PROFESSOR SAHNI'S PALAEOBOTANICAL WORK

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EVEN a cursory glance at Birbal Sahni's work on fossil plants inevitably conveys a vivid impression of its extraordinary compass and variety. His researches, in fact, ranged over practically the whole field of palaeobotany. He not only selected the concrete objects of his investigations from all major groups of vascular plants and from nearly all plant-bearing geological systems; but in dealing with this diverse material, and in his more general discussions, he approached the problems involved from almost every possible angle. Thus his work on fossil plants resulted in contributions to all pertinent branches of botany, as well as to stratigraphy, palaeogeography and other related lines of geological research. One has the impression that he felt on quite familiar ground whether he was studying intricate anatomical structures, analysing taxonomic relationships, describing fossil floras, or discussing their bearings on problems of climatic changes or supposed displacements of continents. The reasons for the comprehensive character of Sahni's work may not be evident to botanists insufficiently acquainted with the study of fossil plants and may, therefore, warrant an attempt at analysis.

It is by no means unusual in fossil botany to find that the publications of one author deal with many matters that are little related except that they concern plants of the past. The palaeobotanist is rarely free to choose his subjects solely with a view to pursuing connected inquiries into certain problems. As a rule he is dependent on the material at his disposal; indeed, most work on fossil plants has been occasioned by access to this or that collection. Fossil plants are scarce, the material is precious and its examination may not infrequently appear to be a duty. It is in fact a characteristic feature of the history of palaeobotany that even the most important advances have often been made by studying and describing accidentally discovered or acquired material. Kidston and Lang, for instance, did not set out to inquire into problems of general morphology. Their primary task was to examine, analyse and describe the structures of the petrified plant-remains from the Devonian of Rhynie; but their work, nevertheless, profoundly influenced our conception of certain fundamental problems connected with the morphology of vascular plants. — No doubt the claims of the material often had a particular significance in Sahni's case. His country is rich in fossil plants, and important undescribed collections as well as imperfectly explored plant-bearing deposits awaited his attention when, at first quite alone, he began work in this vast field. No doubt he was often inspired by a sense of duty not only to botanical science but also to the needs of Indian geology.

At the same time Sahni's researches largely group themselves along certain lines of connected study, which he evidently chose in preference to others because of their bearings on questions of general importance. A very considerable part of his work was also concerned with the analysis and survey of problems which could be studied without direct reference to concrete material. On the whole it would appear that the diversity of his researches was largely an expression of the wide range of his interests, his extensive knowledge and intellectual versatility. Some of the characteristic features of his many-sided scientific personality became apparent at a remarkably early stage of his career as a research worker.

There can scarcely be any doubt that Sahni was first attracted to palaeobotany through the influence of the late Professor Sir A. C. Seward, his teacher at Cambridge. After graduating in 1914, he began research at the Botany School where, under Seward's leadership, studies of living and extinct plants were combined to an extent at that time unparalleled elsewhere. At first Sahni engaged in morphological and anatomical investigations of recent plants, chiefly pteridophytes and conifers. Before long he also took up palaeobotanical work, while continuing his studies of living plants. For the remainder of his stay at Cambridge, till he

returned to India in 1919, he divided his time between these branches of research, doing a surprising amount of excellent work in both.

MORPHOLOGY OF RECENT PLANTS

Sahni's work on living plants will be reviewed separately by Dr. P. Maheshwari. But certain palaeobotanical aspects of his early studies cannot be altogether passed over here. One of the questions dealt with in the theoretical part of his publication on *Acmopyle* (1920a)[1] was concerned with a palaeobotanical matter: the relation of the Cordaitales to the pteridosperms and the conifers. Sahni did not at that time definitely reject the prevailing idea that the Cordaitales were derived from the pteridosperm stock; but he advanced strong arguments against this view and his criticism was later shown to be justified by Florin's comprehensive studies. Sahni's views on various questions relating to the conifers, too, were more in accord with our present knowledge of the oldest fossil conifers than were those of most contemporary authors. In discussing the important problem of the position of the seed[2] in the gymnosperms, he introduced a conception of great general interest from a palaeobotanical point of view. On the basis of one single but important morphological feature he suggested a division of the gymnosperms into two groups: "Phyllosperms", with leaf-borne seeds, and "Stachyosperms" in which the seed is seated directly on a normal or modified axis. This distinction — accepted in a morphological sense rather than for practical use in taxonomic classification — is reflected in the views of later workers in phyletic morphology (e.g. Zimmermann, Florin). It has even been extended to apply to the position of all sporangia in vascular plants ("Phyllospory" and "Stachyospory" of H. J. Lam).

