



NAMING OF PARTS: THE USE OF FOSSIL-TAXA IN PALAEOBOTANY

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Abstract: Fossil plants are extinct plants whose remains (referred to as plant fossils) are found preserved in sedimentary deposits. Plant fossils are classified using fossil-taxa as defined in the International Code of Nomenclature. Fossil-taxa differ conceptually from taxa of living plants in that they often do not refer to whole organisms, but to the remains of one or more parts of the parent organism, in one or more preservational states. There can be complications when two parts of a plant are shown to be connected, or when two preservational states are correlated, and to avoid disrupting the wider palaeobotanical taxonomy it is often best to keep the fossil-taxa separate. Extinct fossil plants reconstructed by piecing together the plant fossils are best not given formal Linnean taxonomic names. There can also be problems using living plant taxa for fossils, even when there is a close morphological similarity of particular plant parts. Fossil-taxa for different plant parts can reflect different taxonomic ranks of the parent plants so care must be taken when using such taxa in floristic or phylogenetic studies. Because of taphonomic factors, a number of “artificial” fossil-taxa have proved useful, despite that they do not fully reflect the systematic positions of the parent plants.

Key words: palaeobotany, nomenclature, fossil-taxa

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Introduction

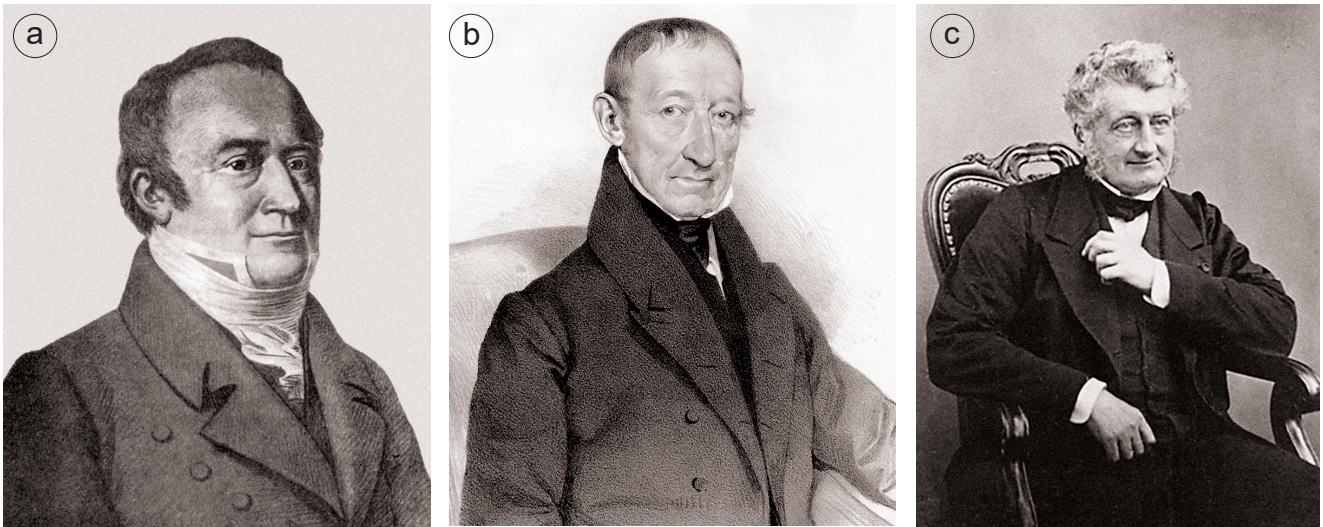
At the time of writing (2020) we are celebrating the bicentenary of the birth of scientific palaeobotany as represented by the publication of the pioneering works of Sternberg (1820), Schlotheim (1820) and shortly afterwards Brongniart (1822). Extracting data from plant fossils to better understand past vegetation is obviously a key aspect of the subject for which many technical advances have been made (for summaries see Jones and Rowe 1999, Cleal and Thomas 2019). Also of fundamental importance, however, is the taxonomy of the fossils as this is central to communicating the observed relationships of the things being studied; without such classifications the observations are merely isolated facts of little epistemological value. Being the remains of plants, palaeobotanists before the 1820s tended to classify the fossils in the same way as living plants, evidently thinking of them as conceptually little different from herbarium specimens (Stafleu 1967). However, with improved understanding of the various taphonomic processes responsible for changing plants into fossils, it became evident that this was oversimplistic and a different taxonomic approach was needed – this was one of major insights of Sternberg and Brongniart.

Although the essence of palaeobotanical taxonomy is still essentially as Sternberg and Brongniart proposed,

there have been changes in detailed approach, especially since the 1950s. There have been several discussions on the subject (e.g., Cleal 1986, Chaloner 1986, 1999, Thomas 1989, Bateman and Hilton 2009, Cleal and Thomas 2010a) but in our opinion there is still some confusion as to the ontological nature of palaeobotanical taxa and how they are used in practice. This paper will review the current position, especially following the changes that were introduced in the 2012 International Code of Nomenclature for Algae, Fungi, and Plants (hereafter referred to as the ICN – McNeill et al. 2012). We will restrict our discussion to the situation relating to plant and fungus macrofossils because palynological taxonomy and nomenclature have been recently reviewed by Gravendyck et al. (2021).

Historical background

The earliest palaeobotanical publications (e.g., Lhuyd 1699, Scheuchzer 1709, Parkinson 1804, Schlotheim 1804; see Andrews (1980) for an historical review) tended to avoid the problems of classifying plant fossils, either by not naming them or naming them as extant species. However, as Schlotheim (1820), Sternberg (1820) and Brongniart (1822) pointed out (Text-fig. 1) any comparison with extant



Text-fig. 1. The pioneers of scientific palaeobotany whose ideas laid the foundations of how we now name plant fossil-taxa. a: Ernst von Schlotheim (1764 – 1821); b: Kaspar Maria von Sternberg (1761 – 1837), reproduced by permission from J. Kvaček (National Museum, Prague); c: Adolphe Brongniart (1801 – 1876). Adapted from Cleal and Thomas (2019: fig. 2.1).

plants is of little value if it is not supported by reproductive structures.

Schlotheim (1820) introduced several generic names suggesting comparisons between certain fossils and extant plants, but without making definite statements as to the affinities of those fossils: for instance, *Palmacites* referred to remains of flabelliform leaves similar to those of the extant European fan-palms, and pinnate fern-like fronds were named *Filicites*. Schlotheim (1820) also established genera for plant remains whose affinities were totally ambiguous, such as *Carpolithes* for isolated seeds or ovules. Schlotheim (1820) unfortunately failed to validly publish these names (Kvaček 1982) but many were later validated by Brongniart (1822) within an improved classification for plant fossils (reviewed by Cleal and Thomas 2018). Importantly, Brongniart (1822) was explicit that his genera consisted of the remains of particular plant parts (e.g., leaves or seeds) and were not intended to represent whole organisms. The Brongniart (1822) classification was further expanded by Sternberg (1825) and Brongniart (1828a), and became the foundation of the palaeobotanical taxonomy still used today.

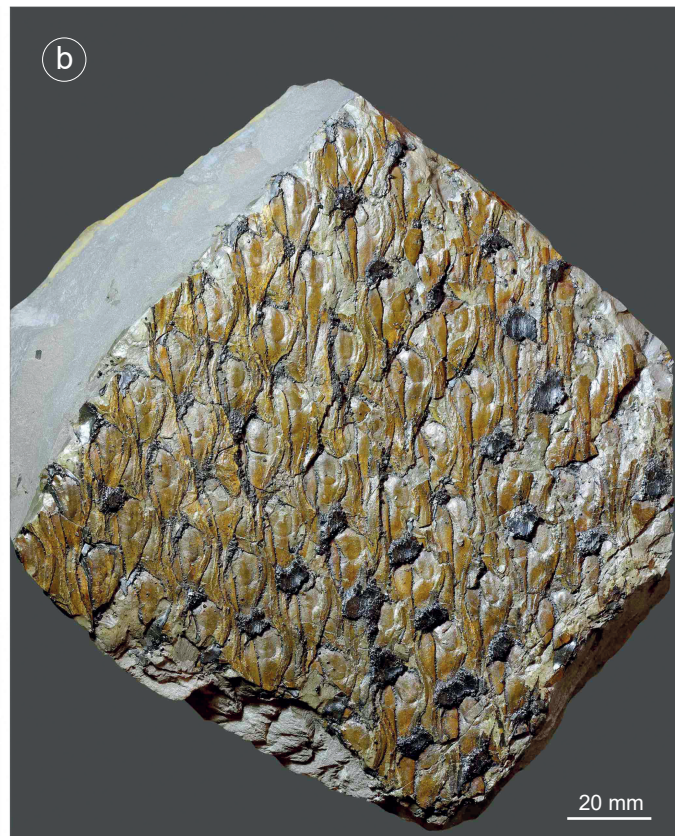
Although the resulting taxa of plant fossils were fundamentally different from the whole organism taxa used for living plants, the way that the two types of taxa were named was essentially the same. The early rules of botanical nomenclature (e.g., Candolle 1867, Briquet 1906) were intended to apply to taxa of plant fossils as well as of living plants, and included no special provisions to take into account the problems faced by palaeobotanists; few if any palaeobotanists seem to have been involved with the formulation of these rules. The situation started to change with proposals made by Thomas (1935) and Jongmans et al. (1935) who argued for the recognition of special types of taxa for use with plant fossils that were to be known as organ-genera and form-genera. A version of these proposals was eventually included in the first International Code of Botanical Nomenclature (Lanjouw et al. 1952; see comments by Malécot 2008) but there then followed a labyrinthine debate extending over half a century about exactly what

was meant by these terms (summarised by Bateman and Hilton 2009 and Cleal and Thomas 2010a); in successive editions of the Code their definitions were changed, organ-genera were removed, and a new concept of morphotaxa was introduced. The result was that many palaeobotanists ignored the concepts of organ-genera, form-genera and morphotaxa, and simply assigned fossils to what they thought were whole-plant genera and species; but this was overlooking the effect that taphonomy was having on the data that were available for classifying the fossils compared with that used with living plant.

