

On the nomenclature of fossil *Aspleniopteris*, *Carpinocarpus*, *Comptonia*, *Comptoniophyllum* and *Dryandrophyllum* (Myricaceae)

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ABSTRACT. *Comptonia comptoniifolia* (Brongn.) Doweld, comb. nov., based on the recently rediscovered *Phyllites comptoniifolius* Brongn., is reinstated based upon priority as the earliest validly published species name in place of the previously incorrectly used *C. acutiloba* Brongn. and *C. difformis* (Sternb.) E.W. Berry (*Aspleniopteris difformis* Sternb.; *Asplenium difforme* Sternb. non R. Br.). *Comptonia japonica* Krysht. is shown to be the earliest validly published name instead of the previously widely accepted *Comptoniophyllum naumannii* Nath. A new genus, *Paracomptonia* gen. nov., is proposed instead of the previously invalidly published *Dryandrophyllum* Velen., being based on the formerly segregated *Comptonia* subg. *Avushia* Zhilin, with transference of two Cretaceous *Dryandra* species, *D. cretacea*, and *D. yakovlevii*, and one Palaeogene species, *D. schrankii*, into *Paracomptonia*. The aberrant fossil species of Western Siberian *Comptonia*, based on fruit endocarps with a superficial resemblance to the extant genus, are reclassified and transferred into the recircumscribed and amplified distinct fossil genus *Carpinocarpus*, which is reinstated as a validly published genus instead of the anomalous *Comptonia* section †*Comptoniella* P.I. Dorof.: *Carpinocarpus debilis* (V.P. Nikit.) Doweld, comb. nov., *C. dorofeevii* (V.P. Nikit.) Doweld, comb. nov., *C. gorbunovii* (P.I. Dorof.) Doweld, comb. nov., and *C. tymensis* (P.I. Dorof.) Doweld, comb. nov. *Comptonia japonica* is neotypified; *Paracomptonia cretacea* (Velen.) Doweld comb. nov., *P. yakovlevii* (Palib.) Doweld, comb. nov. and *P. schrankii* (Sternb.) Doweld, comb. nov. are lectotypified for the first time.

KEYWORDS: botanical nomenclature, palaeocarpology, Cretaceous, Oligocene, Europe, Caucasus, Japan, western Siberia, Myricales

The ongoing editorial work for the *International Fossil Plant Names Index* (IFPNI, 2014–onwards), a global registry of fossil plant names from 1820, compiled with the aim of listing all fossil plant species (Doweld 2015, 2016), has several difficult, still-unresolved cases in the nomenclature of fossil and extant plants. The emphasis of the current study has been on problematic cases of the nomenclature of fossil species of *Comptonia* L'Héritier (in Aiton 1789: 334) and the related fossil forms *Carpinocarpus* P.A. Nikitin (1948: 1103, 1106; 1966: 69), *Comptoniophyllum* Nathorst (1888: 8) and *Dryandrophyllum* Velenovský (1889: 50, 53) (Myricaceae).

New fossil plant names and nomenclatural adjustments (including lecto- and neotypifi-

cations) were registered in a pilot registration version adopted at the XIX International Botanical Congress in Shenzhen in 2017 (Barkworth et al. 2016a–b, Turland et al. 2017) in the International Fossil Plant Names Index (IFPNI 2014–onwards) with unique permanent registration barcodes (LSIDs, Life Science Identifiers).

I. *Comptonia comptoniifolia* vs. *C. acutiloba* and *C. difformis* (*Aspleniopteris difformis* ≡ *Asplenium difforme* Sternb. non R. Br.)

