4, see Supplemental Data with the
675 online version of this article), and *C. cactiformis* also has the smooth seed coat
676 (Verdcourt, 1993). Furthermore, the majority of species in the *Cissus elongata*-*C.*
677 *subtetragona* clade (Fig. 5) share Morphotype 4 characters (Appendix S4, see
678 Supplemental Data with the online version of this article). This evidence suggests
679 that Morphotype 4 occurs throughout the broader *Cissus petiolata*-*C. albiporcata*
680 clade (Fig. 5), and suggests that *C. psilata* belongs in this clade.

681 Further morphological and molecular analyses, with expanded geographic and
682 taxonomic sampling (including those species that failed to amplify for this study), are
683 needed to fully evaluate the systematic significance of seed morphotypes. This study
684 focused on modern African species to place the African Miocene fossils in context.
685 Based on extant species with morphologically comparable seeds, and their
686 phylogenetic position, species from four clades of *Cissus* (or from the ends of their
687 stem lineages) were present during the early Miocene in East Africa. These species
688 were related to the two early-diverging clades of core *Cissus* (the *Cissus integrifolia*
689 and *C. barbeyana* clades), and two later-diverging clades with mainly African species
690 today, the *C. sciaphila* clade and the *C. petiolata*-*C. albiporcata* clade (Fig. 6).

691 **Fossil plant biology and ecology**—Habit and habitat data (Table 2) for
692 nearest living relatives of the fossil *Cissus* (Fig. 6) can be used to consider the likely
693 paleobiology and paleoecology of the fossil plants. In the *Cissus integrifolia* clade,
694 the plants are lianas or herbaceous climbers in wide-ranging habitats, from
695 evergreen forest and woodland to bushland and savanna grassland. Members of the
696 *Cissus barbeyana* clade are herbaceous to woody lianas and predominantly occupy

697 rainforest, gallery and riverine forest fringes. Species in the *Cissus sciaphila* clade
698 are also herbaceous to woody climbers in rainforests or are scrambling shrubs or
699 woody climbers in drier deciduous forest and woodland. The extant species of the
700 *Cissus aralioides*-*C. albiporcata* clade are herbaceous to woody lianas or climbing
701 shrubs, a number of which are succulent (*C. aralioides*, *C. cactiformis*, *C. petiolata*,
702 *C. quadrangularis*, *C. rotundifolia*, *C. sylvicola*). They occur in riverine forest and
703 wooded savanna to rocky outcrops, xerophilic thickets in *Acacia* mixed bushland and
704 grassland (Table 2). The two members of the *Cissus petiolata* sub-clade with
705 different seeds (see previous section) also differ in their habitat preferences, being
706 most often found in moist rainforests.

707 These modern ecologies suggest that a diversity of climbers (either
708 herbaceous or woody or both) were present in the early Miocene on Rusinga Island.
709 These climbers may have occupied gallery or riverine forest (*Cissus andrewsii*
710 related to the *C. barbeyana* clade) and evergreen forest, through woodland to
711 savanna (*C. rusingensis* related to the *C. sciaphila* clade and *C. crenulata* related to
712 the *C. integrifolia* clade). The plant producing the *Cissus psilata* seeds may have
713 been somewhat succulent and hence able to occupy arid habitats as well as riverine
714 forest or savanna, based on the habitats of a number of related extant species in the
715 *C. aralioides*-*C. albiporcata* clade.

716

717

DISCUSSION

718 ***Homology of the ventral surface in Vitaceae seeds***—The current
719 convention for descriptive terminology of Vitaceae seeds (Chen and Manchester 2011)
720 and fossil *Cissus* seeds (Manchester et al., 2012b) has been followed here
721 (Appendix S6, see Supplemental Data with the online version of this article) to allow

722 for ease of comparison with their work. However, an alternative interpretation is
723 possible, particularly for the strongly flattened seeds (e.g. Fig. 1A-L; Fig. 2A-D; Fig. 3;
724 Fig. 6A-F), whereby the ventral surface incorporates both ventral and apical sensu
725 Appendix S6 herein (see Supplemental Data with the online version of this article)
726 and the ventral grooves are short occupying less than half of the dimension of that
727 surface. This alternative seed orientation is followed in all the floras to which we refer
728 in this paper (i.e. the modern seed illustrations in Fig. 6 are all rotated 90 degrees
729 clockwise). These two alternative homologies would best be investigated by a
730 developmental study.

731 ***Cissus origins, phylogeny and Miocene diversity in Africa***—Relationships
732 among genera in the Vitaceae are mostly comparable between our study and the
733 most recent previous studies of *Cissus* (Liu et al., 2013, 2016; Rodrigues et al.,
734 2014), with limited support for the backbone of the trees (but see Wen et al., 2013
735 and Zhang et al., 2015). *Cissus* species are found in three distinct clades in all
736 analyses, identified by Rodrigues et al. (2014) as the *Cissus striata* clade (Clade III of
737 Liu et al., 2013), the *C. trianae* clade (Clade V of Liu et al., 2013) and the core *Cissus*
738 clade, which contains most of the species. As in Liu et al. (2013), the earliest-
739 diverging clades comprise mainly African species, although this is more evident in
740 our study in which the first branches are exclusively African species. This topology
741 provides support for an African origin for the genus, as Liu et al. (2013) also
742 concluded.

743 The new African fossils are entirely consistent with an African origin for
744 *Cissus*. The notable similarities in seed morphology between extant *Cissus* species
745 and Hiwegi Formation fossils across multiple seed morphotypes suggest the
746 presence of four clades or members of their stem lineages, indicating diversity of

747 *Cissus*, by the early Miocene in Africa. Based on the divergence times (Appendix S9,
748 see Supplemental Data with the online version of this article), it appears that all four
749 clades originated much earlier than the ca. 18 Ma age of the Miocene fossils: 41.5
750 Ma (HPD 31.5-51.0 Ma) for the split of the *Cissus barbeyana* clade from the rest of
751 core *Cissus*; 36.0 Ma (HPD 27.6-44.7 Ma) for the divergence of the *C. integrifolia*
752 clade; 24.6 Ma (HPD 18.1-32.1 Ma) for the divergence of the *C. sciaphila* clade; and
753 22.8 Ma (HPD ca. 16.6-30.0 Ma) for the divergence of the *C. aralioides-C.*
754 *albiporcata* clade. The time-calibrated phylogeny (Appendix S9, see Supplemental
755 Data with the online version of this article) therefore suggests that several ghost
756 lineages of *Cissus* await discovery in the fossil record. The new African Miocene
757 seeds, and those from the Oligocene of Peru (see *Comparison with other fossil*
758 *Cissus* below), provide fossil evidence consistent with the suggested phylogenetic
759 history of *Cissus*.

760 ***Comparison with other fossil Cissus***—The fossil record of the grape family
761 (Vitaceae) extends back to the latest Cretaceous or earliest Paleogene in central
762 India (Manchester et al., 2013) and to the Paleogene in North America and Europe
763 (e.g., Manchester, 1994; Fairon-Demaret and Smith, 2002; Chen and Manchester,
764 2007; Collinson et al., 2012). However, for *Cissus*, the oldest, and only other,
765 currently recognised examples are from the late early Oligocene Belén flora of
766 northern Peru (Manchester et al., 2012b). This flora contains two *Cissus* species:
767 *Cissus willardii* Berry and *Cissus lombardii* Manchester, Chen, & Lott. *Cissus willardii*
768 is small and globose with smooth lateral faces and large ventral infolds (fig. 2A-Q in
769 Manchester et al., 2012b), unlike any of the fossils described above from Rusinga
770 Island.

771 Conversely, *Cissus lombardii* shares some characteristics with African
772 Miocene *C. crenulata* and modern *C. integrifolia* (seed Morphotype 1), being
773 bilaterally symmetrical, laterally flattened, elliptical in lateral view with a pronounced
774 median perichalazal rib and a faintly faceted marginal area defined by a marginal
775 ridge on each lateral face (fig. 3A-N in Manchester et al., 2012b). This suggests that
776 *Cissus lombardii* might be related to the *C. integrifolia* clade, extending its fossil
777 record to the early Oligocene (30-28.5 Ma). However, *Cissus lombardii* is smaller in
778 all dimensions than *C. crenulata* and *C. integrifolia*, and lacks the distinct
779 ornamenting ridges that cross the lateral faces in seeds of these species. The
780 specimens of *Cissus lombardii* from the Belén flora are internal casts, which could
781 result in a more subdued surface ornamentation than if the fossils were seeds
782 themselves. However, as has been shown in extant *Cissus* seeds in this study using
783 SRXTM (SRXTM videos of modern *Cissus* seeds (available from the Dryad Digital
784 Repository, <http://dx.doi.org/10.5061/dryad.g9r36>), the inner surface of the endotesta
785 closely parallels the outer surface, which would result in a similar pattern of
786 ornamentation whether a fossil is an internal cast or a replacement of the endotesta
787 itself. There is no indication of even faint ridges across the lateral faces in *Cissus*
788 *lombardii* (fig. 3A-B in Manchester et al., 2012b), suggesting that the ornamentation
789 of the original seed was significantly different from Morphotype 1. The portion of the
790 ventral surface containing the ventral infolds is “more or less planar (not markedly
791 concave)” in *Cissus lombardii* (Manchester et al., 2012b, pg. 936), rather than weakly
792 to strongly concave as in *C. integrifolia* and *C. crenulata*. Therefore, *Cissus*
793 *lombardii*, is clearly distinct from the African Miocene species.

794 **Biogeographic implications**—The position of previously unsampled modern
795 African species near the base of the phylogeny (Fig. 5) reinforces the African origin

796 for the core *Cissus* clade, suggested by Liu et al. (2013). The new African Miocene
797 fossil *Cissus crenulata* has seed Morphotype 1 as do both extant species of the *C.*
798 *integrifolia* clade, confirming the presence of early-divergent members of the core
799 *Cissus* clade in Africa by at least the Miocene.

800 The two modern species outside Africa in the *Cissus sciaphila* clade (*C.*
801 *rostrata* and *C. adnata*) are advanced within this clade. Six of the seven modern
802 African species in this clade are characterized by seeds of Morphotype 3, and the
803 seventh also includes specimens with this seed morphotype. The new African
804 Miocene fossil *Cissus rusingensis* also has seeds of Morphotype 3. These data
805 suggest that this clade originated in Africa. Dispersal during or after the Neogene to
806 Australasia resulted in the modern pantropical intercontinental disjunct distribution.
807 The calibrated phylogeny presented here (Appendix S9, see Supplemental Data with
808 the online version of this article) suggests that the divergence of Australasian species
809 occurred near the end of the Pliocene at 2.7 Ma (HPD 0.8–5.5 Ma) differing from,
810 although within the error of, the late Miocene estimate of 7.8 Ma (HPD 3.0–15.1 Ma)
811 made by Liu et al. (2013).

812 Liu et al. (2013) argued that transoceanic long distance dispersal, rather than
813 terrestrial mammalian dispersal, was the most likely explanation for pantropical
814 intercontinental disjunctions in *Cissus*, because *Cissus* fruits are fleshy and, although
815 in some instances dispersed by mammals, are predominantly bird-dispersed,
816 enabling long-distance transport by bird migration. Multiple large islands across the
817 Indian Ocean may have facilitated an out-of-Africa migration by acting as migratory
818 “stepping stones”, as invoked for dispersal of other vitaceous genera (e.g., *Cayratia*;
819 Lu et al., 2013).

820 The distributions of modern species in all four clades containing nearest living
821 relatives to the fossils extend across Africa from East to West (Table 2). The fossil
822 seeds suggest that the clades containing these living relatives may have had their
823 origins in East Africa with subsequent spread to the rest of the continent. However,
824 additional African fossil records of *Cissus* are needed to document dispersal
825 patterns.

826 ***Paleoenvironmental implications***—Previous paleoenvironmental
827 reconstructions from the Hiwegi Formation have inferred a habitat mosaic inhabited
828 by early hominoids, such as *Ekembo* (see McNulty et al., 2015). Evidence for mosaic
829 habitats comes from gastropod (Verdcourt, 1963; Pickford, 1995) and mammal
830 faunas (e.g., Andrews and Van Couvering, 1975), paleosols (Retallack et al., 1995)
831 and paleobotany (Collinson et al., 2009; Maxbauer et al., 2013; Michel et al., 2014).
832 Collinson et al. (2009) concluded that the overall paleoenvironmental signal,
833 considering the evidence from plants, mammals, gastropods and paleosols, was one
834 of “mixed habitats dominated by woodlands, with waterside environments and small
835 patches of forest big enough to support forest faunas” (p. 161); this is very similar to
836 the possible fossil *Cissus* paleoecologies based on nearest living relatives (see
837 *Fossil plant paleobiology and paleoecology*).

838 The vegetation in which *Cissus andrewsii*, *C. crenulata* and *C. psilata* lived
839 cannot be inferred from associated fossils, as the specimens were surface-picked.
840 However, the context of the *Cissus rusingensis* fossils is well understood as they
841 derive from in situ excavations of plant litter assemblages at the R117 site (Collinson
842 et al., 2009). These litter assemblages were interpreted to have accumulated under a
843 continuous canopy in deciduous, broad-leaved woodland bordering a river, based on
844 the fossil fruits and seeds and their taphonomy (Collinson et al., 2009). *Cissus*

845 *rusingensis* is therefore known to have inhabited a closed riverine woodland,
846 consistent with interpretations made for this species from inferred near living
847 relatives.

848 Recent studies have revealed temporal paleoenvironmental changes through
849 the Hiwegi Formation (Michel et al., 2013, 2014; Garrett et al., 2015) and have
850 suggested that interpretations of mosaic paleoenvironments may be based on time-
851 averaged faunal and floral assemblages that conflate separate, more homogeneous
852 habitats. These studies suggest that more open, drier woodland habitats low in the
853 Hiwegi Formation (e.g., Grit Member) gave way to dense, closed canopy forest
854 further up (e.g., Fossil Bed and Kibanga Members), with early hominoid fossils
855 recovered from both paleoenvironments (Garrett et al., 2015). Since the stratigraphic
856 context of *Cissus andrewsii*, *C. crenulata* and *C. psilata* are unknown and they are
857 not associated with *C. rusingensis*, the four new species of *Cissus* described may or
858 may not have existed contemporaneously. Despite this uncertainty, it is known from
859 in situ excavations in the Fruit and Nut Bed (Collinson et al., 2009) and
860 stratigraphically associated leaf assemblages (Maxbauer et al., 2013) that a riverine
861 mosaic habitat of woodland and forest existed during the deposition of the Grit
862 Member of the lower Hiwegi Formation. The paleoecology of the new fossil species
863 of *Cissus*, inferred from living relatives and supported (for *Cissus rusingensis*) by
864 associated fossils, provides new evidence for mosaic landscapes on Rusinga Island
865 during the early Miocene, ranging from gallery or riverine forest to woodland,
866 bushland and savanna.

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1219

TABLES

1220 Table 1. Seed morphotypes of selected single-seeded, modern African *Cissus*
 1221 species based on internal and external morphology obtained from SRXTM datasets
 1222 and descriptions and illustrations in floras (Dewit and Willems, 1960; Descouings,
 1223 1972; Verdcourt, 1993). H = height, W = width.

1224

Seed morphotype	Species	Description
1 (Figs. 6D, 6E, 7A)	<i>C. integrifolia</i> ; <i>C. populnea</i>	<ul style="list-style-type: none"> • Two-layered, thick fruit wall, with a denser outer layer and more porous inner layer • Seeds laterally flattened (H:W ratio of 1.5–1.8 in median DTS), elongate in the dorsiventral dimension • Obvious break in seed coat near the chalaza • Outer endotesta consists of thin layer with different X-ray attenuation (possibly high mineral content) • Dense and thin seed coat • Seed surface with two marginal ridges, one on each lateral face, a ridged and faceted marginal area, long ridges radiating from ventral margin across lateral faces
2 (Figs. 6B, 7B)	<i>C. barbeyana</i> ; <i>C. dasyantha</i>	<ul style="list-style-type: none"> • Thin to moderately thick fruit wall • Seeds slightly laterally flattened (H:W ratio of 1.3–1.5 in median DTS), elongate in the dorsiventral dimension • Indistinct break in seed coat near the chalaza • Endotesta has uniform X-ray attenuation • Dense and moderately thick seed coat • Seed surface with two marginal ridges; a ridged and faceted marginal area, where ridges sometimes fuse to form a reticulum; short ridges radiating across part of the lateral faces
3 (Figs. 6H, 7C)	<i>C. lebrunii</i> ; <i>C. sciaphila</i> ; <i>C. tiliifolia</i>	<ul style="list-style-type: none"> • Thin fruit wall • Seeds not, or slightly, laterally flattened (H:W ratio of 1.0–1.6 in median DTS), short in the dorsiventral dimension • Indistinct break in seed coat near the chalaza • Endotesta has uniform X-ray attenuation • Thin seed coat of variable texture • Seed surface covered in ridges, forming a complete to incomplete reticulum across the lateral faces
4 (Figs. 6M, 7D)	<i>C. petiolata</i>	<ul style="list-style-type: none"> • Thick fruit wall • Seeds laterally flattened (H:W ratio of 1.5–1.8 in median DTS), short in the dorsiventral dimension • Thickened chalaza with no break in seed coat • Endotesta has uniform X-ray attenuation • Dense and thick seed coat • Seed surface smooth.