Sahni's views on the phylogeny of the stachyosperms were decidedly advanced. He pointed out the strong evidence against a derivation of these plants from megaphyllous ancestors, and was inclined to regard the position of their megasporangia on caulinar branches as a primitive feature. D. H. Scott expressed similar thoughts at about the same time; but it was not until ten years later that W. Zimmermann introduced the telome concept in his *Phylogenie der Pflanzen*, and more than another ten years were to pass before direct evidence was brought forward by Florin in the case of the conifers and the Cordaitales. It would be interesting to know whether Sahni — like Zimmermann at a later date — was influenced by Kidston and Lang's discovery of the axial and terminal position of the sporangia of the Psilophytales. He did not quote the first Rhynie paper, which had appeared about two years earlier, but this may be due to a natural reluctance to enter into comparisons with plants so remote in systematic position and geological age. Only three years later he showed that he was fully alive to the consequences of the Scottish discoveries by his study of the sporangiophores of the Psilotaceae (1923, 1923b).

In his early work on living plants Sahni followed the example of his teacher by mostly choosing those groups which particularly invite comparison with the fossils. It was almost inevitable that from the first he came to adopt a phyletic view in his morphological interpretations and thus to stand out as a decided adherent of what has been named "the new morphology" (H. HAMSHAW THOMAS, 1931). His discussions of phylogenetic relationships at this time throw a vivid light on his analytical mind and his interest in general problems. But they also show that at an early date he had acquired a remarkably extensive knowledge of the morphology and anatomy of both living and fossil pteriodophytes and gymnosperms. One cannot but be impressed with the large amount of high class work which he crammed into the years he spent at Cambridge, dividing his time, as he did, between various little related and most difficult subjects.

Sahni's first contributions to pure palaeobotany, too, were products of his research work at the Botany School. With an interval of only a couple of years between them he published papers on two widely different groups of palaeobotanical subjects: (1) *the anatomy and morphology of Palaeozoic ferns*, and (2) *the fossil plants of the Indian Gondwana formations*. His later publications, too, are largely concerned with these two

1. For full references see the bibliography of Professor Sahni's publications.

2. "Seed" is here used in the customary sense, irrespective of the importance lately attached by some workers to delayed fertilization and the apparent absence of an embryo in the seeds of certain fossil plants. Strictly speaking, however, "ovule" would in most cases be a more adequate term.

fields of investigation. It was fortunate for palaeobotany, no less than for Sahni himself, that, at the very outset of his scientific career, his attention was thus attracted to fruitful branches of research which were to hold his interest to the end of his life. We have Sahni's own words to prove that this important first choice of subjects was chiefly inspired by Seward. Even after Sahni had left England, Seward continued to take a great interest in his gifted Indian pupil who, in after years, frequently expressed his gratitude to the founder and leader of the Cambridge school of palaeobotanical research.

ANATOMY AND MORPHOLOGY OF PALAEOZOIC FERNS

Sahni's work on Palaeozoic fern-like plants was concentrated mainly on the *Coenopteridineae*[3], and more especially on the family *Zygopteridaceae*. As knowledge of this entirely extinct group is not very common among botanists, a few general remarks may not be out of place in order to make it easier to understand the scope and importance of Sahni's work.

The Coenopteridineae are of extraordinary interest in various respects. At the same time they present unusual difficulties as a subject of research. The material is mostly petrified, and the structure is often beautifully preserved; but it is also very fragmentary and gives little information on the habit of the plants. In some cases only the stem is known, more often only the leaf-stalks and the rachises of the leaves; the laminae and the sporangia are seldom preserved. The connexion between the various parts must, as a rule, be established by means of comparative studies. Only very rarely has it been possible to gain more direct evidence by actually piecing together separate fragments, a line of work in which Sahni was to take a leading part. On the whole, the Coenopteridineae scarcely appear to be an attractive subject for a first study in palaeobotany. Sahni, however, came well prepared to the task, since he had done a good deal of research on the anatomy of living ferns as a post-graduate student under Seward (1915 a, 1916, 1917).