Two fossil species names, *Comptonia acutiloba* Brongniart (1828) and *Comptonia difformis* (Sternberg) Berry (1906), have been widely used in systematic palaeobotany and

palaeofloristics for the distinctive myricaceous Tertiary foliage (Kotlaba 1961, Kvaček 2004). Initially these fossil angiosperm leaves were erroneously described as fern leaf remains and named *Asplenium difforme* Sternberg (1821). Vassiljev and Zhilin (1968) were the first to point out that *Asplenium difforme* Sternberg (1821) is a later homonym of *Asplenium difforme* R. Brown (1810). At that time they concluded that *Comptonia acutiloba* Brongniart (1828) should instead be considered the first legitimate name for the fossil (treated as a replacement name, nomen novum, McNeill et al. 2012 (later ICN), Art. 58.1). However, Kvaček and Straková (1997) pointed out that *Aspleniopteris difformis* Sternberg (1825) has priority and therefore should be used in place of *Comptonia acutiloba* Brongniart (1828). Though *Aspleniopteris difformis* was originally published as a new combination, nevertheless it must be accepted as the nomen novum based on the former illegitimate name (ICN, Art. 58.1) (Kvaček 2004, Teodoridis et al. 2017).

In the course of an analysis of early palaeobotanical publications for the IFPNI, a nearly overlooked work of Brongniart (1823) was found, containing a summary of the fossil plant record from the lignites of Soissons (France). In this work he proposed a new replacement name for *Asplenium difforme* Sternberg (1821), *Phyllites comptoniifolius* Brongniart (1823: 359), which has priority and should be used as the earliest known validly published species epithet in place of the earlier incorrectly used *C. acutiloba* Brongn. and *C. difformis* (Sternb.) E.W. Berry. A new combination is therefore validated below:

Comptonia comptoniifolia (Brongniart)
Doweld, **comb. nov.**

IFPNI: DC8B1F65-4141-4AE2-A4AC-B9B34F-52DB8B.

Basionym. *Phyllites comptoniifolius* Brongniart, p. 359. 21–28 Jun 1823 ('*comptoniae-folia*').

Synonymy.

- 1821 *Asplenium difforme* Sternberg, pp. 29, 33, pl. 24, fig. 1 ('*diforme*'), nom. illeg. non *Asplenium difforme* Brown, p. 151. 1810 (ICN Art. 53.1).
1825 *Aspleniopteris difformis* Sternberg, p. xxi, nom. superfl. & illeg.

- 1828a *Comptonia acutiloba* Brongniart, p. 141, nom. superfl. & illeg.
1838 *Zamites difformis* (Sternberg) Presl in Sternberg, p. 198, nom. superfl. & illeg.
1844 *Pterophyllum difforme* (Sternberg) Göppert, p. 137, nom. superfl. & illeg.
1851 *Dryandra acutiloba* (Brongniart) Ettingshausen, p. 735, pl. 33, nom. superfl. & illeg.
1872 *Myrica acutiloba* (Brongniart) Schimper, p. 560, nom. superfl. & illeg.
1906 *Comptonia difformis* (Sternberg) Berry, p. 495, nom. superfl. & illeg.
1927 *Myrica difformis* (Sternberg) Chaney, p. 103, nom. superfl. & illeg.

Type. [fossil leaves] Chomutov, Most, Horní Litvínov, Czech Republic [formerly Komotau, Brüx, Oberleitenau, Bohemia, Austria-Hungary] (holotype, G 2113, Národní Museum, Prague, Czech Republic).

Occurrence. Miocene; Europe.

II. *Comptonia naumannii* as a synonym of *Comptonia japonica*

Recently *Comptonia naumannii* was restudied in detail (Liang et al. 2010). However, the existing name for this leaf fossil is nomenclaturally confused and should be clarified. Nathorst (1888: 8) created a distinct genus, *Comptoniphyllum* Nath., with two described fossil species, *C. naumannii* Nathorst (1888: 8) and *C. japonicum* Nathorst (1888: 13). Since no separate generic diagnosis or description was provided, nor the generic name, neither of the two fossil species (ICN, Art. 35.1) were validly published. This was not realized by later researchers (Florin 1920, Kryshtofovich 1927, 1938, Endo & Morita 1932), who, hypnotized by Nathorst's authority, never questioned the validity of his generic name and its two fossil species. Even Florin (1920) did not recognize Nathorst's fossil species, subsuming them into the synonymy of the previously validly published *Comptonia dryandroides* Unger (= *Comptoniphyllum naumannii* Nath.) and *C. gaudinii* (Heer) Berry (= *C. japonicum* Nath.). Therefore, Nathorst's taxa should have been validated by later researchers who could recognize their distinctness from the previously described *Comptonia*-like fossil forms.