1225 Table 2. Distribution, habit and habitat data of modern *Cissus* species. Sources: (1) Lu (1993); (2) Chen et al. (2007); (3) GBIF
 1226 (2013); (4) herbarium sheet data (Appendix S5); (5) Verdcourt (1993); (6) Keay (1958); (7) Dewit and Willems (1960); (8) Wild and
 1227 Drummond (1966); (9) Descoings (1972); (10) Descoings (1967); (11) Beentje (1994); (12) Yeo et al. (2012).

Species	Distribution	Habit	Habitat	Sources
<i>C. adnata</i> Roxb.	Australasia; E, SE, and S Asia	Scrambling or climbing shrub, or woody liana, up to 10 metres	Primary lowland monsoon forests, riparian forest, disturbed and semi-open scrub and deciduous forest, shrubland and thickets	1, 2, 3, 4
<i>C. albiporcata</i> Masinde & L.E.Newton	E Africa	Climber	Bushland in rocky areas	3, 5
<i>C. aphyllantha</i> Gilg	E Africa	Shrub, scrambler or woody climber, 1 to 4 meters tall	<i>Acacia</i> scrub or desert thornbush, scrubby woodland, rocky outcrops	3, 5
<i>C. aralioides</i> (Welw. ex Baker) Planch.	C, E and W Africa	Vigorous, succulent liana or herbaceous climber, a strong, lofty climber, up to 25 meters	Coastal and riverine evergreen forest, rainforest, coastal bushland, <i>Acacia</i> bushland, grassland, thickets	3, 5, 6, 7, 8, 9
<i>C. barbeyana</i> De Wild. & T.Durand	C and W Africa	Herbaceous to woody, low, small liana	Rainforest, forest clearings, forest fragments and clusters	3, 6, 7, 9
<i>C. cactiformis</i> Gilg	E and S Africa	Succulent climber or scrambler, 1.2 to 4.5 meters long	Woodland, mixed bushland, usually in stony places, rock domes	3, 5
<i>C. dasyantha</i> Gilg & M.Brandt	W Africa	Liana, up to 6 meters	Occasionally flooded forest, gallery forests	3, 7
<i>C. faucicola</i> Wild & R.B.Drumm.	E Africa	Herbaceous climber, several meters long	Evergreen rainforest, especially edges by waterfalls and in grassy clearings	5, 8
<i>C. floribunda</i> (Baker) Planch.	E Africa	Thin woody liana or climber, several meters long	Rainforest, dense moist tropical forest, disturbed forest or forest edge	4, 10
<i>C. integrifolia</i> (Baker) Planch.	C and E Africa	Herbaceous vigorous climber to 5 meters, reaching tops of trees or thicket-forming	Evergreen riverine forest, woodland, bushland and savanna grassland, often on rocky scarps	3, 5, 7, 8, 11
<i>C. lebrunii</i> Dewit	C Africa	Herbaceous climber	Rainforest	3, 7
<i>C. oliveri</i> (Engl.) Gilg ex Engl.	C and E Africa	Herbaceous to woody climbing shrub, up to 6 meters long	Riverine and gallery forest, marshy areas, papyrus swamps, wet grassland with scattered trees	3, 5, 7
<i>C. oreophila</i> Gilg & M.Brandt	C and W Africa	Large herbaceous liana	Gallery and riverine forest, forest edges, swamp areas	3, 4, 6, 9
<i>C. petiolata</i> Hook.f.	C, E and W Africa	Large, somewhat succulent liana,	Riverine forest, occasionally flooded forest edges,	3, 5, 6, 7,

		vigorous climber or scrambler, to at least 10 meters	thickets, <i>Acacia</i> mixed bushland, rocky ground with scattered trees and shrubs, woody/shrub savanna	8, 9, 11
<i>C. phymatocarpa</i> Masinde & L.E.Newton	E Africa	Climber	Thickets on forest edges and coastal bushland	3, 5
<i>C. polita</i> Desc.	E Africa	Herbaceous liana, 1.5 to 3 meters	Calcareous hills and plateaux; dry, deciduous seasonal forest; savanna grassland with dry forest	4, 10
<i>C. polyantha</i> Gilg & M.Brandt	C, E and W Africa	Herbaceous to woody climber/ liana, up to 15 meters	Riverine and gallery rainforest, rocky hollows in grassland and thickets	3, 5, 6, 7, 9
<i>C. populnea</i> Guill. & Perr.	C, E and W Africa	Bushy liana, to 4.5 meters	Wooded savanna, rocky outcrops and scree, bushland, lowland forest edges	3, 5, 6, 7, 9
<i>C. pseudoguerkeana</i> Verdc.	E Africa	Spreading herb, at least 60cm long	Woodland, low shrubs on sand, swampy places	3, 5
<i>C. quadrangularis</i> L.	Arabia; C, E, N, S, and W Africa; SE and S Asia	Succulent bushy liana 1 to 15 meters long, or succulent climbing shrub	Xerophilic thickets, thorny savanna, <i>Acacia</i> woodland, grassland, riverine thicket, coastal forest edges	3, 5, 8, 9, 10
<i>C. quarrei</i> Dewit	C and E Africa	Erect herb or herbaceous climber, 0.6 to 1 meter tall	Riverine vegetation, <i>Brachystegia</i> woodland	3, 5, 7, 8
<i>C. rhodotricha</i> (Baker) Desc.	E Africa	Scrambling and climbing strong liana or erect shrub	Rocky outcrops, deciduous seasonal forest, wooded savanna	10
<i>C. rondoensis</i> Verdc.	E Africa	Herbaceous to semi-woody climber to around 4 meters	Moist, (semi-) evergreen forest, dense forest thicket	3, 4, 5
<i>C. rostrata</i> (Miq.) Korth. ex Planch.	SE Asia	Climber/ liana, up to 10 to 15 meters	Fringe and understory forest; forest river banks, peat swamp/ marshy forest	3, 4, 12
<i>C. rotundifolia</i> Vahl	Arabia; C, E and S Africa	Succulent, herbaceous to woody, vigorous climber/ liana, up to 5 meters	Dry woodland and bush, thorny savanna, <i>Acacia</i> scrub, bushland, thickets, dry forest and forest edges particularly on rocky outcrops	3, 5, 7, 8
<i>C. sagittifera</i> Desc.	E Africa	Creeping or climbing, thin liana	Woodland edges, limestone cliffs, quartzite outcrops	3, 4, 10
<i>C. sciaphila</i> Gilg	E Africa	Woody climber/ liana, 3 to 12 meters long or shrubby	Lowland riverine forest fringes, woodland slopes above river valleys	3, 5, 8
<i>C. smithiana</i> (Baker) Planch.	C and W Africa	Large liana/ climber	Rainforest, forest galleries and edges	3, 7, 9
<i>C. sylvicola</i> Masinde & L.E.Newton	E Africa	Herbaceous, somewhat succulent and fleshy liana, up to 12 meters	Evergreen forest, also forest on rocky hills, coralline limestone and thicket	3, 5
<i>C. tiliifolia</i> Planch.	C and E Africa	Herbaceous to woody climber, up to 10 meters	Forest and thickets in swampy areas, particularly near lake shores, swampy grassland	3, 5
<i>C. welwitschii</i> (Baker) Planch.	C and E Africa	Vigorous, woody climber, 2 to 9 meters long, or shrubby	Semi-evergreen bushland, riverine fringes, thickets and termite mounds in <i>Brachystegia</i> woodland, rocky outcrops	3, 5, 8

APPENDICES

1229

1230 Appendix 1. Voucher information and GenBank accession numbers of *Cissus*
 1231 species, for which new sequences were produced for the present phylogenetic
 1232 analysis. Species; *trnLF*; *rps16*; *trnC-petN*; *atpB-rbcL*; voucher information; Kew DNA
 1233 Bank accession number.

1234

1235 ***Cissus barbeyana*** De Wild. & T.Durand; KX131178; -; -; -; Lisowski, S. 16406 (K);
 1236 31957. ***Cissus bosseri*** Desc.; KX131174; -; -; KX131172; Phillipson, P.B. &
 1237 Rabesihanaka, S. 3140 (K); 31965. ***Cissus petiolata*** Hook.f.; KX131175; -; -; -;
 1238 Luke, P.A. & WRQ 9365 (K); 31952. ***Cissus polyantha*** Gilg & M.Brandt; KX131176;
 1239 -; -; -; Deighton, F.C. 5208 (K); 31955. ***Cissus populnea*** Guill. & Perr.; KX131179; -;
 1240 -; -; Daramola, B.O. 221 (K); 31968. ***Cissus rondoensis*** Verdc.; -; -; -; KX131170;
 1241 Bidgood, S., Abdallah, R. & Vollesen, K. 1553 (K); 31961. ***Cissus smithiana*** (Baker)
 1242 Planch.; KX131177; -; -; -; Louis, J. 559 (K); 31959. ***Cissus tiliifolia*** Planch.;
 1243 KX131173; -; -; KX131171; Eilu, G. 240 (K); 31964.

1244

1245 Appendix 2. Species included in the phylogenetic analysis of family Vitaceae for
 1246 which sequences were obtained from GenBank, with a particular focus on genus
 1247 *Cissus*. Species; *trnLF*; *rps16*; *trnC-petN*; *atpB-rbcL*.

1248

1249 ***Cissus adnata*** Roxb.; JX476858; JX476547; JX476673; JX476429. ***Cissus***
 1250 ***albiporcata*** Masinde & L.E. Newton; JF437304; JX476548; JF437201; JX476430.
 1251 ***Cissus amazonica*** Lindel; JX476859; JX476549; JX476674; JX476431. ***Cissus***
 1252 ***anisophylla*** Lombardi ; AB235010; JX476550; JX476675; JX476432. ***Cissus***
 1253 ***annamica*** Gagnep.; -; -; JX476676; -. ***Cissus antarctica*** Vent. ; JX476860;

- 1254 JX476551; JX476677; JX476433. **Cissus apendiculata** Lombardi; JX313413; -; -; -.
- 1255 **Cissus aphyllantha** Gilg; JX476862; JX476553; JX476679; JX476435. **Cissus**
- 1256 **araguainensis** Lombardi; JX313415; -; -; -. **Cissus aralioides** (Welw. ex Baker)
- 1257 Planch.; JF437305; -; JF437202; -. **Cissus assamica** (M.A. Lawson) Craib;
- 1258 JF437307; JX476559; JF437204; JX476441. **Cissus auricoma** Desc.; JX476866;
- 1259 JX476560; JX476682; JX476442. **Cissus bahiensis** Lombardi; JX313416; -; -; -.
- 1260 **Cissus biformifolia** Standl.; -; JX476562; JX476684; JX476444. **Cissus**
- 1261 **blanchetiana** Planch.; JX313417; -; -; -. **Cissus cactiformis** Gilg.; JX476868;
- 1262 JX476563; JX476685; JX476445. **Cissus campestris** (Baker) Planch.; JX313418; -;
- 1263 -; -. **Cissus cardiophylla** Standley; EF179080; -; -; -. **Cissus cornifolia** (Baker)
- 1264 Planch.; JF437308; JX476567; JF437205; JX476449. **Cissus decidua** Lombardi;
- 1265 JX313419; -; -; -. **Cissus descoingsii** Lombardi; JX313420; -; -; -. **Cissus diffusa**
- 1266 (Miq.) Amshoff; JX476871; JX476569; JX476689; JX476451. **Cissus diffusiflora**
- 1267 (Baker) Planch.; JX476872; JX476570; -; JX476452. **Cissus discolor** Blume;
- 1268 JF437309; -; JF437206; -. **Cissus duarteana** Cambess.; JX313421; -; -; -. **Cissus**
- 1269 **elongata** Roxb.; -; JX476573; JX476691; JX476455. **Cissus erosa** Rich.;
- 1270 HM585942; HM585802; JX476693; HM585526. **Cissus faucicola** Wild &
- 1271 R.B.Drumm.; JX476874; JX476576; JX476694; JX476458. **Cissus floribunda**
- 1272 (Baker) Planch.; JX476875; JX476577; JX476695; JX476459. **Cissus gongylodes**
- 1273 (Burch. ex Baker) Planch.; JX476877; JX476579; JX476697; JX476461. **Cissus**
- 1274 **granulosa** Ruiz & Pav.; JX476880; JX476582; JX476700; JX476464. **Cissus**
- 1275 **hastata** Miq.; AB235012; -; JX476701; JX476465. **Cissus hypoglauca** Durras;
- 1276 JX476881; JX476583; JX476702; JX476466. **Cissus incisa** (Nutt.) Des Moul. Ex
- 1277 S.Watson; HM585944; HM585804; -; HM585528. **Cissus integrifolia** (Baker)
- 1278 Planch.; JX476882; JX476584; JX476703; JX476467. **Cissus javana** DC. ;

- 1279 JX476883; JX476585; JX476704; JX476468. **Cissus lanea** Desc.; JX476884;
- 1280 JX476586; JX476705; JX476469. **Cissus leucophleus** (Scott-Elliott) Suess.;
- 1281 JX476885; JX476587; JX476706; JX476470. **Cissus madecassa** Desc.; JX476886;
- 1282 JX476588; JX476707; JX476471. **Cissus microcarpa** Vahl.; JX476888; JX476590;
- 1283 JX476709; JX476473. **Cissus microdonta** Vahl.; JX476889; JX476591; JX476710;
- 1284 JX476474. **Cissus neei** Croat; JX313424; -; -; -. **Cissus nodosa** Blume;
- 1285 HM585945; JX476592; JX476711; JX476475. **Cissus obliqua** Ruiz & Pav.;
- 1286 JX476890; JX476593; JX476712; JX476476. **Cissus oblonga** (Benth.) Planch.;
- 1287 EF179083; -; -; -. **Cissus oliveri** Gilg. ex Engl.; JX476892; JX476595; JX476714;
- 1288 JX476478. **Cissus paraensis** Lombardi; JX313427; -; -; -. **Cissus paullinifolia**
- 1289 Vell.; JX313426; -; -; -. **Cissus penninervis** (F.Muell.) Planch.; AF300300; -; -; -. **Cissus pentaclada** Jackes; EF179084; -; -; -. **Cissus phymatocarpa** Masinde &
- 1290 L.E. Newton; JF437311; JX476596; JF437209; JX476479. **Cissus pileata** Desc.;
- 1291 JX476893; JX476597; JX476715; JX476480. **Cissus polita** Desc.; JX476894;
- 1292 JX476598; JX476716; JX476481. **Cissus producta** Afzel.; JF437312; JX476600;
- 1293 JX476718; JX476483. **Cissus pseudoguerkeana** Verdc.; JX476896; JX476601;
- 1294 JX476719; JX476484. **Cissus pseudoverticillata** Verdc.; JX476897; JX476602;
- 1295 JX476720; JX476485. **Cissus pulcherrima** Vell.; JX313429; -; -; -. **Cissus**
- 1296 **quadrangularis** L.; JF437313; JX476603; JF437211; JX476486. **Cissus quarrei**
- 1297 Dewit; JX476899; JX476605; JX476722; JX476488. **Cissus reniformis** Domin.;
- 1298 EF179086; -; -; -. **Cissus repanda** Vahl; JX476900; JX476607; JX476724;
- 1300 JX476490. **Cissus repens** Lam.; HM585946; -; -; HM585530. **Cissus rhodotricha**
- 1301 (Baker) Desc.; JX476902; JX476609; JX476727; JX476492. **Cissus rhombifolia**
- 1302 Vahl; JX476905; JX476612; JX476729; JX476495. **Cissus rostrata** Korth.ex
- 1303 Planch.; AB235016; -; JX476731; JX476497. **Cissus rotundifolia** (Forssk.) Vahl;

- 1304 JF437315; JX476614; JF437213; JX476498. **Cissus rubiginosa** Welw. ex Bak.
- 1305 Planch. ; JX476907; JX476616; JX476732; JX476500. **Cissus sagittifera** Desc.;
- 1306 JX476908; JX476617; JX476733; JX476501. **Cissus sciaphila** Gilg; JF437316;
- 1307 JX476619; JF437214; JX476503. **Cissus serroniana** (Glaz.) Lombardi; JX313430; -
- 1308 ; -; -. **Cissus simsiana** Roem. & Schult.; JX476910; JX476620; JX476734;
- 1309 JX476504. **Cissus spinosa** Cambess.; JX313435; -; -; -. **Cissus sterculiifolia**
- 1310 (F.Muell. Ex Benth.) Planch.; EF179088; -; -; -. **Cissus stipulata** Vell.; JX313436; -;
- 1311 -; -. **Cissus striata** Ruiz & Pav.; AB235017; -; JX476747; -. **Cissus subtetragona**
- 1312 Planch.; JX476923; JX476635; JF437216; JX476519. **Cissus sulcaulis** (Baker)
- 1313 Planch.; JX313438; -; -; -. **Cissus surinamensis** Desc.; JX313439; -; -; -. **Cissus**
- 1314 **sylicola** Masinde & L.E.Newton; JX476924; JX476636; JX476751; JX476520.
- 1315 **Cissus tiliacea** Kunth; JX313440; -; -; -. **Cissus tinctoria** Mart.; JX313414; -; -; -.
- 1316 **Cissus trianae** Planch.; JX313441; -; -; -. **Cissus trifoliata** (L.) L.; JX476926;
- 1317 JX476639; JX476755; JX476524. **Cissus trothae** Gilg & M. Brandt; JF437318;
- 1318 JX476640; JF437217; JX476525. **Cissus tuberosa** Moc. & Sesse ex DC.;
- 1319 JX476927; JX476641; JX476756; JX476526. **Cissus tweediana** (Baker) Planch.;
- 1320 EF179089; -; -; -. **Cissus ulmifolia** (Baker) Planch.; JX476928; JX476642;
- 1321 JX476757; JX476527. **Cissus verticillata** (L.) Nicolson & C.E. Jarvis; JX476929;
- 1322 JX476643; JX476758; JX476528. **Cissus vinosa** Jackes; EF179090; -; -; -. **Cissus**
- 1323 **welwitschii** (Baker) Planch.; JX476934; JX476651; -; JX476537. **Cissus**
- 1324 **wenshanensis** C.L. Li; HM585949; -; -; HM585533. **Ampelocissus acapulcensis**
- 1325 (Kunth) Planch.; JF437281; JX476543; JF437172; -. **Ampelocissus africana** (Lour.)
- 1326 Merr. ; JQ182553; JQ182603; -; JQ182448. **Ampelocissus ascendiflora** Latiff ; -;
- 1327 JQ182583; -; JQ182430. **Ampelocissus costaricensis** Lundell; -; -; -; AB234911.
- 1328 **Ampelocissus elephantina** Planch.; HM585932; HM585792; -; HM585516.