To try to clear up this confusion, Cleal and Thomas (2010b) proposed changes to how plant fossil taxonomic nomenclature should operate and these have now been adopted in the ICN (Turland et al. 2018). Following the principle suggested by Chaloner et al. (1998) there are now special taxa at all ranks for classifying plant fossils. These are called fossil-taxa and have the following definition (ICN, Art. 1.2): “A taxon (diatom taxa excepted) the name of which is based on a fossil type is a fossil-taxon. A fossil-taxon comprises the remains of one or more parts of the parent organism, or one or more of their life-history stages, in one or more preservational states, as indicated in the original or any subsequent description or diagnosis of the taxon.” In essence, other than that its name must be based on a fossil specimen, a fossil-taxon can be whatever palaeobotanists decide it should be (just as a taxon of living plants can be whatever botanists decide). Some regret has been expressed as to the loss of organ-genera and form-genera (Bateman and Hilton 2009). In reality, however, these concepts are merely end-members of the continuous spectrum of taxonomic concepts now included within fossil-genera, and it is difficult to see what benefits are to be gained by a sharp demarcation between them.

What are we classifying?

Taxonomy can refer to the classification of anything (e.g., Olivares 2011) but is mostly used in the context of



Text-fig. 2. The distinction between fossil plants (a) and plant fossils (b). a: Reconstruction of a late Carboniferous arborescent lycopoid, often referred to as the *Lepidodendron*-tree; artwork by A. Townsend (formerly of National Museum Wales, Cardiff, UK; see Townsend et al. 1998); b: *Lepidodendron aculeatum* STERNB.; Middle Coal Measures Formation (Duckmantian – upper Bashkiran), Brymbo, near Wrexham, UK (see Thomas et al. 2020: fig. 16b); National Museum Wales specimen 2013.43G.88.

organismal classification. Although some of the philosophical underpinning of biological taxonomy remains contentious (Kendig and Witteveen 2020) most biologists still agree with Huxley (1942) that it should aim to classify organisms into a hierarchical system that reflects their phylogenetic (i.e., cladistic) relationships (Williams and Ebach 2020). However, this overlooks another important practical function of taxonomy – to facilitate the identification and naming of organisms. Plant identifications are still usually based on morphological and anatomical criteria, now supplemented by DNA barcoding (e.g., de Vere et al. 2015). Although morphological and anatomical similarities can reflect phylogenetic relationships, adaptive convergence and divergence mean this correlation is rarely perfect. Consequently, a distinction is often drawn between natural (phylogenetic) and artificial (morphological/anatomical) classifications, the latter sometimes being referred to as parataxonomies (e.g., Sylvester-Bradley 1958, Meyen 1987).

However, this demarcation between natural and artificial taxonomies is itself artificial. All taxonomies are artificial (i.e., man-made) constructs designed to interpret observed patterns in the natural or wider world. In palaeobotany, taxa are developed based on morphological, anatomical and/or histological characters observed in the fossils – these are, after all, the only empirical data available to the palaeobotanist. The choice and weighting of characters that are used to develop the taxonomies are subjective decisions,

but the aim is usually to emphasise those characters thought to reflect the natural relationships of the parent plants. This is important not only for phylogenetic studies; even when the fossils are being used for biostratigraphy, palaeoecology or palaeogeography, the taxonomy will be far more useful if it is reflecting the phylogenetic relationships of the plants in the parent vegetation. It is notable that in palynology, where strictly morphological taxonomies have been developed (e.g., Hughes and Moody-Stuart 1969, Hughes 1970), they have not been widely adopted. However, these natural relationships of the parent plants can never be verified empirically; we can hypothesise that a particular taxonomy is reflecting plant phylogeny by comparing character patterns such as by using parsimony or phenetic similarities, but it cannot be empirically proved. In our view, phylogenetic taxonomies are aspirations, but morphological/anatomical taxonomies are the realities.

To understand what palaeobotanists are dealing with in practice, it is important to differentiate between two quite different concepts (Text-fig. 2): **plant fossils**, which are the fossilised remains of plant fragments preserved in sedimentary deposits; and **fossil plants**, which were the now-extinct plants that produced the remains now preserved as fossils (note the change in tense of the verb used in the two definitions). Plant fossils are the tangible objects that are studied directly by palaeobotanists, who use a range of techniques to extract information about the morphology, anatomy and sometimes histology of the plant fragments

Table 1. Fossil taxa assigned to different plant parts for six representative plant groups in the late Carboniferous tropical coal swamps. Adapted from Cleal et al. (2021).

	Lycopids	Calamites	Sphenophylls	Marattialeans	Medullosaleans	Cordaites
Stems	<i>Lepidodendron</i>	<i>Calamites</i>	<i>Sphenophyllum</i>	<i>Caulopteris</i>	–	<i>Artisia</i>
Foliage	<i>Cyperites</i>	<i>Annularia</i>		<i>Alethopteris</i>	<i>Cordaites</i>	
Reproductive structures	Female <i>Lepidocarpon</i> <i>Lepidostrobophyllum</i>	<i>Calamostachys</i>	<i>Bowmanites</i>	<i>Cyathocarpus</i>	<i>Trigonocarpus</i>	<i>Cardiocarpus</i>
	Male <i>Lepidostrobus</i>					
Rooting structures	<i>Stigmara</i>	<i>Pinnularia</i>	–	–	–	–
Total fossil-genera	6	4	2	2	3	4

that formed the fossils. These data are then used to try to reconstruct and classify the parent fossil plants whose remains have been fossilised. The resulting taxonomy of fossil plants is then sometimes used as the basis for classifying the plant fossils. However, the reconstructions are hypothetical and incomplete conceptual models, and rarely provide a secure basis for the classification of the fossils, which are physical objects; the fossils are more than merely tokens of the parent organisms.

A more robust approach to palaeobotanical taxonomy is to classify the fossils using characters inherent and specific to the fossils themselves (Cleal and Thomas 2010a). As the fossils are tangible objects, their classification can be subjected to direct and complete scientific testing in a way that a classification of the partial, hypothetical reconstructions cannot. The aim is often to make the classification of the plant fossils reflect at least partly what is thought to be the systematic relationships of the fossil plants: for instance, the classification of Palaeogene paratropical fossil seeds has been argued to mirror closely that of extant tropical trees (Reid and Chandler 1933, Collinson 1983). But in practice this correspondence is difficult to test and is often quite poor,

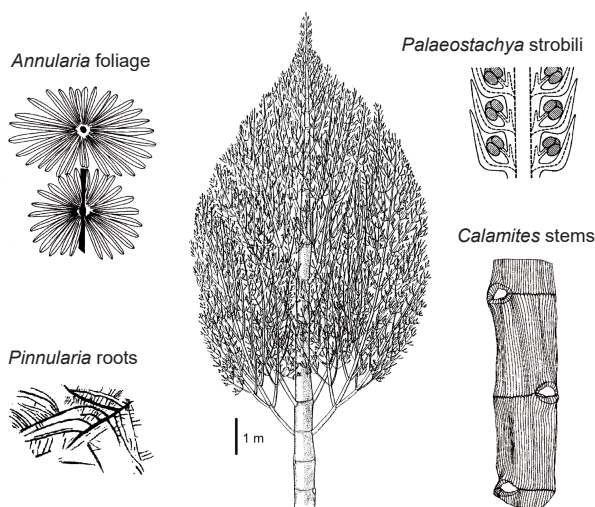
especially with remains of older plant groups: for instance, the fossil-species taxonomy of Carboniferous sphenopsid stems (Stur 1887, Jongmans 1911, Crookall 1969) probably bears little relationship to the systematics of the parent trees. There is a continuous spectrum between how well or poorly the different types of palaeobotanical taxonomy reflect the botanical affinities of the parent plants, and it is obviously important to know where a particular taxon lies in this spectrum when trying to interpret it in a phylogenetic, floristic, palaeoecological or biostratigraphical context.

Naming different plant parts

The aspect of palaeobotanical taxonomy that non-specialists often find counter-intuitive is that different parts of a plant can be assigned to different fossil-taxa (Tab. 1, Text-fig. 3). The confusion partly arises because it is often assumed that, when a taxonomic name is given to a fossil, it is referring to the parent plant from where the fossil came, whereas as we have shown it refers to the fossil which preserves only a part of the plant.