In a preliminary report on the Miocene flora of Kannonzawa in the then-named Echigo (now Niigata) Prefecture of Japan, Kryshtofovich (1920: 19) replaced *Comptoniphyllum*

japonicum Nath. by a new binomial, *Comptonia japonica* Krysht. Overlooking the invalid status of Nathorst's taxa, he did not publish a new combination but rather a replacement name. The requirements of ICN, Art. 41.3, were fulfilled by writing '*Comptonia japonica* Nath.', which is regarded as an indirect reference to the replaced invalid name (basionym), *Comptoniphyllum japonicum* Nath. (1888: 13) (cf. ICN, Art. 41.3, Ex. 3). Later, Kryshtovich (1927: 8) reverted to Nathorst's name, '*C. japonicum* Nathorst'. This, however, could not be taken as a combination based on the validated fossil species name *Comptonia japonica* Krysht. (1920), since no separate generic description was published in his 1927 work.

Comptonia naumannii Kryshtovich (in Kanehara 1926: 54) was also proposed in place of the earlier invalidly published *C. naumannii* Nathorst (1888: 8) by permissible indirect reference as originally writing '*Comptonia naumannii* Nath.', which is regarded as an indirect reference to the invalid basionym *Comptoniphyllum japonicum* Nath. (1888: 8) (cf. ICN, Art. 41.3, Ex. 3).

The generic name *Comptoniphyllum* was inadvertently validated by Japanese authors Endo and Morita (1932: 43) in providing a brief descriptive element for the generic name: "for such fossil *Comptonia*-like leaves until a clear proof is brought forth on some other evidences of that the Tertiary leaves belong to the plants really congeneric with the living species of *Comptonia*". Being unaware of Kryshtovich's replacement names, they continued to accept Nathorst's names as valid. As such, their '*Comptoniphyllum naumannii*' should be regarded as a new combination on the previously validly published *Comptonia naumannii* Kryshtovich (in Kanehara 1926: 54). But since they included the previously validated *C. japonica* Krysht. (1920) in the synonymy of *C. naumannii*, the validated name *C. naumannii* (Krysht.) Nathorst ex Endo & Morita was therefore nomenclaturally superfluous. However, most authors followed Endo and Morita's treatment and incorrectly regarded the species epithet '*japonica*' as a synonym of *C. naumannii* (Endo 1963, Matsuo 1965, Liang et al. 2010). This nomenclatural confusion should be rectified by the use of *Comptonia japonica* Kryshtovich (1920: 19) instead of *C. naumannii* as the earliest available valid fossil species epithet:

Comptonia japonica Kryshtovich,
p. 19. 1920.

Replaced name. 1888 *Comptoniphyllum japonicum* Nathorst, p. 13, pl. 4, figs 2, 3, nom. inval.

Synonymy.

- 1888 *Comptoniphyllum naumannii* Nathorst, p. 8, pl. 2, fig. 2, nom. inval.
 1926 *Comptonia naumannii* Kryshtovich in Kanehara, p. 54 ('*naumannii*') [replaced name for *Comptoniphyllum naumannii* Nathorst 1888].
 1927 *Comptoniphyllum japonicum* Nathorst ex Kryshtovich, p. 8, nom. inval.
 1932 *Comptoniphyllum naumannii* Nathorst ex Endo & Morita, p. 43 (3), pl. 5(1), figs 3–16, nom. superfl. & illeg.
 1961 *Comptonia naumannii* (Nathorst) Huzioka, p. 65, nom. superfl. [isonym].
 1955 *Myrica naumannii* (Nathorst ex Endo & Morita) Tanai, p. 5, nom. inval. [ICN Art. 41.5, lacking basionym] ('*Naumannii*').
 1961 (15 March) *Myrica naumannii* (Nathorst ex Endo & Morita) Suzuki, p. 28, nom. superfl.
 1961 (20 March) *Myrica (Comptonia) naumannii* (Nathorst ex Endo & Morita) Tanai, p. 271, nom. inval. [ICN Art. 36.2, alt. names] & superfl.

