Interpretive morphology.—In 1790 Goethe gave an explicit statement of the view that sepals, petals, stamens and carpels are appendages of the same essential nature as foliage leaves and that the carpel is a leaf folded along its midrib. The relative simplicity of this interpretation has led to wide acceptance and to a status of orthodoxy. The simplicity is a little superficial and conflicting evidence can be found without great difficulty, especially in ontogenetic detail. As a result dissenters are fairly numerous and the present century has seen the birth of several rival theories, some denying the foliar nature of the carpel altogether, others modifying its interpretation. Most of these heterodox theories have been curiously alike in two respects: they have been based on highly selective evidence, and their proponents have not troubled to demolish the orthodox view before presenting a new one.

Professor Eames has a reputation for the brisk slaughter of theoretical monsters, and this is enhanced in his latest book.* But there is more to this volume than mere destruction. Its great value lies in the detailed and cogent presentation of the evidence for a slightly modified orthodoxy. Those who remain unconvinced will now surely appreciate that the onus of disproof lies on their shoulders and that additions to the family of morphological theories must be strictly controlled unless such disproof is presented.

The author states firmly that his viewpoint is comparative, "with emphasis on evolutionary modifications and phyletic implications". He might have added that his main concern is with the origins of the angiosperms and the morphology of the types believed to be primitive. The extension to higher families is decidedly sketchy.

The pattern of these valuable pages is as follows:- vegetative parts and the sterile accessories of the flower (83 pp.); male reproductive parts (82 pp.), female (114 pp.), fertilization, embryos, fruits and seeds (67 pp.); there then follow chapters on the families deemed most primitive (66 pp.) and on the phylogeny of angiosperms (8 pp.). Each chapter has its own bibliography and it is a feature of the book that there is scarcely a reference, or mention of an author's name, in the text. How this eases continuous reading! The difficulty of spotting the precise source of a statement is no great penalty, though to the person who is just using the book for reference it may well be most irritating.

Professor Eames throws his weight against the Eichler-Engler hypothesis that apetalous unisexual flowers (e.g. in Amentiferae) are primitive, and looks for the nearest relatives of extinct early angiosperms amongst the Ranales, as do most botanists in this country. Nevertheless he does not rule out primitive apetaly, for instance in *Trochodendron* or *Eupomatia*. This is something of a surprise, yet it is a logical consequence of the view that the corolla may have originated in two ways, from sepals or by sterilization of stamens. The evidence on this needs more careful handling. In fact there is some confusion in the book itself, for in one place (p. 89) Nymphaeaceae is mentioned as one of the families in which petals have developed as the inner members of a bractlike series, whereas elsewhere (p. 417) the Nymphaeaceous petal is held to be staminodial in origin, as indeed the detailed figures (p. 120) suggest. In *Nymphaea* the four sepals are clearly marked off from the coloured petals, but there is a measure of transition in the fact that the inner surface of the sepals is coloured and petaline while the base of the outer petals may be thickened, greenish and sepaline. The gradual transition from the petals through the outer broad stamens to the inner narrower ones is well known. It is tempting to regard these gradual transitions as primitive, partly because they disappear in families that are certainly advanced, partly because they seem to involve a less precise mechanism of differentiation than does the very abrupt switch from sepals to petals and petals to stamens more usually found.

* Morphology of the Angiosperms. By A. J. Eames. New York. McGraw-Hill. 1961. Pp. xiii×518, figs. 147. Price £5 4s. 6d.

But does transition from petal to stamen indicate that the former is a staminode? Of the origin of the corolla from stamens Eames says (p. 89): "Anatomy demonstrates that the petals of many families are, in vascular structure, unlike the sepals but like the stamens, regardless of extent of superficial resemblance in form to sepals, the number of traces departing to a petal is like that going to a stamen and unlike that to a sepal." This is a point of similarity: not a proof of origin. Even in *Paeonia*, whose petals are said to be sepaline in vasculature and origin, the stamens become petaloid in double flowers.

If the primitive flower was a condensed shoot with numerous appendages we can imagine that the phases of development succeeded one another like a series of waves whose crests mark the maximum expression of sepaline, petaline, staminal or carpellary characters. Thus as the petal-forming characteristics were exhausted the stamen-producing ones gradually came into play. Of necessity carpels are so different in structure from stamens that intermediate states are rare, but Salisbury (in Ann. Bot. xlv, 562: 1931) figured carpels with fertile anther-sacs in *Ranunculus parviflorus*, and his whole study of the fluctuating numerical balance of the floral organs of this species is most instructive. When the male phase wanes before the female begins internal staminodes are formed: simple ones in a *Dillenia* (see Hoogland in Blumea, vii, 14: 1952) or highly modified ones in *Eupomatia*, of which flower Professor Eames gives a full and enthralling account.