- 1329 ***Ampelocissus erdwendbergiana*** Planch.; JF437282; JX476544; JF437173; -.
- 1330 ***Ampelocissus filipes*** Planch.; AB234982; -; -; -. ***Ampelocissus gracilis*** Planch.;
- 1331 AB234983; -; -; -. ***Ampelocissus javalensis*** (Seem.) W.D. Stevens & A. Pool ;
- 1332 AB234984; -; -; -. ***Ampelocissus obtusata*** (Welw. ex Baker) Planch. ; JQ182556;
- 1333 JQ182612; -; JQ182457. ***Ampelocissus thyrsiflora*** (Blume) Planch. ; JQ182546;
- 1334 JQ182593; -; JQ182438. ***Ampelopsis bodinieri*** (H. Lév. & Vaniot) Rehder;
- 1335 JF437284; JX476545; JF437175; JX476427. ***Ampelopsis cantoniensis*** Planch. ;
- 1336 HM585933; HM585793; JX476667; HM585517. ***Ampelopsis chaffanjonii***
- 1337 (H.Lev.)Rehder; JF437286; -; -; -. ***Ampelopsis cordata*** Michx.; AB234997; -;
- 1338 JF437178; -. ***Ampelopsis delavayana*** Planch; HM223253; -; -; -. ***Ampelopsis***
- 1339 ***rubifolia*** (Wall.) Planch.; JF437293; JX476546; JF437186; JX476428. ***Cayratia***
- 1340 ***acris*** F. Muell.; EF179070; -; -; -. ***Cayratia clematidea*** (F.Muell.) Domin.;
- 1341 EF179072; -; -; -. ***Cayratia cordifolia*** C.Y. Wu ex C.L. Li; HM585934; HM585794;
- 1342 JX476668; HM585518. ***Cayratia debilis*** (Baker)Suess.; JF437296; -; -; -. ***Cayratia***
- 1343 ***eury nema*** B.L.Burt; EF179073; -; -; -. ***Cayratia gracilis*** (Guill. & Perr.)Suess.;
- 1344 JF437297; -; -; -. ***Cayratia imerinensis*** (Baker) Desc.; HM585936; HM585796;
- 1345 JX476669; HM585520. ***Cayratia japonica*** (Thunb.) Gagnep. ; HM585937; -; -;
- 1346 HM585521. ***Cayratia maritima*** Jackes; EF179074; -; -; -. ***Cayratia mollissima***
- 1347 Gagnep.; HM585938; HM585798; JX476671; HM585522. ***Cayratia pedata***
- 1348 Gagnep.; AB235005; -; -; -. ***Cayratia saponaria*** (Seem. Ex Benth.) Domin.;
- 1349 EF179075; -; -; -. ***Cayratia trifolia*** (L.) Domin ; HM585940; -; JX476672;
- 1350 HM585524. ***Cayratia triternata*** (Baker) Desc.; HM585941; -; -; -. ***Clematicissus***
- 1351 ***angustissima*** (F.Muell.) Planch.; EF179091; -; -; -. ***Clematicissus opaca*** (F. Muell)
- 1352 Jackes & Rossetto; JX476935; JX476652; JX476767; JX476538. ***Cyphostemma***
- 1353 ***adenocaula*** (A.Rich.)Wild & R.B.Drumm.; JX476936; JX476653; JX476768;

- 1354 JX476539. *Cyphostemma bainesii* (Hook.f.) Desc.; AB235025; -; -; -.
- 1355 *Cyphostemma duparquetii* (Planch.) Desc.; JF437324; -; JF437222; -.
- 1356 *Cyphostemma horombense* Desc.; HM585950; -; -; -. *Cyphostemma jigou*
- 1357 Verdc.; JX476937; JX476655; JX476769; JX476540. *Cyphostemma*
- 1358 *kilimandscharicum* (Gilg) Wild & R.B.Drumm.; JF437327; -; -; -. *Cyphostemma*
- 1359 *mappia* (Lam.) Galet; AB235026; -; -; -. *Cyphostemma maranguense* (Gilg) Desc.;
- 1360 JF437329; -; JF437227; -. *Cyphostemma montagnacii* Desc.; AB235027; -;
- 1361 JF437228; -. *Cyphostemma simulans* (C.A. Sm.) Wild & R.B. Drumm; HM585952;
- 1362 -; -; HM585536. *Leea aculeata* Blume; AB235087; -; -; -. *Leea guineensis* G. Don.;
- 1363 -; JX476657; JF437235; JX476541. *Leea indica* (Burm.f.) Merr.; HM585953; -;
- 1364 JX476771; HM585537. *Leea macrophylla* Roxb. ex Hornem. & Roxb.; JF437335;
- 1365 JX476659; JF437237; -. *Leea spinea* Desc.; HM585955; -; -; -. *Nothocissus*
- 1366 *spicifera* (Griff.) Latiff; JF437336; JX476660; JF437239; -. *Parthenocissus*
- 1367 *chinensis* C.L. Li; HM223263; HM223320; JF437240; HM223373. *Parthenocissus*
- 1368 *henryana* (Hemsl.) Graebn. ex Diels & Gilg; HM223272; HM223329; JF437244;
- 1369 HM223383. *Parthenocissus heptaphylla* (Buckl.) Britton ex Small; HM223256; -; -;
- 1370 -. *Parthenocissus himalayana* Planch.; AB235034; -; -; -. *Parthenocissus*
- 1371 *laetevirens* Rehder; HM223267; -; -; -. *Parthenocissus quinquefolia* (L.) Planch.;
- 1372 HM223275; HM223332; JF437246; HM223386. *Parthenocissus suberosa* Hand.-
- 1373 Mazz.; HM223273; HM223330; JF437247; HM223384. *Parthenocissus*
- 1374 *tricuspidata* (Sieb. & Zucc.) Planch.; HM223274; HM223331; JF437248;
- 1375 HM223385. *Parthenocissus vitacea* (Knerr.) Hitchc.; HM223295; -; -; -.
- 1376 *Pterisanthes eriopoda* Planch.; -; JX476661; -; -. *Pterisanthes heterantha* M.
- 1377 Laws; AB235045; AB234965; -; AB234930. *Pterisanthes stonei* Latiff; AB235046;
- 1378 JX476662; -; -. *Rhoicissus digitata* Gilg & Brandt.; AB235047; -; -; -. *Rhoicissus*

1379 ***rhomboidea*** Planch.; AB235049; -; -; -. ***Rhoicissus tomentosa*** (Lam.) Wild & R.B.
1380 Drumm; JF437342; JX476663; JF437251; -. ***Rhoicissus tridentata*** (L.f.) Wild &
1381 R.B. Drumm.; JF437341; JX476664; JF437250; -. ***Tetrastigma glabratum*** Planch.;
1382 HM585995; -; -; -. ***Tetrastigma hemsleyanum*** Diels & Gilg; HM586000; HM585860;
1383 -; HM585584. ***Tetrastigma lanyuense*** C.E. Chang; HM586009; HM585869;
1384 JF437257; HM585593. ***Tetrastigma laxum*** Merr.; HM586017; -; -; -. ***Tetrastigma***
1385 ***lenticellatum*** Planch.; HM586019; -; -; -. ***Tetrastigma loheri*** Gagnep.; HM586021;
1386 -; -; -. ***Tetrastigma obtectum*** (Wall.) Planch; HM586029; HM585888; -; HM585614.
1387 ***Tetrastigma pachyphyllum*** (Hemsl.) Chun; HM586032; HM585891; JF437259;
1388 HM585616. ***Tetrastigma petraeum*** Jackes; EF179094; -; -; -. ***Tetrastigma***
1389 ***pyriforme*** Gagnep.; HM586039; -; -; -. ***Tetrastigma sichouense*** C.L.Li;
1390 HM586047; -; -; -. ***Tetrastigma triphyllum*** (Gagnep.) W.T. Wang; HM586061;
1391 HM585919; -; HM585646. ***Tetrastigma voinierianum*** Pierre ex Gagnep.;
1392 HM586067; -; -; -. ***Vitis aestivalis*** Michx. ; HM586070; HM585928; -; HM585655.
1393 ***Vitis betulifolia*** Diels & Gilg; JF437352; JX476665; JF437269; -. ***Vitis flexuosa***
1394 Thunb.; HM586071; HM585929; -; HM585656. ***Vitis heyneana*** Roem. & Schult;
1395 JF437354; JX476666; JF437273; -. ***Vitis labrusca*** L.; JX507364; JX507361;
1396 JX507362; JX507360. ***Vitis mengziensis*** C.L. Li; HM223276; HM223333;
1397 JF437270; HM223387. ***Vitis popenoei*** J.L. Fennell; HM586072; HM585930;
1398 JF437276; HM585657. ***Vitis riparia*** Michx; JF437357; -; JF437277; -. ***Vitis***
1399 ***rotundifolia*** Michx.; HM586073; HM585931; -; HM585658. ***Vitis thunbergii*** Siebold
1400 & Zucc.; AB235082; -; -; -. ***Vitis vinifera*** L.; -; -; -. ***Vitis vulpina*** L.; JQ182566;
1401 JQ182622; -; JQ182467. ***Yua austro-orientalis*** (F.P. Metcalf) C.L. Li; AB235085; -;
1402 -; -. ***Yua thomsoni*** (M.A. Lawson) C.L. Li; HM223277; HM223335; -; HM223389.

FIGURE LEGENDS

1403
1404 Fig. 1. External morphology of fossilized *Cissus* seeds from the Hiwegi Formation,
1405 Rusinga Island, Kenya. (A) Lateral, (B) apical, (C) basal, (D) ventral views of the
1406 *Cissus crenulata* (Chesters) comb. nov. holotype (V33753). (E) Ventral, (F) lateral,
1407 (G) apical, (H) basal views of the *Cissus andrewsii* sp. nov. holotype. (I) Lateral and
1408 (J) basal views of a paratype of *C. andrewsii* (V68500), and (K) lateral and (L) apical
1409 views of another paratype (V68502), demonstrating intraspecific variation in seed
1410 size, shape, ornamentation and basal/apical width. (M) Lateral, (N) basal and (O)
1411 apical views of the *Cissus rusingensis* sp. nov. holotype (R117.1981.314). (P, S, V)
1412 Lateral, (Q, T, W) basal and (R, U, X) apical views of paratypes of *C. rusingensis*
1413 (R117.1981.476, R117.1981.604, R117.1981.605 respectively), illustrating
1414 intraspecific variation in seed shape (sub-rounded to pyriform), the number of muri
1415 and enclosed lumina, the extent of the perichalazal rib and the length of the basal
1416 projection. (Y) Lateral, (Z) apical, (AA) basal, (BB) ventral views of the *Cissus psilata*
1417 sp. nov. holotype (V68506). Scale bar is 10 mm in 1 mm increments.

1418
1419 Fig. 2. Ventral infolds revealed in a seed of modern African *Cissus populnea* Guill. &
1420 Perr. by SRXTM (A–B) and in fossil seeds from the Hiwegi Formation, Rusinga
1421 Island, Kenya (C–J), assigned to *Cissus* herein, by μ CT. (A, B) SRXTM digital
1422 transverse section (DTS) through modern *C. populnea*, infill of the endotesta in
1423 yellow in (B) highlighting the position of the ventral infolds. (C, D) μ CT DTS through
1424 the holotype (V33753) of *Cissus crenulata* comb. nov., with (D) showing inferred
1425 position of the ventral infolds (solid yellow lines) and the margins of the endotesta
1426 (dotted yellow lines). (E, F) μ CT DTS through the holotype (V68501) of *Cissus*
1427 *andrewsii* sp. nov., with (F) showing infill of the inferred endotesta in yellow,

1428 highlighting two parallel, broad ventral infolds. (G, H) μ CT DTS through the holotype
1429 (R117.1981.314) of *Cissus rusingensis* sp. nov., with (H) showing infill of inferred
1430 embryo cavity within endotesta in yellow, highlighting two parallel, very broad ventral
1431 infolds. (I, J) μ CT DTS through holotype (V68506) of *Cissus psilata* sp. nov., with (J)
1432 showing inferred position of pair of very short, narrow parallel ventral infolds (solid
1433 yellow lines). All μ CT sections obtained from near ventral part of seeds, where
1434 ventral infolds were most likely to be evident, if concealed externally, based on their
1435 position in modern *Cissus* seeds. All scale bars are 1 mm.

1436
1437 Fig. 3. Virtual taphonomy using digital fossils produced from an SRXTM dataset of a
1438 modern fruit of *Cissus populnea* Guill. & Perr. Specimen oriented in oblique
1439 ventral/apical view to best display ventral infolds. (A) Produced by digitally infilling
1440 space inside endotesta of seed, showing externally conspicuous pair of ventral
1441 infolds, thereby mimicking mineral seed infill processes during fossilization. (B)
1442 Produced by digitally concealing ventral infolds in (A) thereby mimicking taphonomic
1443 processes that could conceal ventral infolds by mineral infill. Scale bar is 1 mm.

1444
1445 Fig. 4. Comparative tissue organisation in *Cissus* (A) and *Cyphostemma* (B) showing
1446 how the endotesta obscures ventral infolds in *Cyphostemma*. (A-B) SRXTM digital
1447 transverse sections through modern fruits. (A) *Cissus populnea* Guill. & Perr. (B)
1448 *Cyphostemma maranguense* (Gilg) Desc. Scale bars in (A) and (B) are 1 mm.