Type. [fossil leaves] Ejiri, Kitago-mura, Igu-gun, Iwaki Prefecture, Japan (neotype, designated here, # 7009, Tohoku University Museum, Sendai, Japan; illustrated by Endo & Morita 1932: pl. 5, fig. 14 [as *Comptoniphyllum naumannii*]).

Stratigraphy. Early–Middle Miocene (Ejiri Formation).

Occurrence. Early–Middle Miocene; Eurasia (Japanese Archipelago, Korean peninsula, China, Russian Far East (incl. Sakhalin Island)).

III. *Dryandrophyllum*, Upper Cretaceous *Comptonia* and allied forms

Velenovský (1889: 50, 53) created a new generic name, *Dryandrophyllum*, for peculiar fossil leaves from the Upper Cretaceous (Cenomanian) sediments of former Bohemia (Austria-Hungary, now Czech Republic). Since he did not provide a separate generic description or diagnosis for the new generic designation, both the generic and the species names (*Dryandrophyllum cretaceum* (Velenovský) Velenovský 1889: 50, 53) were not validly published. They were used in regional geological and palaeontological treatises (Katzner 1892:

1273, 1279, Frič & Bayer 1901: 42) but were not validated in any of them.

Knobloch (1999: 42, 48) acknowledged that monotypic *Dryandrophyllum* was not validly published, but noted that the fossil leaves known originally as *Dryandra cretacea* Velenovský (1883: 26) have nothing in common with the proteaceous genus *Dryandra* Brown (1810: 211). In consequence, Knobloch transferred the fossil species into the formal fossil genus (alternatively termed morphogenus) *Dicotylophyllum* Saporta (1892: 147) pending further study. However, the species from the Czech Republic reveals similarity to the Transcaucasian fossil leaf species *Dryandra yakovlevii* Palibin (1930: 908) in leaf venation and shape, which was also found in coeval Upper Cretaceous (Cenomanian) sediments of the Lesser Caucasus. Takhtajan (1966: 1222) and later Zhilin (1980: 18) treated these leaf fossils as belonging to the myricaceous genus *Comptonia* L'Héritier. However, the fossil taxon is distinct from the extant *Comptonia* in having narrow leaves and in the form and number of leaf lobes, so a distinct subgenus of *Comptonia*, *Comptonia* subg. *Avushia* Zhilin (1980: 18) was created. The Palaeogene fossil species *C. dryandrifolia* Brongniart (1828b: 49) [junior synonym of *D. schrankii* (Sternberg) Heer (1853a: 142, 1853b: 296)] was also placed in subg. *Avushia* on account of similar leaf morphology and venation (see Heer 1870: 326). The subgeneric rank accorded *Avushia* is undoubtedly an undervaluation; the distinctiveness of these fossils (combination of leaf morphology and venation) points to the need to segregate these fossils from the extant *Comptonia* into its own fossil genus which probably originated earlier than subg. *Comptonia* but was a completely extinct Cretaceous–Palaeogene branch of the comptonioid leaf fossil forms (cf. Zhilin 1980). A new generic name, *Paracomptonia* gen. nov., is proposed instead of the invalid *Dryandrophyllum* and is based on *Comptonia* subg. *Avushia* with transference of two Cretaceous *Dryandra* species, *D. cretacea* and *D. yakovlevii*, and one Palaeogene species, *D. schrankii*:

***Paracomptonia* Doweld, gen. nov.**

IFPNI: 50FE6CAB-FCB1-4781-8170-83A1F-5B7ED2F.

Diagnosis. Leaves narrow (2–8 mm in middle part), long (up to 20 cm and more), with many lobes (up to 50). Lobes entire or dentate,

mainly triangular to irregular, with acute, sometimes rounded apex. Midvein thick, lateral veinlets 2–3 per lobe.

Synonymy.

1889 *Dryandrophyllum* Velenovský, p. 50, 53, nom. nud.

