REVIEW

A. TAKHTAJAN, Flowering Plants. Origin and Dispersal. — Oliver & Boyd, Edinburgh. Authorized translation from the Russian by C. Jeffrey, Kew. 1969, pp. X + 310, 32 fig., 13 pl. Net £ 2.10/-

As explained in Takhtajan's preface this book is not a mere translation of his 'The origin of Angiospermous plants' (1961, in Russian), but an entirely new book. I find this true and not true. Comparing it with the Origin (1958 translation of the 1954 Russian version) the essence of the new book was there given in a nutshell. In size, chapter subjects, argumentation, and bibliographic documentation, the work is very much extended and it makes very interesting reading indeed. The sequence of the chapters is logical, almost always leading to distinct synthesis. Properly it is a critical commented survey of many opinions — Takhtajan being clearly in complete command of the huge literature on the subject — but from which the author follows his own line of choice and judgement, accepting or rejecting with brief but clear comments. The whole argumentation is admirably concise and rouses admiration for covering this vast subject, comprising taxonomy, plant distribution, morphology, palynology, genetics, population dynamics, flower biology, anatomy, paleozoology, etc. Major questions are embodied in subsequent paragraphs: polyphyletism is rejected; ancestors must be sought among heterosporous ferns or fern-like plants followed by pteridosperms and certain gymnosperms, although direct ancestors cannot be indicated; the basal flower type of angiosperms was bisexual. Takhtajan attaches great importance to occurrence of plants in small populations, especially in mountain plants, facilitating chance variations and genetic drift, rapid spread of mutant genes, which is important for evolution. This entails that missing links are almost never fossilized. Micro-evolution is equalized with macro-evolution. Neoteny (on which Takhtajan devoted a former work) can lead to despecialisation through which phenotypic simplification the complexity of the genome remains intact; it may provide for a maximum phenotypic effect by a minimal genotypic change. Primitive wood structure of early Winteraceous angiosperms is understandable by neotenic origin. Evolution of angiosperms was not only rapid, but also discontinuous as a result of neoteny. Developing in the mountains 'in many ..... small ..... populations ..... the earliest angiosperms found themselves under conditions most favourable to evolutionary radiation. And if we bear in mind that their evolution was closely tied to the evolution of insects and was based on the complex and peculiar mechanism of mutual selection, then the extraordinary speed of their initial differentiation becomes even more readily understandable.' Protection of the ovules arose as a selection against damage by 'early pollinating insects'; this made simplification of their structure possible which led to smaller ovules (loss of thickened integuments, sclerotesta, etc.) and enabled the angiosperms to observe the greatest economy of material in construction of the ovules and ♀ gametophyte, and it also made possible the perfection of the process of pollination. 'The acquisition of the stigma was undoubtedly a very great event in the evolutionary history of seed-plants.' 'The primitive insects searched for pollen (beetles), nectar searching ones were a further perfection; this again led to a very great advance in cross-pollination; and as a corollary to a greatly increased rate of evolution, which still continues.' 'Isolation of a population is well known to be a prelude to the formation of a new species.'

The question of the hypothetical reconstruction of the first flowering plants is approached by the 'hypothetico-deductive method'. '*Knowing* the basic evolutionary pathways of angiosperms and the main lines of specialisation of their organs and tissues, we may by extrapolation extend these lines mentally into the past to the lowest possible level of specialisation', but somewhat further on he writes 'This reconstruction of the ancestors of the living angiosperms *depends* on the truth of the assumption that they combined in one plant all the most archaic characters that are now found distributed among the living fossils.' I have italicized in the citations two words that are in contradiction; furthermore I would like to point out that whereas each plant we know possesses both primitive and derived characters, we cannot make an exception for an ancestral plant; one which would contain all the archaic characters must logically be an idealized fiction.

The ancestors must have been woody small trees with a weak crown of proportionally few thick branches, evergreen, with stipulate, alternate, simple, penninerved, coriaceous, glabrous leaves, conduplicate vernation, and of course vesselless wood and stomata with subsidiary cells. For their nodal anatomy a new scheme is drawn, three or more gaps being accepted as the most primitive. There is also a discussion on structure of stamens, marginal microsporangia being probably most primitive, with of course monocolpate pollen. Lateral-laminar placentation and stigmas from the conduplicate type led to decurrent stigmas

developed from sutures. Takhtajan proceeds with discussing ovules, gametophyte, seed and fruit, the Drimys type of placentation being most primitive. Finally the karyotype is considered; the number of chromosomes was probably low (7 according to Darlington) from which others are derived by poly- and aneuploidy.

On these grounds the living fossils are selected, *Magnoliales*, *Laurales*, and *Trochodendrales*, and reviewed with respect to characters, adding that primitive forms are also found in *Piperales*, *Nymphaeales*, *Illiciales*, *Ranunculales*, etc., commenting that 'not one of these forms has remained at the ancient gymnospermous stage, and not one of them has retained the whole complex of primitive features; all of them have altered to some extent and become adapted to contemporary conditions. *Indeed, in this way alone could they have survived.*' I have italicized the last sentence, as the hurrah-adaptation-selection theory is in my eyes completely defeated by the wealth of the living gymnosperms which manage to survive under the same contemporary conditions, be it in a fairly small number of species, to produce probably half the biomass of the terrestrial plant world of the globe. There is obviously nothing 'inferior' in being a gymnosperm.