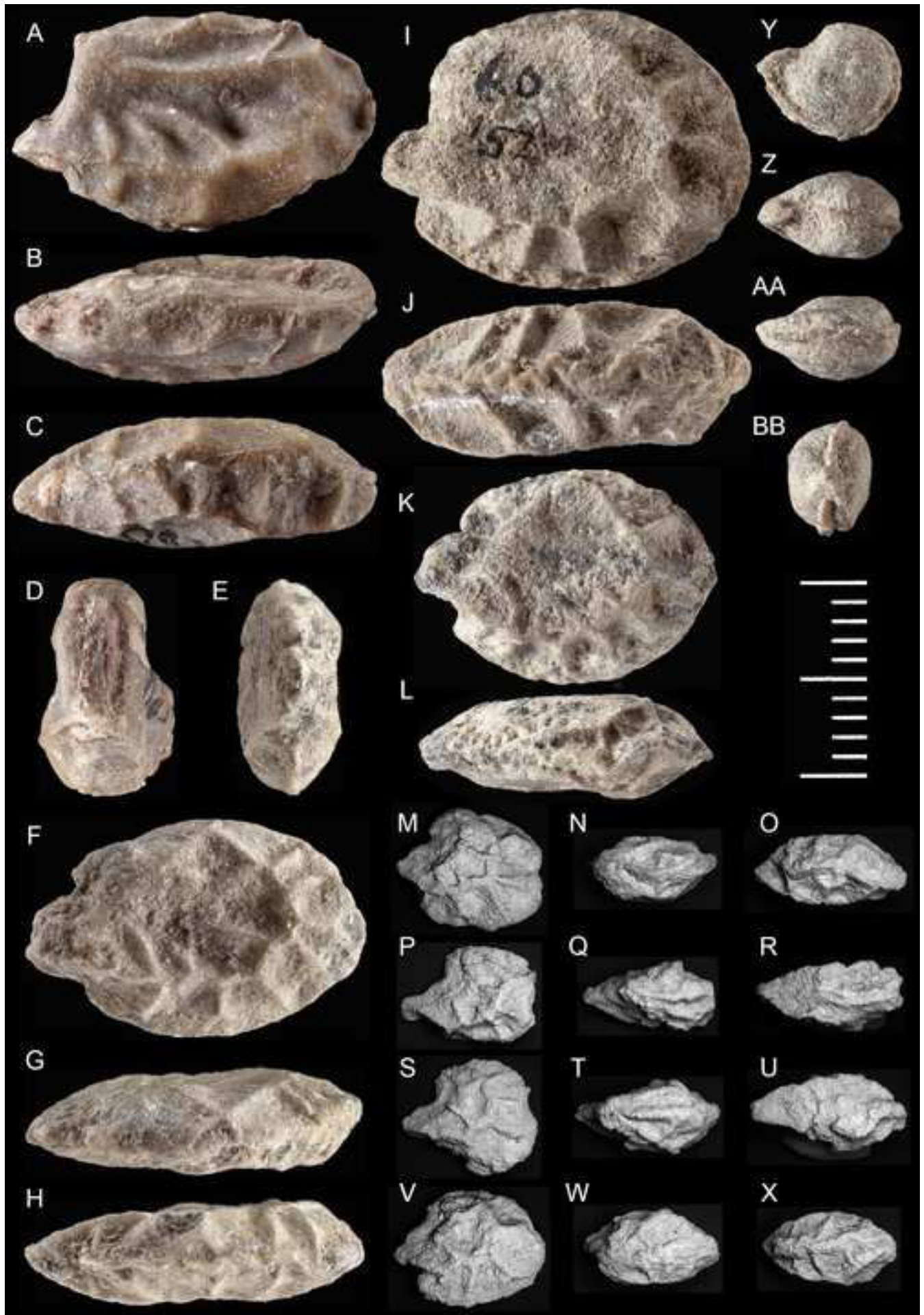
1449
1450 Fig. 5. Phylogenetic tree of core *Cissus* clade obtained using maximum likelihood
1451 criteria, implemented in RAxML (Stamatakis, 2014), based on plastid DNA sequence
1452 data of Vitaceae, with particular focus on genus *Cissus*. Bootstrap values and

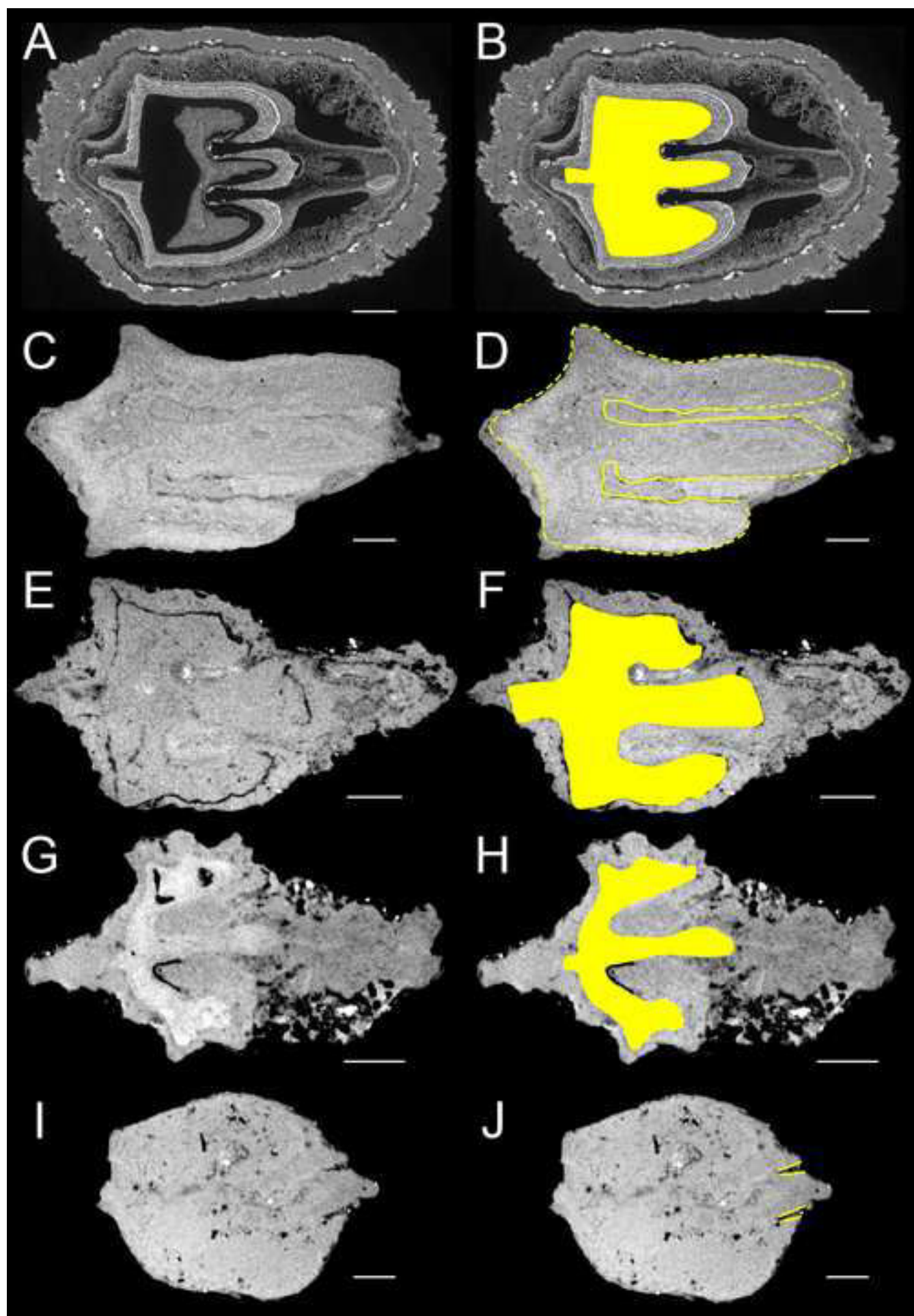
1453 posterior probabilities are indicated at nodes. Clades and seed morphotypes referred
1454 to in text are indicated; species placed in seed morphotypes based on internal and
1455 external morphology are shown with solid colour highlight, and those tentatively
1456 placed in seed morphotypes based on external illustrations and descriptions are
1457 distinguished by coloured outline; distribution ranges indicated after species name
1458 (Af, Africa; As, Asia; Au, Australia; N, Neotropics); species for which new DNA
1459 sequences were produced are highlighted with an asterisk; species for which no data
1460 on seed morphology could be found are denoted by a question mark. Scale bar
1461 shows degree of genetic change (nucleotide substitutions per site) as distance on the
1462 phylogram.

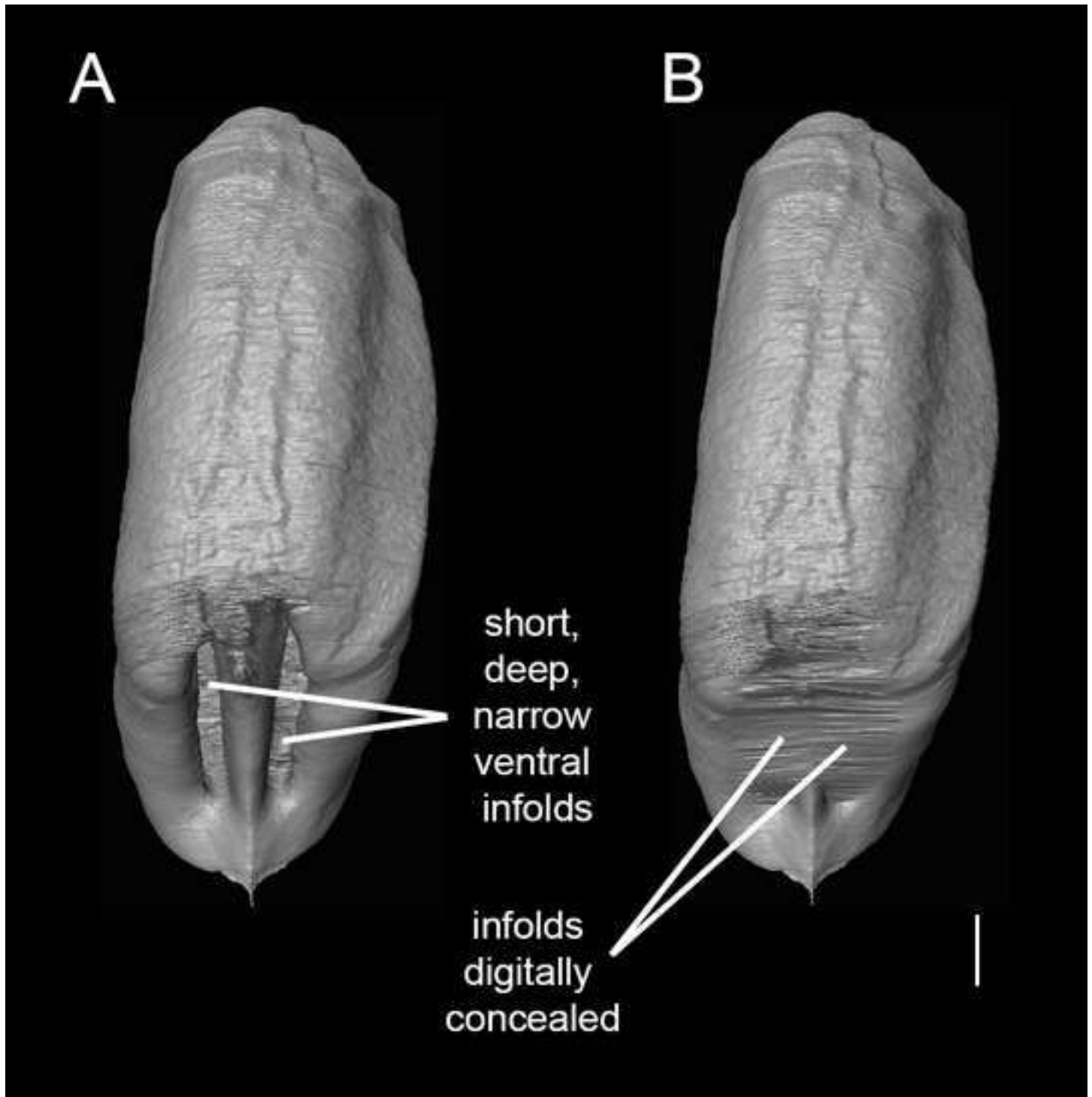
1463
1464 Fig. 6. Major clades recognised in Fig. 5 with representative modern (A-B, D-E, G-H,
1465 J-M, O-W) and fossil (C, F, I, N) seed morphologies. Modern images all rotated 90
1466 degrees clockwise from the original source. Seed Morphotype 1 (A-C) characterises
1467 the *Cissus barbeyana* clade; Morphotype 2 (D-F) the *C. integrifolia* clade;
1468 Morphotype 3 (G-I) the *C. sciaphila* clade and Morphotype 4 (L-N) the *C. petiolata*
1469 clade. Smooth seeds, somewhat similar to Morphotype 4, also characterise the wider
1470 clade (in which the *C. petiolata* clade is basal) indicated by the dotted grey line.
1471 Sources of modern images are as follows: (A) *C. floribunda* (fig. 15.13 in Descoings,
1472 1967); (B) *C. barbeyana* (fig. 13E in Dewit and Willems, 1960); (D) *C. integrifolia* (fig.
1473 13F in Dewit and Willems, 1960); (E) *C. populnea* (pl. 34, fig. 11 in Descoings, 1972);
1474 (G) *C. smithiana* (pl. 52, fig. H in Dewit and Willems, 1960); (H) *C. sciaphila* (fig. 6.1c
1475 in Verdcourt, 1993); (J) *C. bosseri* (fig. 10.8 in Descoings, 1967); (K) *C. leucophlea*
1476 (fig. 14.13 in Descoings, 1967); (L) *C. aralioides* (fig. 13C in Dewit and Willems,
1477 1960); (M) *C. petiolata* (fig. 13A in Dewit and Willems, 1960); (O) *C. elongata* (fig.

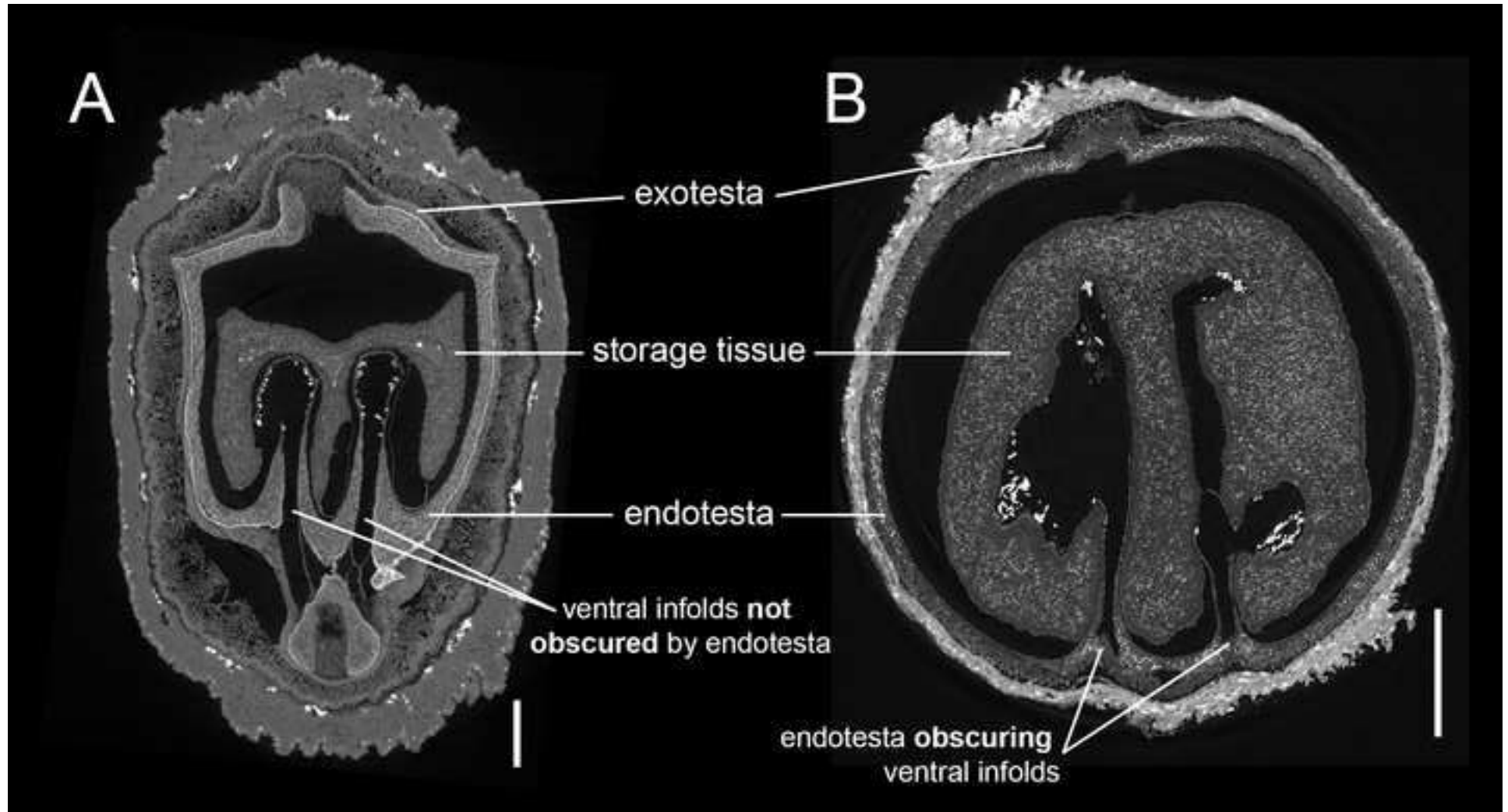
1478 171.10 in Chen et al., 2007); (P) *C. subtetragona* (fig. 171.2 in Chen et al., 2007); (Q)
1479 *C. cactiformis* (fig. 9.8 in Verdcourt, 1993); (R) *C. quadrangularis* (pl. 29, fig. 10 in
1480 Descoings, 1972); (S) *C. cornifolia* (pl. 47, fig. 12 in Descoings, 1972); (T) *C. pileata*
1481 (fig. 13.9 in Descoings, 1967); (U) *C. repens* (fig. 2B in Jackes, 1988); (V) *C. hastata*
1482 (fig. 5C in Jackes, 1988); (W) *C. diffusiflora* (pl. 44, fig. 11 in Descoings, 1972).
1483 Seeds are not to scale and are all shown in lateral view, except (O) and (P), which
1484 are shown in apical view.