1980 *Comptonia* subg. *Avushia* Zhilin, p. 18. – Type: *Comptonia yakovlevii* (Palibin) Takhtajan, p. 1222. 1966.

Type. *Paracomptonia yakovlevii* (Palib.) Doweld.

***Paracomptonia cretacea* (Velenovský)
Doweld, comb. nov.**

Basionym. *Dryandra cretacea* Velenovský, p. 26, 1883.

IFPNI: 902094A3-DF90-463E-8C8F-6280D7B3A19D.

Synonymy.

1889 *Dryandrophyllum cretaceum* (Velen.) Velenovský, p. 50, 53, nom. inval. (ICN, Art. 35.1).

1999 *Dicotylophyllum cretaceum* (Velen.) Knobloch, p. 42, 48.

Type. [fossil leaves] CZECH REPUBLIC. Malá Chuchle, Praha [formerly Kuchelbad, Bohemia, Austria-Hungary] (lectotype, designated here, F 761, Národní Museum, Praha, Czech Republic [figured by Velenovský 1883: pl. 1: fig. 5]).

Stratigraphy. Upper Cretaceous (Cenomanian).

***Paracomptonia yakovlevii*
(Palibin) Doweld, comb. nov.**

Basionym. *Dryandra yakovlevii* Palibin, p. 908. 1930.

IFPNI: E02200EF-B1B2-4EA1-BD9F-51CA94C70F2A.

Synonymy.

1966 *Comptonia yakovlevii* (Palib.) Takhtajan, p. 1222.

Type. [fossil leaves] AZERBAIJAN. Naxçıvan Muxtar Respublikası. Avuş (= Aush, = Chavush) village, Aiotdzorskii (formerly Daralagez) range, Southern Armenian highland, Lesser Caucasus (lectotype designated here, CNIGRMuseum 20/3002, Central Scientific-Research Geological Exploration Museum after S. N. Chernyshev (CNIGRMuseum),

S.-Petersburg, Russian Federation [figured by Palibin 1930: pl. 1: figs 5, 6]).

Stratigraphy. Upper Cretaceous (Cenomanian).

Note. The typification of the fossil species by Zhilin (1980: 18), who erroneously designated specimen 37/3002 as a 'lectotype', is rejected, since this specimen was not illustrated or mentioned in the original protologue (ICN, Art. 9.3). A new lectotype is designated from Palibin's two illustrated specimens (19/3002, 20/3002).

Paracomptonia schrankii (Sternberg)
Doweld, **comb. nov.**

Basionym. *Aspleniopteris schrankii* Sternberg, p. xxii, 1825.

IFPNI: D465F12B-A66E-48E0-8F54-0FAD76B7324F.

Synonymy.

- 1853 *Dryandra schrankii* (Sternberg) Heer, p. 142.
1899 *Myrica schrankii* (Sternberg) Boulay, p. 90 [36].
1906 *Comptonia schrankii* (Sternberg) Berry, p. 514.
1851 *Dryandra brongniartii* Ettingshausen, p. 734 ('*Brongniarti*'), nom. superfl. & illeg.
1878 *Myrica brongniartii* (Ettingshausen) Lesquereux, p. 135 ('*Brongniarti*'), nom. superfl. & illeg.

Type. [fossil leaves] AUSTRIA: Bad Häring, Tyrol (neotype designated here, 1853/001/0072/17, Geologische Bundesanstalt, Vienna, Austria [figured by Ettingshausen 1853: pl. 19: fig. 17]).

Stratigraphy. Lower Oligocene (Rupelian).

- 1828b *Comptonia dryandriifolia* Brongniart, p. 49 ('*dryandraefolia*').
1847 *Comptonites dryandriifolius* (Brongniart) Göppert in Bronn, p. 322 ('*dryandraefolius*').

Type. FRANCE: Armissan, Aude (holotype, MNHN.F.2990, Muséum National d'histoire naturelle, Paris, France [figured by Brongniart 1828b: pl. 3: fig. 7]).

Stratigraphy. Lower Oligocene (Rupelian).

