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# Durianology, discovery, and saltation — the evolution of aroids

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> *"If we become attentive to natural objects, particularly living ones, in such a manner as to desire to achieve an insight into the correlation of their nature and activity, we believe ourselves best able to come to such a comprehension through a division of the parts, and this method is suitable to take us very far. With but a word one may remind the friends of science of what chemistry and anatomy have contributed to an intensive and extensive view of Nature... But these analytic efforts, continued indefinitely, produce many disadvantages. The living may indeed be separated into its elements, but one cannot put these back together and revive them. This is true even of inorganic bodies, not to mention organic ones... For this reason, the urge to cognize living forms as such, to grasp their outwardly visible and tangible parts contextually, to take them as intimations of that which is inward, and so master, to some degree, the whole in an intuition, has always arisen in men of science."*
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> — J.W. von Goethe (1749–1832) in Brady, 2012: 272.

ABSTRACT. It is argued that E.J.H. Corner's 'durianology' is an integrative, holistic approach to the evolution of angiosperm form which complements reductive, atomistic phylogenetic methods involving the reification of individuated high-level abstractions in the concept of morphological 'character evolution'. A case is made that the Durian Theory involved in part the advanced, holistic cognitive mode of insight, and, drawing on recent findings from cognitive science, it is proposed that insight problem-solving may overcome some of the limitations and distortions of dis-integrative character analysis, and lead to discovery of novel morphological relations and global pattern recognition. Evidence drawn from molecular phylogenetic analyses, developmental studies, and from gross morphology is presented that supports an insight-based hypothesis of direct, saltatory derivation of the Araceae from an ancestor with shoot apices not enclosed by sheathing leaf bases, acropetally developed, reticulate-veined compound leaves, and a terminal polymerous strobiloid flower. It is proposed that this saltation led to an array of morphologically hybrid and compound decanalised structures blurring conventional morphological categories such as rhachis, rhachilla, petiolule and venation; leaf base and stipule; leaf and leaflet; leaf and perianth; flower and inflorescence; flower and floral organ; fruit and infructescence; and fruit and seed. The associated perturbation of developmental routines led both to great diversification and to widespread parallel simplification series. It is argued that holistic evolutionary hypotheses cannot usefully be tested using current atomistic phylogenetic methodology applied to morphological characters. It is suggested that holarchical (nested-hierarchical) rather than matrix character sets may provide a more holistic framework for evolutionary hypothesis-testing involving the interplay between molecular phylogeny, evo-devo data and hypotheses, and the quantitative and/or probabilistic analysis of contextualised character distribution.

*Keywords.* Araceae, characters, cognition, Durian Theory, E.J.H. Corner, holistic hypothesis testing, insight problem-solving, saltatory evolution

## Introduction

It is now almost thirty years since Hay & Mabberley (1991) proposed a saltational origin for the Araceae. It involves deep structural reorganisation of both vegetative and reproductive phases in processes which E.J.H. Corner (1906–1996), David Mabberley's mentor, famously author of the Durian Theory (Corner, 1949), and whose work has been characterised as "the most revolutionary contribution to botany of [the 20th] century" (Jacobs, 1976), had highlighted in plants as 'Transference of Function' (Corner, 1958). Corner's proposed evolutionary-developmental process is better known now as homoeosis or homoeoheterotopy [see Baum & Donoghue (2002) for explication of concepts implied in 'Transference of Function']. The case was laid out in some detail in our above-cited paper, and will be updated and corrected as part of a forthcoming book on the classification, evolution and natural history of aroids world-wide (Hay, in prep.), so I will restrict myself here to the key points, address how they stand now in the light of more recent research and thinking, and propose that, in spite of plant macroevolution having been almost entirely usurped by contemporary phylogenetic approaches which perceive it through the (dis)figurative lens of 'character evolution', there is not only room for, but also advantage to be gained by embracing complementary ways of thinking, and exploring what holism might both contribute and entail doing differently. First, though, what has 'durianology' got to do with it? Indeed, what is it?

## Durianology, insight, and method

In Corner's own words, durianology "is a species of tropical holism" (Corner, 1952). The term, rather quaint-sounding now perhaps, and thus possibly distracting from its significance, was coined by Corner not to point directly to the study of durians *per se*, but to the approach he took — his way of seeing, and his insight — in articulating and then further applying the Durian Theory to explain the origin of 'the modern tree' [I have always thought this phrase in the title of the initial paper a little odd, since partly underpinning the Durian Theory is the existence of so many different ways of being a tree — see, for example, Hallé & Oldeman (1970)]. While the durian (*Durio* Adans., now in Malvaceae, then Bombacaceae) certainly figured in it, the theory was brilliantly sweeping: it was, as Corner worked it through over the years, the only holistic, overall conception of the evolutionary development of the now dominant angiosperm vegetation world-wide, as the late Marius Jacobs of Leiden pointed out forty years or so ago (Jacobs, 1976), and so it remains, exactly seventy years later — a great banquet of original, insightful ideas with myriad profound implications for the evolution of development, almost entirely passed over for today's savourless gruel of 'character evolution'.

For the direct purpose of this essay, the Durian Theory's specific propositions (augmented in Corner, 1953, 1954a, 1954b) are perhaps less relevant than the way of thinking that durianology involved. An essential aspect of Corner's approach was to consider plants as integrated systems — integrated not only within themselves but within their ecosystems — systems within systems — the rudiments, at least, of holarchical conceptualisation, of which more later. Of course, I can safely presume that every botanist knows full well that plants are integrated living things, yet the extent to which our science treats them as such not only varies wildly, but is overwhelmingly concentrated at the dis-integrative end of the spectrum. Corner would likely have taken stern issue, for example, with contemporary approaches to reconstructing the flowers of ancestral angiosperms. More than half a century ago he admonished: "[Theories of the origin of the flower] are developed regardless of the fruit to which the flower is a prelude... But they are the purpose of the flower which with its ovules is the neotenic, precociously functioning, reproductive bud... To omit the fruit and the seed from a theory of the flower is academic and abstract, and, if theoretic, cannot be regarded as a working hypothesis; that is to say, a theory so abstract is not useful." (Corner, 1963). Sauquet et al.'s well-publicised recent paper (2017) is a case, among many, in point. It is a major piece of atomistic work in which they claim to 'show' what was 'the ancestral flower'. Yet to someone interested in thinking more integrally, it shirks, first of all, the simple and perfectly straightforward biological truth that flowers do not have descendants — no part does, so there can be no 'ancestral flower'.

Perhaps this is a petty semantic quibble: perhaps 'ancestral flower' is simply shorthand for 'the flowers developed by the original angiosperm plants'. But there is not a plant to be seen in their analysis, so evidently it is not. It is noteworthy that, *inter alia*, their reconstruction itself does not even offer an idea of the *size* of the 'ancestral flower', yet, in botany, as Corner was at pains to point out, size matters (Corner, 1949, 1967) because it impacts on everything else one way or another — e.g. Corner's Rule (Smith et al., 2017). Sauquet et al.'s reconstruction is an abstract flower entirely in a vacuum, divorced not only from the fruit to which it is a prelude, but also from the inflorescence, the twig, the branch, the foliage, the plant as a whole, and the forest; divorced, in fact, from everything that leads to it and to which it leads; divorced from any of the context in which it exists, and on which it entirely depends for its very existence. The reconstruction is at best an elegant methodological edifice teetering on footings of biological sand; at worst a sterling piece of work firmly grounded in what to a holist is a colossal conceptual error. Either way it is meretricious, and a product of mainstream botany's modernist, disintegrative flatland. On the other hand, "The [durian] theory incorporated the classical theory of the carpel and extended, *of course* [emphasis added], to flower, leaf, branch, stem and root" (Corner, 1963).

Corner, as a holist, spoke and wrote unequivocally of plants' parts, and vigorously defended the concepts of classical morphology (Corner, 1966a): "meeuseology is rubbish" he scrawled as a postscript in a letter to me in 1992, referring to Meeuse's (1965) so-called 'new morphology'! Yet he was the very opposite of rigid when it came to plant form: indeed 'Transference of Function' (Corner, 1958), the Durian Theory's key evolutionary mechanism, is a thoroughly dynamic concept which has led to ideas of quite radical morphological novelties, mixed and partial homology, and morphological continua, later articulated in particular by Rolf Sattler and colleagues including Mabberley and myself (e.g., Sattler, 1992, 1993; Hay & Mabberley, 1994; Mabberley & Hay, 1994; Rutishauser & Isler, 2001; Sattler & Rutishauser, 1997). Although Corner clearly thought of plants as systems, he was, as we all are most of the time, shackled to fragmenting language: familiar and largely inevitable nouns such as 'leaf', 'flower', 'stamen' and so on all reify zones of a heterogeneous continuum as discrete components, despite the fact that they emerge seamlessly in the development of a self-organising whole. Of course, that a system is integrated and seamless does not in any way mean that it is homogeneous, and so the concept of parts is only somewhat erroneous, but distorting it inevitably is, particularly if parts are conceptually individuated, whence they may seem to be legitimate fragments.

Corner's approach, however, was almost always to consider parts in relation to one another, and to the plant, and to the forest, that is to say contextually: for example, "...[O]ne must conclude that the leaf has evolved as part of the shoot mechanism, in which progressive simplification has in many ways to render the branch systems more efficient in their elevation of the forest-canopy" (Corner, 1954a); or "The significance [of the fruit of] *Tabernaemontana* cannot be realised except by the hypothesis covering the evolution of the angiosperm forest" (Corner, 1954a); similar statements appear repeatedly in his writing. Since 'parts' are integrated, evolutionary change in one will certainly or probably impact upon others in the system in descendant plants: for example (and simply for the sake of argument now treating one of the propositions of the Durian Theory as given), the evolution of forest-making leptocauls from massive pachycauls will inexorably lead to smaller and/or simpler leaves, more branches, smaller fruits, fewer fruits per shoot, or cauliflory, and affect flower or inflorescence size, pollination, dispersal, predation and so forth, of course in a good deal more detail. What runs through durianology can be characterised as integrative thinking. It involves the interplay of analysis and synthesis — thinking about parts and the connections among them, while striving to grasp the whole at once.

In the opening of the Durian Theory, Corner (1949) hints that it was triggered by a singular event of mind-opening uncertainty:

"One Sunday in July 1944, when Professor Kwan Koriba was acting director of the Singapore Botanical Garden, we found in a patch of virgin forest on the island the fallen fruits of *Elaeocarpus javanicus* (Tiliaceae) [sic — actually *Sloanea javanica* (Miq.) Koord. & Valeton (Elaeocarpaceae)]. They appeared to us to belong to the Meliaceae, Sapindaceae, Flacourtiaceae, Sterculiaceae, Bombacaceae, and even Connaraceae, until we could correct ourselves in the herbarium, *but this very confusion led me to* *inquire* [emphasis added]. It seemed that this kind of fruit — a red loculicidal capsule with large black seeds hanging on persistent funicles and enveloped by a red aril... must have been the ancestral fruit of this group of families. And if of this group, why not of all flowering plants?"

On the face of it, that last question seems extravagantly wild coming from doubt over the identity of a single fruit. Yet it must be remembered that Corner, the mycologist whose thought had not precipitated out into the botanical orthodoxy of the time, had since the late 1920s immersed himself in enough tropical botany to have published his masterly two volume *Wayside Trees of Malaya* (Corner, 1940), of which the text alone exceeded 800 pages, four years before this excursion with Koriba. Thus his mind was replete with the detail of structure and biology of multiple plant families, known first-hand through living for many years with the native vegetation of a region of great diversity. Moreover, he had intended to write a companion to *Wayside Trees* on the larger monocotyledons, but "...war and international responsibility led me to return to academic life" (Corner, 1966b: ix). Nevertheless, his interest in palms, which family he came to regard as core to understanding the monocots, had been cultivated in Malaya at the time by the Goan botanist C. X. Furtado (1897–1980), and later resulted in his consummate durianological interpretation of the sweep of palm evolution in *The Natural History of Palms* (Corner, 1966b).

So Corner possessed quite extraordinary breadth of detailed knowledge, as well as the scintillating intelligence [I cannot forget sweatingly gabbling my responses under his wry, X-ray gaze during my doctoral *viva*] to integrate myriad threads into one coherent explanation, and, of course, captivating rhetorical powers to convey it. Nevertheless, T.C. Whitmore, an erstwhile pupil of Corner's at Cambridge, and a fairly significant figure in tropical forest botany himself, expressed the barbed opinion in his mentor's obituary (Whitmore, 1996), that the Durian Theory relied on style over substance. David Frodin, also among Corner's research pupils, defended his former supervisor's skilled use of rhetoric in a response to Whitmore (Frodin, 1996), but suggested, perhaps with cautious diplomacy in the immediate context of the moment (Frodin, pers. comm.), that the Durian Theory was intended as a provocation to think upon tropical forests, and not necessarily to be taken at face value. Corner was certainly impressed by the need to draw scientific attention to tropical vegetation (e.g. Corner, 1946, 1967) as it was even then disappearing, but assessment of the Durian Theory as an attention-drawing device does not, it has to be said, accord at all with Corner's later publications, and was quite contradicted by his remarks in private correspondence in which he made it very clear to me that he felt that the Durian Theory was indeed a genuine insight into the great intellectual problem of angiosperm origins which had so vexed Darwin and everybody since. Agnes Arber had described (see below) the feeling of conviction, certainty and even joy that accompanies a radical insightful breakthrough, and this accords with the sense that pervades much of Corner's subsequent writing. He remained convinced of the broad veracity of the Durian Theory's insights, and that it would "lead us into new halls of botany" (Corner, pers. comm.), for the rest of his life. It was without doubt no mere provocatively contrived conceit.

The Durian Theory has never been rebutted on its own terms, that is to say by falsification from a holistic perspective or by being supplanted by another holistic theory. In their study of durian phylogeny, Nyffeler & Baum (2000) concluded that "... despite its heuristic and aesthetic appeal, the Durian Theory seems not to be true even for the durians." But while their interpretation may be well justified within the atomistic perspective and methodology they adopted, I would submit that an interpretation from inside that perspective simply cannot speak incisively to the veracity or otherwise Corner's holistic proposition because the approaches are so different. Much earlier, fairly shortly following the Durian Theory's publication, an outraged Van der Pijl (1952) had unwisely worried Corner's ankles, brandishing disconnected and supposedly merely adaptive parts in impotent refutation of Corner's global, contextual hypothesis. In response, Corner rained down upon him superbly elegant derision which perhaps earned him few friends. His paper *Durians and Dogma* (Corner, 1952) particularly infuriated Van der Pijl (Corner, pers. comm.) who fancied himself the chief authority of his day on seed dispersal, and for whom their differences had already become transparently personal. Van der Pijl found himself reduced to simple condescension — "Corner based on the occurrence of arils in tropical fruits his charming but fantastical 'Durian Theory'" (Van der Pijl, 1952) — though years later his attitude softened somewhat. However, John Parkin's measured and thoughtful, though nonetheless piecemeal critique (Parkin, 1953) elicited a more restrained and reflective response in which Corner pondered upon the genuine challenges both of articulating and testing a complex holistic evolutionary idea (Corner, 1954a), challenges now even greater in today's competing climate of highly developed atomistic phylogenetic methodology. More recently, Robert Morley's comprehensive account of the origin and evolution of tropical rainforest (Morley, 2000), heavily reliant as it is on fossil evidence, provides some qualified support for the comparative morphology-derived Durian Theory, but notes that features of Corner's proposed angiosperm prototype appear at quite widely different times in the fossil record (Morley, 2000: 272–273). Corner, however, was clear that he did not expect much support from palaeontology as there was so little prospect of morphologically indicative remains of the relatively short, explosive initial phase of angiosperm diversification surviving herbivory and putrescence. If anything were to put the Durian Theory to the test from a perspective of still greater breadth and depth, it would surely be his own, later, classic study of *The Seeds of Dicotyledons* (Corner, 1976). Yet that vast work of years sowed no doubt, and, as Mabberley has noted, preempted by decades a good deal of the detailed propositions of deep-level angiosperm phylogeny deriving from molecular analyses (Mabberley, 2017: viii).

Corner of course was an excellent taxonomist of both fungi and flowering plants (most notably *Ficus*), and repeatedly emphasised in various of his commentaries on botany the dire need to improve plant classifications, particularly from tropical perspectives, in order to better understand plant evolution. Nevertheless he could be scathing about 'dyed-in-the-wool taxonomists', as he classed some, who made taxonomy an end in itself and quibbled at his general theory of angiosperm forest origins with tedious minutiae. H.E. Moore Jr., the American palm taxonomist, whose work differed so utterly in spirit from Corner's spell-binding palm synthesis, was one such. Corner described him to me as being completely unable to see the wood for the trees. The point of relating that is not to belittle Moore's contribution to palm taxonomy, nor to portray Corner as arrogant (though he clearly had a strong distaste for fools), but to highlight the contrast between the integrative thinking which Corner exercised, and the disintegrative thinking that characterised systematic methodology in Moore's time, and which has crystallised and been formalised to excess in contemporary phylogenetic analysis — insofar as its methods are brought to bear on the evolution of plant form.