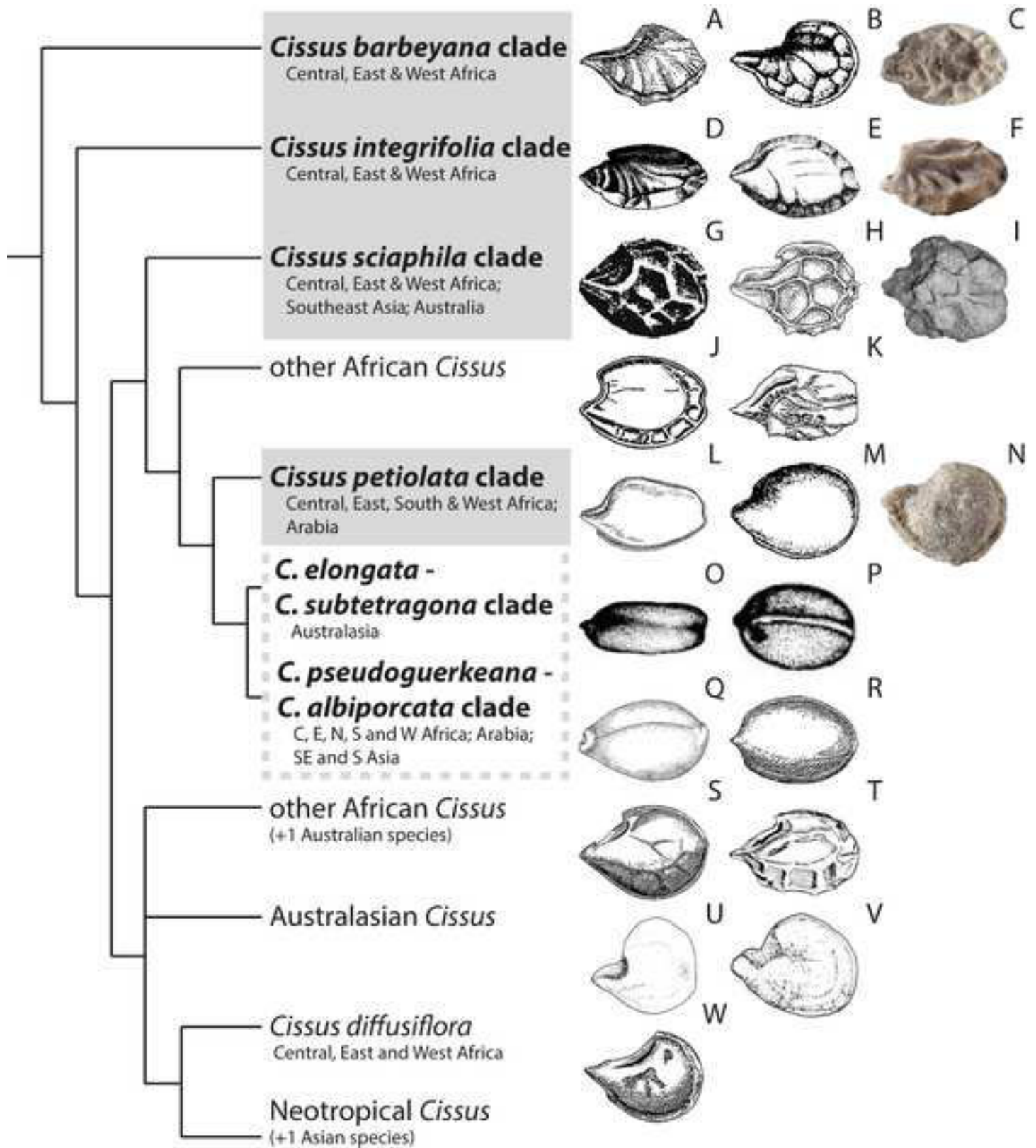
1485
1486 Fig. 7. SRXTM digital transverse sections through fruits of modern African *Cissus*,
1487 using representative specimens to illustrate typical features of each seed morphotype
1488 listed in Table 1. (A) Morphotype 1, *Cissus integrifolia* Guill. & Perr. (B) Morphotype
1489 2, *Cissus dasyantha* Gilg & M.Brandt (C) Morphotype 3, *Cissus tiliifolia* Planch. (D)
1490 Morphotype 4, *Cissus petiolata* Hook.f.. Transverse sections were obtained from
1491 near ventral part of fruits to best show features of ventral infolds and characteristics
1492 of seed coat layers. All scale bars are 1 mm.

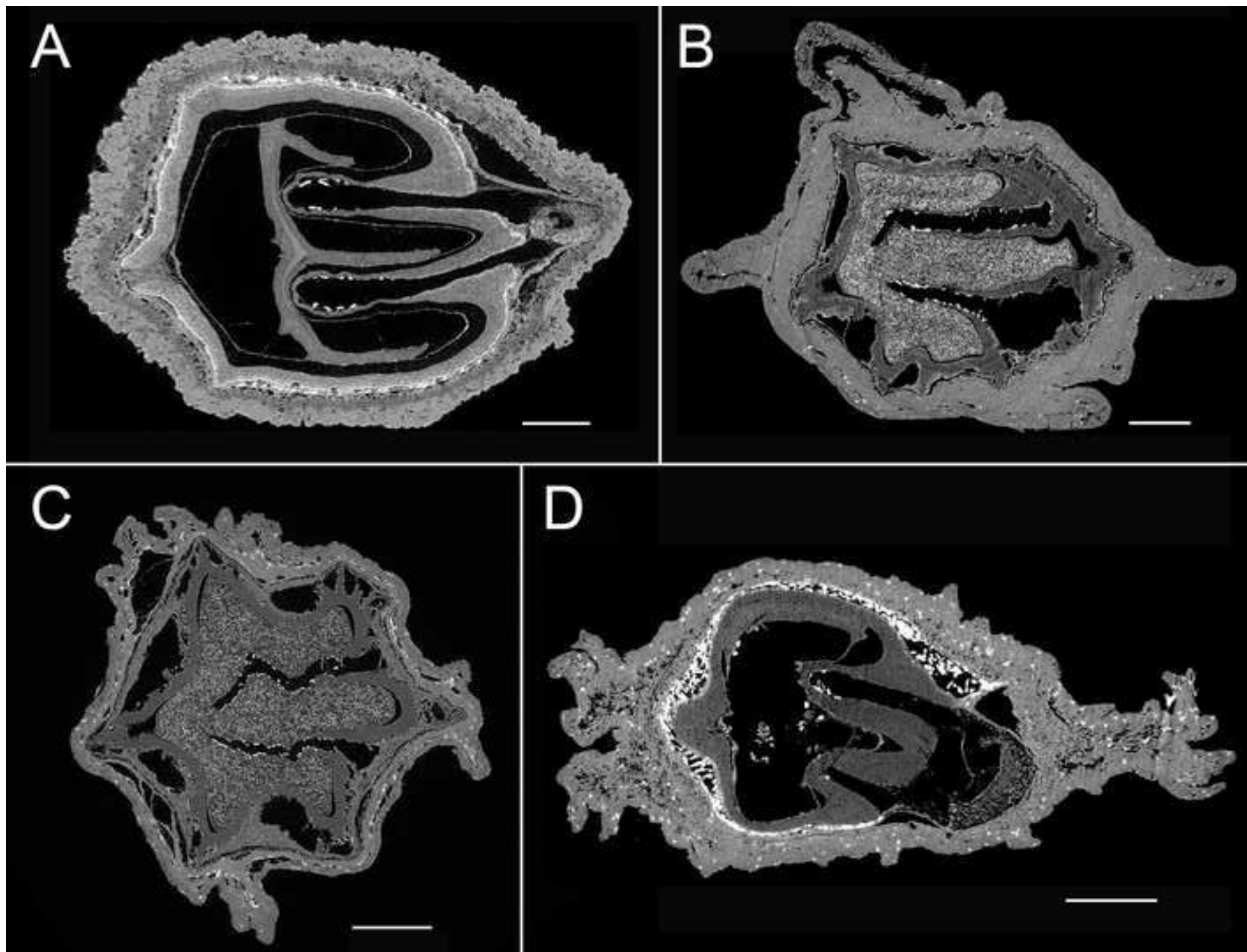












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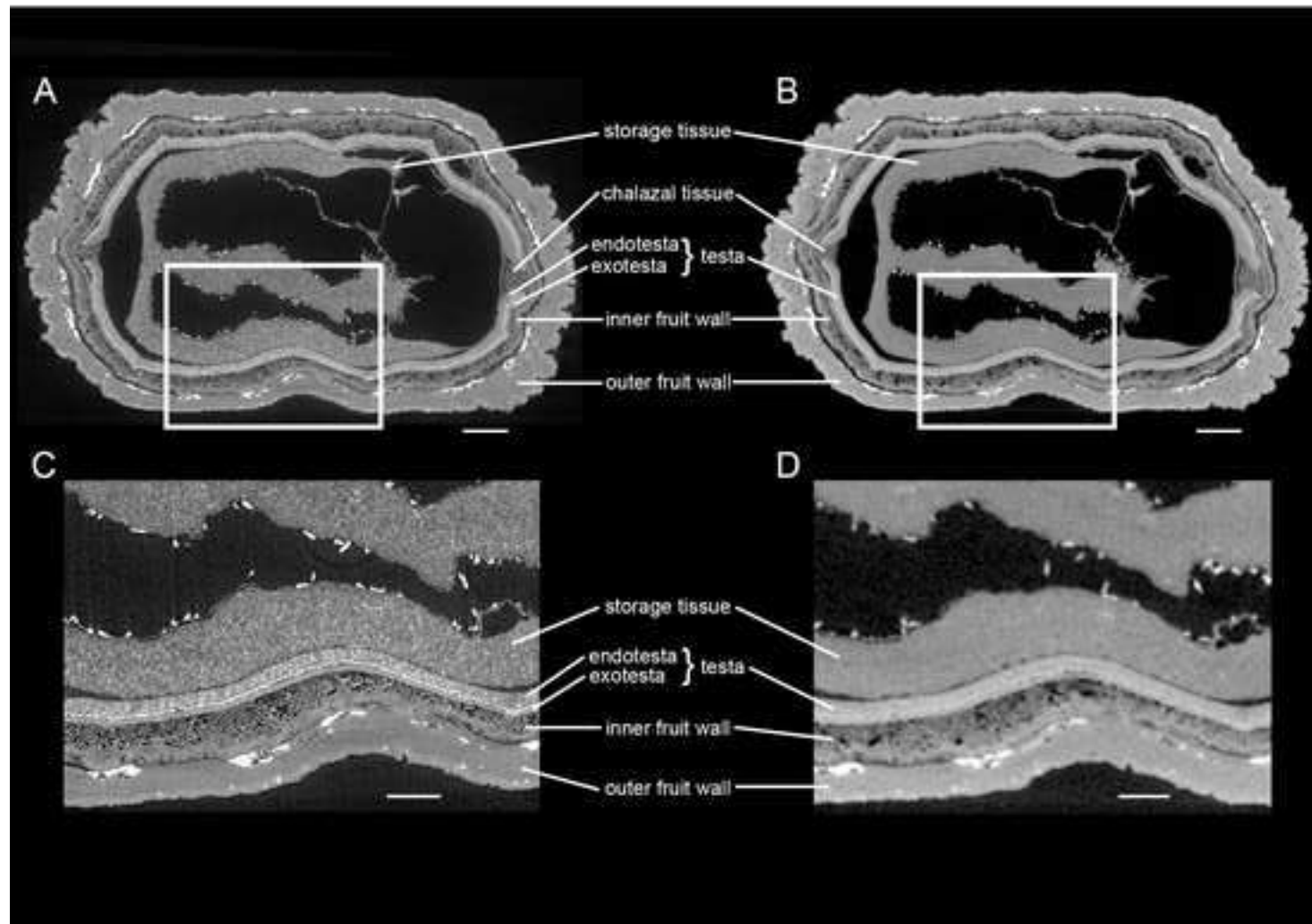
Appendix S1. Herbarium sheet for seed morphotypes of sixteen modern species of African *Cissus* and three species of *Cyphostemma* studied. All specimens sampled from the Royal Botanic Gardens, Kew Herbarium (K), except *C. dasyantha* (from the Botanic Gardens Meise Herbarium (BR), Belgium). References to literature illustrating seeds of these species are also provided.

Species	Collector (collector number)	Country/ region of collection	Seed morphotype (see text and Table 1 for explanation of morphotypes)	Literature with seed illustrations of this species
<i>Cissus barbeyana</i> De Wild. & T.Durand	S. Lisowski (16406)	Zaire (Congo)	2	fig. 13e in Dewit and Willems (1960); pl. 42, fig. 10 in Descoings (1972)
<i>Cissus bosseri</i> Desc.	P.B. Phillipson & S. Rabesihanaka (3140)	Mascarene Islands	Unlike fossils, shares some features with Morphotype 1 but lacks ornament on lateral faces	fig. 10 in Descoings (1967)
<i>Cissus dasyantha</i> Gilg & M.Brandt	J. Louis (13410)	Congo	2	fig. 13j in Dewit and Willems (1960)
<i>Cissus dinklagei</i> Gilg & M.Brandt	A.J.M. Leeuwenberg (5207)	Masok (Tanzania)	Unlike fossils, has very variable seed morphology in floral illustrations, shares some features with Morphotype 1 but differs in that the most prominent ridge is central not marginal	fig. 13g in Dewit and Willems (1960); pl. 40, fig. 10 in Descoings (1972)
<i>Cissus integrifolia</i> (Baker) Planch.	C.M. Taylor, R.E. Gereau & J. Lovett (8517a)	Iringa (Tanzania)	1	fig. 13f in Dewit and Willems (1960)
<i>Cissus integrifolia</i> (Baker) Planch.	C.M. Taylor, R.E. Gereau & J. Lovett (8517b)	Iringa (Tanzania)	1	fig. 13f in Dewit and Willems (1960)
<i>Cissus lebrunii</i> Dewit	B.A. Nkongmeneck (1592)	Cameroon	3	fig. 13k in Dewit and Willems (1960)
<i>Cissus oreophila</i> Gilg & M.Brandt	W.J. Harley (693A)	Liberia	Unlike fossils, as this is a two-seeded specimen	pl. 39, fig. 11 in Descoings (1972)
<i>Cissus petiolata</i> Hook.f.	L.P.A. & W.R.Q. (9365)	Tanzania	4	fig. 13a in Dewit and Willems (1960); pl. 33, fig. 11 in Descoings (1972); fig. 3 in Verdcourt (1993)
<i>Cissus pileata</i> Desc.	H. Humbert (18981)	Madagascar	Unlike fossils, shares some features with Morphotype 3, but has only very irregular ridges on the lateral faces that do not form a reticulum	fig. 13 in Descoings (1967)
<i>Cissus planchoniana</i> Gilg	W. Robyns (606)	Congo	Unlike fossils, shares some features with Morphotype 2 but has long pronounced ridges radiating right across the lateral faces	pl. 43, fig. 11 in Descoings (1972)
<i>Cissus polyantha</i> Gilg & M.Brandt	F.C. Deighton (5208)	Kokoru, Gaura (Sierra Leone)	Unlike fossils, seeds very variable in surface ornament in floral illustrations and SRXTM videos, from smooth to extensively ridged, including specimens that fall into Morphotype 3	fig. 13h in Dewit and Willems (1960); pl. 36, fig. 11 in Descoings (1972)
<i>Cissus polyantha</i>	M. Sacande, L. Sanou,	Burkina Faso	Unlike fossils, seeds very variable in surface	fig. 13h in Dewit and Willems (1960);

Gilg & M.Brandt	M. van Slageren (MSLSMS-1643)		ornament in floral illustrations and SRXTM videos, from smooth to extensively ridged, including specimens that fall into Morphotype 3. This specimen studied by SRXTM is also two-seeded.	pl. 36, fig. 11 in Descoings (1972)
<i>Cissus populnea</i> Guill. & Perr.	R.A.A. Oldeman (350)	Tehini	1	pl. 34, fig. 10 in Descoings (1972)
<i>Cissus rondoensis</i> Verdc.	S. Bidgood, R. Abdallah & K. Vollesen (1553)	Tanzania	Unlike fossils, descriptions in Verdcourt (1993) state that seeds are essentially smooth but have two to three transverse ridges.	
<i>Cissus sciaphila</i> Gilg	B. Mhoro (UMBC287)	Tanzania	3	fig. 6 in Verdcourt (1993)
<i>Cissus smithiana</i> (Baker) Planch.	R.P. Hulstaert (416)	Congo	Unlike fossils, as this is a two-seeded specimen	pg. 533, fig. h in Dewit and Willems (1960); pl. 32, fig. 11 in Descoings (1972)
<i>Cissus tiliifolia</i> Planch.	G. Eilu (240)	Uganda	3	n/a
<i>Cyphostemma adenocaula</i> (Steud. ex A.Rich.) Desc. ex Wild & R.B.Drumm.	H. Ern, B. Leuenberger, H. Scholz, U. Scholz & W. Schwarz (1446)	Togo		pg. 471, fig. e in Dewit and Willems (1960); pl. 28, fig. 11 in Descoings (1972); fig. 20 in Verdcourt (1993)
<i>Cyphostemma heterotrichum</i> (Gilg & R.E.Fr.) Desc. ex Wild & R.B.Drumm.	Carter, Abdallah, Newton (2537)	Tanzania		fig. 18 in Verdcourt (1993)
<i>Cyphostemma maranguense</i> (Gilg) Desc.	C.G. Rogers (2)	Kenya		

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Appendix S2. Comparison of tissue and cellular detail revealed by SRXTM and routine μ CT in a modern fruit of *Cissus populnea* Guill. & Perr., where the digital transverse section (DTS) is through the part of the seed distal to the external ventral infolds. (A) SRXTM and (B) μ CT DTS with labelled identifiable seed tissues (storage and chalazal tissues, testa, fruit wall), the distinction between endotesta and exotesta can be made using the SRXTM DTS but this distinction is not as clear using routine μ CT. (C) SRXTM and (D) μ CT DTS at higher magnification with labelled tissue layers as for (A) and (B), showing the greater cellular detail, ability to distinguish layers in the seed coat and the distribution of phases of different X-ray attenuation in the fruit in SRXTM. White boxes in (A) and (B) outline the areas shown at higher magnification in (C) and (D). Scale bars in (A) and (B) are 1 mm and in (C) and (D) are 0.5 mm.