Note. The original fossils of *Aspleniopteris schrankii* Sternberg are missing (Rüffle 1976: 343, Kvaček & Straková 1997: 137); hence, a neotype is designated from Ettingshausen's illustrated specimens (1853: pl. 19: fig. 17 [specimen #1853/001/0072/17 in Geologische Bundesanstalt, Vienna, Austria]) from Bad Häring, Tyrol, Austria.

IV. Siberian fossil fruits, *Carpinicarpus*,
Comptonia sect. *Comptoniella*
and *C.* sect. *Palaeocomptonia*

The monotypic *Carpinicarpus* P.A. Nikitin, *C. longistylus* P.A. Nikitin (1948: 1103, 1106), was first identified and mentioned in the checklist of fossil plants of the Tertiary floras of Western Siberia, with no description or illustrations. After Nikitin's death in 1950, his manuscripts with descriptions and illustrations of plant fossils were not published for a long time, although they were widely known as typescript copies. Nikitin (inedit., 1948) referred these fossil fruits to the new form genus *Carpinicarpus* on account of their similarity to the fruits of *Carpinus cordata* Blume. After restudy of similar fossil fruit endocarps, Dorofeev proposed the replacement name *Myrica longistyla* P.I. Dorofeev (1955: 1207), nom. inval. [as intended combination '*Myrica longistyla* (Nikitin) m.'] for invalid *C. longistylus* P.A. Nikitin, but he did not provide the necessary descriptions and illustrations to produce a valid species name. Later these fossils were formally described under a new name, '*Comptonia longistyla*' P.I. Dorofeev (1966: 911), nom. inval., but again it was invalidly published due to the lack of a holotype designation (Art. 40.1). The fossil taxon '*Comptonia longistyla*' was validated later as *Comptonia longistyla* (P.A. Nikitin) P.I. Dorofeev (1994: 34).

In a posthumously published monograph, Nikitin (1966: 69) supplied the necessary description and illustrations to validate his monotypic *Carpinicarpus* P.A. Nikitin, *C. longistylus* P.A. Nikitin (l.c.). He acknowledged that these fossils are distantly related to extant representatives of *Carpinus* and *Ostrya*, and that they in fact represented an extinct lineage of *Carpinus*-related plants on account of their supposed similarity to the fruit of *Carpinus cordata* Blume. In contrast, Dorofeev (1966) related them to the extant genus *Myrica* Linnaeus s.l. (1753: 1104), and *Comptonia* in particular, when the genus became widely recognized in plant taxonomy as an entity separate from *Myrica* (Dorofeev 1994). However, he noted that the fossil endocarps from Siberia are significantly different from the extant fruits of *Comptonia* and some related fossil endocarps (*C. crassa* P.I. Dorof., *C. jacutica* P.I. Dorof., *C. peregrinoides* P.I. Dorof.). Their massive, distinctly stalked endocarps, with depressed

sides and numerous crested ribs having acicular attenuate apices, preclude affiliation with the fruits of extant *Comptonia* and allied fossil species based on fruit remains. Even relationships with Myricaceae are very doubtful. Therefore, the Oligocene endemic fossil species from Western Siberia should be better considered as a genus of its own.

These fossil taxa, based mostly on Siberian endocarps, were recently classified as separate sections of *Comptonia* (sect. *Comptoniella* P.I. Dorof. and sect. *Palaeocomptonia* P.I. Dorof.), with an exceptional remark that sect. *Comptoniella* probably deserves generic rank (Dorofeev, 1994). If, due to their very distinctive fruit endocarps, these fossils are to be segregated into a separate fossil genus, the generic name *Carpinocarpus* should be adopted. The confused nomenclature of *Carpinocarpus*, sometimes treated as not validly published (Dorofeev 1994), is summarized and clarified below as follows.