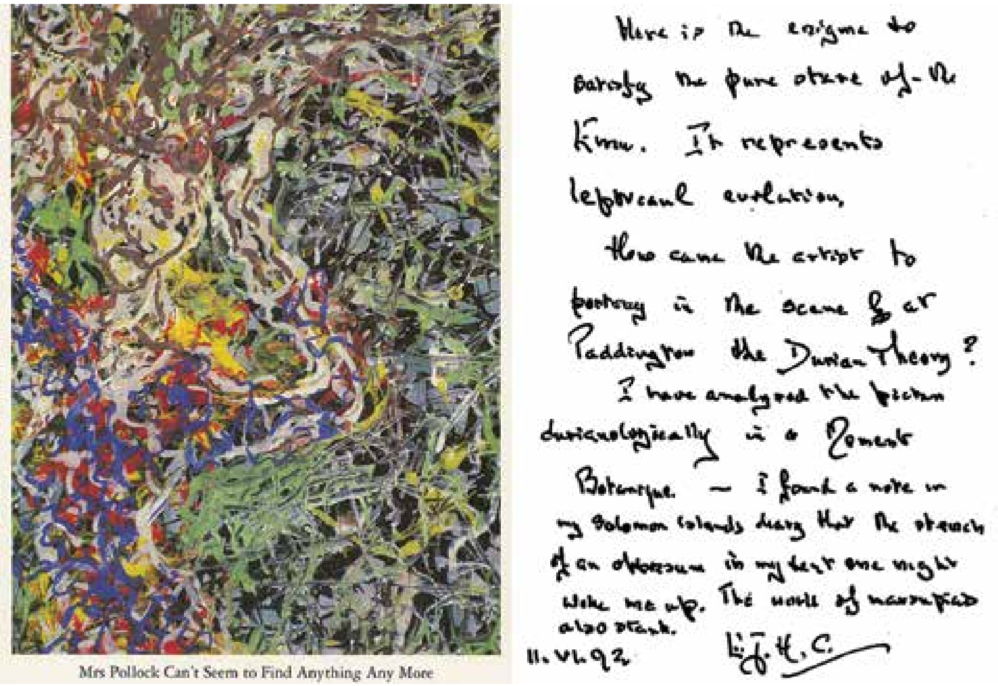
Although Corner was still active during the nascence of cladism, he had retreated as great age, blindness and poor health arrived by the time it grew in musculature to pervade evolutionary botany with the phylogenetic methods and thinking of current hegemony, and, though his mind stayed clear until his death (Mabberley, 1999), he did not publish any commentary. But it was not to his taste: he found it unrealistic and erring in understanding (Corner, pers. comm.), entailing an atomistic approach to looking at plants fundamentally different to his own (though, at the risk of presumption, I imagine he would have embraced molecular phylogenetic systematics with enthusiasm). He had a knack of conveying depth with wit, and in June 1992 he sent me a postcard of a painting by the Sydney artist Sally Swain entitled '*Mrs Pollock can't seem to find anything any more*' (Fig. 1). In it he wrote "Here is the enigma to satisfy the pure stare [sic] of the Emu. It represents leptocaul evolution. How came the artist to portray in the scene at Paddington the Durian Theory? I have analysed the picture durianologically in a *Moment Botanique* [unfortunately unpublished and inaccessible]...". Both intuitively and analytically, he knew that plant evolution is far more interesting, organic and complex than can be allowed by the mapping of atomised abstract characters onto bifurcating cladograms.

Nevertheless, of course, someone with his sharp perception was acutely aware of the pitfalls of classifying grades — defining taxa by homoplasies and plesiomorphies — and as such he was at one with one of the basic tenets of contemporary phylogenetic systematics (Frodin, 1996). Neither did he write of 'primitive groups' of angiosperms (other than disdainfully, e.g. Corner, 1966a, or, to imply groups retaining conspicuous primitive features, but not primitive as in the sense of ancestral, e.g. Corner, 1953), which even now still raise their heads despite conceptual advances in phylogeny; nor did he write of 'basal groups' or 'basal lineages', which are a misinterpretation of phylogenetic trees (Chase, 2004; Crisp & Cook, 2005), though today's literature is still riddled with explicit or implicit statements that living members or features of basal lineages are somehow archaic simply because their lineage traces directly to a deep node. He was emphatic that the features of evolutionary prototypes would be found dispersed among their descendants, and was concerned, of course, with how kinds of part are distributed across taxa. Yet he was not, as I have already emphasised, a mere atomist: parts he analysed and considered in the organic context of other parts or in relation to the organism, not as individuals. This is the essential point.

## The 'character evolution' delusion

Mabberley and I argued that characters are not real and therefore cannot actually evolve at all despite near ubiquitous talk of 'character evolution' (Hay & Mabberley, 1994). We pointed out that characters arise from comparison; in formulating characters one abstracts and reifies the 'sameness' in already abstracted parts that are similar but different: thus they are higher-level abstractions than parts. The 'spathe-and-spadix', for example, a *character* which robustly specifies the family Araceae, does not actually exist in the real world: there are thousands of different, actual manifestations of the theme in all their living complexity, but the family-specifying 'one' is a highly abstracted figment. It is presumed, though, that there was one with actual, intricate specific details developed in the ancestral aroid, but it cannot be captured with what amounts to a three-word slogan which simply symbolises the perceived similarity of aroid blooms absent all their material, biological intricacy. We proposed that the concept of 'character evolution' involves a category error since it imposes a material, biological process on ideas: map is confused for territory when one indulges in the fallacy of misplaced concreteness (Hay & Mabberley, 1994 and further references there). There is of course nothing wrong with abstraction itself: it is how science works. But the problems arise here with a) how good character abstractions are as metaphors for reality, both in themselves (the biological 'content' to which they aim to refer) and in their individuation (the discreteness of that to which they refer), and b) with mistaking higher level abstractions for lower level ones (e.g. confusing morphology based characters with actual parts). Parts are individuated elements of a map of the heterogeneity perceived within an organism's entire phenotye; characters are maps of the perceived commonalities between parts of different organisms. Thus characters are maps of maps, abstractions from abstractions, metaphors about metaphors. A *part* such as a leaf is a concept which refers rather directly to the biological reality [at least in a fragmentist/typological world-view: contrast Rutishauser & Isler (2001), and further references there]. A *character* such as leaf shape only 'contains' the shape aspect of the leaf and nothing more: it, the character, exists in the mind, not in the forest — its reference to reality is that much more remote and more selective than the 'leaf' itself.

Our viewpoint years later drew two curiously incompatible rebuttals. Kluge & Grant (2006), evidently blinded in its commission to the error they deny, were emphatic that there is no category error because both characters (and their states) and transformations are respectively real objects and real events. On the other hand, Weston (2000) had earlier countered that there was no category error because the notions of character *and* character transformation are *both* metaphorical. Clearly there has long been profound confusion over this basic question of character ontology, but Weston was of course correct: it is indeed layer upon layer of metaphors. It cannot be otherwise, which was exactly our point, expressed round about. The widely invoked concept of 'reversal' particularly highlights this truth, since biological evolution simply cannot go backwards (though evolutionary recall or reawakening or re-emergence, defined contextually and, as we might aspire to, in evo-devo terms, are possible, e.g. Mabberley & Hay, 1994; Mabberley, 1995). Form-based character 'evolution' or



Here is the enigma to
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Kew. It represents
leptocaul evolution.
How came the artist to
portray in the scene of at
Paddington the Durian Theory?
I have analysed the picture
durianologically in a Moment
Botanique — I found a note in
my Solomon Islands diary that the stench
of an Alocasia in my tent one night
woke me up. The smell of [illegible]
also stank.
11.vi.92 E.J.H.C.

**Fig. 1.** Postcard, sent by Corner to the author, of Sally Swain's painting '*Mrs Pollock can't seem to find anything any more*', and his inscription. [Image reproduced with the kind permission of the artist. © Sally Swain].

'transformation', far from being a real process, is the metaphorical *translation* of one abstract character into another abstract state where each is a *symbol* communicating an abstracted sameness in similar parts, which themselves are metaphors for an integrated continuum *dismembered* along 'boundaries' *projected*, to significant degree by *convention*, onto its heterogeneity.

But that is hardly how everyone sees it, and, with Weston's explanation of the metaphorical nature of both morphological character and state transformation in mind, we should be aware that any implication that morphological characters are objects, and/or that they actually evolve, automatically invokes category error, and then varying degrees of nonsense may, and indeed do, ensue. If we turn to a fairly recent textbook whose authors are amongst the more erudite practitioners and theorists of plant phylogenetic methods (Judd et al., 2016), and by which, therefore, many a cohort of student systematists has doubtless been introduced to and assimilated concepts of character and character evolution, we find this definition: "A heritable character is any aspect of the plant that can be passed down genetically through evolutionary time and still be recognizable" (Judd et al., 2016: 15). This is the character as object. They point out that the most commonly used heritable characters are those of DNA itself. Molecular-genetic characters are of the replicative, 'digital' (see Walker & Davies, 2013; Baum & Lehman, 2017) genotypic aspect of organism directly transmitted to the next generation. In that sense they are concrete, and indeed objects, and thus ontologically categorically different from abstract morphological characters. However, the authors go on to cite examples of heritable morphological characters, such as flower colour, inflorescence structure and habit (and many others, naturally), under genetic control and generally stably inherited from one generation to the next and which can be used to 'track' evolutionary history (Judd et al., *loc. cit.*). [Nevertheless it must be obvious that for the *vast* majority of plants, the genetic influence on form is assumed vaguely to be present rather than known in detail. Moreover, it has been proposed that genetic 'control' of form may not be all that detailed and that form is 'controlled' in the genetic *and* supragenetic, integrated processes of morphogenesis itself (e.g. Couturier et al., 2009; Prusinkiewicz & Barbier de Reuille, 2010)].

Now, every biologist knows full well that form, the phenotypic aspect of organism, is not *itself* transmitted from one generation to the next (save for the cellular paraphernalia and chemistry passed to the zygote): only its potential for realisation is handed on. Thus the phenotype *re-emerges* each generation as the plant's integrated, seamless developmental trajectory is realised, unfolding from the zygote through to the next generations of seed. The concept of morphological characters as being inherited is thus short-hand or, again, metaphorical. As importantly, if not more so, it is also something of a sleight of hand which appears to legitimise the consideration of fragments or other disembodied aspects of form as real, individuated things which can evolve in particular if they are said to be inherited in particular. We can easily forget that all 'parts' are context-dependent when confronted with morphological characters in a data matrix. Flower colour, say the redness or whiteness of flowers, is highly abstract when elevated as a character, notwithstanding the substance of floral pigment. Although the colour of flowers undoubtedly can and does change during evolution, it surely has extremely little freedom *itself* to evolve even though it may seem to be brought down to earth, so to speak, and made into an entity by the existence of a corresponding floral pigment gene. Flower colour simply does not exist without the flower, which itself is not independent of inflorescence organisation, position, phenology, and the ecological situation in which it develops and behaves. Flower colour is thus almost entirely subordinate to its wider developmental and ecological context (on which its allele too depends for both its developmental activation and its evolutionary persistence). Yet flower colour can be mapped onto a molecular phylogeny, its distribution quantitatively and/or probabilistically analysed, and a hypothesis of its biological *evolution*, completely *in vacuo*, proposed with precisely quantified degrees of confidence or credibility (e.g. Judd et al., 2016: 44). That, i.e. postulating the biological-evolutionary history of an isolated descriptive symbol, is the category error at work.

Another example of a 'bad' or 'metaphorically inadequate' character, particularly pertinent here in the context of aroids, is that of leaf venation. Much has long been made of monocot leaves being typically parallel-veined, and 'dicot' leaves typically having reticulate venation. Of course venation can be observed and described, and obviously it has changed during angiosperm evolution, but can *it* evolve? The answer is categorically not: it has virtually *no* freedom to evolve *itself*. Although we use the terms quite validly (but symbolically) as descriptors, parallel and reticulate venation do not exist in the domain in which evolution occurs: as characters they are high level abstractions, notwithstanding that veins can be directly seen and felt. Symbols created and used for descriptive purpose arising from comparison cannot necessarily be simply flipped to become the heritable objects of analysis: something that is a perfectly good taxonomic character may be perfectly useless as a supposedly individuated element of evo-devo syntax. Just as flower colour is to be understood in the context of flowers, pollination syndromes, inflorescences and so forth, leaf venation can only be understood in the context of leaf development which in turn cannot be adequately understood outside of the context of dynamic shoot apex architecture, habit, life form, habitat and so on. The idea that one should map venation onto a phylogeny, coding, for example, *Dracontium* L., *Caryota* L., and *Ravenala* Adans. equally as 'net-veined' (e.g. Givnish et al., 2005) is a patently misguided one beaten to the peak of metaphorical inadequacy only by the idea that one could infer the actual evolutionary history of leaf venation this way. Because leaf venation *per se* cannot evolve, it *per se* does not have an actual evolutionary history at all in any meaningful sense, despite obviously having systematic distribution, and use, as a character (cf. Mabberley & Hay, 1994).

Phylogenetic systematic literature is replete with propositions about 'character (or trait) evolution', usually without the slightest acknowledgement that the meaning is both metaphorical and tied up with implicit assumptions about morphogenetic causation. While phylogenetic systematics rightly places itself in a central role in the study of evolution, itself a real, overarching process and a core theme of biology, we can reasonably expect and indeed demand that 'evolution' mean something real (and surely the same for 'transformation') in this evolutionary biological context, or at the very least set a very high bar for metaphorical adequacy. Problems with morphological characters in phylogeny inference have long been recognised and thankfully morphology-based inference of phylogenesis has largely given way to the analysis of molecular data (e.g. Scotland et al., 2003), not that that is by any means pitfall-free (e.g. Jenner, 2004), though the issues are open to empirical solution in principle. However, the problem of morphological characters persists in their use in the study of evolutionary transformation of form by mapping them over molecular phylogenies. The 'objectivity' of morphology-based phylogenetic method is illusory: it is intersubjective, not objective — that is to say cultural, not objectively real, even though little of it is completely arbitrary — we are, after all, intelligent dedicated scientists standing on the shoulders of others. Nevertheless, we *agree* to atomise; we agree to atomise in particular ways (see also Cusset, 1982); we agree to further abstract and reify the same samenesses; we analyse their patterns in agreed ways; we take comfort in and often make over-reaching success-claims about our results; and yet we may not think deeply and dispassionately enough about what we are doing, until we eventually wake up to the most fundamental limitations, and indeed harm, to understanding involved — as Goethe pointed out centuries ago (see epigraph).

The examples I cited earlier were particularly egregious instances of 'character evolution' quite unable even to refer symbolically in any useful way to a real biological process, far less actually being real in themselves. Nevertheless the problem applies in principle to all form-based characters and their proposed translations: they are all abstractions at risk of symbolising processes of evolution which do not or cannot take place, though to varying degree. Metaphors are only as valuable as they are apt, and if thoroughly unapt they are no more than hollow verbiage, as then are the proposals of evolutionary trends arising from their use, regardless of how rigorous the analytical tools applied. Indeed, the defence of characters, both their content and the validity of their individuation, should be compulsory in the inference of morphological ‘character evolution’, but characters are almost invariably taken as given, as directly empirical objects whose real world systematic distribution can be analysed and which can materially transform through time. That is the category error at work, again. So while Weston (2000) was right to point out that there is no category error in the concept of character transformation *in principle*, category error nevertheless arises again and again *contingent* upon characters being treated as objects and not explicitly as ideas.

It is of course possible to vastly improve how characters are formulated, in particular using understanding of development and developmental genetics to arrive at characterisations that refer more adequately to the syntax of morphogenesis, and therefore to elements that perhaps can be said to evolve. Baum, for example, has proposed a concept of individuated ‘phenes’ corresponding to organismal features that are caused by DC (developmental-causal) genes “made up of the genetic information (which might or might not be physically contiguous in the genome) that is needed for the production of the organismic attributes that comprise the trait” (Baum, 2013; see also Baum, 2019 in this volume). I have no doubt that will be extremely informative, but it is still based on the premise that organisms are atomisable, despite the potential of the idea to exclude ‘parts’ that are morphogenetic-syntactical nonsense from a developmental genetic point of view. The phene concept in principle allows for more rational atomisation, providing greater adequacy of reference of the metaphor of individuated character to the heterogeneity of the whole, but it concerns me that, despite the potential identification of DC genes related to *individuated* traits, phenes, dependent on DC genes though they might be, as a straightforward matter of fact still require the entire developmental resources of the organism in order to emerge generation after generation at all. Phenes arise in the seamless, not atomised, context of development as a result of interlaced and encased developmental processes, and while potentially being a (more) rational fragment, the phene is still an abstracted bit. While DC genes may be the particular (proximate) developmental cause of phenes, their integral (ultimate) developmental cause is the organism itself, including the inherited environmental developmental resources deriving from its specific ecological station, from the context of which both the phene and its particular cause cannot escape.