With this view of the flower in mind the transitional organs of *Nymphaea* which intergrade between petals and stamens may be accepted as just what they appear to be: transitional organs. Flowers which show an abrupt and consistently localized change-over from one set of organs to another are not likely to be primitive in this respect. There can be little argument that the flower of an antirrhinum or orchid depends for its normal development on a higher degree of morphogenetic precision than does that of a buttercup or water-lily.

This line of thought leads to an interesting comparison with vegetative patterns. While a generalized flower seems likely to be near to the primitive type, in the vegetative body evolution within angiosperms may well have run from a high-precision and complex pattern (foliage leaves, bud scales or stipules, etc., often a differentiation of long and short shoots and special inflorescences) to the very much looser one of the advanced dicotyledonous herb. This is probably a consequence of the speeding up of the vegetative phase and the advancement of flowering connected with the herbaceous habit.

Professor Eames gives qualified approval (pp. 3, 21 &c.) to the tendency to regard only root and shoot as the major morphological categories, a view which probably owes more to the study of herbaceous than of woody angiosperms. Is there not something of a paradox between this idea, now widely held, and the continued argument on the foliar or cauline nature of the floral organs? It is not merely that there is no clear-cut physical boundary line. Flowers (reproductive shoots) or vegetative branches may develop at leaf-sites on the rhizome of *Nymphaea* (Cutter in Phytomorphology, vii, 45-73: 1957); the floral emergencies in the capitula of those Compositae with naked receptacles are initially indistinguishable from those of bracts when these are present in the head (Philipson in Biological Reviews, xxiv, 40: 1949). Corner has similarly pointed out that while the lower flowers of *Capsella* arise in the axils of inhibited bracts, higher up in the inflorescence the rudiments which should have become bracts become flower buds directly (see Journ. Linn. Soc. Lond. Bot. lvi (Zool. xliv), 33: 1958). Professor Eames is at pains to show that carpels or ovules borne in apparently terminal positions are really pseudoterminal (p. 227). I do not question the correctness of his facts, but neither should I question his foliar interpretation of the Ranalian carpel if some carpels were actually found to be terminal. If an effectively terminal carpel is required we may expect that it will ultimately be developed in the most straightforward manner: terminally.

The evidence which Professor Eames sets out for the primitively foliar nature of the angiosperm carpel seems to me overwhelmingly strong. Little attention, however, is

paid to the subsequent evolutionary diversification. Admittedly syncarpy is dealt with in some detail, though much is left to rest on the orientation of vascular bundles. The complex and outrageously unleaflike behaviour of the ovary wall after fertilization (consider, for instance, the fleshy outer covering and complex endocarp of some Anacardiaceae: Hill in Ann. Bot. N.S. i, 249-254: 1937) escapes comment.

That the carpel was primitively foliar need not condemn us to seeking foliar carpels in all angiosperms. McLean Thompson's acarpous theory of flowering may not have been so wildly wrong in Scitamineae as when he tried to impose it on Ranunculaceae. If there are plants which fulfil Lam's conditions of stachyospory (cf. Scitamineae; also *Datura*—see Satina & Blakeslee in Amer. J. Bot. xxx, 453: 1943) this does not mean that the angiosperms are dirheithric (diphyletic in normal terminology). It means, rather, that in certain groups the site of ovular emergence has been shifted away from a demonstrably foliar position. Professor Eames will have nothing to do with the cauline origin of any reproductive structure, but I have less faith in the morphological consistency of angiosperms (cf. p. 104). There is a level in the higher families where recognition of foliar carpels depends, to use W. B. Crow's phrase, on the imaginative apprehension. There may be a level where it just is not true: where the foliar carpel has been superseded.