At this time the Coenopteridineae had recently been dealt with in important publications by several leading authors: D. H. Scott, A. G. Tansley, R. Kidston and D. T. R. Gwynne-Vaughan, W. T. Gordon, and especially P. Bertrand. The interest centred, then as now, round the largest subdivision, the Zygopteridaceae. This family is remarkable for the extraordinary branching of the highly compound leaves : in most genera the primary pinnae are placed in four rows, two on either flank, and they are always orientated so that their planes form right angles to the plane of the mother rachis. In this peculiar type of symmetry, and in some anatomical features, the fronds of the Zygopteridaceae are very unlike normal leaves; at least in their proximal parts they can even be said to combine characters of both stem and leaf. P. Bertrand actually considered their petioles to represent a special kind of organ, which he named *phyllophores*; however, this term will not be used here.

Sahni's first paper (1918) on these plants was a critical study of the branching of the zygopteridean leaf. As it was chiefly concerned with discussion of current views, one might conclude that Sahni was first attracted to the subject of the Coenopteridineae by a study of the literature in connexion with his investigations of the anatomy of living ferns. But in the same publication he referred briefly to a specimen of a zygopteridean fern from Australia, of which he had given a preliminary account before the Cambridge Philosophical Society as early as in February 1917. The work on this specimen, which had been suggested by Seward, grew, later, through the addition of more material and was probably the immediate cause of Sahni's taking up the study of the Coenopteridineae as one of his chief lines of research.

Sahni's continued investigation of the Australian zygopteridean stem resulted in several publications (1919 a, 1928 d, 1930 a, 1932 c). The species proved to be of great interest. The peculiar combination of its structural features is reflected in the various generic names that have been applied to it at different times: *Zygopteris, Ankyropteris, Clepsydropsis*, and finally *Austroclepsis*,

3. The name Coenopteridineae was not much used at the time when Sahni's first publications appeared. Several names had been proposed, but none agreed on ; Sahni, working chiefly on the subdivision then named the Zygopterideae, did not discuss the name of the whole group. The simplified classification adopted here is, except for the rank of the group, that of Arnold's *Introduction to Paleobotany*. The Coenopteridineae are accordingly regarded as divided into only three families : the Botryopteridaceae (including the Anachoropteridaceae), the Zygopteridaceae and the Cladoxylaceae.

a new genus founded by Sahni. Mrs. E. M. Osborne had already noted that the plant agreed with the genus *Ankyropteris* in the structure of the stele and the leaf traces, but that the petiolar bundles were of the type of *Clepsydropsis*. This much-discussed genus had been founded by Unger in 1856 for isolated petioles with a somewhat hour-glass or dumb-bell-like form of the vascular bundle as seen in transverse section. The combination of *Clepsydropsis* petioles with a stele of the *Ankyropteris* type seemed very surprising, for other *Ankyropteris* stems were known to bear petioles in which the cross-section of the bundles resembles the letter H or a double anchor — the latter feature having given the genus its name. By examining a large material and fitting together various fragments, Sahni was able to give an unexpectedly complete account of the anatomy of the stem and also to picture the extraordinary habit. He found that the plant was a large tree-fern with an almost unique type of trunk: numerous slender, bifurcating axes are embedded in a thick mass of adventitious roots and aphlebiae and thus kept together so as to form a "false stem", somewhat reminiscent of that of the Cretaceous genus *Tempskya*. In conformity with the rules of nomenclature for living plants, Sahni at one time (1919 a, 1928 d) named this species *Clepsydropsis australis*. However, his subsequent studies of another petrified stem, to be mentioned presently, showed that this would lead to absurd consequences, and he, therefore (1932 c), proposed the new generic name *Austroclepsis* for the Australian plant. In doing this he adopted a palaeobotanical nomenclatorial practice which has later been submitted to the International Botanical Congress for sanction: that a new name may be given to a "combination genus" (natural genus) though separate parts of the type species have been described under older generic names, and these — in the sense of "organ genera" or "form genera" — continue to be used for other detached plant fragments with similar characters.