The integrity of plants as organisms is not just developmental: plants, as whole organisms, exhibit behaviour and intelligence (Trewavas, 2014); nerve-analogous pathways facilitate communication and behavioural responses throughout the entire plant; and so it should not be up to the holist to prove the plant is whole, but up to the atomist to prove it is not — perhaps a futile task (but see above and Baum, 2019 in this volume). Nevertheless plants, having a strong colonial aspect, sit somewhere between (or better, straddle the concepts of) a holon — something which cannot be extrinsically divided without destroying its nature (an atom, a cell, a dog), and a society — a group to which individual holons can be recruited and which individual holons can leave, which thus can be divided without altogether destroying its nature (e.g. a population). A clumping plant which can be divided and retain its intrinsic nature is evidently towards the society end of the spectrum on which colonial organisms sit. Note however, that when, for example, trees are characterised as 'populations' of meristems (or shoots, or architectural reiterations, or roots etc), this is somewhat misleading as a tree is nearer to a holon than a society — neither a meristem, nor a shoot, nor a root, nor an architectural reiteration, can up sticks and join another tree, nor can a phene leave one shoot and join another: the shoot is not a society of phenes. While the phene concept would at least to some extent filter out evolutionarily nonsensical characters, one would still have to contend with the shortcomings of inferring evolutionary transformation through the quantitative or probabilistic analysis of the systematic distribution of individuated phenes. The idea of individuated phenes (and metamers) encourages the rationalisation of the modernist error of forcing differential, contextual (i.e. integral) evolution to be disassociated, mosaic (i.e. atomised) evolution (cf. Kirchoff, 2002). The (trans-modernist, 'systems') idea of phenes being recognisable but integrated, on the other hand, accords with the reality of differential evolution, but would reject disassociation. In principle there is a spectrum from phenes in lockstep to phenes in which change has almost no impact on certain other morphogenetically 'distant' phenes, but which are still only quasi-independent: morphological subunits are not merely juxtaposed to make the whole shoot-unit, but 'encased' within it (see Jeune et al., 2006). The phene is thus perhaps only meaningful syntactically in a top-down context of the development of the whole, and its 'individual' evolution is only comprehensible in the top down context of the evolution of the whole, constrained by, among other things, the nature of prototypes at nearer and further levels in the taxonomic hierarchy. In both developmental and evolutionary terms, then, the identity of the phene will be partly intrinsic (drawing on genetic information) but partly extrinsic or context-dependent (drawing on its relations with other phenes and the whole organism).

Weston (2000), discussing the potential impact (or otherwise) of Rolf Sattler's integrated, dynamic, process-conceptualisation of form (e.g. Sattler, 1992) on phylogenetic methods, stressed that in many instances molecular and (more or less static, fragmenting) morphology-based phylogenies show considerable congruence, implying that form-based, atomistic analysis sometimes 'works' in phylogeny reconstruction. Nevertheless, molecular methods have certainly taken us much further and more sure-footedly forward in phylogeny reconstruction generally, but, in acknowledgement of Weston's point, it is not inconceivable that morphologically atomistic approaches might be less violating in some groups than in others. For Araceae there has been only one entirely morphology-based cladistic analysis of the whole family, admittedly in the author's own estimation a tentative one (Grayum, 1990), and it, like all other post-Darwinian form-based classifications of Araceae, cladistic or not (including our own: Hay & Mabberley, 1991), completely missed, among other points, the now well-corroborated and extremely striking molecular-phylogenetic inference that the monoecious aroids form a single large clade which comprises about two thirds of the family (where previously it had been thought that monoecism had arisen repeatedly in different clades also including bisexual-floreted representatives). From a holistic perspective, the problem is fundamentally that current phylogenetic methods of inferring evolutionary transformation of form represent a purely bottom-up, atomistic endeavour, absent the top-down context of the constraining progenitor and the evolving whole, and this can be profoundly misleading.

## Holism

Scientific, that is to say largely exterior or objectivist holism (cf. Wilber, 2000: 70–72), cannot exist without analysis, though analysis, self-evidently, can exist without holism. Holism is thus trans-analytical and so, in principle, the more advanced mode of prehension — atomism and holism are not merely alternatives. Arguably, pure (i.e., in a sense, extreme) holism is aesthetic and non-scientific, a contemplative exercise, though Kirchoff (2002) has rightly made the point that appreciation of the holistic aesthetic is likely to enhance the reductionist enterprise. Rutishauser (2018), contrasting post-modernist and modernist views, observes that (post-modern) proponents of holism emphasise the heuristic value of complementing, seemingly contradictory, perspectives, while (modernist) reductionists appreciate crisp concepts and usually accept just one view as the right one. It can be said that holism in science stands in a holarchic, nested relationship to atomism/reductionism: holism transcends atomism, just as post-modernism transcends modernism. But it is arguable that holism is really post-post-modern, since post-modern ideas leave one with a mixed salad of perspectives rather than a greater integrated view, though post-modern thinking and values are a step on the way. That is all to say holism is more than (or extends beyond) atomism, while at the same time including it, and represents the integrative glue and contextual orientation needed for the deeper understanding of complex developing and/or evolving whole systems. However, when saying that holism transcends atomism, it is necessarily the case that holism, as a higher level integral enterprise, rejects *aspects* of lower level atomism (and of post-modern perspectivism) that are incompatible with higher level, holistic reality (objective realm), cognition (subjective realm) and values (intersubjective, cultural realm). Holism thus requires us not to reject atomism itself, but to reconfigure how it is done.

Where botany seeks to deal with the development and evolution of form, language itself is a challenge. Empirical botany generally is itself reductive and fragmenting, as is the language used to communicate it: most morphological terms are nouns, the majority of which enshrine pieces in stasis, and formal taxonomic descriptions still mostly exclude verbs, the words of process. The study of development clearly addresses dynamic change, but tends to rest on or launch itself from statically conceptualised pieces, e.g. ‘the development of leaves’. The limitations and/or distortions created by fragmenting morphological terms have been raised by Sattler (1992, 1993), Hay & Mabberley (1994), Ingrouille & Eddie (2006), Hesse et al. (2009), and other authors, Peter Stevens neatly putting it thus: “our thoughts as it were get trapped inside the terms we use” (Stevens, 2001 onwards). Despite our advocacy of process (and thereby, systems) conceptualisation (Hay & Mabberley, 1994), observing and describing organisms as process-systems is extremely difficult, and practically impossible in systematics where multiple taxa are necessarily involved: imagine generating process-descriptions for the entire Palmae, or *Euphorbia*! Kirchoff et al. (2008) provided a review of several conceptual ways out of the difficulty of fragmentation, typology and stasis, including developmental genetics, process morphology, continuum morphology and cladistically organised image-based, non-verbal representations. None of them, in those authors' own assessment, is altogether satisfactory, though each is meritorious to some extent. It is not surprising then that "[d]espite the efforts of Hay, Mabberley, Jeune, Sattler and Rutishauser, much of descriptive plant morphology [and with it form-based characterisation and the conceptualisation of evolution in phylogenetic methodology] is still based on a limited set of empirically based rules." (Ingrouille & Eddie, 2006: 132).

At the root of the empirical and linguistic challenges associated with the analysis and understanding of form is cognition. *Conceptual* solutions to the problem, such as those outlined by Kirchoff et al. (2008) may mitigate the violations of stasis, typology and fragmentation, but they are still analytical, and holism, by definition of course can never successfully be prosecuted solely analytically, though more dynamic and relational analysis and perhaps the use of non-verbal representations could in principle yield clearer glimpses. The impasse perennially faced by holists is thus as much cognitive (mental processing) as conceptual (the projection of mental representations onto the world). So, is there a *cognitive* way through? Is there a holistic cognitive mode which can be brought to bear on these fundamental issues? And might it complement purely analytical approaches which, while so entrenched, widely accepted and methodologically well-developed, suffer from inherent limitations and distortions imposed by the abstract morphological atomisation of holons, and by the assumptions that underlie the interpretation of the distribution of abstracted figment-fragments in vacuo (principally that they are acceptably individuated *a priori*).

## Insight problem-solving

While it may seem unorthodox to divert (even fairly briefly) into cognitive psychology in a botanical paper, it is nevertheless essential to the present discussion to do so, and I will start with a botanist who raised the matter decades ago. The enduringly celebrated Cambridge plant morphologist and biophilosopher Agnes Arber (1879–1960) sketched the advanced cognitive process of insight in her book *The Mind and the Eye*, which first appeared in 1954. Drawing upon the French mathematician Henri Poincaré (1854–1912), she described wrestling with the assorted minutiae of analytic observation, struggling to make multiple logical connections within complex phenomena, clearing the mind and, then, perhaps only if one is lucky, having the experience of an intuitive, integrative, revelatory flash of *insight* as it all comes together in new understanding, or perhaps in a more gradually realised coalescence around a significant insight to a key aspect:

"[Poincaré] noticed, broadly, that in each example [of his mathematical discoveries] there was first a period (or periods) of conscious work, which apparently failed to lead to any conclusion. Secondly, there was a *change* from conscious work. This change might take various forms: he instances either simple rest, or else variation of place or pursuit, diverting the attention for a time to other matters... [Then] a third stage — in which the question he had been pondering passed from darkness into full light — suddenly supervened. This illumination put him in possession of a 'roughed out' solution of his problem which carried with it, at least for the time being, an irresistible conviction of truth — *une entière certitude...* A great teacher of China was voicing something cognate when he spoke of "the long expenditure of strength, and then one day, in a flash, everything becoming linked up together"... [But, in biology as an empirical science first of all] new hypotheses come into mind most freely when discursive reasoning (including its visual component) has been raised by intense effort to a level at which it finds itself united indissolubly with feeling and emotion. When reason and intuition attain to this collaboration, the unity into which they merge appears to possess a creative power which was denied to either singly... [T]he moment at which a fruitful combination of ideas enters the awareness, is often charged with a peculiar feeling of joy, which precedes and seems independent of, the rational goal-attainment. (Arber, 2009: 18, 20, 21)."

Corner, as far as we know, left little explicit indication of how he arrived at the great integrative synthesis that the Durian Theory represented, though his son, John K. Corner, quotes from notes his father left him that:

"[The Durian] has brought to me a whirlwind of thought [sic]. Chance [sic] had directed me and I have built a Durianology about the evolution of the tropical forest, the evolution of flowering plants, their fruits and their seeds; and of course the natural history of those forests up to the descent of man" (E.J.H. Corner in J.K. Corner, 2013: 399–400).

Corner (the elder) characterised it as having "...arisen from a comprehension, or grasping together, of many tropical sights" (Corner, 1954a). It is, I think, significant that he deliberately restated a literal meaning of 'comprehension', in such a way as perhaps to suggest arriving at an insightful understanding of a lot of things at once, in an omnispective view. As I indicated earlier, the Durian Theory was grounded in a vast amount of detailed knowledge of living plants in their natural settings, was apparently triggered by a singular event of uncertainty, was characterised as holistic, and was held by its author with great conviction, pride and certainty, all of which, as we will see, point to it being insight-derived, at any rate in part.

Interestingly, Corner himself had wondered about the origin of the revolutionary ideas on the conquest of land by plants put forward by Oxford's A.H. Church (1865–1937) who had been a great influence on him (Corner, 1981). It seems likely that Corner himself had had the experience of insight to such matters, for he put it, implicitly at least, first in a series of possibilities: "A revolution in thought sets the historian looking for the roots. In this case there are none. It is not disclosed in any of his pages how Church came upon the new synthesis, suddenly [sic], gradually, through the vision of a predecessor, or of his own accord, perhaps as he listened to [Oxford zoologist] Ray Lankester's lectures or as he fashioned his own" (Corner, 1981). [Material has since come to light showing that Church clearly recognised the importance of the subconscious in problem solving, writing in a letter to Antony Gepp (1862–1955), phycologist at the Natural History Museum, London: "One only gets 1 or 2 ideas a day & it is slow work collecting them. ... I had not read Darwin's *auto*biography before last week. It is very illuminating after the sort of rubbish biographers compile. I was pleased to find he had the idea of scribbling down ideas as they came, in illegible writing [!], & then sorting them out later. Doing this sets the subconscious mind at work and the result turns up often in a few days" (see Mabberley, 2000: 68 & 70)].

Intuition and insight can have overlapping meanings, and both terms are used in more than one sense. Were one to say something like 'molecular techniques have brought new insights into phylogenesis', the meaning of insight is (cognitively) pedestrian, and it merely alludes to drawing on a new (and fruitful) source (and type) of information, without implying the engaging of a different kind of cognitive process. Likewise intuition has relatively quotidian meanings, such as an instantaneous mental sense about something, not involving consciously articulated thought processes. Sometimes, but certainly not always, this is a mischaracterisation of instinct and then pre-rational. However, intuition refers at a rational but subliminal level to, for example, an expert's immediate feeling that something makes sense, or the near instant identification of a plant without engaging conscious analysis — intuitive taxonomy. [See Hodgkinson et al. (2008) for a review of concepts of intuition as distinct from insight]. However, both intuition and insight can have another, higher-level meaning, referring to direct (i.e. without an explicit series of mental steps of which the subject is aware) problem-solving: the eureka moment, to fall back on a cliché.

Because of the confusing use of the word intuition in other senses which might mislead one to equate this high-level intuition with mere hunch, guessing or opinion, one might call this intuitive insight, rather than just intuition; but cognitive science now simply calls it insight. It must be remembered when interpreting earlier authors' use of the word 'intuition' that insight and intuition have often been used interchangeably, and it is necessary to take care to decipher the intended meaning. Moreover, "The words intuitive [insightful] and subjective must not be conflated. Intuition [insight] is a bright idea grounded in thorough familiarity with data and theory, while [merely] subjective means existing only in the mind or illusory. Intuition [insight] is fundamental to hypothesis generation, which is part of an objective scientific endeavor" (Zander, 2013: 30). The cognitive-scientific definition of insight remains somewhat problematic in that different researchers define it more or less widely, including or excluding various related cognitive phenomena. However, Kounios & Beeman (2014) in their review of the cognitive neuroscience of insight adopted a middle-path definition, as "any sudden comprehension, realization, or problem solution that involves *a reorganization of the elements of a person's mental representation of a stimulus, situation, or event to yield a nonobvious or nondominant interpretation*" [emphasis added]. They further noted that insight may be especially salient following impasse (e.g. after intensive, unsuccessful, rational analysis), and may be associated with emotional affect, but that, in their definition, these are not indispensable characteristics.

Some cognitive scientists have classed problem-solving in general into two approaches, ‘Search’ and ‘Insight’. Non-insight Search is analytical, logical, step by conscious step (including technological proxies such as the use of analytical software), while, as we have seen, “Insight is the sudden awareness of the solution to a problem (i.e. the “Aha!” phenomenon) with little or no conscious access to the processing leading up to that solution” (Kounios et al., 2008 and further references there). While some simple problems may be solved either by Search or by Insight (e.g. anagrams), in complex problems, it is likely that insight *follows* Search effort, and in very complex problems with multiple parameters, it must be so, if it occurs at all. This resonates precisely with the idea mentioned earlier that holism transcends atomism: insight is reliant on analytical effort, follows expert immersion in and grasp of detail, but yields something qualitatively greater than the piecing together of analytic observations. In the history of science, insight/intuition has been enormously important in both discovery and establishing a global view of problems (Blazhenkova & Kozhevnikov, 2012). In Poincaré’s aphorism: ‘it is by logic that we prove, but by intuition [insight] that we discover’.

The idea that the right hemisphere of the brain is the ‘seat of creativity’ belongs largely in the domain of pop psychology [but see Mihov et al. (2010) for a meta-analytic review of the lateralisation of creativity]. However, “certain *advanced* cognitive processes, such as the ability to recognise non-obvious insightful solutions to problems, may not rely on [more left hemisphere] language, and indeed may even be hampered by it” (Fiore & Schooler, 1998; emphasis added). Fiore & Schooler (1998) noted that insight may rely on cognitive processes associated with the brain’s right hemisphere, which may uniquely influence creative thought in its interaction with the left hemisphere. They drew a link between key properties of insight problem-solving and cognitive characteristics of the right hemisphere, including reliance on non-verbal processes, avoiding perseveration/fixation, access to non-dominant interpretations, and perceptual restructuring, and cited several strands of evidence supporting the idea that the non-verbal right hemisphere is particularly adept at global pattern recognition. [Possibly corresponding neuroanatomical asymmetry between the hemispheres has been summarised by Kounios & Beeman (2014).] Such cognitive abilities can be characterised as loosely associative, non-linear and *holistic* (DeYoung et al., 2008).