Assigning different parts of the plant to what are now known as fossil-taxa goes back to the pioneering work of Brongniart (1822, 1825) and Sternberg (1825), and arose because most plants fragment during fossilisation (Thomas 1989, Thomas and Cleal 1999, Forey et al. 2004); it is rare to find the different parts still attached to each other. Fragmentation is of course not unique to plant fossils: conodont animal remains are almost always found as dispersed elements (parts of their feeding-apparatuses) and Sylvester-Bradley (1954) argued that “parataxa” similar to form-genera (as used in the older botanical codes) might be applicable to their classification (see also Bengtson 1985). However, this has never been incorporated formally into palaeozoological taxonomy – fossil-taxa remain a distinct and distinctive feature of palaeobotany.

There are no formal rules about how a plant is divided up into its component sets of fossil-taxa. Sometimes it is fairly self-evident – when a particular organ is regularly abscised from the plant and preserved as a coherent structure (e.g., seeds) it makes sense to assign it to its own set of fossil-taxa. But compound structures can be more problematic.



Text-fig. 3. Some of the fossil-genera produced by a Carboniferous arborescent sphenospid. Redrawn from Cleal and Thomas (2019).

For instance, although cones and strobili are often abscised whole from the plant and have their own fossil-taxa, some also regularly disarticulated so their component parts can also occur as isolated fossils: Carboniferous *Lepidocarpon* D.H. SCOTT (Scott 1900) strobili regularly disaggregated as part of the plant's dispersal strategy (Text-fig. 4) and so the resulting isolated sporophylls are assigned to the fossil-genus *Lepidostrobophyllum* HIRMER (Hirmer 1927, Allen 1961, Boulter 1968, Habgood et al. 1998); in the same way, isolated leaf-scales that subtended Mesozoic bennettitalean "flowers" such as *Williamsonia* CARRUTH. (Carruthers 1870) are assigned to *Cycadolepis* SAPORTA (e.g., Saporta 1874, Harris 1969, Watson and Sincock 1992). Although such isolated bracts and scale-leaves can be important for indicating the presence of a particular group of plants, it would be misleading to record them using fossil-taxa defined on the whole reproductive structures; for instance, not all *Lepidostrobophyllum* were produced by *Lepidocarpon* strobili.

Another factor that has to be taken into account is, will



Text-fig. 4. *Lepidocarpon* cone in the process of disarticulating as part of the dispersal strategy of the plants. When preserved isolated, the sporophylls are assigned to the fossil-genus *Lepidostrobophyllum*. Refigured from Thomas (1981). Grovesend Formation (upper Asrturian – lower Moscovian), Kilmersdon Tip, Radstock Coalfield, UK; Natural History Museum (London) specimen V.60431.

having separate fossil-taxa for particular isolated plant parts be useful to palaeobotanists? For example, medullosalean fronds that abound in the upper Carboniferous fossil-record represent clearly-defined organs but are usually found as isolated pinnae or even pinnules. Consequently, most early classifications tended to be based on characters of the individual pinnae and pinnules (e.g., Brongniart 1822, 1828a). Such taxa were useful for recording the presence of particular frond fragments but they ultimately proved to be of little practical value for understanding the systematics of the parent plants, which in turn reduced their value for biostratigraphical and floristic studies. Improved generic schemes were subsequently developed using architectural characters of the complete fronds reconstructed from the fossil fragments (e.g., Gothan 1941, Laveine 1997). The fronds of only a few fossil-species have been reconstructed, and assigning the other species has had to be based on comparisons using criteria such as epidermal structure preserved in cuticles (e.g., Cleal et al. 1990, Cleal and Shute 2012) or on evidence of association of other frond parts such as cyclopterid epiphytic leaves (e.g., Laveine 2005). This has allowed the vast majority of the known fossil-species defined on isolated pinnae to be placed in the classification based on frond-architecture (Cleal and Shute 1995, 2012).

An alternative solution was proposed by Gothan (1953) based on the trinomial taxonomic nomenclature used by Kidston (1884) for fern fossils: for instance, "*Neuropteris (Imparipteris) heterophylla*" indicated that the species had pinnules that corresponded to the fossil-genus *Neuropteris* (BRONGN.) STERNB. (Sternberg 1825) and a frond architecture corresponding to *Imparipteris* GOTHAN (Gothan 1941). A species with *Neuropteris*-like pinnules but for which frond architecture and cuticles are unknown would just use the first generic name, e.g., *Neuropteris teberdensis* SHCHEG. (Shchegolev 1979). However, viewed in the context of today's taxonomic nomenclature this would imply that the botanically more-meaningful *Imparipteris* was a subgenus of the more loosely defined *Neuropteris*, which it is not. Consequently, this nomenclatural approach has been generally rejected.

Alternative solutions are to use satellite taxa (discussed later under taxonomic rank) or open nomenclature as used in palaeozoology (Matthews 1973, Bengtson 1988). Using the open nomenclature scheme suggested by Matthews (1973), *Laveineopteris? dussartii* (LAVEINE) LAVEINE (Laveine 2005) would imply that the transfer of the species to *Laveineopteris* should be regarded as provisional because neither frond architecture nor cuticles are known. Although, this would not be possible with a new species as ICN Art. 35.2 states that a combination "is not validly published unless the author definitely associates the final epithet with the name of the genus or species", it does offer a solution when taxonomically revising previously published species. However, it should be noted that an open nomenclature "?" has been used in a rather different context, for a fossil that agreed in all available data with a living taxon, but where certain critical criteria were absent (Collinson 1980). Evidently, if open nomenclature is to be adopted in palaeobotany, an agreed procedure will be needed but, as it deals with taxonomic rather than strictly nomenclatural issues, this is unlikely to be in the ICN (it is also not covered

by the Zoological nomenclatural code – see comments by Sigovini et al. 2016).

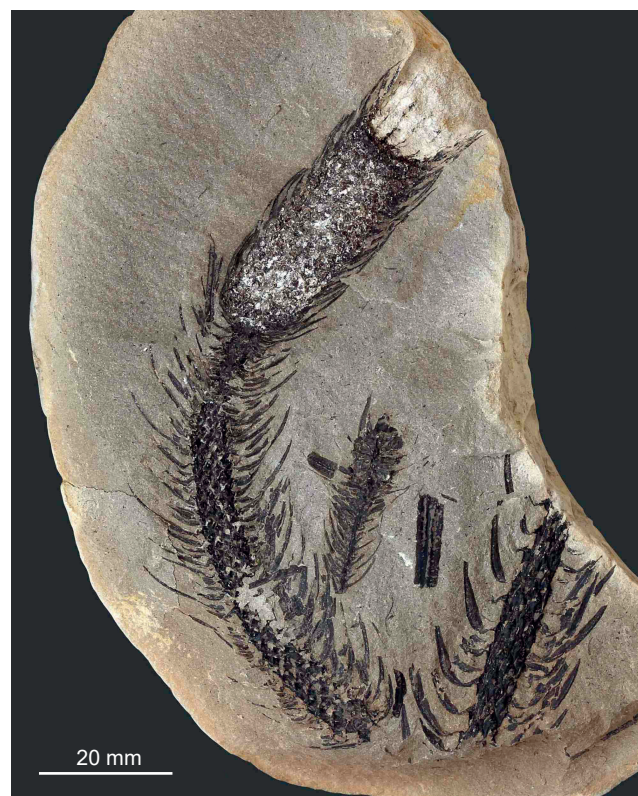
What happens when plant parts are correlated?

As palaeobotany has advanced, the connection between organs in various plants has been demonstrated, either on direct evidence of attachment, or indirect evidence such as the regular co-occurrence of remains of plant parts, or similarities in anatomical or surface features (Chaloner 1986). But how should this be reflected in the taxonomic nomenclature? The least disruption to the taxonomy and nomenclature results from simply continuing to use the separate fossil-taxa for the different plant parts. For instance, both the heterosporous lycopsid cone *Flemingites* and the microsporangiate cone *Lepidostrobus* have been found attached to leafy shoots (e.g., Text-fig. 5), but most accounts merely list a named cone species attached to a named shoot (e.g., Chaloner 1953, Thomas and Seyfullah 2015a); the taxonomic and nomenclatural issues surrounding these lycopsid cone fossils are discussed later in the section on “Artificial” fossil taxa. However, palaeobotanists often seem to be drawn to the idea that the connection between the plant parts should be reflected in the taxonomy of the fossils and that this will improve understanding of the systematics of the parent plants, but this can often have unforeseen consequences.

It is perfectly legitimate to designate a new fossil-taxon for the combination of plant parts, but what should this new combination fossil-taxon be named? One option is to expand the circumscription of one of the existing fossil-taxa so it now includes both plant parts. Wang et al. (2009) described noeggerathialean foliage of the fossil-genus *Paratingia* HONG ZHANG, 1987 with attached strobili from the lower Permian Wuda Tuff of north China, and established a combination fossil-genus for the foliage and strobili. There was at the time no valid generic name for the strobili (see comments by Pfefferkorn and Wang 2016) and so the only existing name of fossil-genus whose type could unequivocally be placed within the new combination fossil-genus was *Paratingia*. Since remains of *Paratingia* foliage appear to be not particularly diverse, it seems reasonable to assume that all plants with such foliage formed a systematically coherent group and bore the same strobili, and so expanding the circumscription of the foliage fossil-genus to include the strobili appeared reasonable.