Sahni's later work on *Austroclepsis* was much influenced by his investigation of another species, which he also referred to a new genus, *Asterochlaenopsis* (1930 a). This species has a curious history. A fine petrified stem of a tree-fern from Siberia had long before been cut transversely into several slabs, some of which must have found their way to different museums in Germany. When Sahni began to search for the pieces, they were no longer known to belong together; two of them had even been described as species of different genera: *Asterochlaena* and *Rhacopteris*. By rediscovering and fitting together these two fragments Sahni could prove that they were actually parts of the same specimen. His reconstruction of the stem, incorporating three other pieces as well, revealed another interesting combination of characters. The petioles were of the *Clepsydropsis* type, but the leaf-trace sequence resembled that of *Asterochlaena*, and the previously unknown stele proved to be of a type somewhat intermediate between those of *Asterochlaena* and *Ankyropteris*.

The nature and affinities of *Clepsydropsis*, which Sahni has done so much to clear up, might seem a trivial matter. Actually, the genus has played an important rôle in the discussions of the Coenopteridineae. Not only has it been regarded as the type of a family, but its interpretation must affect the very basis of classification in a considerable part of the whole group. Sahni's investigations, here reviewed at a length which would otherwise have been uncalled for, thus have wide bearings in various respects. One of his conclusions, inevitable in the opinion of the present writer though not accepted by P. Bertrand, was that *Clepsydropsis* should not be regarded as a real taxonomic unit, but can only be upheld as a form genus for petioles and rachises having a certain type of structure, which may occur in different groups of plants.

Bertrand had once made the suggestion, later withdrawn, that Unger's *Clepsydropsis* rachises belonged to the stems of the peculiar genus *Cladoxylon*, which occur associated with them in the Lower Carboniferous at Salfeld in Thuringia. Sahni (1930 a, 1932 c) entertained the same idea, and the two colleagues actually tried, in friendly co-operation, to establish the organic connexion between the rachises and the stems. But no definite proof came to light, and in 1941 Bertrand retained *Clepsydropsis* as an independent genus, constituting the type of the family Clepsydraceae. He even placed this family and *Cladoxylon* in different orders: the Pyllophorales and the Cladoxylales! Whatever may be the upshot of this extremely complicated controversy, Unger's old type species *Clepsydropsis antiqua* was

left alone and unattached after all attempts to provide it with a stem.

While still engaged in studying the various plants involved in the *Clepsydropsis* problem, Sahni began research on a different kind of zygopteridean ferns (1932 d). During his tour in Europe in 1929 he not only collected material for the investigations already referred to, but also turned his attention (1932 d) to the obscure species *Zygopteris primaria* (Cotta) Corda. The old genus *Zygopteris* (CORDA, 1845), which has given its name to the family, once included several species. All except one of these were later transferred to other genera — in fact divided between no less than four. The remaining species, *Z. primaria*, had been founded only on the structure of fern petioles preserved in a silicified specimen from the Permian of Chemnitz. This specimen was believed to be the only one in existence, but sawn-off parts of it had been widely scattered. Sahni identified and studied these fragments of petioles in no less than half a dozen museums in England, France and especially Germany. But on his arrival in Berlin he was shown another specimen, previously overlooked, in which a protostelic stem was preserved. In this case, too, Sahni could reconstruct the habit of the plant, which proved to be a tree-fern with a slender axis supported by an armour of petiole-bases and adventitious roots. The investigation of the anatomical structure of the various parts led to the most unexpected results. The stem, the leaf-trace sequence and the roots were found to be of the type previously known in the genus *Botrychioxylon*, which is remarkable as a primitive fern with a large amount of secondary wood. The petioles, on the other hand, had the structure of *Etapteris*, a large genus of which only the characteristic leaves were known. The salient features of three genera, all familiar from the usual text-books, were thus found combined in one single specimen! If this stem had been known and satisfactorily studied at the time, it is probable, Sahni remarks, that the genera *Botrychioxylon* and *Etapteris* would never have been founded. However, Sahni was reluctant to accept the obvious but disturbing nomenclatorial consequence of his discovery, and did not merge the two other genera in *Zygopteris*.