Insight solutions are, of course, not necessarily right, as Poincaré (1913) himself observed, but Salvi et al. (2016) have found that insight solutions are more likely to be right than analytic solutions, something supported by Webb et al. (2016) who related that “accuracy is often heralded by feelings of insight [‘Aha’] and insight-related affect (such as Confidence, and Pleasure)”, which in turn resonates with Agnes Arber’s observation quoted earlier. Insight has been the subject of psychological research for over a century, but the cognitive neuroscience of insight is a new area with connections to fundamental neurocognitive processes (Kounios & Beeman, 2014). Different individual preferences for Search or Insight problem-solving approaches appear to be related to resting-state brain activity, with higher right hemisphere resting state activity in high-insight individuals than in low-insight individuals, likely influenced by individual differences in neuroanatomy, microcircuitry, and neurotransmitter systems, all of which may be influenced by genetics and past experience, which in turn suggests that different individuals may be intrinsically more predisposed to insight problem solving than others (Kounios et al., 2008). The proclivity for creative insightfulness may also be associated with the ability to pick up on peripheral information, where non-insight problem solvers may be more focussed. Being more focussed can result in not-obviously germane information being discarded: consider, for example, in the process of character generation — with characterisation abstracting the sameness from things that are different, 'looking for characters' may blind one to the whole even within the narrow and artificial confines of the 'things' being characterised. Besides these possible aspects of intrinsic variation in individual insight potential, activation of certain parts of the brain may prepare it for insight problem-solving (Kounios et al., 2006), suggesting the aptitude can be cultivated, or at least facilitated.

Contemporary phylogenetic method, besides perhaps appealing, aesthetically, to those with an idiosyncratic preference for Search rather than Insight problem-solving, more importantly (and potentially deleteriously) places an impediment to insight problem-solving by obviating the impasse which may trigger a shift [or "cognitive phase transition" (Gabora, 2017 and further references there)], to 'right brain' cognition: there simply is no impasse when method merely demands data are passed through analytic software. With impasse so averted, and more advanced mental processing bypassed via the diversion of method and software, the result is methodological 'proof' (parsimony, confidence, credibility) which does not necessarily correspond to discovery. Every particulate character simply passes through computerised pattern analysis with its definition unchanged. The total product of observation has no opportunity to be mentally processed and reprocessed, undefined and redefined, and its contextual linkages and relations unrealised and re-realised subliminally during processing by the insightful mind. I am not suggesting, of course, that counter-intuitive results are not questioned, but even with re-characterisation, the process is fundamentally the same. The consequence is that phylogenetic-analytical character-based 'solutions' to questions of evolution of form are fixated in the limits, rigidity, categorical preconceptions and prejudices of abstract typological and atomistic character definition, with algorithms robotically seeking patterns within matrices of artefacts. Formulation of the problem of inferring an integrated ancestral or precursor organism in terms of conceptually immutable individuated fragments actually makes it impossible to solve, while at the same time rendering it susceptible to generating a robust methodological result. On the other hand the inherent limitations and distortions of 'left brain' conceptualisation and logic seem to be melted away in 'right-brain' processing, leading to insightful global pattern recognition, perception of novel contextual relations and, potentially, genuine discovery.

Plant molecular phylogenetic systematics, based on pattern analysis of concrete replicant objects, is the true modernist triumph in this context, though it is self-evidently not yet fully mastered and rests on many assumptions. However, 'tracking' evolution (and creating phylogenies) via abstract individuated morphological character/taxon matrices is a very unfortunate case of modernist over-reach which must be transcended to make real progress toward coming closer to understanding the historical transformation of integrated form. I have already used use the word 'transcend' here several times, carefully, stripped of mystical connotations, to mean 'to move beyond but include'. In this context 'moving beyond' is into a holistic mode, and 'include' means entraining those compatible, strengthening elements of modernist, reductionist achievement, while rejecting those of its distortions and weaknesses that may be avoidable.

In summary, as a complement to contemporary modernist, atomistic phylogenetic methods, integrative 'durianology' prioritises post-formal insight *and* formal-operational analysis; holistic integration *and* reductive fragmentation; process *and* pattern; contextuality *and* particularity; and a top-down (progenitor to descendant) approach *and* a bottom-up (descendant to progenitor) approach.

That is all well and good, but of limited scientific value if holistic hypotheses cannot be appropriately tested (though at least they may throw up quite radically new ideas of primary homology to think upon). So, how are they to be tested, and can there even be a holistic test at all? I will return to that question later, bringing 'characters' back into the picture, but first, the aroids and the articulation of an insight-based solution to the questions of their origin and their very diverse and pervasively ambiguous morphology.

## Aroids

Corner regretted that he had not paid much attention to aroids during his time in Singapore and Malaysia: "I never studied them as deeply as I should", he wrote to me in August 1991, "because I left them to Furtado in Singapore. [Furtado] knew astonishingly little formal botany and I used to take him round the Singapore Gardens and explain simple and compound leaves and so on! He thought well and wrote vaguely — round and round the point which often lay outside the circle. Holttum and I more or less rewrote his articles". So, while Furtado produced some publications on Araceae between 1930 and 1964 (see Hay et al., 1995), aroids barely featured in Corner's writings at all.

What led me, aged twenty-two, to inquire into them was the excruciating pain of hurtling, prone, down a muddy forest ravine at Gurakor in Papua New Guinea's Morobe Province, and grabbing reflexively at a clump of what transpired to be the tough and extremely prickly petioles of *Cyrtosperma macrotum* Becc. ex Engl. (Araceae—Lasieae), which lacerated my right palm as they slid through its grip. Astonishment and confusion followed expletives: aroids (such of them as I then knew) just do not have spines! David Mabberley's stellar lectures and mildly intimidating tutorials at Oxford had exposed me to his and Corner's writing, and tropical botany had burst into bright colour amid the beige of most other teaching. The Durian Theory had, among other things, recast armature from a mere surface adaptation into a sign of potentially deeper evolutionary consequence (Corner, 1954a). Scrambling filthy and bleeding back up to the plant, there it was: in the centre of the thorny basket of petioles was a newly emerged leaf blade; it was about 5 cm long, while the mature expanded hasto-sagittate leaf blades, with their unequivocally reticulate venation and spiky undersides, were about fifteen times that length. And looking at other plants round about in various stages, it was clear that the leaves expand in an acropetal wave, the petiole from the base up carrying the little blade aloft until it, at last, unrolls and expands. Why would any monocotyledon, that great lineage in which intercalary growth is so pervasive, allowing leaves and inflorescences to be exposed to the vagaries of the environment only in the latest stages of development, have so much of its shoot development externalised like this? The comparison I made on the spot was with *Euryale* Salisb. and *Victoria* Lindl. (Nymphaeaceae), but the inflorescence, though also exposed in an unexpanded state and carried up on a long, slender, acropetally maturing armed peduncle, being, it seemed, a compressed raceme of neatly hexamerous monocotyledonous flowers and a very modest bract-like spathe, was at first impossible to reconcile.

Since different taxa express differently such diversity as they exhibit, and taxonomic rank is somewhat arbitrary, it is risky to claim that one has the most among other very diverse families, but it is nevertheless readily apparent that Araceae are among the most diverse families of any plants in both their vegetative and reproductive organisation. There can be no doubt that they are by far the most diverse and speciose family in the Alismatales to which they are now widely agreed to belong, the other families being numerous and small (APG, 2016), and it is at least arguable that Araceae is more diverse than the rest of the Alismatales taken together, to which they are sister in some molecular phylogenies (see Stevens, 2001 onwards), though that distinction may go to Tofieldiaceae (e.g. Luo et al., 2016). Alismatales are sister to the rest of the monocots, barring *Acorus* L., which is sister to all the monocots (APG, 2016). In turn, monocots trace to a deep node within 'dicots', with magnoliids sister to [monocots plus eudicots] (APG, 2016). Crown group molecular age estimates for both monocots and Alismatales vary significantly but tend to centre on 140 million years, i.e. early Cretaceous at the end of the break-up of Pangaea, though some estimates extend well back into the Jurassic, and hence before the break-up of Pangaea (see Stevens, 2001 onwards). Araceae were already well divergent, with fossils exhibiting characteristics of all subfamilies by the early Cretaceous, and are one of the oldest families of angiosperms in the fossil record (Nauheimer et al., 2012). In short, the ancestors of aroids, alismatids, and monocots all take us right back into early angiosperm divergence, and the origin of Araceae is thus very close to the question of the origin of monocots. It remains the case then, that the origin of aroids is an important piece in understanding the early evolution of angiosperms, as we argued before the molecular revolution had taken hold (Hay & Mabberley, 1991). Here I will generally address form and diversity in the 'macro-aroids', since the 'micro-aroid' Lemnoideae, interesting as they are, do not seem to do much to illuminate the rest of the family.

## Vegetative phase

Overall vegetative form of aroids is extremely varied, but here I will emphasise diversity in leaf form and behaviour, mostly at the macroscopic level, and its relation with shoot modularity. Examples are illustrative rather than an exhaustive survey.

1. While many aroids have long leaf sheaths (or long leaf-enclosing cataphylls) within which the late stages of leaf development are almost completed, and the new blade emerges from the preceding sheath at almost full size in 'typical monocot' fashion, several groups have leaves which emerge in a highly unexpanded state, and several groups show a range of intermediate conditions. Both (at least relatively) early and late leaf emergence are found in all major clades of Araceae except Monsteroideae (all late), though very early emergence occurs only in Pothoideae (*Anthurium* Schott, but not *Pothos* L.) and Lasioideae (all genera; Fig. 2), with Zamioculcadieae, *Nephthytis* Schott and *Anchomanes* Schott (all Aroideae) similar in this respect.

2. The sheathing leaf base, and more importantly the deep internalisation of the shoot apex that goes with it, which Corner (1966b) discussed so eloquently, is characteristic of monocotyledons as a whole [bar some highly modified forms, e.g., in Araceae most species of extreme leptocaul, climbing and ramified *Heteropsis* Kunth in which the sheath is interpreted as fully adnate to the subtended internode (Mayo, et al. 1997: 116), as well as some similar *Pothos* species, where developing leaf blades are wrapped in older leaf blades]. In Araceae there is not only enormous variation in the sheath length relative to overall leaf size (and hence bud depth) but frequently also a sharp distinction in texture and behaviour between the petiole base and the sheath wings. Stipule-like cataphylls, usually bearing a qualitative resemblance in texture, colour and persistence/marcescence/deliquescence to the wings of the sheath, form when petiole and blade are not expressed in what is conventionally interpreted as a leaf primordium.

3. All species with early leaf emergence have reticulate leaf venation, while all with fully striate venation have late leaf emergence. In some relatively low-level ranks (tribes downwards) reticulate and striate venation intergrade (e.g. Monstereae; *Philodendron* Schott, both with late leaf emergence). Not only are late and early (or later and earlier) leaf emergence and reticulate and striate venation patterns found on both sides of deep phylogenetic divergences in Araceae, but they also occur together in more recently differentiated tribes; for example, among the monoecious Aroideae, in Spathicarpeae (e.g. *Dieffenbachia* Schott vs. *Taccarum* Brongn. ex Schott) and Aglaonemateae (*Anchomanes* and *Nephthytis* vs. *Aglaonema* Schott and *Aglaodorum* Schott).

**Fig. 2.** An emerging, highly divided leaf of a juvenile plant of *Dracontium gigas* Engl. (Araceae–Lasioideae), subtended by a short cataphyll and the petiole of the previous leaf (adult plants bear solitary leaves). The leaf emerges petiole apex first, hence the hooked shape. This blade is ca. 5 cm long and will eventually expand to almost a metre across. Near La Selva, Costa Rica, February 2018. (Photo: A. Hay)

4. There is a very strong, but not absolute correlation between divided (i.e. at the very least, trilobed, and at the most, decompound, and including fenestrate) leaves and reticulate venation, and of striate venation with simpler leaves: while there are many examples of aroids with simple leaves and reticulate venation, there are exceedingly few with striate venation and compound blades (e.g. the parallel-pinnately veined, pedately arranged leaflets of *Philodendron goeldii* G.M.Barroso).

5. Aroid shoots are very diverse, but most are physiognomically unbranched sympodia with a range of more or less precisely canalised numbers of foliage leaves and cataphylls per module. There is a tendency for more highly divided leaves to occur in species (or genera or tribes) with monophyllous (i.e. with one foliage leaf; there are also cataphylls present) modules, and in these, the role of protecting the next younger leaf before it emerges is transferred from the leaf base to the cataphyll. For example, in *Philodendron* subgenera *Philodendron*

and *Meconostigma* (Schott) Engl., which both have unifoliar modules, there are (a minority of) species with truly compound or strictly-speaking simple but very highly dissected leaves (e.g. pedate *P. leal-costae* Mayo & G.M.Barroso; 3–4 × pinnatifid *P. warszewiczii* K.Koch & C.D.Bouché), while in subgenus *Pteromishum* (Schott) Mayo, which has plurifoliar modules, all leaves are simple and entire (Grayum, 1990); in Pothoideae, divided leaves are uncommon and only represented (in a small minority of) *Anthurium* species, e.g. the pedate/radiate *A. clavigerum* Poepp. & Endl. with pinnately lobed leaflets, among others. These are evergreen plants whose leaves each persist for a considerable period and the crown consists of several successive unifoliar modules, a 'shoot of shoots' or meta-shoot. By contrast in those Monsteroideae with divided — including perforate — leaves (as well as those with entire leaves), the modules are almost always plurifoliar, but the leaf blades are always divided intramarginally — e.g. the complex hierarchies of perforations in *Monstera deliciosa* Liebm., *M. dubia* (Kunth) Engl. & K.Krause, *M. punctulata* (Schott) Engl. (Fig. 3A), *M. siltepecana* Matuda, and others. In Lasioideae the majority with plurifoliar modules have simple, entire (other than being sagittate to hastate) leaf blades, exceptions being 1 x perforate *Dracontioides* Engl., sometimes pinnatifid *Lasia spinosa* (L.) Thwaites and the uniquely 3–4 × pinnatifid *L. concinna* Alderw., the most highly divided of any marginally dissected plurifoliar aroid. However, the most highly compound of all leaves in Araceae almost all occur in the unifoliar modules of those deciduous geophytes which have only one leaf at a time (as adult plants), such as *Dracontium* and *Pycnospatha* Thorel ex Gagnep. (both Lasioideae), *Gonatopus* (Aroideae — Zamioculcadieae), *Taccarum* (Aroideae — Spathicarpeae), *Anchomanes* and *Pseudohydrosme* Engl. (both Aroideae — Aglaonemateae *sensu lato*) and *Amorphophallus* Blume ex Decne. (Aroideae — Thomsonieae); there are also single-leaved deciduous geophytes with simpler and indeed entire leaves. We return to the length of the leaf sheath in considering monophyllous modules: it is always short, regardless of whether the leaves emerge early or late in their expansion, because the sheath's role is taken over by more or less stipule-like cataphylls, as noted earlier. Curiously this is also the case in *Rhaphidophora neglecta* A.Hay & P.C.Boyce, the only case in the Monsteroideae with text-book perfectly pinnate leaves with fully individuated pulvinate leaflets, though it is not yet clear if this species has unifoliar modules (Hay & Boyce, 2019; see also below).

6. There are two broad classes of developmental pathway to divided leaf blades in Araceae — marginal and intramarginal. Marginal division is by blastozone fractionation (*sensu* Hagemann & Gleissberg, 1996), as in 'dicots'; intramarginal dissection (including fenestration) is, where known, by programmed cell death. These processes recur in various lineages, often in close systematic proximity to one another, in the same tribe, the same genus, and even in the same plant, and both occur in more or less close systematic proximity to undivided leaves with reticulate or striate venation. In the Monsteroideae, intramarginal dissection

**Fig. 3.** Examples of perforated and intramarginally divided leaf-blades in aroids. **A.** The complex hierarchy of lacunae in the leaf blade of *Monstera punctulata* Schott ex Engl., cultivated at the Jardín Botánico Lankester, Costa Rica, January 2019. **B.** The intramarginally derived leaflets of *Amydrium zippelianum* (Engl.) Nicolson each showing pinnate and reticulate venation and submarginal veins, cultivated in the Royal Botanic Gardens Sydney, March 2019. **C.** Intramarginally differentiated leaflets of *Monstera filamentosa* Croat & Grayum each with pinnate and reticulate venation and intramarginal veins, and each derived from the rupture of the thread-like residue of connecting lamina around ca. 5 lacunae to give the narrowed base and somewhat lobed margins. At Mogos, Puerto Jiménez, Costa Rica, February 2019. (Photos: A. Hay).