Appendix S3. Further details of the phylogenetic analyses.

Total genomic DNA was extracted from 0.2 g of herbarium specimen material using a modified version of the 2× cetyltrimethyl ammonium bromide (CTAB) method (Doyle and Doyle, 1987). The total DNA was purified using a caesium chloride/ethidium bromide gradient (1.55 g/mL) followed by a dialysis procedure for long-term storage in the DNA & Tissue Collections at RBG Kew (<http://apps.kew.org/dnabank/homepage.html>). The *trnL* intron and *trnL*–*F* spacer were amplified in two reactions using primers *c/d* and *e/f*, respectively (Taberlet et al., 1991). The *rps16* intron was amplified using the primers *rps16F* and *rps16R* (Shaw et al., 2005). The polymerase chain reactions (PCRs) for the above markers were performed in 25 µL volumes, containing 12.5 µL of DreamTaq PCR Master Mix (2x) (4 mM MgCl₂; Thermo Fisher Scientific, Waltham, Massachusetts, USA), 4 µL TBT-PAR (trehalose, bovine serum albumin (BSA), and polysorbate-20 (Tween-20); Samarakoon et al., 2013), 0.5 µL of each primer (100 ng/µL) and 1 µL of DNA template. A ‘long and cold’ programme was used with an initial denaturation at 80°C for 5 mins, followed by 35 cycles of 95 °C for 1 min, 50°C (*trnL*–*F*) or 48 °C (*rps16*) for 1 min and 65 °C for 5 mins, completed with a final extension of 65°C for 4 mins. All amplifications were performed on a 9700 GeneAmp thermocycler (ABI, Warrington, UK). All PCR products were purified with either the QIAquick PCR kit (Qiagen, Hilden, Germany) or the Nucleospin Extract II kit (Machery-Nagel, Düren, Germany), following the manufacturer protocols. Cycle sequencing reactions were performed in 5 µL reactions using 0.5 µL of BigDye® Terminator cycle sequencing chemistry (v3.1; ABI, Warrington, UK) and the same primers as for PCR. Complementary strands were sequenced on an ABI3730 automated sequencer and then assembled and aligned in Geneious (Biomatters Limited, Auckland, New Zealand). The newly produced DNA sequences are available from GenBank (see GenBank accession numbers in Appendix 1 of main paper).

Publically available sequences (Appendix 2) were downloaded using Geneious 7.0.2 (Biomatters Limited, Auckland, New Zealand) and matrices (including sequences produced for the present study) were aligned using MUSCLE (Edgar, 2004) in Geneious. Alignments used to produce the phylogeny are available at from TreeBASE (<https://treebase.org>; study 18491). A phylogenetic analysis was performed using the maximum likelihood criterion as implemented in the programme RAxML v8.1.24 (Stamatakis, 2014) using the rapid bootstrap algorithm with 1000 replicates and a search for the best-scoring tree. The analysis was run on the Cipres Science Gateway portal (www.phylo.org). Divergence time estimates were obtained using the Bayesian inference approach implemented in the package BEAST v.1.8.2 (Drummond and Rambaut, 2007). The plastid regions were combined and the GTR+I+G evolutionary model was applied to the resulting matrix. An uncorrelated relaxed molecular clock with a lognormal distribution of rates and a birth-death speciation model were used. Two analyses were run on the Cipres Science Gateway portal (www.phylo.org) for 50 million generations each, sampling one tree every 1000th generation. Parameter convergence was confirmed using the software Tracer v1.6 (Rambaut et al., 2014). Following the combination of these two runs using LogCombiner v1.8.2 (Drummond and Rambaut, 2007), a maximum clade credibility tree with median branch lengths and 95% highest posterior density (HPD) interval on nodes was reconstructed using TreeAnnotator 1.8.2 (Drummond and Rambaut, 2007), after an initial burn-in period of five million generations had been removed (10%).

Appendix S4. Seed morphotypes for all seeds from clades within core *Cissus* (Fig. 5) containing African species (fifty-two species in total); those highlighted in grey were studied by SRXTM.

Species	Clade in phylogeny (Figs. 5 & 6)	Seed morphotype	Seed illustration and/or description in literature
<i>Cissus adnata</i> Roxb.	<i>C. sciaphila</i> clade	3	fig. 3B and 3C and p. 489 in Jackes (1988) p. 701 in Lu (1993); fig. 172.7 and 172.8 and p. 188 in Chen et al. (2007)
<i>Cissus albiporcata</i> Masinde & L.E.Newton	<i>C. pseudoguerkeana</i> - <i>C. albiporcata</i> clade	no published illustration or description found	
<i>Cissus annamica</i> Gagnep.	<i>C. elongata</i> - <i>C.</i> <i>subtetragona</i> clade	no published illustration or description found	
<i>Cissus aphyllantha</i> Gilg	<i>C. sciaphila</i> clade	3	p. 38 in Verdcourt (1993)
<i>Cissus aralioides</i> (Welw. ex Baker) Planch.	<i>C. petiolata</i> clade	4	fig. 13C and p. 548 in Dewit and Willems (1960); pl. 30, figs. 10-12 and p. 88 in Descoings (1972); fig. 11.10 and p. 47 in Verdcourt (1993)
<i>Cissus auricoma</i> Desc.	<i>C. microdonta</i> - <i>C.</i> <i>auricoma</i> clade	3	figs. 12.6 and 12.7 and p. 89 in Descoings (1967)
<i>Cissus barbeyana</i> De Wild. & T.Durand	<i>C. barbeyana</i> clade	2	fig. 13E and p. 525 in Dewit and Willems (1960); pl. 42, fig. 10 and p. 118 in Descoings (1972)
<i>Cissus bosseri</i> Desc.	<i>C. microdonta</i> - <i>C.</i> <i>auricoma</i> clade	unlike fossils	fig. 10.8 and p. 83-84 in Descoings (1967)
<i>Cissus cactiformis</i> Gilg	<i>C. pseudoguerkeana</i> - <i>C. albiporcata</i> clade	4	fig. 9.8 and p. 40 in Verdcourt (1993)
<i>Cissus cornifolia</i> (Baker) Planch.	<i>C. cornifolia</i> - <i>C.</i> <i>trothae</i> clade	unlike fossils	p. 519 in Dewit and Willems (1960); pl. 47, figs. 11-12 and p. 132 in Descoings (1972); fig. 8.9 and p. 36 in Verdcourt (1993)
<i>Cissus dasyantha</i> Gilg & M.Brandt	unknown	2	fig. 13J and p. 543 in Dewit and Willems (1960)
<i>Cissus diffusa</i> (Miq.) Amshoff	<i>C. elongata</i> - <i>C.</i> <i>subtetragona</i> clade	no published illustration or description found	
<i>Cissus diffusiflora</i> (Baker) Planch.	<i>C. diffusiflora</i> clade	unlike fossils	p. 528-529 in Dewit and Willems (1960); pl. 44, figs. 11-12 and p. 124 in Descoings (1972); p. 24 in Verdcourt (1993)
<i>Cissus dinklagei</i> Gilg & M.Brandt	unknown	variable seed morphology	fig. 13G and p. 515 in Dewit and Willems (1960); pl. 40, fig. 10 and p. 114 in Descoings (1972)
<i>Cissus elongata</i> Roxb.	<i>C. elongata</i> - <i>C.</i> <i>subtetragona</i> clade	4	fig. 171.10 and p. 186 in Chen et al. (2007)

<i>Cissus faucicola</i> Wild & R.B.Drumm.	<i>C. pseudoguerkeana</i> - <i>C. albiporcata</i> clade	4	p. 48 in Verdcourt (1993)
<i>Cissus floribunda</i> (Baker) Planch.	<i>C. barbeyana</i> clade	2	figs. 15.12 and 15.13 and p. 138 in Descoings (1967)
<i>Cissus integrifolia</i> (Baker) Planch.	<i>C. integrifolia</i> clade	1	fig. 13F and p. 514 in Dewit and Willems (1960); p. 16 in Verdcourt (1993)
<i>Cissus javana</i> DC.	<i>C. elongata</i> - <i>C. subtetragona</i> clade	unlike fossils	fig. 170.8 and 170.9 and p. 187 in Chen et al. (2007)
<i>Cissus lanea</i> Desc.	<i>C. microdonta</i> - <i>C. auricoma</i> clade	no published illustration or description found	
<i>Cissus lebrunii</i> Dewit	unknown	3	fig. 13K and p. 543 in Dewit and Willems (1960)
<i>Cissus leucophlea</i> (Scott-Elliot) Suess.	<i>C. microdonta</i> - <i>C. auricoma</i> clade	unlike fossils	figs. 14.12 and 14.13 and p. 132 in Descoings (1967)
<i>Cissus madecassa</i> Desc.	<i>C. microdonta</i> - <i>C. auricoma</i> clade	unlike fossils	figs. 13.4 and 13.5 and p. 112 in Descoings (1967)
<i>Cissus microdonta</i> (Baker) Planch.	<i>C. microdonta</i> - <i>C. auricoma</i> clade	unlike fossils	figs. 15.4 and 15.5 and p. 100 in Descoings (1967)
<i>Cissus oliveri</i> (Engl.) Gilg ex Engl.	<i>C. petiolata</i> clade	unlike fossils	p. 535 in Dewit and Willems (1960); p. 32 in Verdcourt (1993)
<i>Cissus oreophila</i> Gilg & M.Brandt	unknown	3	pl. 39, fig. 11 and p. 112 in Descoings (1972)
<i>Cissus pentaclada</i> Jackes	<i>C. cornifolia</i> - <i>C. trothae</i> clade	unlike fossils	fig. 3D and p. 491 in Jackes (1988)
<i>Cissus petiolata</i> Hook.f.	<i>C. petiolata</i> clade	4	fig. 13A and p. 515 in Dewit and Willems (1960); pl. 33, fig. 11 and p. 97 in Descoings (1972); fig. 3.9 and p. 16 in Verdcourt (1993)
<i>Cissus phymatocarpa</i> Masinde & L.E.Newton	<i>C. pseudoguerkeana</i> - <i>C. albiporcata</i> clade	no published illustration or description found	
<i>Cissus pileata</i> Desc.	<i>C. cornifolia</i> - <i>C. trothae</i> clade	unlike fossils	figs. 13.9 and 13.10 and p. 119 in Descoings (1967)
<i>Cissus planchoniana</i> Gilg	unknown	unlike fossils	p. 520 in Dewit and Willems (1960); pl. 43, figs. 11-12 and p. 120 in Descoings (1972); p. 23-24 in Verdcourt (1993)
<i>Cissus polita</i> Desc.	<i>C. petiolata</i> clade	no published illustration or description found	
<i>Cissus polyantha</i> Gilg & M.Brandt	<i>C. sciaphila</i> clade	variable seed morphology, including specimen like Morphotype 3	fig. 13H and p. 536 in Dewit and Willems (1960); pl. 36, figs. 11-12 and p. 104 in Descoings (1972); p. 30 in Verdcourt (1993)
<i>Cissus populnea</i> Guill. & Perr.	<i>C. integrifolia</i> clade	1	p. 531 in Dewit and Willems (1960); pl. 34, figs. 10 and 11 and p. 100 in Descoings (1972); p. 19 in Verdcourt (1993)

<i>Cissus producta</i> Afzel.	<i>C. cornifolia</i> - <i>C. trothae</i> clade	unlike fossils	fig. 13B and p. 524 in Dewit and Willems (1960); pl. 46, fig. 10 and p. 130 in Descoings (1972); p. 22 in Verdcourt (1993)
<i>Cissus pseudoguerkeana</i> Verdc.	<i>C. pseudoguerkeana</i> - <i>C. albiporcata</i> clade	no published illustration or description found	
<i>Cissus quadrangularis</i> L.	<i>C. pseudoguerkeana</i> - <i>C. albiporcata</i> clade	4	p. 513 in Dewit and Willems (1960); p. 91 in Descoings (1967); pl. 29, figs. 10 and 11 and p. 87 in Descoings (1972); p. 41 in Verdcourt (1993)
<i>Cissus quarrei</i> Dewit	<i>C. sciaphila</i> clade	3	p. 537 in Dewit and Willems (1960); p. 32 in Verdcourt (1993)
<i>Cissus reniformis</i> Domin	<i>C. elongata</i> - <i>C. subtetragona</i> clade	4	figs. 2F-G in Jackes (1988)
<i>Cissus rhodotricha</i> (Baker) Desc.	<i>C. sciaphila</i> clade	3	figs. 12.15 and 12.16 and p. 116 in Descoings (1967)
<i>Cissus rondoensis</i> Verdc.	<i>C. petiolata</i> clade	unlike fossils	p. 20 in Verdcourt (1993)
<i>Cissus rostrata</i> (Miq.) Korth. ex Planch.	<i>C. sciaphila</i> clade	3	p. 326 in Yeo et al. (2012)
<i>Cissus rotundifolia</i> Vahl	<i>C. petiolata</i> clade	4	p. 519 in Dewit and Willems (1960); p. 21 in Verdcourt (1993)
<i>Cissus rubiginosa</i> (Welw. ex Baker) Planch.	<i>C. cornifolia</i> - <i>C. trothae</i> clade	unlike fossils	pl. 53, fig. E and p. 540 in Dewit and Willems (1960); pl. 31, figs. 12 and 13 and p. 92 in Descoings (1972); fig. 4E and p. 26 in Verdcourt (1993)
<i>Cissus sagittifera</i> Desc.	<i>C. barbeyana</i> clade	2	figs. 14.8 and 14.9 and p. 130 in Descoings (1967)
<i>Cissus sciaphila</i> Gilg	<i>C. sciaphila</i> clade	3	figs. 5.10 and 6.1 and p. 30 in Verdcourt (1993)
<i>Cissus smithiana</i> (Baker) Planch.	<i>C. sciaphila</i> clade	3	pl. 52, fig. H and p. 534 in Dewit and Willems (1960); pl. 32, fig. 11 and p. 94 in Descoings (1972)
<i>Cissus subtetragona</i> Planch.	<i>C. elongata</i> - <i>C. subtetragona</i> clade	4	fig. 171.2 and p. 185 in Chen et al. (2007)
<i>Cissus sylvicola</i> Masinde & L.E. Newton	<i>C. petiolata</i> clade	4	p. 18 in Verdcourt (1993)
<i>Cissus tiliifolia</i> Planch.	<i>C. sciaphila</i> clade	3	p. 35 in Verdcourt (1993)
<i>Cissus trothae</i> Gilg & M.Brandt	<i>C. cornifolia</i> - <i>C. trothae</i> clade	no published illustration or description found	
<i>Cissus welwitschii</i> (Baker) Planch.	<i>C. petiolata</i> clade	4	p. 19 in Verdcourt (1993)

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Appendix S5. List of herbarium sheets used to provide habit and habitat data for modern *Cissus* species (source 4 in Table 2 of main paper). Herbarium abbreviations: DSM (University of Dar es Salam Herbarium, Tanzania); G (Geneva General Herbarium); IFAN (Institut Fondamental d'Afrique Noire Herbarium); K (Royal Botanic Gardens, Kew Herbarium); L (National Herbarium of the Netherlands at Leiden University); MO (Missouri Botanical Garden Herbarium); P (Muséum National d'Histoire Naturelle Herbarium, Paris); TAN (Tsimbazaza Herbarium, Madagascar).