In his work on *Grammatopteris Baldaufi* (1932 g) Sahni dealt with a tree-fern which had been placed in a different family, the Botryopteridaceae. This study, too, involved the comparison of several scattered pieces into which the only known stem from the Lower Permian of Chemnitz was found broken when discovered in 1915. The new interpretation of the structure and affinities of this species — and of Renault's imperfectly known genus *Grammatopteris* — was another important result of Sahni's European tours in 1929 and 1930. He found convincing evidence for removing *Grammatopteris* from the Botryopteridaceae, and with some hesitation placed it in the Zygopteridaceae, while emphasizing the great resemblance to the Osmundaceae.

These examples will have shown that Sahni's work on the Coenopteridineae did not, as a rule, consist in describing new and interesting collections which might easily yield important results. Instead, he followed up definite lines of study, and to that end had to search for material in many museums and in various countries. The specimens that he had an opportunity of studying were rarely new; often they had been repeatedly examined by previous workers, and sometimes they were the actual types of species and genera. A characteristic feature of his investigations, repeatedly exemplified above, was that he hunted up and fitted together the scattered and sometimes forgotten fragments of one and the same stem. For this purpose he often had to trace the fate of old collections and reconstruct past happenings in something like the manner of a detective. Considering the high value placed on petrified material of primitive ferns, Sahni was remarkably successful in having important specimens placed at his disposal. No doubt his tact and his engaging personality often helped him to obtain rather more than the customary facilities accorded to a distinguished investigator; he often dwelt gratefully on the assistance and courtesy that he met with everywhere.

It was largely this "fossil hunting" in museums that enabled Sahni to reconstruct the general organization and habit of some very interesting plants (always excepting the configuration of the missing leaves). This reconstruction work, in its turn, influenced the conception of relationships in the Coenopteridineae not only in particular instances, but in a more general way. It clearly revealed the unsettled state and artificial nature of the present classification,

by showing that too great reliance had often been placed on single anatomical features. While much of Sahni's work on the Coenopteridineae thus had a critical trend, the criticism was decidedly positive and constructive. Combined with his other work it did much to hasten the slow and difficult synthetic process of building up a more natural taxonomic classification in this group.

Sahni's study of *Grammatopteris* was his last original publication of any great length on the subject of the Coenopteridineae. Other pressing work, chiefly on the fossil plants of his own country, took up nearly all the time that he could spare from his duties as a teacher and a leader of research. But he never gave up his interest in the petrified Palaeozoic ferns, and used every tour in Europe to procure additional material. While staying for a couple of months in Stockholm in 1948 he studied various coenopterids at the Swedish Museum of Natural History, and a few specimens were actually being sectioned for him there when the news of his death arrived.

As a final expression of what Sahni's work meant to our knowledge of the Coenopteridineae it seems fitting to quote a remark — brief, but to the point — by the great authority Paul Bertrand. These two prominent workers in the same field always remained fast friends, but they were far from always of the same mind in palaeobotanical matters. Sahni had lately criticized some of his colleague's views when, in 1933, Bertrand sketched the most important stages in the investigation of the Coenopteridineae. Beginning with the pioneer work of von Cotta, Corda and Unger, he distinguished four main periods in the history of these investigations. Of the last of these he wrote: " 4:e période, de 1920-1933: cette période inrégistra des progrès décisifs, dus surtout aux travaux remarquables de B. Sahni . . .".

EARLY REVISIONS OF INDIAN FOSSIL PLANTS, ESPECIALLY FROM THE GONDWANAS

Indian Gondwana plants claimed a very large share of Sahni's interest and work from his Cambridge days till his death. No field of research could, of course, have been more natural for a young Indian botanist to choose while working with A. C. Seward. After the appearance of the classical monographs that were published in 1863-86 by T. Oldham and O. Morris, and especially by O. Feistmantel, followed a period of over thirty years during which comparatively little work was done on the fossil plants of the Gondwanas, or indeed on any Indian fossil flora. In the British Museum *Catalogue of the fossil plants of the Glossopteris flora* (1905) E. A. Newell Arber included descriptions of many Indian specimens. Original papers on Indian Gondwana plants were also published by several European authors, notably by Zeiller, Arber, Nellie Bancroft and especially Seward; but they were neither numerous nor extensive. Of greater importance were the many contributions that Seward made to the subject in other connexions. In his " Fossil Plants " and in his publications on various fossil floras — especially those from other parts of the old Gondwanaland — he often discussed plants that also occur in the Indian Gondwanas. No palaeobotanist, however, had made the Indian Gondwana floras the subject of special and connected study since 1885, when Feistmantel left India, until Sahni returned to his own country in 1919.