(and dissection of any form) occurs in just one member of the Heteropsideae, the (probably) monotypic Amazonian relict *Alloschemone* Schott*,* which is possibly nested in *Heteropsis* (Zuluaga et al., 2019). It further occurs in several lineages of the Monstereae, including *Amydrium* Schott*,* where *A. zippelianum* (Engl.) Nicolson, which virtually never has fenestrate juveniles and whose leaflets are remarkable for their pinnate venation running to conspicuous intramarginal veins and strongly reticulate finer venation (Fig. 3B), has been recently recorded (but not illustrated) as having leaves dissected by blastozone fractionation (Henriquez, 2015: 173). However, I have observed that the most newly emerging leaves of *Amydrium zippelianum* have the leaflet tips connected by an extremely fine and rather long thread of tissue which breaks at the slightest movement, and withers early on leaving leaflets which show little if any visible sign of having been connected (unlike the truncate-falcate leaflet tips of most dissected-leaved Monstereae, with more robust, though still necessarily fragile, leaflet tip connections). Either way, the leaflets of this species are remarkable for their complex, reticulate venation pattern and extraordinarily strong resemblance to leaflets developed through blastozone fractionation. In other species [*Amydrium medium* (Zoll. & Moritzi) Nicolson and *A. hainanense* (H.Li et al.) H.Li] the leaves are dissected intramarginally and/or fenestrate (the two remaining species, *A. humile* Schott and *A. sinense* (Engl.) H.Li, both diminutive, have entire leaves). In *Monstera*, there is a strong correlation between reticulate venation and fenestration: those species without fenestration either resemble juveniles of fenestrate species with reticulate venation and thus exhibit neoteny, or are robust plants with striate leaf venation (e.g. *M. anomala* Zuluaga & Croat; *M. standleyana* G.S.Bunting). *Monstera membranacea* Madison is remarkable in this group for having perforate and intramarginally dissected leaves with particularly conspicuous fully reticulate tertiary venation and pinnately arranged secondary venation along the lobe midribs (primary veins), though it is not unique in that respect. *Monstera filamentosa* Croat & Grayum is even more remarkable for intramarginally dissected very shallowly lobed leaflets, deriving from the breaking of several perforations aligned between the primary veins, yet each leaflet is pinnately veined and has intramarginal collective veins (Fig. 3C), again bearing very striking resemblance to marginally differentiated leaflets, though with the falcate/truncate tips seen in most dissected Monstereae. A similar correlation can be observed in the Old World relative *Rhaphidophora* Hassk., though the same level of leaf blade complexity is not found there. Nevertheless vestigial secondary veins along the leaflet or lobe midribs are also apparent in some *Rhaphidophora*, including the recently described *R. neglecta* which additionally has fully (and intramarginally) formed discrete leaflets (Fig. 4) — though its juvenile or sub-adult plants have decurrent leaflet lamina like the rest of the members of the tribe with pinnate leaves, and the adult leaflets lack intramarginal veins. Nevertheless all these variations are strongly suggestive of derivation not from an ancestor with entire, pinnately striate-veined leaves, but from one with

**Fig. 4.** The intramarginally differentiated leaflets of *Rhaphidophora neglecta* A.Hay & P.C.Boyce, with, uniquely in the Monstereae, no lamina decurrency at all onto the rhachis (except near the leaf tip, and also throughout the rhachis in juvenile plants). Each leaflet is separated from the next by a single lacuna making fully individuated leaflets joined in bud only at their tips. In the Royal Botanic Gardens, Sydney, June 2018. (Photo: A. Hay)

reticulate-veined leaves of higher complexity. How and why this might be so is addressed below. In the Lasioideae, *Dracontioides* has fenestrate leaves while *Anaphyllum* Schott, *Lasia* Lour. and *Pycnospatha* are dissected, sometimes highly so, with no sign of fenestration. Within *Anaphyllopsis* A.Hay (though the mode of dissection is unconfirmed in two of the three species, which are extremely rare), *A. americana* (Engl.) A.Hay clearly has intramarginally dissected leaves, *A. pinnata* A.Hay to outward appearance has marginally dissected pinnate and bi-pinnate leaves (with petiolulate, narrowly ovate-elliptic, acuminate-tipped leaflets), and *A. cururuana* A. Hay appears, again to outward appearance, to have both in the same leaf [with the anterior and posterior divisions apparently marginally differentiated and each part of the lamina fenestrate to intramarginally dissected; Hay (1988b), Gonçalves (2005)]. While it is of course rash to make that claim in *Anaphyllopsis* without developmental study, both modes of dissection were proposed to occur together in the *same leaves* in closely allied *Dracontium* (Hay & Mabberley, 1991), and have since quite clearly been observed operating together in the developing leaf of *D. polyphyllum*

L. (Poisson & Barabé, 1998). Intramarginal and marginal dissection occur in greater or lesser taxonomic proximity not only in the Monsteroideae/Pothoideae clade and the Lasioideae, but also in Aroideae, in the clade incorporating the Culcasieae (intramarginal or entire), which is sister to [Philodendreae (marginal or entire) + Aglaonemateae (*sensu lato*, intramarginal or entire)] (Nauheimer et al., 2012). Divided leaves in the rest of the Aroideae are marginally dissected. However, the manner of intramarginal dissection, at least in Aglaonemateae (i.e. *Anchomanes*) and possibly Culcasieae (*Cercestis* Schott) appears to be rather different from processes involving perforations arising from patches of programmed cell death in Lasioideae and Monsteroideae (see below). [A largely unknown possible dicotyledonous case of marginal and intramarginal dissection in close taxonomic proximity is the neotropical pachycaul megaphyllous genus *Pentagonia* Benth., apparently first alluded to by Madison (1977) in his revision of *Monstera*. It is the only member of the huge, otherwise simple- and entire-leaved family Rubiaceae in which compound and divided leaves occur (including truly pinnate — e.g. *Pentagonia osapinnata* Aguilar et al. and *P. imparipinnata* Cornejo, and bipinnatifid — e.g. *P. tinajita* Seem.), while NW Ecuadorean *P.* cf. *lanciloba* Cornejo has leaves which appear to be both pinnately lobed and conspicuously fenestrate: https://green-24.de/forum/wer-kennt-diese-155-pflanze-aus-ecuador-t80922.html.]

7. Simple, entire leaf blades in Araceae exhibit an extraordinarily wide range of venation patterns, even amongst almost identical leaf shapes. For example, sagittate and cordato-sagittate blades, differ in shape principally by the outline of the posterior lobes (pointed and rounded respectively). In sagittate blades, for example in many Lasieae, some *Philodendron*, *Nephthytis*, *Xanthosoma* Schott, *Alocasia* (Schott) G.Don and so forth, the posterior costae each run straight from the sinus at the top of the petiole to the tip of the respective posterior costa, with pinnately arranged primary veins on either side. In cordato-sagittate leaves, most notably in many species of *Anthurium*, particularly in but not restricted to Sect. *Belolonchium* Schott, as well as a number of *Philodendron* species, the posterior costae are basiscopically arcuate and on the acroscopic sides serially emit primary veins of decreasing size in a pedate array, each with pinnate secondary venation. These contrasting forms are suggestive of two evolutionary developmental routes to the simple, sagittate leaf from compound form: one process is the substitution of a branched rachis with ‘leaflet’ and the other is webbing or connation of the anterior and posterior lobes and of the leaflets of a pedate leaf, and the two in combination. Indeed much of the diversity of leaf form in Araceae can be accounted for relatively simply by invoking the replacement of all or each of the major branches of a highly compound leaf with either ‘leaflet’ or ‘ultimate rhachilla’ (for example where anterior and posterior lobes, or the segments/leaflets of a pedate-radiate leaf, are pinnatifid, e.g. *Anthurium clavigerum* etc), and the connation of divisions. In the pedate leaf itself every acroscopic branch of the leaf, including the entire anterior lobe,

and the acroscopic branch of every subsequent fork of the posterior rhachis are replaced by ‘leaflet’.

8. Some of the most complicated leaf-blades in Araceae, indeed of all monocots if not all flowering plants, are found in *Dracontium, Lasia concinna* and *Pycnospatha* (Lasioideae), and in *Anchomanes* (incl. *Pseudohydrosme*), *Taccarum* and *Amorphophallus* (all Aroideae). Their complexity derives not simply from the high order of division (to 4 or 5 x divided), but also in that the blades are not divided wholly hierarchically: low order branches bear (or fork into) not only next higher order branches, but also *directly* bear still higher order branchlets and leaflets (or leaflet-like segments) in a more or less irregular array. [This very complex form is also found in some species of *Tacca* J.R.Forst. & G.Forst. (Dioscoreaceae). Some species of *Gonatopus* Hook.f. ex Engl. (Araceae) also have very highly compound leaf-blades, but here in contrast the division is more regularly hierarchical, and *Anaphyllopsis* (cf.) *pinnata*, very recently rediscovered in the Colombian Amazon (Allison Muñoz, pers. comm.), also has individuals apparently with perfectly hierarchically bipinnate leaves]. In each case they develop rather differently (where known), and vary considerably in the state of expansion in which they are released from their enclosing bud, but the most extraordinary is *Anchomanes* where the whole blade emerges sagittate, entire and supervolute, and, as it unfurls, splits along predetermined narrow lines of weakness. The resulting highly compound mature blade is barely distinguishable in form from those of other highly compound leaved genera in which the blade develops from a branching primordium. Rhachis, rhachilla, and even petiolule (where present, e.g. *Anchomanes nigritianus* Rendle) and leaflet/segment all have their boundaries defined *within* the developing entire lamina. Indeed the resemblance to complex leaf blades deriving from marginal blastozone fractionation is so strong, that one has to question whether such a leaf is justifiably called ‘pseudocompound’, and then in turn question whether ‘pseudocompound’ is a good description even of the leaves of palms (cf. Cronk, 2009: 106), which are quite like those of *Anchomanes* but with striate venation and plication (which go hand in hand). Despite the plants being easily cultivated and propagated, leaf development of *Anchomanes* has not been studied recently, and it is not known either how or when the splitting lines in the lamina are formed. Nevertheless it would seem likely that this process occurs later in the development of the lamina than the initiation of patches of cell death that produce lacunae in the laminas of, for example, *Monstera*, which in turn occurs later, and of course in different positions, than the initiation of blastozone fractionation in marginally dissected aroid leaves (Gunawardena & Dengler, 2006).

This necessarily brief tour round the vegetative diversity of Araceae could be presented more exhaustively, clade by clade, and in far more detail but nevertheless it should be clear that these macroscopic, easily observed features are integrated with one-another and taken as such represent much of the extraordinary range of ways in which the vegetative phase of aroids emerges as a whole and extends itself into the environment. Early leaf emergence, short leaf sheaths and reticulate venation are linked, reticulate venation and leaf dissection (marginal or intramarginal) are linked, striate venation and simple entire leaves are linked, reticulate venation and leaf dissection together are linked to monophyllous sympodia, and so on, but none of these links is hard.

These examples of linkage encapsulate the tension between the one and the many, the whole and the part, constraint and freedom, synthesis and reduction that should be embraced at the core of biology, yet we seem intoxicated by the mechanistic and particulate. We could of course codify all these features (notwithstanding their generally continuous variation) into ‘characters’ and ‘states’, analyse their distribution with the variety of tools for statistical inference now available, and generate methodologically robust hypotheses of their ‘polarity’. Yet for all the talk of economy of hypotheses of ‘character evolution’ in phylogenetic systematics, whether based on or applied to morphology, shattering organisms into data matrices is necessarily an uneconomical start from which, as Goethe noted, there is no hope of recovery. Doing so addresses their ‘partedness’ to the exclusion of their ‘oneness’. Yet to the extent organisms *are* ‘parted’, it works, but because at the same time they *are not*, it is limited, and so gutting the live organism on the altar of (atomistic) method yields findings which may be implausible in an integrative context even if repeatable in a disintegrative one. To cite just one such example from fairly recent phylogenetic work on Araceae, Cusimano et al. (2011), followed by Nauheimer et al. (2012), determined that “monsteroid leaves”, which the reader is left to suppose means intramarginally dissected and/or perforate, evolved “at least twice” in the Monsteroideae [once in Heteropsideae which, as noted above, includes the intramarginally dissected monotypic relic *Alloschemone* — all the remaining genera have simple, entire, pinnately striate-veined leaves; and again in Monstereae where *Amydrium*, *Epipremnum* Schott (as currently circumscribed), *Monstera* and *Rhaphidophora* all include intramarginally dissected and or perforate-leaved as well as entire-leaved species, while *Scindapsus* Schott and *Anadendrum* Schott are simple- leaved]. This assertion appears to be drawn merely from the distribution of this ‘character’ and that of simple, entire leaves in Monsteroideae. It is made otherwise entirely *in vacuo*, and therefore seems capricious, regardless of analytical rigour. I mention this example in particular because intramarginally dissected and perforate leaves are a key piece in a more integrative insight to aroid shoots (see below) which draws a very different inference about the ‘meaning’ and evolution of leaf fenestration and intramarginal dissection in Araceae.

Returning to the diversity of shoot expression in Aroids, it is clear that there are evolutionary trends involving early through late leaf emergence, reticulate through striate venation, compound through simple leaves and so on, repeatedly in a number of clades, whichever way the series are initially read. There is parallelism everywhere. Any reconstruction or inference of an ancestral shoot state must account for both the enormous diversity and the extensive parallelism. Grayum (1990) and Mayo et al. (1997) are among those that have, using cladistic approaches, proposed that leaves of the ancestral aroid were simple, entire, striate-veined and distichous. Aroids with these without exception exhibit late leaf emergence, and they sound a lot like the 'typical monocots' of my 1960s British school biology text-books. Is this really a precursor state to *Anthurium*, *Monstera*, *Dracontium*, *Anchomanes*, *Amorphophallus*, *Xanthosoma*, *Gorgonidium* Schott, *Arisaema* Mart. and so forth? It does not offer any explanation for repeated parallel trends in the direction to the 'opposite' state of highly compound, reticulate veined, often early (or earlier) emerging leaves in those and further genera and deeper clades.

Developmental studies of leaves tend to focus on early stages of initiation and secondary morphogenesis while glossing over later stages of emergence and unfolding, and the appearance of venation patterns. The latter are easier and far less labour-intensive to observe, and hence afford the possibility of readily making comparisons over many taxa, and while shoots and leaves of course require, ideally, to be understood at all stages of development, there are nevertheless still insights to be gained at the macroscopic level. Curiously this striking feature of early leaf emergence to which Mabberley and I drew attention in Araceae many years ago has gone completely ignored. It does not appear in any morphological analysis, nor in any commentary on morphological 'character evolution' arising from the numerous molecular phylogenies of Araceae that have appeared in the 21st Century. Early leaf emergence occurs across a wide range of habits in Araceae, from climbers to more or less arborescent herbs, rhizomatous herbs, epiphytes and geophytes, each with counterparts with late (or at least later) leaf emergence. Within whichever habit the comparison is made, the contrast is between a relatively shallow apical bud exposing leaves early in their acropetal expansion, and relatively deep apical buds which retain the more vulnerable parts within the protection of more mature tissues for much longer. It is the key because it surely strains credulity to breaking point to envisage the repeated loss, as an evolutionary advancement, in largely relict aroid lineages of a self-evidently successful mode of shoot growth and leaf presentation that broadly characterises all the major clades of monocots which arise from less deep phylogenetic divisions. It must be noted here that neotropical *Anthurium,* the largest genus of Araceae by far, exhibits early leaf emergence in the great majority of its species; it is on the one hand a somewhat isolated group leading from a deep division in the family, but, on the other, its species show evidence of rapid, recent diversification (Carlsen & Croat, 2013). However, the second group which shows strikingly early leaf emergence is the undeniably relictual, pantropical Lasiodeae of whose ten genera, only three possess more than three species (*Cyrtosperma* Griff., *Dracontium* and *Urospatha* Schott). Amongst the Aroideae (*sensu lato* — including all monoecious aroids), there are but very few small, relict genera with late leaf emergence and striate venation [striate-veined Schismatoglottidieae now has over 30, mostly small genera, but this is a recent, specialised diversification — see Low et al. (2018) and Boyce & Wong (2019, in this volume)].

Champagne & Sinha (2004) viewed compound leaves as either equivalent to collections of simple leaves on a branch system, or as equivalent to divided simple leaves, and inconclusively discussed whether it was possible to answer which of these applies in terms of developmental genetics. On the other hand Efroni et al. (2010) in a review of simple and compound leaf morphogenesis, focussed on the usual few model plants, concluded “despite the use of common genetic components in the development of leaflets, lobes, and serrations, leaves are different from leaflets, leaflets from lobes, and lobes from serrations, each representing a distinct morphogenetic entity” (but see Runions & Tsiantis, 2017 who suggest a more realistic continuum view). In Araceae (and several other families) there are so many states and configurations intermediate between simple and compound leaves that such binary, categorical concepts of identity cannot possibly hold. Even in *Dracontium*, whose leaves are quite reasonably characterised as highly compound, some of the most highly divided such as those of *D. gigas* Engl. would be, according to text-book definition, classed as simple as there is narrow continuous blade decurrency along all rhachises, while in other species such as *D. spruceanum* (Schott) G.H.Zhu, also highly divided, the rhachises are naked and the leaves thus text-book compound. Likewise in intramarginally dissected (by cell death) *Rhaphidophora*, fenestrate, entire-margined leaves intergrade with entire, striate veined leaves on one hand, and on the other with deeply pinnatifid leaves with very narrow lamina decurrency on the rhachis through to pinnate species in which the lamina of the leaflet runs into the rachis but is discontinuous, to *R. neglecta* in which the leaflet bases are rounded and articulated to the rhachis on a pad, and are by any definition fully compound in the mature leaf. As described earlier, cases such as *Amydrium zippelianum, Rhaphidophora neglecta* and *Monstera filamentosa* clearly show the expression of ‘leaflet’ (as opposed to merely having lacunae) *within* the leaf blade. And lastly, of course, the whole highly complex and highly compound leaf blade of *Anchomanes* is derived from within an entire leaf blade, splitting along very narrow lines of weakness yielding rhachises, rhachillas, petiolules and leaflets with brochidodromous venation. Developmental genetics certainly has some interesting questions to answer in aroid leaves.