The inferior ovary brings up another interesting point of outlook. Eames has shown that the wall of most inferior ovaries may be regarded as formed by the concrescence of the outer floral whorls. In certain groups, such as Santalaceae (pp. 247-8), the ovary wall is interpreted as being receptacular in origin because of the course followed by the vascular bundles supplying the ovules. These run up to the rim of the ovary, giving off branches to petals and stamens before turning downwards to the ovules within the hollow of the ovary: they are aptly described as recurrent. H. L. Mason, discussing the homologies of the angiosperm flower (in Madrono, xiv, 93: 1957), says that if the inferior ovary of Santalaceae is interpreted as receptacular it cannot be because of these recurrent vascular bundles; they are quite foreign to the normal receptacle and therefore cannot provide the evidence for the homology of the two structures. This is an unduly formal approach, or an attempt to think in terms of homology when it is not the appropriate tool. Eames's interpretation, confirmed ontogenetically, is that this pattern of vasculature is only comprehensible if considered as resulting from the upgrowth of an annular zone of the receptacle that carries the vascular supply with it. This is a question of evolutionary change, which escapes the strict concept of homology, just as does Corner's principle of the transference of function. Homology is a good chisel; bluntish, perhaps, but it can be used to produce useful work. The morphologist, however, has other tools and homology is by no means always the right one. Eames himself does not, I think, altogether avoid its inappropriate use. At one point he lapses into the type of morphological pedantry responsible for the disrespect into which the discipline has fallen. I refer to his description of the teeth or outgrowths of the filament in certain species of *Allium* as the stipules of the stamens (p. 12). Are there any grounds for such a statement? There are no recognizable stipules in *Allium*. These staminal structures are surely mere outgrowths, connected perhaps with pollination. Elaborate interpretations of floral innovations of this nature (cf. also the "corona" in Amaryllidaceae) do not help.

A more flexible approach is suggested by Eames's remarks on the telome theory (p. 218) "Consideration of the primitive plant body as made up of basic units, telomes, is doubtless of value for the understanding of the more primitive taxa, but its value in the interpretation of the higher taxa, where axis and appendages have become established as morphological units, is doubtful". This passage may seem inconsistent with his support of the 'root and shoot' view, but it is quoted for its recognition that a theory may be justifiable (useful) in one group yet not in another at a higher level. Elaboration of this attitude within the Angiosperms may well be the key to our future pattern of morphological thought. The carpel theory appropriate in Ranales may not be so in Compositae.

I have referred above to "valuable pages". In fact they cost, in Britain, nearly 2½d.

each. Metcalfe's Anatomy of Gramineae (O.U.P., 1960) is, despite its more specialist appeal, just over a penny a page less. The exorbitant price of Eames's book simply means that it cannot be recommended to the individual student. Departments must buy it if they can, but most students should be able to make better use of £5 4s. 6d.

There are some oddities that can scarcely be passed over without comment. In terminology, 'vein eyelets' for 'vein islets' (p. 11); the definition of 'adelphous' (p. 105) is a little ambiguous but appears to be 'without bundles', which should clearly be 'anadelphous' (if such a word exists or is needed). In descriptive matter, the stipules of *Galium* are interpetiolar, not intrapetiolar (p. 12); the venation of *Austrobaileya* is pinnate (fig. 5, p. 20 & p. 408), not palmate (p. 30); the receptacle of *Eupomatia* is hollow (pp. 395) not flattened (p. 429). In classification, '*Caryophyllaceae* (*Anagallis*)' strikes an odd note, as does '*Elatostemon*' (presumably *Elatostemma*—p. 81); *Costa* in the caption to fig. 128 (p. 334—not indexed) is presumably *Costus* (used p. 322), but the index reference under *Costa* is to 'costa' (midrib); *Arceuthobium* is referable to Loranthaceae, not Santalaceae as might be inferred (p. 280), and the reference to 'families of Santalaceae' (p. 281) should presumably be Santalales. The use of Helobiales (p. 438) to include Butomaceae and Alismataceae is contradicted by acceptance of Alismatales (p. 442) and later of Butomales also (p. 464). In the same way Ranales may be used in a wide sense to include Magnoliales and Laurales, or these orders may be referred to as distinct. These inconsistencies will not worry the experienced taxonomist, but they are liable to confuse the student abominably. A single page tabular outline of a reference classification would surely be worthwhile.

To sum up, Professor Eames's main thesis is clearly the foliar nature of the fertile appendages of the primitive angiosperm flower. Here he has marshalled his evidence in a most convincing fashion, and has added some novel details in his interpretation —for instance the idea that the microsporangium is naked, that placentation was primitively laminar not submarginal, that carpels may be either involute or conduplicate, that syncarpous ovaries have sometimes arisen before the closure of the carpels. All this is excellently done and merits careful consideration. If some of his further, and minor, argument is less satisfactory, the contrast could serve a useful purpose in leading towards a morphology which is more flexible and accords greater recognition to the changes which may have taken place within the angiosperms.

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