In the meantime much new material had been accumulated through the field activity of the Geological Survey of India, and part of it had been briefly recorded in the publications of the Survey. Palaeobotanical science, too, had passed through a period of great changes. A revision of Feistmantel's work, good though it was for its time, had thus become ever more pressing. At Seward's request a collection of fossil plants, most of them previously figured by Feistmantel, had been sent to him by the Geological Survey of India. Sahni, still working at Cambridge, became associated in this investigation, which resulted in a joint publication by Seward and Sahni (*Indian Gondwana Plants: A Revision*, 1920b). The material included species from both the Lower and the Upper Gondwanas. The need of a revision was clearly demonstrated not only by the creation of four new genera, but especially by the considerable amount of new and valuable information on morphological and anatomical matters, partly gained by study of cuticular structures.

Seward had always held that the differences between the Mesozoic Gondwana floras and the contemporaneous floras of Europe had been exaggerated. It may have been largely due to the influence of the senior author that the joint memoir strongly

reflects this view, which is scarcely generally accepted at the present time; indeed, Sahni himself later found cause to modify his first opinion. In the case of the Palaeozoic flora of the Lower Gondwanas, too, the results of the survey were believed to indicate that Northern and Southern floras show a closer resemblance than had previously been realized. The principal evidence, the generic identification of *Noeggerathiopsis* and *Cordaites*, however, scarcely appears convincing; in a later publication by Sahni alone (1933 b) he reverted to the use of the generic name *Noeggerathiopsis*. The material from the Mesozoic part of the Gondwanas, on the other hand, yielded especially one plant of considerable interest in this respect. A species which had been wrongly determined by Feistmantel was now identified as a conifer resembling the recent *Torreya* and was given the new generic name *Torreyites*. Through this discovery, later confirmed, the important northern group Taxales was for the first time shown to have extended to Gondwanaland in Jurassic times.

After his return to India in 1919 Sahni resumed the work on the Gondwana plants in earnest; now working alone and on more ambitious lines. In his Presidential Address to the Botany Section at the Eighth Indian Science Congress (1921 c) he summarized the position of Indian palaeobotany at that time, and briefly hinted at the principles which ought to guide future studies. Though he expressed himself with his customary modesty, he nevertheless made clear his intention to extend his investigations to the whole field of Indian palaeobotany. When continuing the work of revision, he accordingly included material from various formations, and gave his next comprehensive publications the title *Revisions of Indian Fossil Plants*. As his first subject he chose the Coniferales. One might wonder at this decision, as the conifers are by far the most difficult group among all fossil gymnosperms and pteridophytes; probably he was influenced by his previous studies of recent genera of this group.

The revision of the Coniferales appeared in two separate parts, one dealing with the impressions and incrustations (1928 c), the other with the petrifactions (1931 c, with a supplementary note, 1931 d). The great majority of the plants came from the Gondwana formations. Among the rest, some fossil woods and three types of petrified cones were probably, in some cases certainly, derived from the Deccan Intertrappean beds, which are now generally placed in the Eocene. Two female cones, for which Sahni founded the new genera *Indostrobus* and *Takliostrobus*, are particularly interesting and have attracted considerable attention. Sahni found their structure to be in the main abietinean, but also noted some peculiar features which, at least in the case of *Indostrobus*, suggested some approach to the Podocarpaceae. These podocarpean features were later overmuch stressed by Hirmer and Hörhammer, while Florin, like Sahni, left the question of phylogenetic relationships open. Irrespective of the formal classification, the combination of characters demonstrated by Sahni is remarkable in view of the young age of the cones.

The number of " species " recorded in the two parts of the Revision was 61, of which over a dozen were left unnamed while 21 were described as new to science. The examination of this large material was most certainly a very difficult and laborious task. In addition to the renewed investigation of practically all types and figured specimens, other scattered and often unsatisfactory records were revised, placed in their correct relations, and made easily accessible. The Revision also included descriptions, discussions and illustrations of much and important material, especially petrified woods and cones — partly mentioned above — as well as a welcome summary of the stratigraphical and geographical distribution.