## Reproductive phase

Araceae are replete with ambiguous reproductive structures, and, as with the vegetative phase, there is very great diversity. There follow a number of key general points about aroid blooms and infructescences. Examples are, again, illustrative rather than an exhaustive survey.

1. No aroid multiplies its florets into a paniculate arrangement: there are no branched spadices. Indeed there is absolutely no sign whatsoever within Araceae, across its thousands of species and immense diversity of reproductive structure, ecology, and above all, size, that the spathe-and-spadix is reduced or condensed from a more elaborate inflorescence. Multiple groups of aroids produce several to many blooms together, and they are in every case arranged in variously cymose sympodia. [Except the highly modified climber *Pothoidium lobbianum* Schott (almost certainly better treated as a member of *Pothos* subgenus *Pothos*), in which there are sometimes multiple lateral blooms on a monopodial foliage-leafless shoot]

2. The spathe-and-spadix unequivocally functions as a flower in virtually the whole of the monoecious subfamily Aroideae, as is practically self-evident, and well known. However, in those groups with bisexual florets, such as *Anthurium*, many of which more readily accord, superficially, with the idea of the spathe and spadix as basically a spicate inflorescence subtended by a bract, it is also the main unit of pollination (Chouteau et al., 2008), and indeed the spathe is intimately involved in the structure and function of the bloom in most of the bisexual-floreted taxa, including most Orontioideae, many Monsteroideae, most Lasioideae, as well as many Pothoideae (Díaz Jímenez et al., 2019). This is not a new observation, of course: it has long been known that in all major clades of Araceae the spadix is almost always protogynous as an entity.

3. While the spathe is indeed sometimes bract-like (in the sense of a bract as a scale-leaf derived from the primordium base) and seemingly not involved in pollination, it is also often far more elaborate, resembling a perianth, a leaf or a combination of the two. The resemblance of the gigantic spathe of *Amorphophallus titanum* (Becc.) Becc. (Aroideae) to a perianth–leaf 'hybrid' is very striking, with the convolute lower portion corresponding to the leaf base, the forked ribs of the mid-portion echoing the forked rhachises of the leaf blade and the lobed margin and looped venation recalling the leaflets. Indeed the largest and/or most elaborate spathes in Araceae all show to some extent obvious expression of 'leaf' in what is functionally 'perianth': for example, the spathe of *Pseudohydrosme gabunensis* Engl. (Aroideae) has the upper part of the limb with a midvein issuing conspicuously reticulate and looped venation, and in *Dracontium* (Lasioideae), the spathe of *D. croatii* G.H.Zhu, for example, has conspicuous brochidodromous venation towards the margins and a thick convolute lower part, again with a midvein off which pinnate veins run. In both these latter, the anterior division of the leaf has a rhachis which reaches virtually to the leaf tip. Such a pinnate veined midvein is not observable in elaborate-spathed species of *Amorphophallus*, and here the anterior division of the leaf blade does not have a single rhachis as it is repeatedly forked, hence the spathe again echoes the leaf. Corner (1967) lamented that academic, excessively temperate-prejudiced botany failed to take seemingly extreme plants seriously and tended to dismiss them as adaptive curiosities, perhaps one of the reasons why he thrust *Durio* into the spotlight. However, that the spathe is in part a leaf and not a mere bract is readily discernible in members of the family with less elaborate spathes too, even if it takes the most elaborate to show the way: again in the Lasioideae (bisexual florets), *Lasia concinna* has a narrow spathe differentiated into a basal 'tube' separated by a constriction from the distal limb, and the spathe limb of *Dracontium plowmanii* G.H.Zhu & Croat is sometimes trilobed (Zhu & Croat, 2004) echoing the tripartite first division of the leaf blade, and what is probably a variant of *D. gigas* with a trilobed spathe has recently been found in Costa Rica (https://www.flickr.com/photos/charlierussell/6879509173/in/photostream/), in each case with the central lobe considerably exceeding the two lateral lobes. In Pothoideae, the spathe of *Pothos mirabilis* Merr., though simple (like the leaves),

clearly has leaf, not bract venation — it has a midvein with pinnate primaries running to an intramarginal collective vein; *Anthurium andraeanum* Linden ex André has spathe shape and venation that reflects its leaf blade. *Anthurium* does of course have a great many species in which the spathe is ostensibly bract-like, seemingly doing nothing more than protecting the immature spadix (though it nevertheless almost always persists well into fruiting, often growing and retaining or changing distinctive colour, perhaps suggesting more than a transient protective bract function) and others in which it is petaloid in appearance but with simple striate longitudinal venation. Yet there are also *Anthurium* species with elaborate spathes, such as the recently described *A. roseonaviculare* Croat & O.Ortiz with its convolute base and big flag-like limb. In most of the Monsteroideae the spathe is quite simple in gross aspect — mostly more or less boat-shaped, though in *Monstera barrieri* Croat et al. it is basally convolute with a cowl-like limb, and of course in *Spathiphyllum* Schott the spathe hardly differs at all in form from the (simple, pinnately striate-veined) leaf blade. Elsewhere in the family, most clearly in the monoecious groups in Aroideae, over and over again it can be seen that the spathe has a defined convolute base and more or less open and expansive limb which are open to interpretation as respectively expressing the much modified base and blade of a leaf. Interestingly, in the mutant cultivar *Alocasia* 'Stingray', where the distal half of the leaf blade is almost completely absent, reduced to a tail-like extremity, the distal part of the spathe limb is also wanting, bar a small, narrow, central extremity. The widespread received wisdom that the aroid spathe is merely an elaborated bract still seems open to question, to say the least.

4. Across the family, there is, broadly, a strong correlation between elaborate spathes and complex leaves with reticulate venation, and between simpler spathes and simple leaves with striate venation (note here that the Schismatoglottideae, with entire leaves and striate venation, exhibit very intricate and varied pollination-related spathe and spadix *behaviour*, but the spathe is nevertheless relatively simple at the gross morphological level; inversely, *Biarum* Schott, which have simple, though reticulate veined leaves have complex spathes). However, while virtually all aroids with the most elaborate spathes have elaborate leaves, not all aroids with elaborate leaves have elaborate spathes. So, as with relationships between venation, leaf form and emergence discussed above, there is a continuum between integration and independence of spathe form and leaf form.

5. It is true of all aroids that there are no bracts subtending the florets, and in species that have been examined in sufficient developmental detail, none is even initiated and then suppressed nor incorporated into a tepal (Buzgo, 2001; Remizowa et al., 2013).

6. Even amongst the groups with bisexual, tepalate florets, the number of floral parts is seldom canalised at generic or higher level: while 4-tepalate, 4-staminate florets are frequent (and characterise the huge number of species of *Anthurium*,

and most Monsteroideae except *Spathiphyllum*), other groups are predominantly but not entirely hexamerous (*Pothos*); the Gymnostachydoideae/Orontioideae clade has tetramerous and hexamerous representatives (*Orontium* L. is mixed); some Lasioids are also variable, especially *Dracontium* with up to 8–10 tepals per floret and sometimes a considerably greater number of stamens — up to 19 per floret, and up to 10 locules per ovary (Zhu & Croat, 2004). Most other Lasioids have unilocular ovaries, each possibly composed of a single carpel (Barabé, 2013), though *Dracontioides* is bilocular and *Urospatha* bilocular or unilocular. *Urospatha* and *Cyrtosperma* have (3), 4, 5 or 6 tepals and usually the same number of stamens per floret, while both species of Indian *Anaphyllum* are each recorded as having differing numbers (up to 5) of tepals and stamens per floret (Dominic, 2012), and so on. Amongst monoecious groups, *Philodendron* has enormously variable locule numbers, up to almost 50 per ovary. Male florets in monoecious groups, while often clearly recognisable and then often with large and/or variable stamen numbers, or smaller and more regular numbers, are in many monoecious taxa practically or actually undefinable, simply forming a mass of stamens in the male zone, or, as in the remarkable *Homalomena monandra* M.Hotta, male florets are reduced to single stamens arranged on the spadix in more or less regular parastichies. Male floral identity is thus often lost altogether, and likewise, female floral identity *per se*, while recognisable in those taxa where the pistils are regularly associated with staminodes, is lost when the female zone is reduced to a collection of pistils which are *functionally* indistinguishable from carpels on the female zone of the spadix axis.

7. Molecular phylogenies of Araceae since French et al. (1995) have all converged on the finding that the monoecious aroids very likely belong to a single large clade. This is by far the most striking and important outcome of the application of modern research techniques to aroid phylogeny (the second being the now rather well-corroborated position of Lemnoideae as sister to the Pothoideae/Monsteroideae clade plus the rest of Araceae).

8. All monoecious taxa (except a few cases of extreme modification and/or reduction) have the male zone of the spadix distal to the female.

9. It has been proposed, on the basis of detailed developmental study of the spadix of various *Philodendron* species and members of other monoecious genera, that there is a morphogenetic gradient between the gendered zones at the level of the spadix itself; indeed in the transition zone, gender identity cuts across florets themselves (especially when they are close-packed), with those on the interface being bisexual (though sterile) but with the male elements distal (with reference to the spadix axis) and the female element proximal (Barabé & Lacroix, 2000; Barabé et al., 2000, 2004a, 2004b). An earlier study on *Montrichardia* Crueg. (Boubes & Barabé, 1997), also showed this gendered split cutting across sterile bisexual florets in the transition zone. Somewhat different transition patterns

have been found in *Cercestis* and *Culcasia* P.Beauv. (Barabé & Bertrand, 1996), in *Caladium* Vent. (Barabé & Lacroix, 2002), and in *Schismatoglottis* Zoll. & Moritzi (Barabé et al., 2004b), but all are consistent with the spadix itself being the reference for gender differentiation, rather than being a neutral axis on which gendered florets develop.

10. The fruiting stage in Araceae exhibits a wide and extraordinary range of ambiguous structures and functions. An ordinary spike of individually distinct berries with little or no involvement of the spathe is common and widespread in the family (e.g. *Gymnostachys* R.Br., *Pothos*, *Anthurium*, *Podolasia* N.E.Br., *Aglaonema*, *Amorphophallus*, *Anchomanes*, *Arisaema*, *Arum* L. and many more). However, many Monstereae have transversely dehiscent fruits in which the upper thickened stylar portion of the fruit breaks away, usually attached to neighbours so that the infructescence is irregularly dehiscent *as a unit* (a 'monsterocarp': see Boyce et al., 2011), in curious analogy to the circumcissile carpels of, for example, *Talauma* Juss. [*Magnolia* sect. *Talauma* (Juss.) Baill.], which also come away in plate-like groups exposing seeds with pulp (sarcotesta; Romanov & Dilcher, 2013). In *Monstera*, at least, the exposed seeds can be easily pulled out and they come away in a neat, aril-like envelope of flesh which comes away from the fruit wall, functionally a sort of 'fruit-aril' rather than a seed-aril (Fig. 5A). Some *Anthurium* (Pothoideae) and *Anaphyllopsis cururuana* (Lasioideae) actively expel the berries from the fruiting spadix where they sit precariously or drop, while many other *Anthurium* and *Cyrtosperma cuspidispathum* [Lasioideae — so far the only species in this subfamily recorded with this behaviour, Hay (1988a)] not only expel the fruits but maintain them hanging, like arillate seeds, but here held by strips of tepal epidermis (an 'anthuriocarp'), in analogy to the etaerio of other *Magnolia*. Some *Anthurium*, such as the recently described *Anthurium decipiens* A.Hay & M.Cedeño (Fig. 5B) from Tatamá, Colombia, take the analogy with arillate seeds further still, indeed to an extraordinary degree, with the exposed tips of the immature fruits black (or otherwise sombre in most other species) through development, and the flanks, only visible when the fully ripe fruit is abruptly expelled from the tepals and left to hang, bright orange-red (or otherwise contrasting in other species) (Hay & Cedeño-Fonseca, 2019). The red-and-black colour contrast quite often found in tropical fruits, manifests in various other ways in some aroid infructescences. In some *Pothos* and in *Cyrtosperma bougainvillense* A.Hay, the tepals become very dark, almost black, and contrast with the orange to red fruits; in some *Arisaema*, such a *A. serratum*, the infructescence axis swells into a 'receptacle' and becomes black in contrast to the now separated red fruits, in analogy to an 'etaerio of berries'. In various groups, the spathe persists into fruiting evidently with a role protective of the developing berries in those cases where it encloses them. In some instances, such as in Philodendreae, it is generally the whole spathe which persists, while in others, such as *Alocasia*, *Dieffenbachia,* most *Schismatoglottideae,* and *Xanthosoma* (all now placed in quite divergent clades of Aroideae) it is only the basal convolute portion. In these groups the spathe is dehiscent when the berries

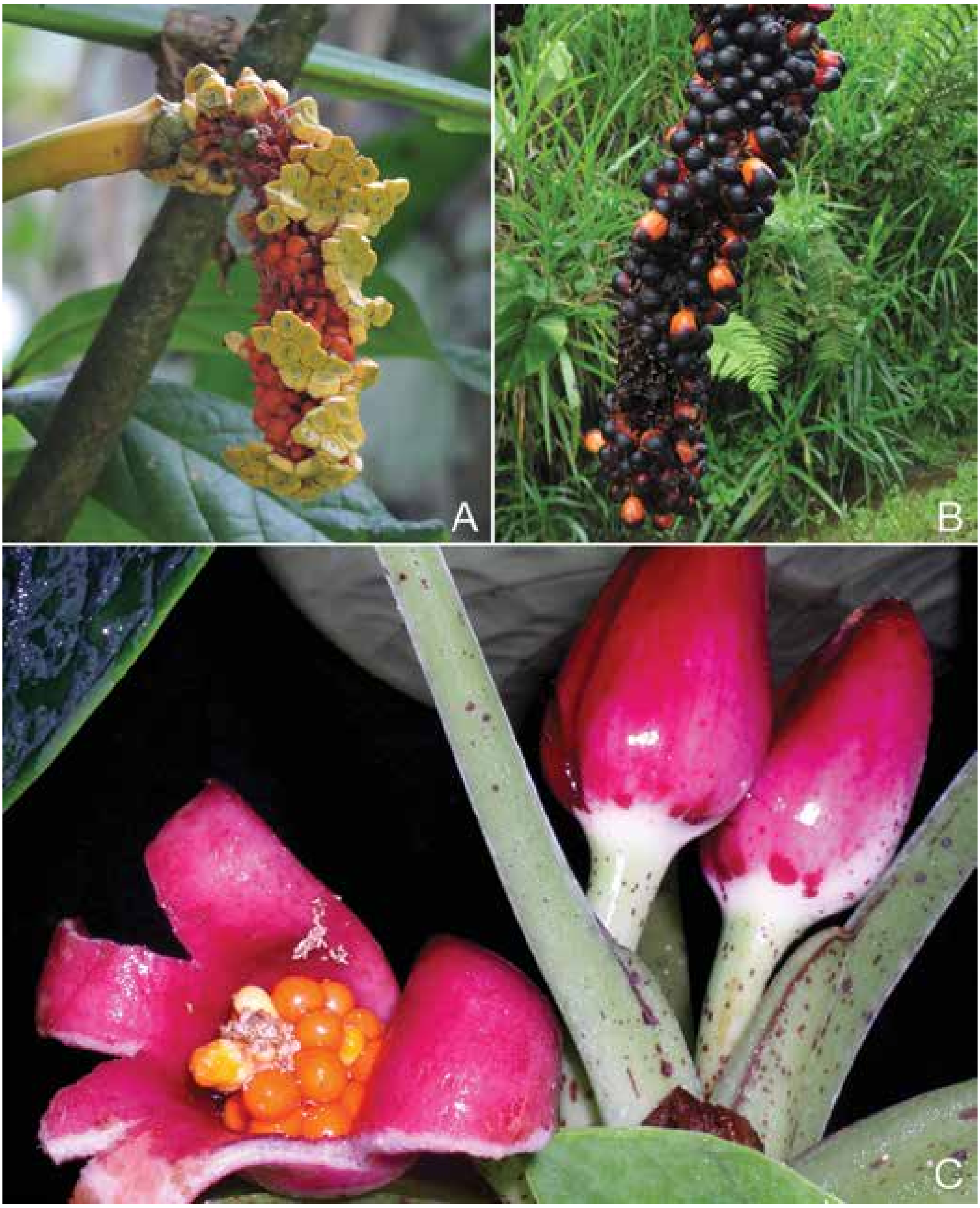

**Fig. 5.** Examples of fruit-like infructescences in aroids. **A.** The collectively circumcissile fruits of *Monstera membranacea* Madison revealing seeds encased in red pulp — a 'monsterocarp'; at Manzanillo, Costa Rica, August 2017. (Photo:). **B.** Ripe fruits of *Anthurium decipiens* A.Hay & M.Cedeño expelled from the spadix revealing orange flanks and hanging by inner epidermis of the tepals, so mimicking arillate seeds — an 'anthuriocarp'; at Cerro Montezuma, Risaralda, western Colombia, July 2018. **C.** The 'schizocarp' of *Alocasia chaii* P.C.Boyce, with the spathe base as 'fruit wall'; at Kapit, Hose Mts, Sarawak, Malaysia. (Photos: A, M. Cedeño Fonseca; B, A. Hay; C, P.C. Boyce.).

are ripe, and in some cases the spathe lining is brightly coloured (or white) and contrasting with or highlighting the berry colour (e.g. *Alocasia chaii* P.C.Boyce; *A. sarawakensis* M.Hotta and others). The result is a sort of 'capsule of berries' analogous to a dehiscent fruit containing arillate or sarcotestal seeds (Fig. 5C). In *Syngonium* Schott, meanwhile, the berries are connate and form what would conventionally be termed a multiple fruit, but it is enclosed in the persistent, *indehiscent* spathe base which becomes brightly coloured, forming, as it were, a 'berry of (connate) berries'. All of these examples can, of course, readily be discounted individually as somehow conjured-up curious adaptive novelties — that is the zoomed in 'trees' view [about which Corner (1952) had been so scathing], but taken together they form part of an extensive pattern of ambiguous structures in Araceae which straddle, blend or blur the hierarchical morphological categories both of flower and inflorescence, and of fruit and infructescence — i.e. seen in the zoomed out 'wood' view.