Another similar example was where the circumscription of the peltaspermalean ovuliferous fossil-genus *Autunia* KRASSER (Krasser 1919) was expanded by Kerp (in Kerp and Haubold 1988a) to also include foliage. In this case, the generally-used generic name for this foliage (*Callipteris* BRONGN.; Brongniart 1849) was having to be suppressed for nomenclatural reasons and so a new generic name would have been needed. The taxonomic revision proposed in Kerp and Haubold (1988a) avoided the creation of such a new generic name, although a number of other names were needed for peltaspermalean-like fossil-genera for which fructifications were unknown (Kerp and Haubold 1988a, b).

But other examples are more problematic. *Sphenophyllum oblongifolium* (GERMAR) UNGER (\equiv *Sphenophyllites*



Text-fig. 5. Fossil remains of a leafy *Lepidodendron ophiurus* BRONGN. shoot bearing a *Flemingites* strobilus produced by a tree similar to that shown in Text-fig. 2a; Middle Coal Measures Formation (Duckmantian – upper Bashkirian), Brymbo, near Wrexham, UK (see Thomas et al. 2020: fig. 16b); National Museum Wales specimen 2013.43G.120.

oblongifolius GERMAR) (Germar 1845, Unger 1850) is a fossil-species of sphenophyllalean leafy shoots found widely in the Upper Pennsylvanian and Permian of Euramerica and China. Barthel (1976, 2015) reported a distinctive type of strobilus attached to *S. oblongifolium* shoots from the lower Permian of Germany. If found isolated, such strobili would normally be assigned to a species of *Bowmanites* BINNEY (Binney 1871), but Barthel (1976) instead emended the diagnosis and circumscription of *S. oblongifolium* so that it now included the strobili (he made no comment on the circumscription of the fossil-genus). However, Zodrow and Gao (1991) later reported other shoots of *S. oblongifolium* from the Middle Pennsylvanian of Cape Breton (Canada) that bore a different type of strobilus with much smaller, different-shaped sporophylls, each of which bore more sporangia; the Canadian fossils were, therefore, placed in a new fossil-species and fossil-genus, *Leeites oblongifolius* ZODROW et Z.F.GAO (this was clearly stated to be a new species, not just a new combination of the Germar species epithet with a new genus). Although the generic significance of these differences in strobili has been questioned (Libertin et al. 2014) the differences at the rank of species appear real. This clearly presents problems when isolated shoots are found: do they belong to *S. oblongifolium* sensu Barthel (1976, 2015) or *L. oblongifolius*? It might be argued that this is not a problem – that it is not necessary to have a valid species name for shoots without strobili. However, *S. oblongifolium* in its traditional sense refers to very distinctive and widely-

reported leafy shoots with well-defined stratigraphical and geographical distributions, and the loss of this fossil-species would be detrimental to floristic and biostratigraphical studies. If only from a utilitarian perspective, it would seem to be preferable to retain separate fossil-taxa for the sphenophyllalean leafy shoots and the strobili.

Hoskins and Cross (1943) also tried to correlate sphenophyllalean shoots and strobili, but they instead changed the circumscription of the strobilus fossil-genus *Bowmanites* to include the shoots and proposed a series of new combinations of species formerly assigned to *Sphenophyllum*. The difficulty here is that the type species of *Sphenophyllum* (*S. emarginatum* BRONGN.; Brongniart 1828a) bore *Bowmanites* strobili (e.g., Bek 2018) and so normal nomenclatural practice would require *Bowmanites* to be suppressed in favour of the earlier published *Sphenophyllum* BRONGN. (Brongniart 1828a). This would require all of the *Bowmanites* species to be transferred to *Sphenophyllum*, whether or not the leafy shoots were known. Again, the practical benefits of combining the fossil-taxa for the strobili and foliage would seem to be marginal, while the disruption to the taxonomy and nomenclature would be considerable.

An alternative solution for situations where plant parts are shown (or indicated) to have been originally connected is to create a completely new fossil-taxon for the combination, but this can also introduce taxonomic problems. *Zamites gigas* (LINDL. et HUTTON) MORRIS (\equiv *Zamia gigas* LINDL. et HUTTON) (Lindley and Hutton 1835, Morris 1841) was established for fossil fronds resembling those of living cycads. Carruthers (1870) subsequently correlated these fronds with reproductive structures (“flowers”), and established a new genus *Williamsonia* to include both plant parts, with three species with names based on epithets whose types were fronds; of these, *Williamsonia gigas* (LINDL. et HUTTON) CARRUT. was later designated as the type (Seward 1917). The problem is that there are other *Williamsonia*-like bennettitalean flowers that have been correlated with different types of frond of the fossil-genera *Ptilophyllum* MORRIS (Morris 1840) and *Pterophyllum* BRONGN. (Brongniart 1825) (e.g., Harris 1969, Watson and Sincock 1992); it is also far from certain that all *Zamites* fronds were borne on plants with *Williamsonia* flowers. If we were to retain *Williamsonia* as a combination fossil-genus for fronds and flowers it would, therefore, either have to have (1) a very wide circumscription to include a wide range of fronds and flowers currently placed in different genera or (2) a very narrow circumscription restricted to those bennettitaleans with **only** *Zamites* fronds **and only** *Williamsonia*-like flowers. Neither solution is taxonomically satisfactory and Harris (1969) argued that it is far more sensible for *Williamsonia* to be restricted to the fossils of bennettitalean flowers and the fronds assigned to one or other of their own set of fossil-genera. Although sensible, to do this it has been necessary to conserve the name *Williamsonia* with a different type (Zijlstra and van Konijnenburg-van Cittert 2020). None of this confusion would have arisen if Carruthers (1870) had not tried to create a combination fossil genus for the fronds and flowers.

Another series of fossils from the Wuda Tuff showed connections between stems, leafy shoots and strobili of a subarborescent sphenophyte, and was the basis of a

combination fossil-species that was called *Palaeostachya guanglongii* LI LIU, PŠENIČKA, BEK, M.WAN, PFEFFERK. et JUN WANG bis. No emended diagnosis was provided but by inference Liu et al. (2021) were expanding the circumscription of the fossil-genus *Palaeostachya*; previously it had been restricted to strobili, but now it was to also include stems and leafy shoots. There is nothing intrinsically illegitimate about changing the circumscription of a fossil-genus in this way but, in this case, it will cause significant practical taxonomic difficulties. It is implicit in the Liu et al. (2021) proposal that *Palaeostachya* must include both the remains of this distinctive Chinese sphenophyte and the remains associated with the generic type (*Palaeostachya elongata* (C.PRESL) C.E.WEISS) (Weiss 1876) but, as pointed out by Liu et al., they were produced by plants with two very different growth strategies. Unless the name *Palaeostachya* were to be formally conserved with a new type (with all of the species formerly included within *Palaeostachya* requiring a new fossil-genus and new combinations), the inevitable consequence of their proposal is that all arborescent (“calamitid”) sphenophytes will have to be included in a single whole-plant genus, irrespective of their significantly different growth strategies, which systematically makes little sense. What evidently seemed to be a logical solution to a problem encountered in one particular fossil flora has the potential for causing confusion for the wider palaeobotanical community.

An alternative approach was taken by Weiss (1884), who described numerous Carboniferous sphenophyte fossils linking stems, foliage and strobili. To demonstrate these relationships, he used the same species epithet but combined with a different generic name for each plant part: for instance, he described stems as *Calamites ramosus* ARTIS (Artis 1825), the attached foliage as *Annularia ramosa* C.E.WEISS and the strobili as *Calamostachys ramosa* C.E.WEISS. Unfortunately, it was not clear from his descriptions if he was regarding these as one species but assigned to a different genus according to which plant part was being referred to (which goes against normally accepted nomenclatural practice that a species can only belong to one genus), or that there were three separate fossil-species with the same epithet but placed in different fossil-genera. It is not formally illegitimate to name different fossil-species for different plant parts using the same epithet but assigned to different fossil-genera, but those species must be clearly and separately diagnosed and typified, which Weiss failed to do. Because it is not clear how Weiss (1884) was envisaging the circumscription of these fossil-taxa it has proved difficult to use them in practice (Jongmans 1911).

Yet another solution has been to place fossil-species for different plant parts in genera with names with a similar root but with suffixes indicating what plant parts are being referred to. This again is totally legitimate within the nomenclatural rules and in some cases can be taxonomically acceptable, but in other cases can cause difficulties. Renier and Stockmans (in Renier et al. 1938) established *Ulostrobos* for cones attached terminally to slender, leafy shoots that Renier (1926) had earlier identified as *Ulodendron* RENIER et STOCKMANS. However, Thomas (1967) showed that the Renier (1926) leafy shoots do not belong to *Ulodendron* sensu Lindley and Hutton (1832), in which the wider stems

have persistent leaves; they are, in fact, terminal shoots of *Lepidodendron* which abscised its leaves from the wider stems (Thomas and Seyfullah 2015a). The type of *Ulostrobilus* is, therefore, a strobilus attached to a *Lepidodendron* shoot and is morphologically indistinguishable from the other strobili found attached to *Lepidodendron* and normally placed in *Flemingites* (Text-fig. 4). The name *Ulostrobilus* is therefore both nomenclaturally misleading (it does not refer to the strobili attached to *Ulodendron*) and is almost certainly a later heterotypic synonym of *Flemingites*.