Species	Habit	Habitat	Region/ Country of Collection	Collector (Collection Number)	Herbarium (Herbarium Barcode)	Accession Number	Web Link
<i>Cissus adnata</i> Roxb.	Scrambler	Remnant primary forest on south facing slope	Yunnan, China	Li Heng (9095)	(Unknown)	(Unknown)	http://www.tropicos.org/Specimen/1402887
	(Unknown)	Forest margin	Yunnan, China	Zhan Huo Tsi (91-109)	MO (MO-162633)	4250721	http://www.tropicos.org/Specimen/1344197
	Climber	Riparian forest	Sarawak, Malaysia	Abang Mohtar et al. (S49581)	MO (MO-162639)	3844467	http://www.tropicos.org/Specimen/1344238
	Climbing woody vine (stem very corky)	Semi-open scrub forest	Sri Lanka	F.R. Fosberg et al. (50818)	MO (MO-162634)	2213855	http://www.tropicos.org/Specimen/1344199
	(Unknown)	Deciduous forest	Northern Thailand	T. Shimizu et al. (T10433)	MO (MO-162637)	2580082	http://www.tropicos.org/Specimen/1344231
	Woody vine (10-15m long)	Primary evergreen seasonal broad-leaved closed lowland forest on very steep slopes	Thanh Hoa, Vietnam	L.V. Averyanov, P.K. Lôc, D.T. Doan & N.T. Vinh (3880)	MO (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/2774452
	Vine (common)	Primary evergreen seasonal broad-leaved closed lowland forest on very steep slopes	Thanh Hoa, Vietnam	L.V. Averyanov, P.K. Lôc, D.T. Doan & N.T. Vinh (3939)	MO (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/2774468
	(Unknown)	Monsoon forest	Sumbawa, Indonesia	J. Elbert (3667)	L (L 0746186)	L.2334734	http://medialib.naturalis.nl/file/id/L.2334734/format/large
	(Unknown)	Light monsoon forest	Lombok, Indonesia	J. Elbert (1963)	L (L 0746179)	L.2334741	http://medialib.naturalis.nl/file/id/L.2334741/format/large
	Evergreen woody climber	Open, disturbed thicket along a seasonal stream with secondary growth in a destroyed primary, evergreen, seasonal, hardwood forest	Chiang Mai, Thailand	J.F. Maxwell (01-295)	L (L 0761745)	L.3928867	http://medialib.naturalis.nl/file/id/L.3928867/format/large
	Woody climber	Open, degraded, disturbed, fire-prone	Champasak, Laos	J.F. Maxwell (98-1041)	L (L 0762737)	L.4254525	http://medialib.naturalis.nl/file/id/L.4254525/format/large

		thicket bordering deciduous secondary growth forest					
Climber	Riparian forest	Borneo, Indonesia	A. Kostermans (21453)	L (L 0672603)	L.2334780	http://medialib.naturalis.nl/file/id/L.2334780/format/large	
Climbing-scrambling vine	Open areas in evergreen forest and open rocky thickets	Saraburi, Thailand	J.F. Maxwell (74-546)	L (L 0194871)	L.2328773	http://medialib.naturalis.nl/file/id/L.2328773/format/large	
Deciduous woody climber	Open degraded mixed deciduous secondary growth, margins of evergreen and deciduous seasonal forest, canopy to 25m	Ubon Ratchathani, Thailand	Martin Greijmans (184)	L (L 0761507)	L.3928674	http://medialib.naturalis.nl/file/id/L.3928674/format/large	
Vine	Thicket	Queensland, Australia	B.R. Jackes (unknown)	L (L 0761883)	L.4254130	http://medialib.naturalis.nl/file/id/L.4254130/format/large	
Creeper	Dipterocarp forest	Borneo, Indonesia	M.M.J. van Balgooy (5746)	L (L 0672608)	L.2334775	http://medialib.naturalis.nl/file/id/L.2334775/format/large	
Slender climber	Mixed lowland forest	Borneo, Brunei	M.J.E. Coode et al. (6797)	L (L 0672609)	L.2334774	http://medialib.naturalis.nl/file/id/L.2334774/format/large	
Solitary climber, 1m high	Much disturbed primary forest ca. 40m high, on alluvial soil near a river. Terrain flat to gently sloping.	Sulawesi, Indonesia	E.F. de Vogel (5103)	L (L 0483122)	L.2334730	http://medialib.naturalis.nl/file/id/L.2334730/format/large	
Woody climber	Partly open, alluvial area along a small stream in degraded mixed evergreen and deciduous hardwood forest with much bamboo, in overall deciduous dipterocarp-oak and pine, seasonal forest	Chiang Mai, Thailand	J.F. Maxwell (95-449)	L (L 0762949)	L.4254251	http://medialib.naturalis.nl/file/id/L.4254251/format/large	
Shrubby creeper	Sandstone outcrop in broadleaf scrub	Northern Territory, Australia	Martensz & Schodde (AE 706)	L (L 0746142)	L.2334721	http://medialib.naturalis.nl/file/id/L.2334721/format/large	
Climber (5 m)	Forest edge with clearing in remnant primary forest	Sumatra, Indonesia	W.J.J.O. de Wilde and B.E.E. de Wilde-Duyfjes (21320)	L (L 0746262)	L.2328679	http://medialib.naturalis.nl/file/id/L.2328679/format/large	
Climber (ca. 8m)	Forest edge in primary	Sumatra,	W.J.J.O. de Wilde	L	L.2328682	http://medialib.naturalis.nl/file/id/L.2328682/format/large	

	tall)	rain forest	Indonesia	and B.E.E. de Wilde-Duyfjes (19351)	(L 0746260)		.2328682/format/large
	(Unknown)	Mixed deciduous forest	Phitsanulok, Thailand	Kai Larsen, T. Smitinand & E. Warncke (877)	L (L 0194878)	L.2328770	http://medialib.naturalis.nl/file/id/L.2328770/format/large
	Vine	Partly shaded area in the mixed evergreen/deciduous forest in a burned area with some bamboo	Chiang Mai, Thailand	J.F. Maxwell (89-600)	L (L 0194777)	L.2328772	http://medialib.naturalis.nl/file/id/L.2328772/format/large
	(Unknown)	Monsoon forest, busy and light	Sumbawa, Indonesia	J. Elbert (4204)	L (L 0746182)	L.2334738	http://medialib.naturalis.nl/file/id/L.2334738/format/large
	Climber	Bushes by forest stream	Ranong, Thailand	A.F.G. Kerr (16877)	L (L 0194781)	L.2328775	http://medialib.naturalis.nl/file/id/L.2328775/format/large
	Sprawling vine	Open place along a river, on granite bedrock, in a dry dipterocarp forest	Chiang Mai, Thailand	J.F. Maxwell (87-687)	L (L 0194778)	L.2328774	http://medialib.naturalis.nl/file/id/L.2328774/format/large
	(Unknown)	Deciduous forest	Chiang Mai, Thailand	T. Shimizu, H. Koyama & M. Hutoh (T10433)	L (L 0194837)	L.2328776	http://medialib.naturalis.nl/file/id/L.2328776/format/large
	Deciduous vine	Open, disturbed, degraded, secondary growth thicket in degraded mixed evergreen and deciduous, seasonal, hardwood forest with bamboo	Phayao, Thailand	J.F. Maxwell (98-747)	L (L 0762744)	L.4254532	http://medialib.naturalis.nl/file/id/L.4254532/format/large
	Solitary climber, 8m high	Disturbed primary forest near streamlet	Sulawesi, Indonesia	E.F. de Vogel (5592)	L (L 0483124)	L.2334731	http://medialib.naturalis.nl/file/id/L.2334731/format/large
	(Unknown)	Partly shaded areas in the mixed evergreen & deciduous forest, base of limestone cliffs, rugged limestone terrain	Kanchanaburi, Thailand	J.F. Maxwell (93-923)	L (L 0762963)	L.4254263	http://medialib.naturalis.nl/file/id/L.4254263/format/large
	Vine	Second growth forest	Luzon, Philippines	H.G. Gutierrez (61-75)	L (L 0746209)	L.2334793	http://medialib.naturalis.nl/file/id/L.2334793/format/large
	Climber	Riparian forest	Borneo, Malaysia	Abang Mohtar et al. (S.49581)	L (L 0672610)	L.2334773	http://medialib.naturalis.nl/file/id/L.2334773/format/large
<i>Cissus</i>	Vine	Rainforest	Antananarivo,	L.C. Barnett &	MO	3333595	http://www.tropicos.org/Specimen

<i>floribunda</i> (Baker) Planch.			Madagascar	Laurence J. Dorr (187)	(MO-163568)		/177642
	(Unknown)	Forest	Antananarivo, Madagascar	Georges Cremers (1299)	(Unknown)	(Unknown)	http://www.tropicos.org/Specimen/1204127
	Vine (climbing to 3m)	Tropical moist forest	Antsiranana, Madagascar	George E. Schatz (2405)	MO (MO-163570)	3708677	http://www.tropicos.org/Specimen/178235
	Liana	Rainforest towards a small lake	Antsiranana, Madagascar	Armand Rakotozafy & Jeannine I. Raharilala (2295)	TAN (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/1103606
	Liana	Dense rainforest	Antsiranana, Madagascar	Richard Razakamalala (3598)	MO (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/3453897
	Liana (4m in height)	Forest	Antsiranana, Madagascar	C. Rakotovao & et al. (3148)	MO (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/2982381
	Liana	Rainforest	Fianarantsoa, Madagascar	Armand Rakotozafy (196)	TAN (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/1204111
	Vine	Disturbed forest and edges	Fianarantsoa, Madagascar	Thomas B. Croat (30103)	MO (MO-163571)	2322603	http://www.tropicos.org/Specimen/1354458
	(Unknown)	Rainforest	Fianarantsoa, Madagascar	Bernard M. Descoings (1110)	MO (MO-163121)	2211740	http://www.tropicos.org/Specimen/176965
	Liana	Dense rainforest	Fianarantsoa, Madagascar	N.M. Andrianjafy & et al. (670)	MO (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/2704015
	Climbing liana	Dense rainforest	Fianarantsoa, Madagascar	N.M. Andrianjafy & et al. (747)	MO (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/2705111
	Slender liana (to ca. 10m long)	Rainforest	Fianarantsoa, Madagascar	S.T. Malcomber (1288)	MO (MO-163596)	4574042	http://www.tropicos.org/Specimen/176950
<i>Cissus oreophila</i> Gilg & M.Brandt	Climber	Riverine forest border	Gabon	Adriaan M. Louis (1019)	MO (MO-163214)	4573103	http://www.tropicos.org/Specimen/1348861
	(Unknown)	Forest regrowth remains on the edge of a Sphagnum pond	Brazzaville, Congo	Bernard M. Descoings (5917)	MO (MO-163221)	2211723	http://www.tropicos.org/Specimen/1348913
	Liana	Swamp region	Brazzaville, Congo	Bernard M. Descoings (6988)	MO (MO-163215)	2211724	http://www.tropicos.org/Specimen/1348877
	Herbaceous vine (20-25m)	Dense primary forest with large trees and vines	Equatorial Guinea	Manuel Fidalgo de Carvalho (3596)	MO (MO-163206)	4325779	http://www.tropicos.org/Specimen/1348780
	Climber	Forest edge	Ivory Coast	J. Bokdam (2785)	MO (MO-163217)	2422492	http://www.tropicos.org/Specimen/1348885
	Creeping herb	Secondary forest	Ivory Coast	C. Geerling & J. Bokdam (2471)	MO (MO-163216)	2469995	http://www.tropicos.org/Specimen/1348881
	(Unknown)	Savanna edge and hill forest regrowth	Central African Republic	Bernard M. Descoings (10441)	MO (MO-163219)	2211725	http://www.tropicos.org/Specimen/1348892
	Creepers	High forest	Liberia	P. Adames (565)	IFAN	IFAN52664	http://plants.jstor.org/stable/10.55

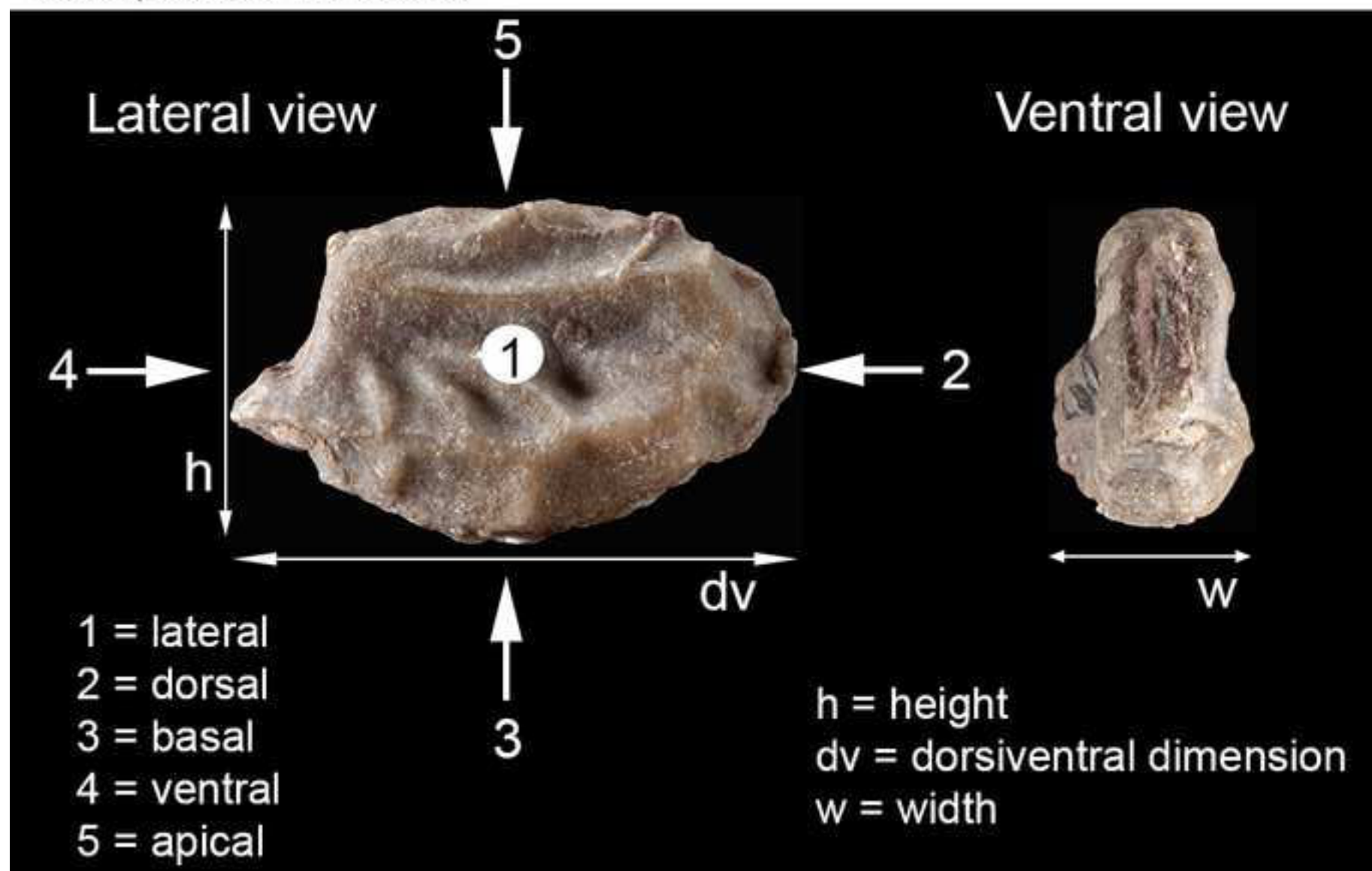
					(IFAN52664)		55/al.ap.specimen.ifan52664
<i>Cissus polita</i> Desc.	(Unknown)	Hills and limestone plateau, seasonal deciduous forest	Antsiranana, Madagascar	H. Humbert (19215)	P (P00061314)	P00061314	http://plants.jstor.org/stable/10.5555/al.ap.specimen.p00061314
	Liana (3m)	Dry forest	Antsiranana, Madagascar	F. Ratovoson (1234)	MO (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/3225598
	Liana (3m height)	Dry forest on sandy soil	Antsiranana, Madagascar	Andriamalala Rakotondrafara (400)	MO (MO-1059463)	5957540	http://www.tropicos.org/Specimen/2844837
	Liana	Degraded dry forest	Antsiranana, Madagascar	Stéphan Rakotonandrasana (938)	MO (MO-1441510)	5996128	http://www.tropicos.org/Specimen/2871026
	Climbing shrub	Rocky sandstone woodland	Antsiranana, Madagascar	H. Perrier de la Bâthie (6185)	P (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/177361
	Liana (1.5m)	Dense dry forest	Antsiranana, Madagascar	L. Nusbaumer & P. Ranirison (1128)	G (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/100647659
	Liana	Savanna grassland with residual groves of dry deciduous forest	Antsiranana, Madagascar	M. Bardot-Vaucoulon & G. Véné (1607)	P (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/100333665
<i>Cissus rondoensis</i> Verdc.	Herbaceous climber to ca. 4m	Moist evergreen forest	Lindi, Tanzania	G. Sally Bidgood, R.D. Abdallah & K.B. Vollesen (1553)	DSM (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/2855173
	Semi-woody climber to 3m tall	Dense forest thicket	Lindi, Tanzania	G. Sally Bidgood, R.D. Abdallah & K.B. Vollesen (1442)	K (K000322840)	K000322840	http://plants.jstor.org/stable/10.5555/al.ap.specimen.k000322840
<i>Cissus rostrata</i> (Miq.) Korth. ex Planch.	Liana	Secondary forest	North Maluku, Indonesia	Tjut Jul Fatisa Bangun, Mary Merello, Iska Gushilman, Idris Haris & Roji Mahroji (11)	MO (MO-2702487)	6434347	http://www.tropicos.org/Specimen/100530014
	Liana (at 1m high)	Disturbed forest	North Maluku, Indonesia	Lalao Andriamahefarivo, Deby Arifiani, Richard Razakamalala & Bahar Fabanyo (137)	MO (MO-2702471)	6431952	http://www.tropicos.org/Specimen/100554547
	Climber	Foothill primary rain forest	Negeri Sembilan, Malaysia	Eric Gardette (E.G 2112)	L (L 0761437)	L.4254449	http://medialib.naturalis.nl/file/id/L.4254449/format/large