11. In the Lasioideae, again, there are the only two examples of armed fruits in the entire family — *Lasia spinosa* and *Pycnospatha arietina* Thorel ex Gagnep.: in both the fruit is indehiscent, leathery-fleshy and single-seeded, and the spines are vestigial with no apparent function.

## The hopeful monster — vegetative and reproductive phases

The proposition was that 'monocotyledonous' sheathing leaf bases and enclosed shoot apical buds were new at the beginning of Araceae, or Alismatales, perhaps derived from the homoeotic connation of leaf base and stipule of a more open shoot apex (Hay, 1986; Hay & Mabberley, 1991), and since it is now well supported that the beginning of the Alismatales was very near the beginning of the monocots, this hardly seems enormously controversial. However, in this saltatory scenario, the newly enclosed shoot apex is (still) associated with acropetally developing leaves and would have represented a very significant perturbation to the integrated processes of shoot development, since the environment in which pre-emergence stages of leaf development take place would have been radically altered. It would particularly impact on ancestrally compound acropetal leaves which would have to adapt to developing within and being extruded from a series of conic, tightly enclosing leaf bases. This leads to a series of more or less parallel trends towards ever simpler leaves, deeper sheaths, intramarginal dissection in some clades, and increased intercalary leaf development ultimately arriving at simple, entire, late-emerging, pinnately striate-veined leaves of many Monsteroideae, many *Philodendron*, *Homalomena* Schott, *Zantedeschia* Spreng., *Anubias* Schott, *Dieffenbachia*, Schismatoglottideae and so on, driven by internal adaptation to the inherited developmental constraint of the sheathing leaf base. Thus the most conventionally 'monocot' leaves in Araceae are the most derived, as understood in the context of the saltatory enclosure of a more or less open precursor shoot apex.

Since there is no evidence that aroid blooms are reduced from branched inflorescences, nor even from bracteate racemes, and since they unequivocally function as flowers, and since spathes are evidently leaves with the function of perianth, it was proposed that the aroid bloom was directly derived from a polymerous, apocarpous strobiloid flower (in which case, incidentally, the evolutionary status of floral polymery of Alistmataceae might require reappraisal). It is noteworthy in this context that over a century ago Church (1908: 76) expressed the view that in the evolution of the aroid inflorescence "a long series of phylogenetic stages may have been omitted". What we (Hay & Mabberley, 1991) proposed was the homoeotic shift of expression of 'perianth' into the subtending foliage leaf, and the re-expression of 'flower' in the floral organs of the strobiloid axis which became the spadix, yielding a meta-flower, a flower of flowers. This not only parsimoniously accommodates the key facts of the principal family reproductive character, but also offers a coherent explanation for the remarkable diversity of reproductive form, from flowering through to fruit and seed, arising in part through the novel recombination of developmental routines, i.e. a negative evolutionary constraint, as well as pervasive parallel evolutionary trends brought about by positive developmental constraints deriving from saltational transformation. Again, the major evolutionary trends are to be understood contextually, not merely by the analysis of character distribution. Since, in this scenario, the aroid bloom is a hybrid structure drawn from both vegetative and reproductive phases of its precursor, the evolution of reproductive parts cannot but be influenced at least to some extent by vegetative context: one cannot hope to understand the evolution of, for example, pollination systems in Araceae without an explicit theory of the spathe, which in turn in part relies on a contextual theory of the leaf. Merely mapping pollination syndromes or pollinator interactions onto molecular phylogenies largely misses the point, because without a holistic context there is little or no insightful clue about whence came the wherewithal to form these syndromes (cf. Bröderbauer et al., 2012; Chartier et al., 2013).

## Saltation

"Before the advent of evo-devo, the very idea of saltational evolution as an explanation for macroevolutionary transitions... was strictly banned as heretical. However, an appreciation of the non-linear character of the genotype → phenotype map is enough for us to realise how major phenotypic changes can be accomplished in a leap" (Minelli, 2018: 334). The principal objections to saltational evolution, i.e. dichotomous saltation — the mutational creation of a new lineage with radical phenotypic rearrangement in a single generation (Bateman & DiMichele, 1994, 2002) — had been the issues of whether radical phenotypic change required large-scale genetic change, and of the likelihood of survival and establishment of a suddenly re-organised organism. Saltational evolution in plants had been proposed by that other great pillar of 20th Century tropical botany, C.G.G.J. van Steenis, principally through allopolyploidy and neoteny (Van Steenis, 1969, 1977). It was curious, particularly given Van Steenis's second paper appeared in a volume dedicated to Corner's 70th birthday (Mabberley

& Chang, 1977), that he did not even mention, let alone countenance Transference of Function (homoeosis, homoeoheterotopy) as a means of saltation. It is of course now very well known that large-scale genetic change is not necessarily required for radical phenotypic change, and hence it is not necessary to assume that the generation of hopeful monsters is an impossibly rare event — rather it is likely occurring all the time (Bateman & Di Michele, 1994). Establishment, Bateman & DiMichele further argued, though this stage will undoubtedly filter out many failure pro-species, only requires vacant niches and relatively low environmental intrinsic stress: not an impossibly high bar either. [Van Steenis had relied on the not generally accepted idea that plants as a whole are not subjected to anything like the same intensity of selection pressures as animals]. More recently Theißen (2009) concluded that "the complete dismissal of saltational evolution is a major historical error of evolutionary biology tracing back to Darwin that needs to be rectified."

As noted earlier, the radical homoeotic reorganisation of the vegetative and reproductive phases of the living plant represents a massive perturbation of a highly complex, integrated developmental system, which may have two broad classes of consequence for subsequent evolution.

- In one, "saltation breaks [prior] canalisation, toppling the hopeful monster from the adaptive optimum of its parent(s) but also freeing the potential lineage for radical reorganisation of form" (Bateman & Di Michele, 1994) — i.e. it introduces the potential for the explosive diversification, through the exploitation of the novel recombination of developmental subroutines, and may include further saltational changes, particularly prior to the reestablishment of canalised/stabilised developmental trajectories. These consequences are thus broadly negative constraints.

- The second class of supposed consequence is the progressive evolutionary stabilisation of developmental routines of novel organogeny — i.e. a response to the need to recover developmental efficiency, leading to a great deal of parallel change in multiple lineages generated in the first consequence. This consequence is broadly a positive constraint.

The hypothesised new developmental environment of the acropetal compound leaf now in an enclosed bud, created perhaps by or consequent to the intercalary union of petiole base and stipule giving the winged sheath, would surely have been an enormously significant change. It would lead in every subsequent lineage (leaving aside Lemnoideae) to further structural/developmental adaptation for containing leaves in confined space and enabling their efficient release in every more fully developed states, including monophyllous sympodia, fenestration, simplification, deepening of the bud and so forth. Parallel reduction/simplification series under such circumstances blur the distinction of homology and homoplasy, and arguably place them on a continuum rather than in dualistic opposition as they are usually conceived. If descendants respond in similar ways independently (from each other) to their shared inheritance of one or more radical developmental perturbations, here principally the enclosed vegetative bud and the replacement of floral organs with florets on a strobiloid reproductive axis, those 'self-adaptive' changes occur homoplasiously with regard to place and time but consequent upon inherited, homologous cause/constraint. One cannot say they are fully independent if evolution is driven structurally as well as adaptively (cf. Wake, 1991). They stand somewhere on a spectrum between full homology and full homoplasy. Bottom-up, atomistic cladistic phylogenetic methods will likely obfuscate this state of affairs, by quantitatively or probabilistically testing for either homology or homoplasy based on the distribution of discrete states mapped onto a phylogeny, with insufficient regard for a top-down, integrative context. It is therefore refreshing to see it recognised that while reductionist approaches may be essential to the proposal of phylogenies, "when interpreting the results of such reductionist studies, a more holistic viewpoint often proves helpful, given that the developmental processes that together ultimately generate a mature organism are undeniably holistic" (Sokoloff et al., 2018), or as Bateman & Di Michele (1994) had put it "...[S]cientific analysis requires reciprocal illumination between different hierarchical levels of evidence... as well as between pattern and process... [P]rogress requires interaction between character-based analysis and evolutionary theory.

The following is a discussion of selected aspects of diversity of Araceae considered in the light of a proposed saltatory origin.

## Fenestrate and intramarginally dissected leaves

Among the steps accommodating compound leaves developing within leaf sheaths is proposed to be intramarginal dissection which can allow developing, complicated leaf blades to be more easily fitted into the bud. Thus the 'monsteroid' intramarginally dissected and/or fenestrate leaf is to be interpreted as primitive relative to undivided and imperforate leaves in the Monsteroideae. If it is not, it would appear to have evolved *de novo* at the very least three times (and possibly six): once in the relict Alloschemone (Heteropsideae), once in a clade of Monstereae including *Monstera*, *Amydrium*, *Epipremnum pinnatum* (L.) Engl. and part of *Rhaphidophora*, and at least once again in *Rhaphidophora* (which is probably paraphyletic; Tam et al., 2004; Zuluaga et al., 2019), and then to have been repeatedly lost, but no-one offers the least idea of how or why.

It is true that most of the examples given earlier of very high leaf blade complexity are usually single-leaved deciduous geophytes, which might suggest that such leaf complexity is a homoplasious adaptive novelty. However, as was also noted earlier, leaves as highly complex, or almost so, are found, albeit rarely, in other aroid groups with quite different habits. There is actually a more systematically widespread correlation between highly divided (i.e. at least to the third degree) leaves and unifoliar modules (though many species with unifoliar modules in a range of habits have simple leaves) than there is between highly divided leaves and geophytic habit. Highly divided leaves (i.e. including several orders of perforation, or several orders of marginal lobing or of actual divisions) are very rare in aroids with plurifoliar modules, unless the division is intramarginal (consider *Monstera* spp., versus *Lasia concinna*). In the absence of a clear adaptive rationale for the convergent evolution of such leaf form, their common extreme complexity must give one pause to wonder if the *pattern* is not homologous even if the ways of realising it are radically different, and whether the developmental environments (context) of the leaf — within the older leaf in plurifoliar modules; within a cataphyll or cataphylls in unifoliar modules — do not represent significantly differentiated evolutionary constraints on the retention of highly complex leaf blades. It is for this reason that mapping, say, lamina shape onto a phylogeny, and analysing its pattern *in vacuo*, is a misguided exercise (cf. Canal, 2018) because there is direct evidence, in the form of some correlation of lamina complexity with variation in shoot modularity, that leaf evolution may indeed be positively or negatively constrained by leaves' own structural and developmental context.

Nevertheless, it is tempting (and not unreasonable, on the face of it) to counter that more or less similar leaf blades differing so radically in their development must be convergent in these different aroid groups. This is the standard view, and is apparently supported cladistically, i.e. on the basis of analysis of atomised, acontextual 'character distribution'. From a developmental homology standpoint Gunawardena & Dengler (2006) repeated the old notion that, because intramarginal (apoptosis; cell death) and marginal (blastozone fractionation) dissection are developmentally different processes, the dissected aspect of the leaves of *Monstera deliciosa* and *Zamioculcas zamiifolia* (Lodd.) Engl. (two abundantly common house plants which they compared with little rationale for the selection of subject matter, and in the absence of consideration of contextual factors such as modularity and habit) are not homologous. They thereby made the case that dissected leaves are derived in Araceae. What is problematic about this interpretation is that it disallows without rationale the possibility of one developmental pathway to dissected leaves evolving from another. Yet evolutionary change in the development of conserved phenotypes [in this case divided leaves] in the form of developmental system drift, is now regarded as a frequent, even ubiquitous evolutionary phenomenon (e.g. True & Haag, 2001). According to the interpretation of Hay & Mabberley (1991), such leaves of *Zamioculcas* Schott and *Monstera* are homologous as compound leaves, but with quite radical modification to development. That does not necessarily involve the creation of entirely new developmental-genetic pathways: the close systematic proximity of marginal and intramarginal dissection more generally in certain aroid groups, together with the extraordinarily close morphological similarity between intramarginally dissected leaflets (such as those of *Amydrium zippelianum*, *Monstera filamentosa*, *Anchomanes* spp.) and marginally differentiated leaflets in some other taxa, suggests that these seemingly very different processes may be connected rather than independently achieved, perhaps expressing conserved patterns (i.e. various degrees of compound lamina) via modified and/or co-opted existing gene regulatory networks, and/or the activation of existing genes in new domains (e.g. Sanetra et al., 2005). The genetic aspect of leaf development in most aroids is hardly known (but see Henriquez, 2015).

## Monoecy and the re-emergence of the strobiloid flower

Two major saltational changes (and arguably more, but less radical) appear to have taken place subsequent to the saltational origin of the Araceae. The first is the Lemnoideae, now understood in multiple molecular analyses to be sister to the [Lasoideae plus Aroideae], and thus arising from a deep node in Araceae, a huge down-grade (in terms of complexity) leap into extreme neoteny, with the supposedly linking intermediate *Pistia* L. now universally agreed to occupy a distant position (within the Aroideae) in the family phylogeny. In addition, quite radical but very different reorganization of the body of the plant seems to characterise monotypic *Gymnostachys*, and the re-emergence of bisexual but tepal-less florets in the still-enigmatic *Calla palustris* L., in both cases an apparent dead end.

The second, of more importance in the sense that it has led to the large majority of the extant aroid genera, is the appearance of monoecy. Again, molecular analyses are generally agreed that all the monoecious aroids, including several erstwhile subfamilies, represent one clade (French et al., 1995; and later analyses). This is of particular interest because it supports the idea that none of the extant bisexual-floreted lineages have generated monoecy, despite the not infrequent occurrence of partially sterile florets at the apices and/or bases of the spadices in these taxa, which might otherwise have been persuasive of gradual evolutionary transitions to monoecy. Notwithstanding the relatively recent proposals that the monoecious Zamioculcadioideae be distinguished from the Aroideae (i.e. all the rest of the monoecious clades; Bogner & Hesse, 2005), or Keating's earlier proposal that the monoecious clade be divided into several subfamilies (Keating, 2002), a likely single origin for monoecy is unshaken. [However, a qualification must be made in that Cabrera et al. (2008) provided two alternative proposed positions for the monoecious *Zamioculcas*/*Stylochaeton* clade, in one of which it is sister to (Lasiodeae + Aroideae), which might imply a dual origin for monoecy (further discussion in Mayo et al., 2013). Nevertheless later (and earlier) analyses concur in maintaining this switched about, with Lasioideae sister to an Aroideae *sensu lato* including the Z/S clade.]

Monoecy in aroids produces what is in effect a strobiloid flower, with a spathe — frequently modified in both structure and behaviour to manage the movement of pollinators — instead of a perianth, and the 'staminate' zone distal to the 'pistillate' zone. The systematic distribution of monoecy, confined as it is to a single (large) clade, together with the developmental evidence from several clades that the spadix axis itself (rather than florets individually) is the reference for gender, suggests the distinct possibility of a single, saltatory event in which each gender is *suppressed* along the spadix in the same order in which each gender is differentiated in a strobiloid flower — proximal male and distal female. In other words, monoecy in Araceae can be interpreted as the re-assertion of the strobiloid flower out of the strobiloid, bisexual-floreted meta-flower. With monoecy comes rapid anthesis (this also in most Monsteroideae), and subsequent to the zoned suppression of each gender is the suppression of perianth (still present in the 'basal' Aroideae, i.e. the Zamioculcadieae *sensu lato*), and a suite of other anatomical and palynological attributes (Hesse, 2006), and, as noted earlier, the eventual almost total loss of floret identity along the spadix in various clades, via various stages of more or less clearly to tenuously definable unisexual florets.