Apetalous dicotyledons are considered derived and the nucleus of *Monochlamydeae* had its origin in the *Hamamelidales* (standing near are *Eucommiales*, *Urticales*, *Casuarinales*) which in turn are derived from *Magnoliales*. *Amentiferae* are descendants of *Hamamelidales*. But this group is a mixed assemblage, and *Salicales* have a different affinity.

The chapter on monocots indicates that they originated very early from very primitive dicots; moreover, monocots show to some degree 'infantilism' (neoteny) in their vegetative organs, and as neoteny is usually connected with extreme environmental conditions, their ancestors were probably rhizomatous herbs of marshy places. In monocots there is, however, no order combining all primitive characters of a similar standing as *Magnoliales* among dicots.

The first traces of flowering plants 'undoubtedly originated long before the Cretaceous,' obviously in the Triassic, but undoubted fossils are scarce and fully authentic fossils only date from the Early Cretaceous. Some early data are mentioned.

Chapter 11 deals with the question 'The Cretaceous Expansion. Why and Wherefore?' This is answered by stating that during the Triassic and Jurassic Periods not much happened on the globe and 'vegetation went on under comparatively stable conditions'. But the close of the Jurassic was marked by marine transgressions and, in places with increased aridity, by the start of continental uplift, intensification of mountain building, and general diversification of conditions; so was the Cretaceous. This brought changes sufficient 'to lead *gradually* to an *abrupt* transformation of the organic world' (a contradiction, p. 129). 'For reasons we do not fully understand the plants that had been dominant in the Jurassic gave way to the angiosperms', either by becoming extinct (*Bennettitales*) or by fading into the background (cycads and ferns). 'Evidently they did not possess sufficient evolutionary plasticity to enable them to produce forms adapted to the novel conditions of a more diverse and rapidly changing environment. Therefore, first in the mountains and then in the lowlands, the dominant position passed to the angiosperms'. ....'Thus on the one hand new, unoccupied land surfaces were created or regions of new environmental conditions established'. ....The rapid change was no doubt due to the great evolutionary plasticity and unusual adapt ability of the angiosperms, as shown by Scott (1911). Personally, I feel that such reasoning seems very plausible but if one contemplates these changes, it seems unrealistic to think that before the Jurassic there were no shores, oceans, mountains, continents, and islands, wet areas and dry areas; it is unthinkable that there were no orogenetic changes etc., there has never been a stable topography. Second, no real reason is given for the plasticity, this is only accepted as a fact. If one accepts the origin of a more plastic group it would have led to this explosion at any time in the earth's history. Further on in the chapter Takhtajan mentions the relationship with insect pollination, but this is only thinkable as secondary. Takhtajan does not take a definite decision by mentioning authors who object to this idea of accepting the palaeogeographic changes responsible for the rapid expansion of the angiosperms (p. 134), and the chapter ends with his doubt.

Then follows a chapter on the 'cradle of the flowering plants'. This is more positive. No definite stress is laid on Wegenerian drift; one concludes that he is not in favour of this (but instead of (insular) land bridges), and neither of random long-distance dispersal. Certain is to him (and many others) that the angiosperms must have arisen somewhere in South East Asia-Australasia-Melanesia, and that this is not a refugium but a fragment of the ancient area which was first colonized by the angiosperms.

Chapter 13 on the 'ecological evolution of flowering plants and the origin of the temperate flora' repeat in a generalized way what is contained in earlier chapters.

Chapter 14 deals with the differentiation of floras and the major phytochoria. Early differentiation of hemisphere floras in Middle Cretaceous and their zonation. And the importance of the Tethys, especially as source of arid plants. He then proceeds to review in bird's eye flight with examples the botanical history of the various regions in these phytochoria in Upper Cretaceous and Tertiary. Direct connections between the amphi-Atlantic tropics ruptured very early, though probably not completely (leaving large archipelagos). Australia had a link with South East Asia for a very long time, a link which still exists today. To the book are added two appendices, the first embodying an outline of the classification of flowering plant families

with very brief argumentation; it is an abstract from a Russian book (1967) with a full explanation. The hierarchy is Class, Subclass, Superorder, Order, and Family. In all there are 94 orders. The second appendix is an outline of the Floristic Regions, with Subkingdoms and Regions. Each region of the 37 is briefly characterized by the number of endemic families and genera.

A very interesting work, stuffed with a large amount of information and surprisingly few errors. It reflects a condensation of much contemporary thought towards a synthesis in many fields and I would strongly recommend its reading. The contradictions in explanation found here and there, and the alternatives which Takhtajan gives himself, reflect that he realizes that many points rest on assumption and hypothesis, especially the why of phanerogam evolution. It is refreshing that this criticism is not hidden, but offered to the reader; it sets him thinking.

Due emphasis is laid on the fact that Hallier (and Bessey) were leaders for the modern reform of phylogenetic angiosperm taxonomy (p. 96). It is also appreciated that Takhtajan gives due credit for new ideas to predecessors by quoting them literatim. Among them are not a few Russian authors whose work was unknown to western botanists by being written in Russian. Of course, he had to lean in no mean degree on publications by others and these are sometimes pitfalls: e.g. on the strength of Hofmann's paper (1948) he quoted mangrove pollen from Flysch in Central Europe; however, J. Muller tells me that these identifications are wrong.

We may indeed be grateful for the large task Mr Jeffrey set himself to enable us to have this material available in English.

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