In conclusion, when two or more plant parts are shown to be in organic connection or can be reliably correlated by other means (e.g., similarity of epidermal structures), there are three main options: (1) keep the fossil-taxa for the different plant parts separate; (2) emend the diagnosis of the fossil-taxon used for one of the plant parts so that its circumscription becomes expanded to include the other plant part(s); or (3) create a new fossil-taxon to include all the plant parts. There are no fixed rules for deciding which option to follow but the guiding principle should clearly be to try to avoid causing significant disruption to the taxonomy. For instance, expanding the circumscription of a fossil-taxon of foliage to include strobili might appear attractive if an example of connectivity has been found, but it might cause significant disruption to the widely-used taxonomy of the foliage, requiring numerous new combinations to be created.

Whole-plant reconstructions

A related problem is how to name the whole-plant reconstructions that regularly appear in palaeobotanical and other textbooks (e.g., Text-figs 2a, 3, 6b). Reconstructions of the smaller, herbaceous species may be based on more or less complete fossilised remains of the plants, notably among Devonian taxa (e.g., Lele and Walton 1961) but also in some younger floras (e.g., Barthel 1968, Pšenička et al. 2021); these can potentially be named and classified in the same way as any plant fossil. Rarely, larger, subarborescent plants have been found at least partly complete, such as when they have been very rapidly preserved in situ by volcanic ash-fall (e.g., Liu et al. 2021). However, these are exceptions and the vast majority of larger plants have been reconstructed by connecting their component parts through evidence of co-association or similarity in anatomical features (e.g., Kvaček 2008, Bomfleur et al. 2013). Even the best examples of these are mostly only gross-morphological reconstructions showing the form of the plants; only rarely is the cellular structure also fully-preserved. Ultimately, most such whole-plant reconstructions based on the plant fossil record are theoretical “biofantasies” (DiMichele and Gastaldo 2008) that exist just as hypothetical constructs in the minds of palaeobotanists, or as illustrations or models created by artists (Townsend et al. 1998).

When such reconstructions are published in the literature, they are often given a Linnean-style taxonomic name usually based on the name of one of the best-known component fossil-taxa: for instance, reconstructions of one of the Carboniferous arborescent lycopsids (Text-fig. 2a) are often named *Lepidodendron*, after the fossil-genus used for the stem adpressions (Text-fig. 2b); Unger (1850) even

emended the diagnosis of *Lepidodendron* to include the whole plant. This may seem a straightforward and harmless validation of the legitimacy of the reconstruction. However, if this was to be regarded as a change in the formal use of the name *Lepidodendron*, it implies a change in the generic diagnosis so that it also includes the other organs such as strobili, foliage and rooting-structures (Thomas and Cleal 2020). If this was accepted, many of the *Lepidodendron* species for which the associated other plant parts are unknown could not be safely included within the new genus, and a new genus and name would be required for these less well-understood fossils. The resulting flurry of new combinations would cause significant nomenclatural disruption and could be ignored by many palaeobotanists.

If this was to be a real gain for palaeobotany, helping improve the understanding of the systematics of the plants, then this disruption might be regarded as a price worth paying. However, it is difficult to see what real scientific gain is to be obtained by assigning a formal Linnean taxonomic name (implying a binomial) to such a reconstruction. Linnean taxonomic names are not merely labels to identify a particular organism; they are part of a systematic hierarchy within which the organisms are classified either phylogenetically or morphologically, and this implies there are numerous similar organisms to form that hierarchy. In this case, there are only a small number of reconstructed fossil plants, most of which are monotypic at the rank of genus and even family, and so there is no taxonomic hierarchy in which to place them much below the rank of order. There are of course living monotypic families and genera of living organisms that are assigned binomial Linnean taxonomic names, and there is nothing formally to prevent this from being done for the reconstructed fossil plants, but the question must be asked, what is to be gained scientifically?

This is not to disparage the development of whole-plant reconstructions, but what is the real scientific justification of providing them with a formal Linnean name? As pointed out by Chaloner (1986), a much better solution is to merely give them an informal label such as “*Lepidodendron* plant”, which achieves everything that is needed, without the potential disruption to other parts of the palaeobotanical taxonomy (compare similar comments by Crane 1984, Bomfleur et al. 2013).

Naming life-history stages

ICN, Art. 1.2 also allows different life-history stages to be given separate taxonomic names. Gametophytes of pteridophytic plants are usually too delicate to be preserved as fossils but, where they are found, they have been given separate taxonomic names to the sporophytes: for instance, in the Lower Devonian Rhynie Chert fossil flora, *Lyonophyton* W.REMY et R.REMY, *Kidstonophyton* W.REMY et HASS and *Langiophyton* W.REMY et HASS (Remy and Remy 1980, Remy and Hass 1991a, b) are the gametophytes of the plants with sporophytes *Aglaophyton* D.S.EDWARDS, *Nothia* A.G.LYON and *Horneophyton* BARGH. et DARRAH, respectively (Barghoorn and Darrah 1938, Lyon 1964, Edwards 1986; see Kerp et al. 2003 for a review). An example of the taxonomic distinction of different life stages

of a sporophyte are the saplings of what is often referred to as the “*Archaeopteris* tree” (Late Devonian trees with *Archaeopteris* DAWSON leafy shoots and *Callixylon* ZALESKY woody stems; Dawson 1871, Zalessky 1911) which are referred to the fossil-genus *Eddyia* C.B.BECK (Beck 1967; Text-fig. 6).

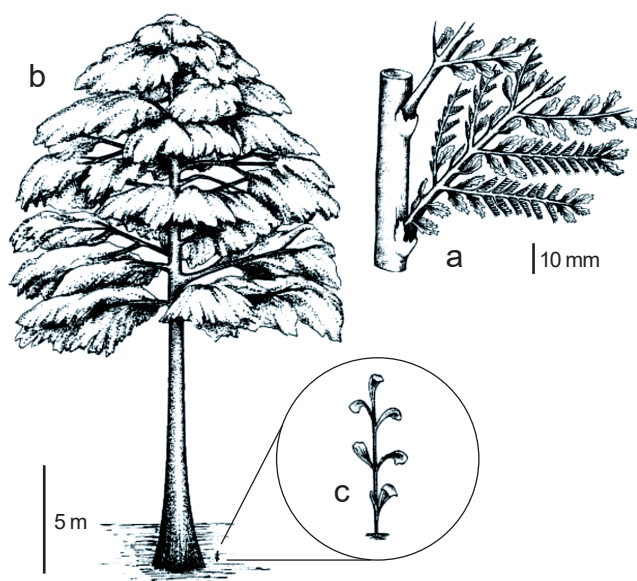
Fossil fungi present particular problems. Living fungi can occur in either their asexual stage (anomorph) or sexual stage (teleomorph), and historically it has often proved difficult to correlate these stages. Consequently, the older nomenclatural codes allowed these stages to be assigned different taxonomic names. More recently, however, molecular studies have enabled some of the different stages to be correlated and the resulting whole organism is known as a holomorph. Since the Melbourne ICN (McNeil et al. 2012) only one name can be given to a living fungus taxon and priority must be given to the first named regardless if its type is an anamorph or teleomorph (Hawksworth 2011, May et al. 2019). However, as fossil fungi will lack molecular data this remains a significant problem for palaeomycology (Taylor et al. 2015).

Recognising living plant taxa in the fossil record

There is a gradation between today’s living vegetation and the extinct vegetation preserved in the fossil record, with a transition represented by historical herbaria and archaeological samples (Collinson 1986). This raises the question, when is it legitimate to use taxa of living plants for plant fossils? Especially with angiosperm remains, plant parts such as leaves may seem indistinguishable from the equivalent parts of extant taxa (Text-fig. 7) but this can be misleading; there have been cases where seeds resembling those of one living genus have been found attached to leafy shoots attributable to another living genus (e.g., Crane 1984). Collinson (1986) has, therefore, argued that it is normally best if extant species and genera are not used for

fossil remains. At the time of writing her paper, Collinson pointed out that the Code presented a number of hurdles to developing a practical taxonomy and nomenclature for these fossils, but these have mostly disappeared with the use of fossil-taxa as allowed in the current ICN (Turland et al. 2018). As pointed out by Collinson (1986), however, there remains the problem of the gradation between the fossil record and today’s vegetation; it would make little sense to use fossil-taxa for historical herbarium specimens or even archaeological samples, but where should the line be drawn?