Carpinocarpus P.A. Nikitin ex P.I. Dorofeev (1963: 278), nom. inval., was proposed as a monotypic fossil genus, *C. longistylus* P.A. Nikitin ex P.I. Dorof., nom. inval., based on fruit remains from Miocene sediments of Kireevskoe village, Ob' river, Tomsk region, Russian Federation (Western Siberia), but not validly published, since Dorofeev failed to designate a holotype for the fossil species. Later, *Carpinocarpus* P.A. Nikitin (1966: 68) was validated in his posthumously published monograph *Aquitanean flora of Lagerny Sad (Tomsk)*. However, Dorofeev (1994) questioned the validity of Nikitin's name, and 'validated' '*Comptonia longistyla* P.I. Dorofeev sp. nov.' (1994: 34) on the basis of the type of *C. longistylus* P.A. Nikitin (1966: 69). In 1966, Nikitin fulfilled all the requirements of the International Code of Botanical Nomenclature and provided a description (in Russian), illustrations and a type designation as 'Holotype. Specimen from the sediment of Lagerny Sad (Lag. II)' [translated]. Nikitin did not specify the holotype among several figured specimens (pl. 9, figs 8–12); this is permissible and did not infringe the provisions of the previous and modern versions of the Codes. The obligatory specification of the holotype among figured specimens became effective from 1 January 2001 (ICN, Art. 43.3). Thus, Dorofeev (1994) in fact designated the lectotype from the specimens of Nikitin (1966); his '*Comptonia longistyla* P.I. Dorofeev sp. nov.' (1994: 34) should be

technically treated as a new combination based on the previously validly published basionym, *C. longistylus* P.A. Nikitin (1966: 69).

Since the fruit endocarps of the fossil species *Comptonia gorbunovii* P.I. Dorofeev (1994: 36) serving as the type of *Comptonia* sect. *Comptoniella* P.I. Dorof. (1994) do not show any resemblance to the fruit endocarps of putatively suggested (but not proven) *Comptonia*, although they do have a full range of intermediate forms with *C. longistylus*, section *Comptoniella* (Nikitin 2007: 71–72) is not recognized as a distinct taxonomic entity and is placed in the synonymy of *Carpinocarpus*. The fossil genus is amplified and recircumscribed below by inclusion of the aberrant fossil species of *Comptonia*, based on distinctive fruit endocarps from Western Siberia: *Comptonia debilis* V.P. Nikitin (1976), *C. gorbunovii* P.I. Dorofeev (1966, 1994), *C. tymensis* P.I. Dorofeev (1994) and *C. dorofeevii* V.P. Nikitin (2007):

Genus *Carpinocarpus* P.A. Nikitin (1966: 68) emend. Doweld, **emend. nov.**

IFPNI: DF276863-29A2-4E21-80DB-30A0305F1F38.

Synonymy.

1994 *Comptonia* section †*Comptoniella* Dorofeev, p. 31.

1994 *Comptonia* section †*Palaeocomptonia* Dorofeev, p. 31, excl. typo, p.p.

Diagnosis. Infructescences racemiform, ellipsoidal, with heterocarpic fruits. Fruit (endocarps) large, massive, 3.3–6.7 × 1.75–3.75 mm, ellipsoidal, elongate and short, nearly rounded, short-stalked. Wingless. Apex obtuse wedge-shaped to acute, sometimes attenuate, column short. Sides depressed, turned over, interrupted at apex; face acute, rarely obtuse. Ribs numerous (5–12), entire and interrupted at apex, crests acute, smooth to toothed, in upper part with distinct short crests or conical to obtuse tubercles. Fruit endocarp walls thick, cells of inner part elongate, in longitudinal series.

Type. *C. longistylus* P. A. Nikitin.

Carpinocarpus debilis
(V.P. Nikitin) Doweld, **comb. nov.**

Basionym. *Comptonia debilis* V.P. Nikitin, p. 175, pl. 66, figs 6–9. 1976.

IFPNI: 52AB7706-15D9-4711-B589-BC5B-11CA70C0.

Type. [fossil fruits (endocarps)] RUSSIAN FEDERATION. Tomsk region, Belyj Jar, Kompasskij Bor, right bank of Tym river below Pyl'-Karamo, V.P. Nikitin Coll. (holotype, TB-4, Komarov Botanical Institute, Russian Academy of Sciences, S.-Petersburg, Russian Federation) [figured by Dorofeev 1994: pl. 72, fig. 1a].