Climber	Secondary forest, flatland	Borneo, Malaysia	A.A. Nordin (86099)	L (L 0672368)	L.2333842	http://medialib.naturalis.nl/file/id/L.2333842/format/large
Climber	Forest river bank	Borneo, Malaysia	Aban Gibot (94480)	L (L 0672371)	L.2333839	http://medialib.naturalis.nl/file/id/L.2333839/format/large
Scrambling shrub	River banks in rainforest seral growths	New Guinea, Indonesia	L.J. Brass (13064)	L (L 0745287)	L.2333803	http://medialib.naturalis.nl/file/id/L.2333803/format/large
Vine	Secondary growth in area intermediate between heath and dipterocarpaceous forests	Borneo, Malaysia	Ding Hou (391)	L (L 0672375)	L.2333834	http://medialib.naturalis.nl/file/id/L.2333834/format/large
Tall woody climber (30 feet)	River bank in disturbed primary forest	Borneo, Malaysia	P.S. Ashton (S.18398)	L (L 0672365)	L.2333845	http://medialib.naturalis.nl/file/id/L.2333845/format/large
Climber (6m tall)	Forest edge in primary peat swamp and marshy forest on flat land	Sumatra, Indonesia	W.J.J.O. de Wilde and B.E.E. de Wilde-Duyfjes (20538)	L (L 0745311)	L.2333873	http://medialib.naturalis.nl/file/id/L.2333873/format/large
Climber	Rainforest (Eucalyptus deglupta dominant)	Sulawesi, Indonesia	M.M.J. van Balgooy (3421)	L (L 0745292)	L.2333797	http://medialib.naturalis.nl/file/id/L.2333797/format/large
Climber	Bank of a forest brook	Borneo, Indonesia	F.H. Endert (3387)	L (L 0672539)	L.2333923	http://medialib.naturalis.nl/file/id/L.2333823/format/large
Soft climber	Riverside vegetation in mixed lowland forest	Borneo, Brunei	M.J.E. Coode (6443)	L (L 0672388)	L.2333889	http://medialib.naturalis.nl/file/id/L.2333889/format/large
Twining climber	Lowland dipterocarp primary rain forest	Negeri Sembilan, Malaysia	Eric Gardette (E.G 1643)	L (L 0762757)	L.4254436	http://medialib.naturalis.nl/file/id/L.4254436/format/large
Climber	Secondary regrowth forest in disturbed lowland rainforest	Borneo, Malaysia	C.E. Ridsdale (2130)	L (L 0672384)	L.2333826	http://medialib.naturalis.nl/file/id/L.2333826/format/large
Climber (4m long)	Riverside in forest	Borneo, Malaysia	Asik Mantor (118747)	L (L 0672382)	L.2333828	http://medialib.naturalis.nl/file/id/L.2333828/format/large
Climber (20m above ground)	Lowland mixed forest	Palawan, Philippines	D.D. Soejarto, D.A. Madulid, F. Gaerlan, E. Sagcal, O. Fernando (8661)	L (L 0761399)	L.3298568	http://medialib.naturalis.nl/file/id/L.3298568/format/large
Climber	Disturbed open area on evergreen forest margins	Singapore	J.F. Maxwell (83-9)	L (L 0745318)	L.2333866	http://medialib.naturalis.nl/file/id/L.2333866/format/large
Climber	River side in secondary forest	Borneo, Malaysia	A.A. Nordin (86041)	L (L 0672367)	L.2333843	http://medialib.naturalis.nl/file/id/L.2333843/format/large
Climber	Undergrowth on open bank of a stream in	New Guinea, Indonesia	L.J. Brass (12397)	L (L 0745286)	L.2333804	http://medialib.naturalis.nl/file/id/L.2333804/format/large

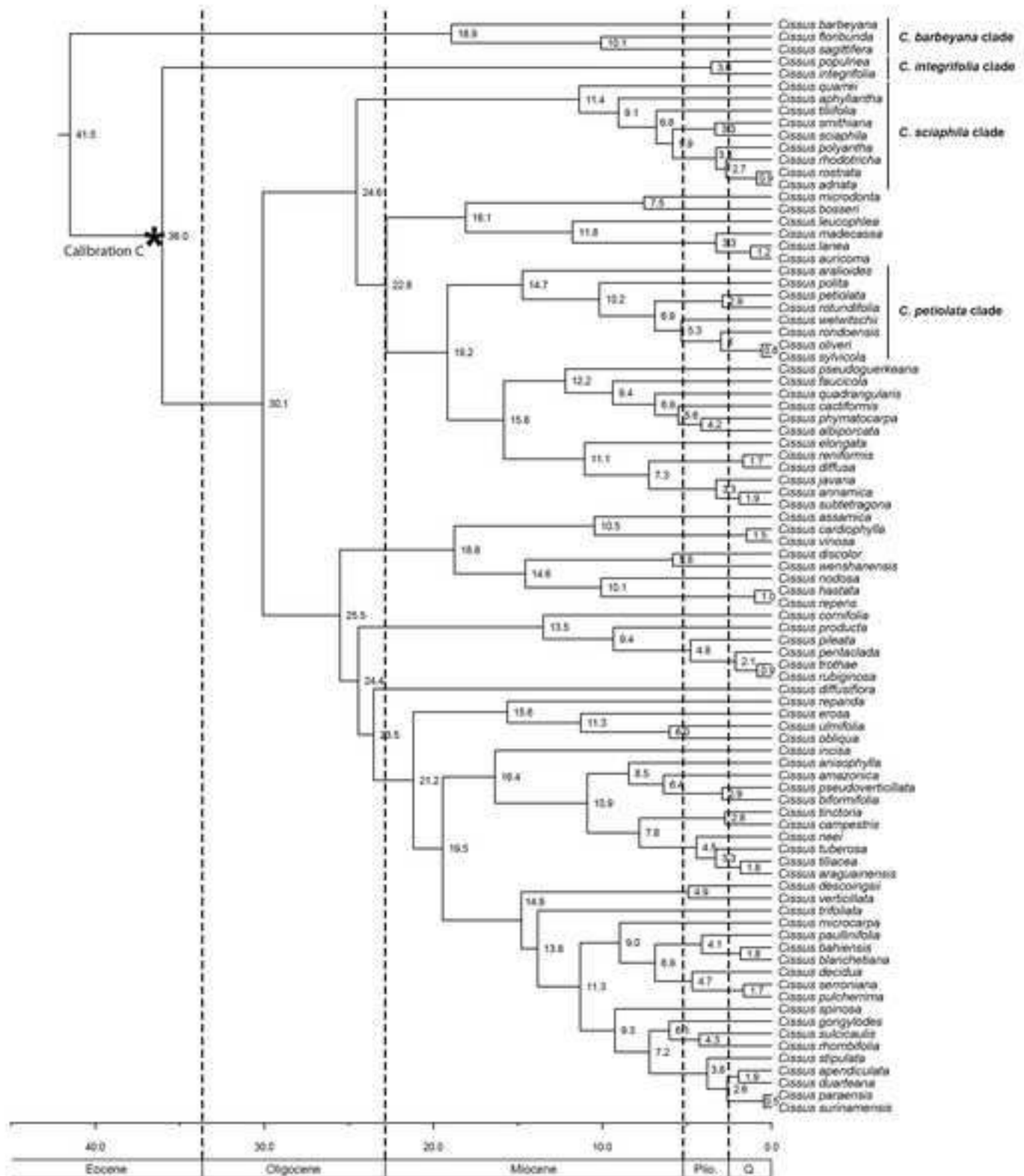
		rainforest					
	Climber (to 60 feet)	Near a stream in primary forest	Borneo, Malaysia	J.A.R. Anderson and Ilias bin Paie (S.28316)	L (L 0672373)	L.2333836	http://medialib.naturalis.nl/file/id/L.2333836/format/large
	Climber (6 m)	Primary riverine forest	Borneo, Indonesia	J.P. Mogeia and W.J.J.O. de Wilde (3766)	L (L 0672370)	L.2333840	http://medialib.naturalis.nl/file/id/L.2333840/format/large
	Climber	Undulating disturbed forest	Borneo, Malaysia	Maidil Amin & Matin Amin (69988)	L (L 0672386)	L.2333824	http://medialib.naturalis.nl/file/id/L.2333824/format/large
	Climber	Riverine forest	Moluccas, Indonesia	M.M.J. van Balgooy (4676)	L (L 0745289)	L.2333800	http://medialib.naturalis.nl/file/id/L.2333800/format/large
	Climber (2m high)	Mixed dipterocarp forest	Borneo, Malaysia	H. Othman, Rantai & Jugal (S.56497)	L (L 0761832)	L.4254181	http://medialib.naturalis.nl/file/id/L.4254181/format/large
	Climber	Riverside of fast flowing river with steep banks, almost precipitous in places, in primary forest	Borneo, Malaysia	J.A.R. Anderson & Ilias bin Paie (S.28876)	L (L 0672374)	L.2333835	http://medialib.naturalis.nl/file/id/L.2333835/format/large
	Climber (ca. 5m long)	Forest hillsides	Borneo, Malaysia	T. Sawan (125281)	L (L 0762871)	L.4254355	http://medialib.naturalis.nl/file/id/L.4254355/format/large
	Climber	Lowland dipterocarp primary rain forest	Negeri Sembilan, Malaysia	Eric Gardette (E.G 2255)	L (L 0762759)	L.4254438	http://medialib.naturalis.nl/file/id/L.4254438/format/large
<i>Cissus sagittifera</i> Desc.	(Unknown)	Cracks and fissures in quartzite	Fianarantsoa, Madagascar	H. Perrier de la Bâthie (12540)	P (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/177505
	Climbing liana	Woodland edge	Mahajanga, Madagascar	H. Perrier de la Bâthie (1371)	P (Unknown)	(Unknown)	http://www.tropicos.org/Specimen/177497
	(Unknown)	Limestone cliff	Madagascar	Bernard M. Descoings (2445)	P (P00061317)	P00061317	http://plants.jstor.org/stable/10.5555/al.ap.specimen.p00061317
	(Unknown)	Base of a limestone cliff	Toliara, Madagascar	Bernard M. Descoings (2443)	MO (MO-163554)	2211717	http://www.tropicos.org/Specimen/1354431

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Appendix S6. Definitions of lateral, ventral, dorsal, basal, apical views and the dorsiventral dimension, height and width of the seeds used in the systematic descriptions of the fossils.

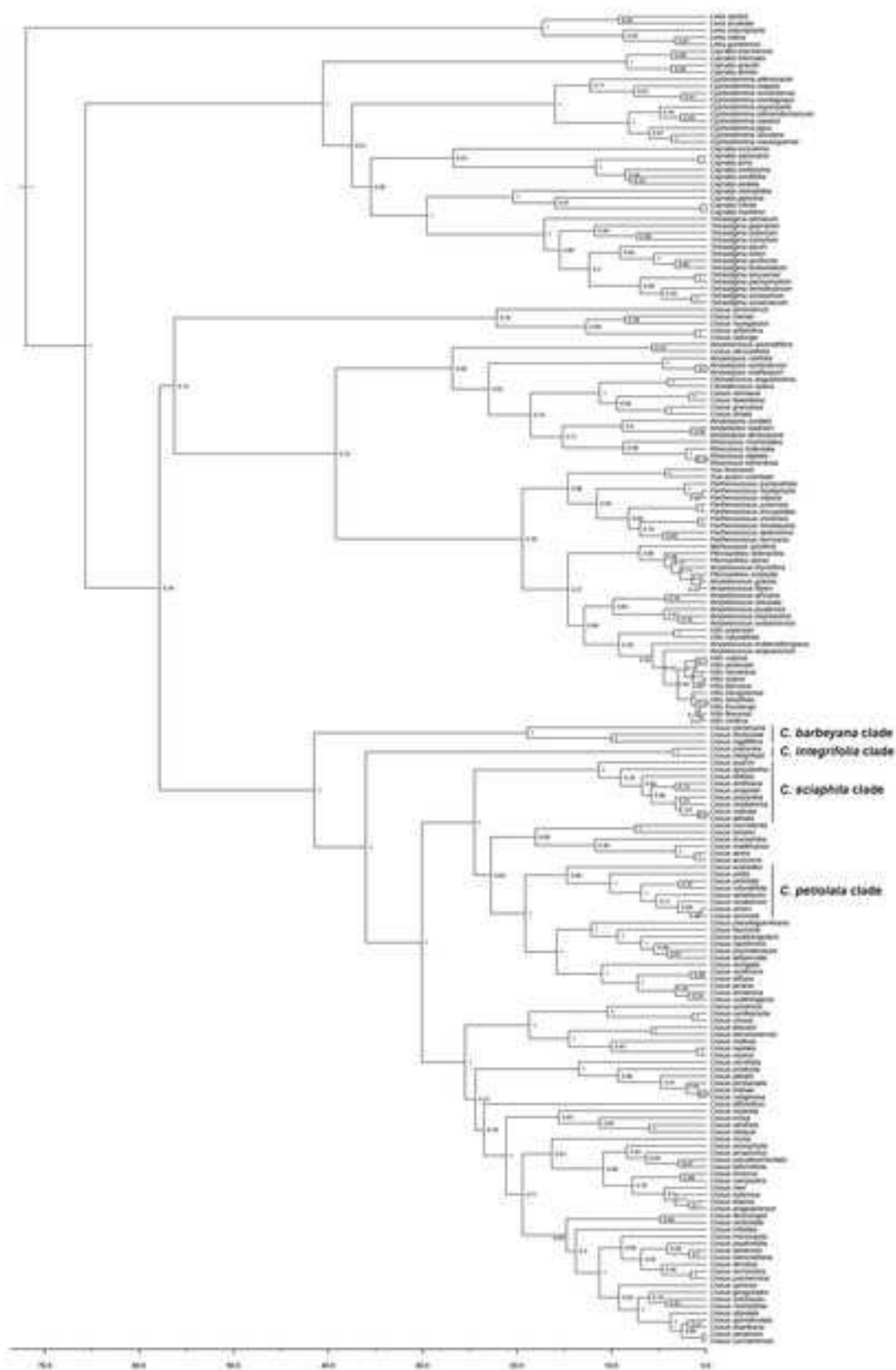


Appendix S9. Chronogram of the core *Cissus* clade obtained using the Bayesian approach implemented in the software BEAST with the fossil *Cissus* from the Oligocene Belen flora used as a calibration point (indicated by asterisk; see text for details). Ages in millions of years (Ma) are indicated on the nodes. Scale is in millions of years.



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Appendix S10. Maximum credibility tree obtained for the Vitaceae family from the Bayesian analysis as implemented in the software BEAST. Posterior probability values are indicated at the nodes. Scale is in millions of years.



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Appendix S11. Chronogram obtained using the Bayesian approach implemented in the software BEAST and three Vitaceae fossils as calibration points. Bars on nodes are the 95% highest posterior probability intervals on the age estimates. Scale is in millions of years.