The problem is less acute with small, herbaceous plants where whole or near-whole organisms may be preserved. In the Carboniferous floras of the low-palaeolatitudes of Euramerica, there are herbaceous lycopsids that are very similar morphologically to extant species of *Selaginella*. These fairly rare fossils have usually been placed in the fossil-genus *Selaginellites* ZEILLER (Zeiller 1906) which was intended for *Selaginella*-like fossils but whose botanical affinities at least at the rank of genus could not be definitely verified (similar to how Schlotheim (1820) and Brongniart (1822, 1828a) used names such as *Filicites* for fern-like fossils). However, the type of *Selaginellites* from the upper Carboniferous Blanzky Coalfield in France (*S. suissei* ZEILLER) has a dichotomously branched stem, dimorphic leaves, and a terminal bisporangiate cone with apical microsporangia and basal megasporangia, which is very similar to many living anisophyllous species of *Selaginella* with tetragonous strobili (e.g., *S. vogelii* SPRING, *S. cathedrifolia* SPRING, *S. pervillei* SPRING; see Thomas and Quansah 1991, Quansah and Thomas 2021). Thomas (2005) therefore took the view that it was legitimate to include at least some of the Carboniferous herbaceous lycopsid fossils within the extant genus *Selaginella*, but assigned to a separate subgenus *Hexaphyllum* B.A.THOMAS: *Selaginella gutbieri* (GÖPP.) B.A.THOMAS (Thomas 2005), *Selaginella stachygyndroides* (GEINITZ) B.A.THOMAS and *Selaginella zeilleri* (T.HALLE) B.A.THOMAS (Thomas 1997).

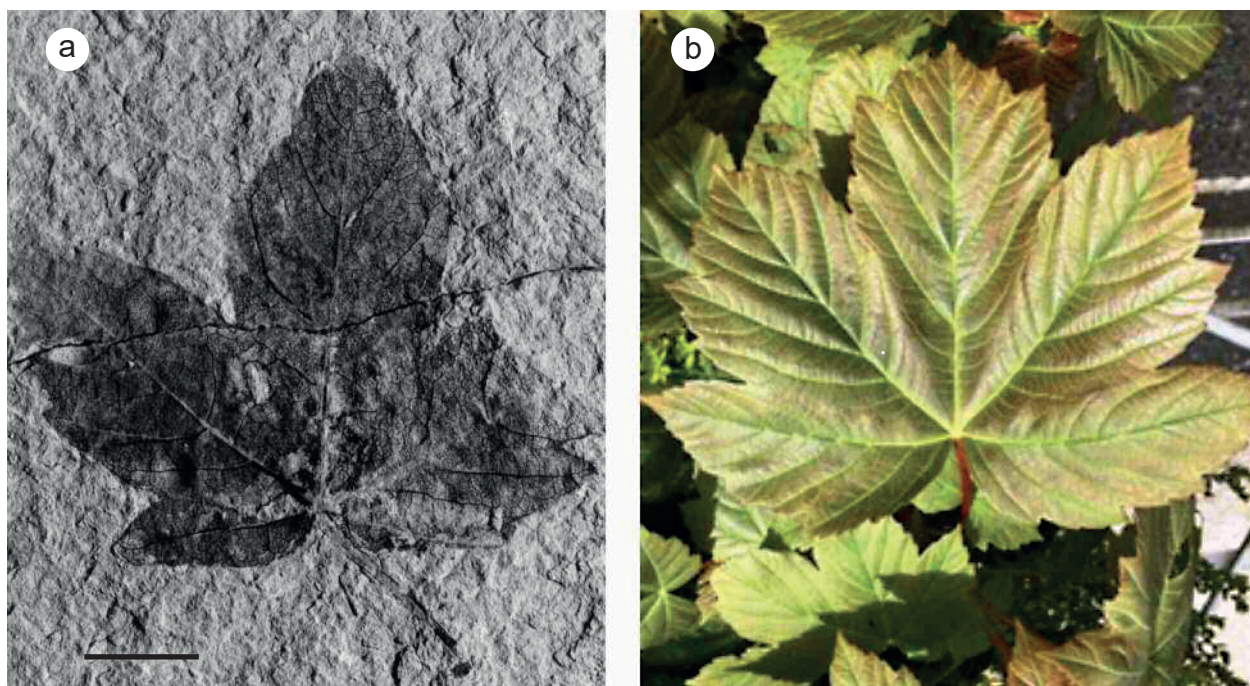


Text-fig. 6. a: Reconstruction of the fertile shoot *Archaeopteris* from the Late Devonian; b: Reconstruction of tree that bore *Archaeopteris* shoots; c: Juvenile form (“sapling”) of *Archaeopteris*-bearing tree. Redrawn from Cleal and Thomas (2019).

The effect of different states of preservation

Art. 1.2 of the ICN (Turland et al. 2018) states that a fossil-taxon can also represent plant remains in a particular preservation state. Different preservation states can yield different types of information about the plant, and a fossil-species diagnosed on cellular details seen in anatomically-preserved fossils may be unrecognisable in adpressions; similarly, species diagnosed on morphological characters from adpressions (e.g., frond architecture) may be difficult to recognise in anatomically-preserved fossils.

There are cases where some morphological data can be obtained from anatomically preserved fossils. For instance, Beeler (1983) described coal-balls with anatomically preserved medullosalean pinna fragments where paradermal sections showed the pinnules to be similar in shape and venation to those in the adpression fossil-species *Neuropteris ovata* FR.HOFFM. (Hoffmann 1826). In this case the taxonomic assignment seems reasonable as the pinnules were relatively flat and so the paradermal sections provided a reasonable representation of the overall pinnule shape. However, in other medullosaleans such as *Alethopteris*



Text-fig. 7. Fossil and living examples of leaves of *Acer*. **a:** *Acer* sp. (fossil), Pleistocene diatomaceous deposits near Fau-fouille, France (scale bar = 10 mm); National Museum Wales specimen 86.54G.1a; **b:** Leaf from living *Acer* growing near Machynlleth, mid-Wales, UK; photo by B. A. Thomas.

STERNB. (Sternberg 1825) the pinnule limb is significantly vaulted and so paradermal sections do not normally show the pinnule shape so well (Raymond et al. 2013). Moreover, the generic taxonomy of the medullosalean adpression foliage is heavily dependent on frond architecture (Laveine 1967, 1997, Cleal and Shute 1995), which is rarely determinable in the much smaller fossils found in coal-balls; for instance, Beeler (1983) found no evidence of the basal dichotomy of the primary rachis, which is a key diagnostic character of *N. ovata* frond adpressions (e.g., Zodrow and Cleal 1988). Either the anatomically preserved fronds were non-dichotomous and borne on different plants to those preserved as adpressions (probably unlikely) or the morphological data provided by the anatomically preserved fossils are incomplete. There are also other adpression taxa similar to *N. ovata* that are distinguished on the shapes of the pinnae and terminal pinnules that would be difficult to see in the coal-ball fossils (Saltzwedel 1969, Cleal and Zoderow 1989). Since, it is impossible to identify reliably all of the characters used to define the taxa distinguished in adpressions in anatomically-preserved fossils, it is best not to use the adpression taxa for coal-ball fossils. In this case, anatomically-preserved medullosalean pinnae are best retained in the fossil-genus *Myeloxylon* BRONGN. (Brongniart 1849) which was defined on purely histological characters.

There can also be problems with identifying in adpressions the histological features used to define taxa of anatomically preserved fossils. *Lepidodendron* STERNB. is a well-documented fossil-genus of Palaeozoic arborescent lycopsid stems preserved as adpressions and casts (Crookall 1964, Thomas 1970a, Tenchov 1987, Álvarez-Vázquez and Wagner 2014). However, stems of the same plants have been divided into fossil-genera based on data that can rarely be seen in adpressions (e.g., *Diaphorodendron*

DiMICHELE, *Synchysidendron* DiMICHELE et BATEMAN, *Hizemodendron* BATEMAN et DiMICHELE (DiMichele 1985, Bateman and DiMichele 1991, DiMichele and Bateman 1993); for a summary see Bateman et al. 1992). There have been attempts to integrate the classifications for these stems in different preservation states (e.g., Cleal and Wang 2002, DiMichele et al. 2013, Bateman and DiMichele 2021) but Laveine et al. (2003) argued that the morphological characters recognisable on the adpressions were simply not reliable enough guides to distinguishing the fossil-genera based on anatomical criteria; the two sets of fossil-genera are best kept separate (Thomas and Cleal 2020).

This is not to say that fossils in different preservation states must always be assigned to different fossil-taxa; if it is possible to map with reasonable reliability the fossil-taxa between the different types of fossil then it obviously makes sense to use the same taxa (DiMichele and Bateman 2020). For instance, most strobili of Carboniferous sphenopsids are assigned to either *Calamostachys* SCHIM. or *Palaeostachya* C.E.WEISS based mainly the position of the sporangiophores relative to the bracts, and these characters can be seen in both adpressions and anatomically-preserved floras (Gastaldo 1981, Cleal and Shute 2016). Similarly, the large dichotomising rhizophore bases of the arborescent lycophytes are called *Stigmara* BRONGN. in both full-sized or fragmentary casts and anatomically preserved fragments found in coal balls (Williamson 1887, Thomas and Seyfullah 2015b).

However, such unequivocal one-to-one mapping of the taxa between preservation states tends to be rare and, to avoid taxonomic confusion, it is normally advisable to keep separate the fossil-taxa for different preservation states.

Taxonomic rank

Palaeobotanical taxonomy uses the same hierarchical structure as the taxonomy of living plants. Fossil-taxa can be of any rank, but the most commonly encountered are fossil-species and fossil-genera. Species of living plants were traditionally defined on distinctive morphological characters, but more recently with the added criteria of reproductive isolation (although the importance of this has been questioned – Rieseberg et al. 2006) and molecular data (e.g., de Vere et al. 2015). Reproductive isolation and molecular data clearly cannot be used with the fossil record and so fossil-species can only be defined on morphological or histological criteria, e.g., the consistent co-occurrences of a particular range of morphotypes. Consequently, although fossil-species are broadly similar in practice to whole plant species in that both are mainly defined by morphological characteristics, there is a fundamental conceptual difference: there is at least the potential for using reproductive and/or molecular evidence in defining whole plant taxa, but this can never be used for the fossil-taxa.