## Floral merosity

The subfamily Lasioideae, comprising the 10 genera of the relict pantropical tribe Lasieae, is particularly interesting as the subfamily of bisexual-floreted aroids in which the number of floral parts per floret is the least canalised. The plants are generally rather rare and it can be difficult to obtain sufficient material to study them developmentally, but Denis Barabé and colleagues have analysed spadix and floret development in a species of each of three of the four neotropical genera forming the New World lasioid clade in the molecular analysis of Cusimano et al. (2011): *Anaphyllopsis americana* (Barabé & Lacroix, 2008), *Dracontium polyphyllum* (Poisson & Barabé, 2011), and *Urospatha sagittifolia* (Rudge) Schott (Barabé et al., 2011); only *Dracontioides* is lacking. In their publication on *Anaphyllopsis*, Barabé & Lacroix (2008) concluded that it might be hypothesised that the tetrameous flowers such as predominate in *Anaphyllopsis* may be derived from an ancestor with polymerous flowers such as in *Dracontium*.

However, in the later paper, on *Urospatha,* Barabé et al. (2011) reversed course on this not unreasonable proposition, concluding that the condition in *Urospatha* (predominantly tetramerous with some pentamerous and occasional trimerous and hexamerous florets) is the primitive. Indeed they allege that the latter study "shows" this to be the case, using all too familiar over-reaching success language. They propose that placing their study of floret development in phylogenetic context enables them to discover the evolutionary direction of merousness here. Their conclusion is however, unwarranted and their certainty perhaps over-blown. First, they seem (the language is somewhat equivocal) to begin with the premise that because (in the phylogeny used) *Urospatha* is sister to the other genera of the new world clade, and is thus 'basal', it shows the 'basal' morphological condition. This is a misconception which sneaks back in the long-debunked concept of 'primitive groups' albeit clothed in more modern phylogenetic jargon, based on the misinterpretation of cladograms (see earlier). There is no *a priori* reason why *any* of the morphology *at all* of a molecular-founded 'basal' group should necessarily be primitive for the group to which it is sister. The duckweeds, 'basal', it is now quite well established, in relation to all the Araceae except the Orontioideae/Gymnostachydoideae clade, prove the point. Second, while they acknowledge the spathe-and-spadix as the [sic] reproductive unit, their studies atomistically home straight in on 'flowers' while avoiding any explicit structural consideration of the origin of the spathe-and-spadix which surely must, or at the very least might, contextually impact the inference of evolutionary trends within it [see also Barabé's more recent (2013) review of floral morphogenesis in aroids, which persists with interpretation of floral evolution, absent an explicit context of the whole bloom and its origins]. Third, they described floral development in *Dracontium* on the one hand, and *Anaphyllopsis* and *Urospatha* on the other, as appearing to be "completely different" (Barabé et al., 2011). That rhetorical flourish seems a trifle over-colourful; the development of florets in those very closely allied genera is demonstrably slightly different, as are the mature florets: so no surprise there.

What their studies show is that, in summary, floret primordia are initiated acropetally on the spadix and then their further development proceeds in a wave from the top of the spadix down; within the florets themselves development is acropetal; a whorl of tepals is initiated first; then, in *Dracontium polyphyllum,* a whorl of stamens is initiated in positions alternating with the tepal primordia, then a second whorl of stamen primordia is initiated in positions alternating with the stamens of the first whorl, and thus opposite the tepals, but that the positioning and number is not absolutely rigid, where in *Anaphyllopsis americana* and *Urospatha sagittifolia* there is only one whorl of stamens initiated and these arise opposite the tepals; finally the gynoecium develops, unilocular in *Anaphyllopsis* and plurilocular in *Dracontium*. They assert that in the (as they characterise it) more organised or integrated floret development of *Anaphyllopsis* and *Urospatha* the close association of stamen with tepal constitutes a tepal-stamen complex or unit or sector not found in *Dracontium*, yet delete the outer whorl of stamens in *Dracontium* and surely positionally corresponding tepal-stamen 'sectors' would appear there too. Moreover, the clear conceptual definition of tepal/stamen sectors breaks down in those *Urospatha* florets with three tepals and four stamens (Barabé et al., 2011: fig. 3a). Furthermore, *Anaphyllum*, which molecular studies suggest may be most immediately allied to rather strictly tetramerous *Lasimorpha* Schott, also routinely has differing numbers of tepals and stamens, sometimes with only three tepals but up to five stamens (Dominic, 2012). So, the association of stamen and tepal is looser than they suggest; indeed that there is a tepal-stamen unit at all seems defined only by relative position — the tepal and corresponding stamen do not develop from a common primordium, nor at the same time, so it seems extravagant to say that an increase in number of floral parts is achieved by adding tepal-stamen units or sectors: the whorls each merely develop three, four, five or six parts, the members of the inner whorl opposite the members of the outer whorl in those cases where there is such regularity. They conclude "one can hypothesise that the only way to produce more than six floral parts... is for a sudden change to take place in the mode of development". Yet they provide us no clue as to why seemingly canalised, or at least conventional, equal tepal and stamen numbers, should be broken, and what contextually would drive this mini-saltation.

What they propose can be read the other way: a counterhypothesis is that lower numbers of floral parts with stricter correlation between tepal and stamen number is the more or less stabilised end point — a developmentally efficient attractor — in parallel reduction series taking place in most lineages in which a key step is the deletion of an outer staminal whorl. Then the unanswered question would be why has *Dracontium* not itself followed that parallel path of reduction, or at least not completed it — there is in fact a number of species with smaller numbers of floral parts (Zhu & Croat, 2004). A third interpretation is that, given its phylogenetic position, it is possible that the somewhat irregular polymerous flowers of *Dracontium* are both primitive *and* novel — that is to say a case of evolutionary recall or re-emergence; but again, why remains a mystery. A fourth consideration is of course that the topology of the Lasioideae clade may simply be wrong. *Dracontium,* with variable and the largest number of locules in the Lasioideae, is the only known case in Araceae of a gynoecium apocarpous in early development (Poisson & Barabé, 1998, 2011), and one of only two [the other being multilocular *Philodendron* subgenus *Meconostigma* (Aroideae)] groups with individual stylar canals in the ovary (united in the style) (Poisson & Barabé, 2011). Poisson & Barabé (2011) note this is difficult to explain, but just as simpler leaves may be achieved in parallel in clade after clade driven in each by the homologous context of possession of sheathing leaf bases and conical shoot apices, so too predominantly tetramerous florets with 1–2-locular fully syncarpous ovaries may be achieved in parallel, time and time again, driven by their shared, homologous context of spathes-and-spadices derived by saltation directly from a polymerous strobiloid flower.

## Fruit

The widespread occurrence in Araceae of ambiguous fruiting structures that blur conventional hierarchical distinction between fruit and infructescence in the same way that aroid blooms blur the hierarchical distinction between flower and inflorescence, may, in addition to being interpreted adaptively, also be interpreted from a structuralist perspective in the context of saltation from an etaerio. For example the monsterocarp and anthuriocarp, with their curious analogy to fruits of various species of *Magnolia* Plum. ex L., can thus be interpreted as possibly realising deep evolutionary potential of the strobiloid gynoecium in the structurally hybrid metaflower in which ovaries are both pistils of the florets *and* carpels of the spadix-receptacle (or structures which straddle both categories): hence the ‘fruit arils’ of dehiscent *Monstera* and the hanging ‘aril fruits’ of indehiscent *Anthurium*. Likewise in the Aroideae, the various manifestations of a ‘schizocarp of berries’, which appear in several lineages apparently independently, can be interpreted as hybrid or intermediate structures, this time also incorporating the spathe into the infructescence, deriving again from the saltational origin of the aroid bloom. In all of these, it is speculated that novelty and diversification are enabled through the recombination of developmental routines, and the breakdown of erstwhile hierarchically and/or sequentially segregated developmental systems.

## The Durian Theory and saltation

Corner never, to my knowledge, proposed a saltational origin for any plant group, despite being a leading and early proponent of homoeosis as an evolutionary process in plants. I assume this was for the general reason that the idea of hopeful monsters had been discarded: that no mutation could occur ‘big’ enough to viably reorganise the plant body plan more or less at a stroke. Indeed he had initially thought my proposed saltational origin of aroids extravagant, though he later changed his mind (Corner, pers. comm.). However, while saltation leads to a notional decanalised prototype, a key thread in Corner's views on angiosperm evolution is a not dissimilar idea — that of the 'well-equipped' prototype, an idea which can be traced to his mentor Church (e.g. Church, 1919). Corner proposed that major clades, down at least to big genera, have been initiated in general by pachycauls which, due to their complexity and massiveness of primary structure and form, may have greater potential for diversification than plants whose primary construction is simpler and more diminutive (e.g. Corner, 1975). This intersects with ideas of saltatory origins of novel body plans as a, if not the, means of arriving at well- (and differently-) equipped starter species imbued with high evolutionary potential, and resonates with Zander's (2013: 147) concept of the dissilient genus with a supergenerative core species. In all, it is implicit that evolution is to be understood partly in terms of the constraints, positive and negative, provided by the progenitor, and thus that 'character evolution', given that it is entirely metaphorical, is better conceived contextually, not purely atomistically.

## Testing holistic evolutionary hypotheses

I have already noted the considerable incompatibility of language with holism, and hence a key role for non-verbal mental processing, associated with cooperation of the right hemisphere with the analytical, verbal left, in providing insight solutions (holistic hypotheses) to complex problems such as the origin of and major morphological evolutionary trends in a plant family (e.g. Hay, 1986; Hay & Mabberley, 1991), or the flowering plants as a whole (Corner, 1949 and other references here). I also noted that the Durian Theory had never been rebutted on its own terms: how is one to test an insight-based holistic evolutionary hypothesis? Arriving at it involves analysis, impasse, insight and finally articulation. But because articulation involves regressing to language and 'left-brain' logic (regressing in the sense of involving a less advanced, formal-operational mode of cognition), what is exposed to rebuttal is the insight solution as it were in pieces ripe for the plucking by atomist nit-pickers. It is also essential to point out that insight solutions to such complex problems are probably unrepeatable at least *in practice*, and therefore the focus must be on testing the hypothesis, rather than devising replicability in arriving at it. Corner was clear that the test of the Durian Theory was, of course, systematic, but he was aware of the challenge: again, "My problem is how to explain and test a theory that has arisen from a comprehension, or grasping together, of many tropical sights" (Corner, 1954a). Phylogenetic systematic methodology has become highly developed, but atomistic through and through, and it of course makes no sense to apply an entirely atomistic test to a holistic theory, yet the test must, obviously, be verbal, analytical and logical.

I have pointed out that concepts such as the phene potentially represent significant improvements in how characters are formulated to be metaphorically more adequate in evo-devo terms, though that addresses but one dimension of the problem while remaining entrenched in fragmentation or dis-integrative thinking. The challenge for methodologists in this context is to address another, complementary dimension to work towards a rigorous analytic approach to holistic hypothesis testing which does not lose sight of the integrated organism. Earlier I stressed the ease with which ‘character evolution’ can slide into nonsense, by highlighting a couple of examples where the evolution of the features concerned is necessarily contextual in reality, and which constitute largely meaningless ‘busy work’ when conceptualised as characters ‘evolving’ *in vacuo*. A further clue to the direction this should take is provided by Jeune et al. (2006) noting that, holistically speaking, morphological subunits are not juxtaposed (in the shoot) but ‘encased’ by it. While leaves, for example, are encased by the shoot, the leaf in turn encases orders and patterns of venation and other subordinate characteristics. What follows then is the need for a *holarchical* rather than matrix conceptualisation of systematic morphological data sets, in which less inclusive characteristics are included within and below the hierarchical level(s) of structurally more inclusive, contextual features.

A holarchical, or nested, dataset could be visualised as a set of concentric circles with a sector for each taxon in the clade in question. The fields created by the intersection of concentric circles and sectors are populated by features of which the most ‘encasing’ or most overarchingly contextual in the clade concerned are in the outermost circle and progressively subordinate features populate the remaining fields centripetally. For each most contextual feature, a transformation is proposed drawing on the holistic insight-hypothesis, based on the premise that each transformation constrains the evolution of the next and possibly more subordinate features positively (leading to parallel change), negatively (leading to diversification), both with respect to different aspects of the subordinate feature (e.g. a positive constraint towards leaf simplification combined with a negative constraint realized by multiple modes of leaf simplification and thus multiple simpler forms), or neutrally (having no significant impact on evolutionary change in subordinate parts).

As I have indicated in the discussion of aroids, an example of a high-level contextual vegetative feature in all lineages (except duckweeds) concerns the enclosed monocot shoot tip, or more specifically, the proposed homoeotic transformation from an open pre-aroid or pre-monocot shoot tip to an enclosed shoot tip with leaves developing within older sheathing leaf bases. It is proposed that this constrains leaf evolution towards later leaf emergence, simpler laminas, intramarginal dissection, and the extension of intercalary growth leading progressively to deep-budded plants with less complex leaf shapes and parallel-pinnate leaf venation. Does the diversity and systematic occurrence of leaf form and development down-lineage accord quantifiably or probabilistically with that hypothesis? Another high-level contextual vegetative feature concerns modularity, specifically a change proposed to be from plurifoliar to unifoliar modules (with respect to foliage leaf number per module) which occurs in a number of lineages leading to a sort of ‘compound shoot’ where the modules are persistent, or a plant body consisting of one or two modules only, as in some deciduous geophytes. As I have noted, highly compound leaf blades are disproportionately, but not exclusively, found in taxa with unifoliar modules. Since all aroids have leaf sheaths (barring some highly modified exceptions) the leaf sheath is universally contextual for leaf evolution; modularity is also universal but different modularity states (plurifoliar versus unifoliar) appear to be differentially contextual, with the unifoliar state associated with cataphylls and exceedingly short leaf sheaths, so the evolution of leaf blades is to be understood in the context of *both* sheaths and modularity states, with different contexts of the latter in different clades. For example in the Philodendreae there occur plurifoliar modules in *Homalomena* (except *H. elegantula* A.Hay & Hersc. and allied species; all simple blades) and *Adelonema* Schott (all simple blades), unifoliar modules in *Philodendron* subgenus *Meconostigma* (simple, entire, highly divided and truly compound blades), plurifoliar modules in *Philodendron* subgenus *Pteromischum* (all simple blades) and unifoliar modules in *Philodendron* subgenus *Philodendron* (simple, entire to very highly divided blades). The next question then posed in the framework of a molecular phylogeny on the one hand and holarchical morphological cladal datasets on the other is — does the diversity and systematic occurrence of divided and simple blades accord quantifiably with the hypothesis that unifoliar modules with leaves developing within cataphylls is a weaker positive constraint on blade complexity than plurifoliar modules with leaves developing within leaves? These are all evo-devo issues, and it is would seem that holarchical character set conceptualization provides a better basis than an atomised data matrix for both incorporating contextualised evo-devo findings, and hence providing stronger evidence for the direction of evolutionary change and the identification of parallelism and re-emergence ('reversal'), and for formulating carefully targetted, contextualized evo-devo questions involving the interplay between molecular phylogenies, evolutionary hypotheses, and the analysis of biologically contextualised character patterns.

## Conclusion

It probably goes without saying that methodological rigour is a good thing in science, though one might well ask whether enslavement to method is. Should approaches with lesser methodological rigour step aside for those which are well developed? Molecular phylogenetic systematics has been a great success though I am not aware of anyone intellectually mature who thinks we have arrived at the final phylogeny nor the ultimate means to it for any group (notwithstanding the over-reaching success language with which the literature is rife), or even that phylogenies are best represented as bifurcating. Yet, while a great many improvements seem to have been and continue to be made, and the work justly lauded, how little has changed is as remarkable as how much (Mabberley, 2008: ix). Much generated from taxonomy before the phylogenetic methodological revolution still stands, and, to return briefly to Corner, *Seeds of Dicotyledons,* based on keen observation and intelligent unaided interpretation, preempted much of far more recent molecular systematic propositions of relationships. So while the line of development of atomist approaches has proceeded to a level at which it can claim methodological rigour, such that there is now a tsunami of publications concerning 'character evolution', the fact that what actually evolves is the developmental routine of whole integrated organisms, not characters, is often overlooked. Yet we seem now so enamoured of the view through the 'character' lens that form-based characters are seldom if ever defended as elements of the genetic, epigenetic, or morphogenetic syntax of development, nor their individuation questioned. Hence phylogenetic methodology is in danger of sacrificing organismal integrity merely to satisfy its own demands, with the consequence that 'results' are being confused with discovery. What seems very clear is that there is room to recognise and invigorate the line of development of integrative approaches, and also a need to be willing to embrace and encourage more anarchic, insight-thinking wherein illuminating connections may be made which might never have otherwise been inferred.

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