Stratigraphy. Upper Oligocene (Chattian).

Carpinicarpus dorofeevii (V.P. Nikitin)
Doweld, **comb. nov.**

Basionym. *Comptonia dorofeevii* V.P. Nikitin, p. 71, pl. 6, fig. 15. 2007.

IFPNI: 14D8B866-EDC6-4292-9D41-B0256F4116A5.

Type. [fossil fruits (endocarps)] RUSSIAN FEDERATION. Tomsk region, Kompasskij Bor, right bank of Tym river, V.P. Nikitin Coll. (holotype, Co-7/2. TB-4, Komarov Botanical Institute, Russian Academy of Sciences, S.-Petersburg, Russian Federation) [figured by Nikitin 2007: pl. 6, fig. 15].

Stratigraphy. Upper Oligocene (Chattian).

Carpinicarpus gorbunovii
(Dorofeev) Doweld, **comb. nov.**

Basionym. *Comptonia gorbunovii* Dorofeev, p. 36, pl. 76, figs 6, 7. 1994.

IFPNI: 7C4C20E0-80A1-4007-A014-71C6EE451E14.

Synonymy.

1966 *Comptonia gorbunovii* Dorofeev, p. 911, fig. 1: 25–27, nom. inval. (ICN, Art. 40.1).

Type. [fossil fruits (endocarps)] RUSSIAN FEDERATION. Tomsk region, Rezhenska village, Bol'shaja Kirgizka river (holotype, 2/6-K516, Komarov Botanical Institute, Russian Academy of Sciences, S.-Petersburg, Russian Federation).

Stratigraphy. Lower Oligocene (Rupelian).

Carpinicarpus longistylus P.A. Nikitin,
p. 69, pl. 9, figs 9–12, 1966,
emend. V.P. Nikitin, p. 71. 2007.

IFPNI: 6BA1B7E3-C8FD-4056-8C51-6A0FDE00E34F.

Synonymy.

1948 *Carpinicarpus longistylus* P.A. Nikitin, p. 1103, 1106, nom. nud.

1955 *Myrica longistyla* Dorofeev, p. 1207, nom. nud. (Art. 40.1).

1963 *Carpinicarpus longistylus* P.A. Nikitin ex Dorofeev, p. 278, nom. inval. (Art. 40.1).

1966 *Comptonia longistyla* (P.A. Nikitin) Dorofeev, p. 911, nom. inval. (Art. 41.5).

1976 *Comptonia longistyla* (P.A. Nikitin) Dorofeev ex V. P. Nikitin, p. 175, nom. inval. (Art. 41.5).

1994 *Comptonia longistyla* (P.A. Nikitin) Dorofeev, p. 34.

1994 *Comptonia thalictroides* Dorofeev, p. 34, pl. 71, figs 1–22.

Type. [fossil fruits (endocarps)] RUSSIAN FEDERATION. Tomsk region, Lagernyj Sad, P.A. Nikitin coll. (lectotype designated by Dorofeev (1994: 34), specimen 34/3, coll. Lag 59-3 # 150, Komarov Botanical Institute, Russian Academy of Sciences, S.-Petersburg, Russian Federation) – figured by Nikitin 1966: pl. 9, fig. 11.

Stratigraphy. Upper Oligocene (Chattian).

Carpinicarpus tymensis (Dorofeev) Doweld,
comb. nov.

Basionym. *Comptonia tymensis* Dorofeev, p. 36, pl. 70, figs 1–19. 1994.

IFPNI: ED6CF4E5-9872-4838-91A6-4C8792150DAB.

Synonymy.

1966 *Comptonia tymensis* Dorofeev, p. 911, fig. 1: 10–12, nom. inval. (ICN, Art. 40.1).

Type. [fossil fruits (endocarps)] RUSSIAN FEDERATION. Tomsk region, Belyj Jar, right bank of Tym river (holotype, 17/2–K519, Komarov Botanical Institute, Russian Academy of Sciences, S.-Petersburg, Russian Federation) [figured by Dorofeev 1994: pl. 70, fig. 2].

Stratigraphy. Upper Oligocene (Chattian).

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