Fossil-species are sometimes divided into taxonomic varieties or even forms. This is usually based on characters that are not always preserved in the fossils: for instance, Cleal and Zodrow (1989) proposed the recognition of varieties of *Neuropteris ovata* FR.HOFFM. fronds based on epidermal features that can only be recognised if cuticles are preserved.

Fossil-species are grouped into fossil-genera. It would seem logical to try and make fossil-genera agree with the genera of the plants that produced those fossils but this is often not possible. For instance, the Medullosales were trees and woody scrambling plants that occurred widely in late Carboniferous and early Permian wetland floras. All of the plants in this order seem to have had similar distinctive stems with a dissected stele that when anatomically preserved are assigned to the fossil-genus *Medullosa* COTTA (Cotta 1832; hence the name of the order). This fossil-genus can, therefore, in effect be taken as a proxy for a whole-plant order rather than a genus of whole-plants. In contrast, the large ovules that are assigned to the fossil-genus *Pachytesta* BRONGN. (Brongniart 1874) appear to be restricted to just one of the medullosalean families, the Alethopteridaceae. Hence, fossil-

taxa for different parts of the plant can indicate different ranks of whole-plant taxa: in this case, an ovule genus indicates a family whereas the stem genus indicates an order.

This does not make a fossil-genus such as *Medullosa* artificial, as it clearly correlates with a natural taxon of whole plants – just not a taxon of the same rank as the fossil-taxon. Similarly, foliage adpressions probably yield relatively limited evidence as to their systematic position in terms of families or orders, but their fossil-species and fossil-genera have proved invaluable in floristic and palaeoecological studies (e.g., Cleal et al. 2010). All of these fossil-taxa are natural (in the normal accepted taxonomic sense of natural) as they provide evidence of the systematic position of the parent plants, but not necessarily at the same rank.

For situations where there are discrepancies between the rank of a fossil-taxon and the rank of the plant that produced the fossils, Meyen (1978) introduced the concept of satellite taxa (the term satellite taxon was later used by Hanski (1982) in a quite different sense in ecological studies). In the above quoted example, *Pachytesta* would be attributable to the family Alethopteridaceae (order Medullosales) whereas *Medullosa* would be a satellite-genus of the order Medullosales (Tab. 2). This is perfectly compatible with the ICN as the sequence of taxonomic ranks is not being disturbed; it just means that one or more ranks are omitted when describing the systematic position of a fossil-taxon. An example of the use of satellite taxa was in a classification of lycopsids by Thomas and Brack-Hanes (1984) that attempted to incorporate fossil-genera of stems, rooting structures and even some of the less well-defined fructifications; see also their use in classifying Permian noeggerathioid remains by Gao and Thomas (1987).

The ICN allows for the recognition of fossil-taxa at supra-generic ranks; for instance, Cleal and Shute (2003) proposed a set of fossil-families of medullosalean fronds. More commonly, however, fossil-genera from different plant parts are combined to form what are in essence whole-plant families, although emphasis has often been given to the reproductive organs when defining the circumscription (e.g., Meyen 1984, Thomas and Brack-Hanes 1984, Anderson et al. 2007). Being more like whole-plant taxa was one of the arguments for using families rather than lower-

Table 2. Systematics of selected medullosalean fossil-genera and satellite-genera.

Class	Order	Fossil-family	Fossil-genus	
Cycadopsida	Medullosales	Alethopteridaceae	<i>Alethopteris</i> STERNB.	
			<i>Neuralethopteris</i> CREMER	
			<i>Lonchopteris</i> BRONGN.	
		Satellite-genus: <i>Pachytesta</i> BRONGN.		
		Cyclopteridaceae	Neurodopteridaceae	<i>Neuropteris</i> (BRONGN.) STERNB.
				<i>Odontopteris</i> (BRONGN.) STERNB.
				<i>Macroneuropteris</i> C.J.CLEAL et al.
				<i>Laveineopteris</i> C.J.CLEAL et al.
				<i>Margaritopteris</i> GOTHAN
				<i>Callipteridium</i> C.E.WEISS
Satellite-genus: <i>Medullosa</i> COTTA				
Satellite-genus: <i>Myeloxylon</i> BRONGN.				

ranked fossil-taxa for investigating large-scale patterns in vegetation history, such as the effects of mass extinctions (e.g., Cascales-Miñana et al. 2013, Cleal and Cascales-Miñana 2014).

“Artificial” fossil taxa

Another distinctive aspect of palaeobotanical taxonomy is that it is possible to have taxa for poorly preserved fossils that cannot be placed in a phylogenetic classification, except perhaps as satellite-taxa of a division or maybe class. Although such “artificial” taxa may be of limited phylogenetic or floristic interest, they have proved useful in palaeoecological studies or even just for curatorial purposes. Jongmans et al. (1935) suggested that the nomenclature of such taxa should not have to follow all of the normally-accepted rules for botanical nomenclature but this was rejected by most in the palaeobotanical community; some palynologists have also suggested using different taxonomic categories to those covered by the ICN (Hughes 1970, Hughes and Moody-Stuart 1969, Visscher 1971, Van der Zwan 1979) but these have also not been widely adopted. Although the ICN does not prevent the use of such “artificial” taxa, it does place some constraints on how they are defined if nomenclatural stability is to be achieved, in particular on the choice of type. This is best explained using a series of examples.

Hostinella BARRANDE ex STUR, 1881

Silurian and Devonian fossil floras regularly yield fragments of slender, dichotomous axes that lack spines, leaves or attached sporangia, but determining their taxonomic affinities is virtually impossible. In stratigraphically younger fossil floras, such remains would normally be dismissed as merely unidentifiable plant debris and would not be named taxonomically. However, they play a more important role in understanding the development of the earliest terrestrial biotas and (following Høeg 1942, 1952) they are often placed in a separate fossil-genus (e.g., Edwards 1979, 1980, Prestianni et al. 2012). The problem is that the generic types are Middle Devonian stems that appear to be parts of early progymnosperm fructifications (Matten and Schweitzer 1982). Since none of Stur’s types can really be incorporated within the generic concept as envisioned by Høeg (1942), it is illegitimate to use the name *Hostinella* in this way.

Psilophytites HØEG, 1952

Høeg (1952) created this fossil-genus to be similar to *Hostinella* as he had defined it, but for axes with “... spreading undivided spines.” Most of the specimens that Høeg listed as typifying the fossil-genus had either not been published with a species name or had been assigned (incorrectly, according to Høeg) to other, better-known species such as *Psilophyton princeps* DAWSON. However, one was the holotype of *Psilophyton rectissimum* HØEG (Høeg 1945), which consisted of a spiny axis lacking reproductive structures or anatomy, exactly as Høeg had defined *Psilophytites*. Since it is unlikely that reproductive structures or cell structure will ever be found for the *P. rectissimum* holotype, it is unlikely to be ever transferred to another, more natural taxon. It

therefore makes complete sense also to designate the Høeg (1945) specimen the generic lectotype for *Psilophytites*, thereby effectively stabilising the name for the fossil-genus envisaged by Høeg (1952).

Pecopteris (BRONG.) STERNB., 1825 (≡ *Filicites* (*Pecopteris*) BRONGN., 1822)

Fern-like frond fragments with small dentate pinnules are common in many Carboniferous and Permian adpression floras. When evidence of reproductive structures has been available, they have been assigned to one of various fossil-genera (e.g., *Acitheca* SCHIMP., *Cyathocarpus* C.E. WEISS and *Seftenbergia* CORDA; Corda 1845, Weiss 1869, Schimper 1879) but for many species these structures are unknown (many such species can be found in the monographs by Corsin (1951) and Dalinval (1960)). Traditionally these fossils have been assigned to the fossil-genus *Pecopteris*, adopting the original diagnosis given by Brongniart (1822), but this overlooks the fact that the reproductive structures of the type of *Pecopteris* (*P. penniformis*) are well documented: they compare with the sori of the tedeleacean fern *Senftenbergia* (Bertrand 1912, Bek and Pšenička 2001, Frojdová et al. 2020).

There are two potential solutions to this problem. The original Brongniart (1822) taxon could be retained (with the change of rank suggested by Sternberg 1825), and all fern-like fossil fronds with small, linguaeform to dentate pinnules assigned to *Pecopteris*, irrespective of affinities. This has the advantage of inclusivity, as no fossils of this type need be excluded, but has the disadvantage of lacking any taxonomic resolution. Since it is now accepted that at least two distinct orders of ferns (Marattiales and Filicales) have fronds with such dentate pinnules, and they even occur in some seed-plants (e.g., Callistophytales – e.g., Crookall 1930), such a lack of resolution would be clearly disadvantageous.

It was for this reason that a more natural classification was developed that takes into account the reproductive structures (summarised by Cleal 2015). But what happens to the species for which the reproductive structures are unknown? It would be possible to create a new fossil-genus for the fossil-species for which reproductive structures are unknown. But for this to be a stable concept, the type would have to be chosen such that reproductive structures would be impossible or unlikely ever to be found – otherwise, as soon as those structures were discovered, the type would be excluded from the fossil-genus and a new name would need to be created. The only real solution is to make comparisons with the framework species of the classification (i.e., those for which sori/synangia are known) based on morphological features of the sterile pinnae, and named maybe using open nomenclature – not a totally satisfactory solution but maybe the only practical one.

Lepidostrobis variabilis LINDL. et HUTTON emend. by Chaloner (1953)

Brongniart (1828b) named and briefly described as the holotype of *Lepidostrobis* a fossilised cone figured by Parkinson (1804). From then on, all cones that even vaguely fitted Brongniart’s morphological criteria were included in this genus. Sporophyll morphology later came to be

regarded as the most important character for taxonomic purposes. *Lepidostrobus* was generally accepted to be a heterogeneous group including both bisporangiate cones with megaspores and microspores, and microsporangiate cones with just microspores.

However, it eventually became obvious that, wherever possible, the in-situ spores in the cones need to be thoroughly investigated for an accurate determination (Chaloner 1953, Felix 1954). The earlier taxonomic efforts emphasized the characteristics of the megaspores rather than those of the microspores. Although microspores from *Lepidostrobus* can be correlated with the genus *Lycospora* J.M.SCHOPF, L.R.WILSON et BENTALL (Schopf et al. 1944), it is often difficult to relate them to the dispersed spore species. Nevertheless, studies of in-situ spores have suggested that there are at least two groups of *Lycospora*: those with distinctive proximal ornamentation and broad equatorial flange occur within microsporangiate *Lepidostrobus* strobili, whilst those with smooth proximal surfaces lacking broad equatorial flanges occur within bisporangiate strobili (Thomas 1970b, 1978, Thomas and Dytko 1980). Since the type of *Lepidostrobus* contained microspores of the type found in microsporangiate cones, Brack-Hanes and Thomas (1983) redefined *Lepidostrobus* as a fossil-genus of microsporangiate strobili; bisporangiate cones formerly included in *Lepidostrobus* were transferred to *Flemingites* CARRUTH. (Carruthers 1865).

So, what should the strobili that lack evidence of their spore content be called? They originally tended to be referred to as *Lepidostrobus* sp. but there was also a tendency to give them specific names based on morphological features. This could imply they were microsporangiate cones, which might not necessarily be correct and could be misleading. Chaloner (1953) suggested that the fossil-species *Lepidostrobus variabilis* as emended by Arber (1922) should be retained as a designation for such barren cones (the revision of this species by Sen (1958) should probably be rejected as having been based on contaminated samples – Bek 2012). This seems to us as an admirable suggestion and would leave no doubt about its use when applied to figured cones or identifications in species lists.

***Taeniopteris* BRONGN., 1828a**

Cycad-like fronds are common in Mesozoic fossil floras but it has been recognised since Thomas and Bancroft (1913) that they include both cycadalean and bennettitalean foliage, two groups of seed plants that are only distantly related. The two types of frond can be easily distinguished if cuticles are preserved but is less so in impressions. Some of these foliage genera are sufficiently distinctive morphologically that they can be separated without cuticles, and hence assigned to either the cycads or bennettites; the distinctive *Otozamites* BRAUN (Braun 1844) fronds, for instance, are generally regarded as bennettitalean (Harris 1969). Other genera are more problematic, however, not least the more or less entire leaves of the *Taeniopteris/Nilssonina/Nilssoniopteris* complex.

The nomenclatural confusion surrounding the cycadalean *Nilssonina* BRONGN. (Brongniart 1825) and bennettitalean *Nilssoniopteris* NATH. (Nathorst 1909) has

been extensively discussed (Cleal and Rees 2003, Cleal et al. 2006, van Konijnenburg-van Cittert et al. 2017, Pott and van Konijnenburg-van Cittert 2017) and need not be repeated here. The lectotype of *Taeniopteris* as designated by Cleal and Rees (2003: 763) is a very similar shaped leaf but with no cuticle preserved. Since this fossil originated from the Middle Jurassic Stonesfield flora that hardly ever yields cuticles, it will almost certainly be impossible ever to place the *Taeniopteris* lectotype within the circumscription of either *Nilssonina* or *Nilssoniopteris*. To further clarify the situation, Cleal and Rees (2003: 762) emended the diagnosis of the genus containing the type of *Taeniopteris* so that it can only include species that have not yielded cuticles. By strictly following ICN, therefore, we have ended up with three fossil-genera of essentially similar-shaped entire or near-entire cycadophyte leaves: *Nilssonina* for those species attributable to the Cycadales, *Nilssoniopteris* for those attributable to the Bennettitales, and *Taeniopteris* for the less-well known species unattributable to either group.

***Androstrobus* SCHIMPER, 1870 emend. by Glasspool et al. in Deng et al. (2014)**

Androstrobus has been widely used for adpressions of Mesozoic cycadalean pollen organs (e.g., Harris 1964, Watson and Cusack 2005). The genus was originally defined through relatively generalised morphological characters but van Konijnenburg-van Cittert (1971) refined the definition using cuticular and pollen characters, and a morphologically similar set of fossil cones was separated off into a second fossil-genus, *Hastystrobus* VAN KONIJNENBURG-VAN CITTERT.

However, Archangelsky and Villar de Seoane (2004) pointed out that the holotype of *Androstrobus* preserves neither cuticles nor pollen, so it is impossible to confirm if it in fact belongs to either *Androstrobus* sensu Konijnenburg-van Cittert (1971) or *Hastystrobus*. Consequently, Deng et al. (2014) proposed that *Androstrobus* sensu Konijnenburg-van Cittert (1971) should be placed in a new fossil-genus, *Schimperoastrobus* GLASSPOOL, J.HILTON, S.H.DENG et DEJAX. Deng et al. (2014) also emended *Androstrobus* to include only cycad-like microstrobili of this type, but for which pollen or cuticles are unknown. As pointed out in Deng et al. (2014), this limits the use of *Androstrobus* in phylogenetic studies, but is a useful taxon for recording cones of this type in museum collections and geological studies.

Conclusions

Palaeobotanical taxonomy would appear to differ conceptually from that used for living plants for the simple fact that it deals with the classification of inanimate objects and not of living organisms. As we have discussed in this paper, the separation is not always so clear-cut in practice because plant fossils are the remains of once living organisms and sometimes have remnant organic tissue such as cuticle or spores in reproductive organs. However, there are things that you can do with taxa of living plants (e.g., examine the complete organism, analyse DNA, fully investigate reproductive biology) that cannot be done with fossils and, for this reason, the two taxonomies have to be regarded as distinct.

Plant fossils are classified as fossil-taxa that can represent a part or combination of parts of the parent plant in one or more states of preservation, and at one or more stages of its life history, depending on the diagnosis. The circumscription of a fossil-taxon is not constrained by the ICN, which only specifies that the name of such a taxon must be a fossil specimen. This flexibility allows palaeobotanists to make decisions that could lead to taxonomic disruption or instability, but is this any different from the situation in neobotany? It should surely not be the role of the ICN to police palaeobotanists when making taxonomic decisions.

It is obvious that palaeobotanists must have a clear understanding of the diagnoses and circumscriptions of the fossil-taxa they are using because this can significantly affect the information that the taxonomic names are conveying. Although there is normally the aspiration that palaeobotanical taxonomy will at least partly reflect the phylogenetic relationships of the parent plants, the correspondence will rarely if ever be perfect. A fossil-species of foliage, for instance, may have been borne by more than one plant species; and in some cases, a plant species may have different types of leaf that when found isolated would be placed in different fossil-species or even fossil-genera (e.g., Shute and Cleal 2002). The ranks of the taxa may even be different – a fossil-genus may reflect a family or even order of the parent plants. Moreover, for a particular plant group, the fossil-taxa for different plant parts may reflect different taxonomic ranks of the plants: a fossil-genus of seeds may reflect the plant family whereas a fossil-genus of stems of the same plant may only reflect the taxonomic order. Uncritically collating fossil-taxa such as for diversity, biostratigraphical or floristic studies will evidently, therefore, be fraught with danger (see Cleal et al. 2012 for ways of overcoming this problem of taxonomic inflation).

Provided that fossil-taxa are used carefully, the flexibility of this system has many benefits as such taxa will provide an accurate picture of the taphonomically-complex plant fossil record. Nevertheless, this flexibility requires care when fossil-taxa are revised as information improves; for instance, combining fossil-taxa when two or more plant parts are shown in attachment can unwittingly disrupt the wider palaeobotanical taxonomy. Combining fossil-taxa might seem a good idea when working with an unusually well-preserved flora, but in fact delivers relatively little real scientific benefit to improving understanding of that flora and may disrupt the taxonomy being used by many others.

Ultimately, our only direct source of empirical evidence of past vegetation in deep time is the plant fossil record, and our models of phylogenetic and vegetation history have to be grounded in sound palaeobotanical taxonomy. This is particularly important for diversity and floristic studies, where accurate recording of taxonomic distributions is vital. It is critical that palaeobotanists understand exactly what is meant when a fossil-taxon is being recorded and how it is providing a different set of data compared with when a botanist is recording a taxon of living plant.

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