The most interesting general result of the Revision was perhaps that Sahni noted a certain difference between the fossil conifer floras of India and of Europe. The large material from Peninsular India was not found to include a single typical representative of the northern families Pinaceae and Cupressaceae, nor of the northern genera of the Taxodiaceae. This negative conclusion particularly deserves to be remembered as being the first indication of a general and important feature of conifer distribution which Florin was later able to confirm and extend on the basis of more extensive and positive evidence. — It was unfortunate, from one point of view, that the results of Florin's comprehensive studies of living and fossil conifers had not been published at the time, as they would certainly have facilitated Sahni's work; and might have influenced some of

his conclusions. Thanks to the earlier appearance of the Revision, on the other hand, the large amount of valuable information which it contains could be used in Florin's review of the southern conifer floras, as shown by the numerous references there given to the Indian work. Since that review appeared much later (1940) and could be based on many years' special studies of the conifers on universal lines, it is not surprising if it led to a different interpretation of some Indian forms. The same thing happened in the case of practically all previous work on the conifers in local Southern floras — not least that of the present writer.

Sahni's continued study of the Gondwana plants was less concerned with revisions of the floras than with investigation of undescribed material, particularly in morphological and anatomical respects. The latter kind of work probably appealed more strongly to his inquiring mind. But the decisive factor was no doubt that much new and interesting material urgently demanded examination; even the second part of the Revision had chiefly dealt with undescribed specimens. The sequel proved the wisdom of this change of plan, as the new lines of study led to unexpected results of great importance.

At about this time, too, Sahni began to share part of his research work with others. He had become Professor of Botany at the Lucknow University in 1921, and some of his numerous students had specialized in palaeobotany. Gradually he gathered round him a staff of able and enthusiastic assistants and collaborators, to whom he could entrust special tasks fitting into the general plan of his researches. Sometimes the work resulted in joint papers; when Sahni's name did not appear on the title page, the authors' grateful acknowledgements never failed to make clear how much the teacher's directing influence had meant to their work.

THE FOSSIL PLANTS OF THE RAJMAHAL SERIES

The subject that dominated Sahni's continued investigation of the Gondwana plants was the Jurassic Rajmahal flora. The Upper Gondwana beds of the Rajmahal Hills had yielded a large part of the Jurassic plants described by Oldham and Morris and by O. Feistmantel. Rich as the flora was then found to be, it was, however, scarcely more remarkable than some other local floras of the Indian Mesozoic Gondwanas at the time when Sahni began his researches. His work introduced a new epoch, and when it came to a premature end, the Rajmahal flora had become famous through the discovery and excellent investigation of a number of peculiar and interesting fossil plants.

The Rajmahal material contained both impressions and petrified specimens. A list of leaf-impressions collected by Mr. G. V. Hobson was given in the Annual Report of the Geological Survey for 1928. Other new specimens, most of them collected by Sahni, his collaborators and students, were described and discussed in joint papers by Sahni and A. R. Rao (1933a, 1934d, 1935d). Some new species and two new genera, *Ontheodendron* and *Rajmahalia*, were discovered.

It was, however, the petrifactions which formed the main subject of the work on the Rajmahal plants. A silicified secondary wood has caused a good deal of discussion (1932e). The specimen resembled coniferous wood in being devoid of true vessels and markedly pycnoxylic, that is compact, with narrow medullary rays. But it was found to differ in the structure of the medullary rays, in the varied type of the pitting of the tracheids, and in the presence of scalariform tracheids in the secondary wood. Sahni then compared the specimen with some species of *Cycadeoidea* and *Williamsonia* which likewise have pycnoxylic wood; but he found a close relationship improbable because of the large amount of massive secondary wood and some features of the medullary rays. On the whole, the most perfect agreement seemed to be with some genera of the modern Magnoliaceae, which are also devoid of vessels and had for that reason been somewhat artificially grouped together by van Tieghem and others, under the name Homoxyleae. Sahni made the fossil species the type of a new genus and named it *Homoxylon rajmahalense* (1932e). A well-known phylogenetic theory regards the homoxylous genera of the Magnoliaceae as belonging to the most primitive dicotyledons; the presence of similar wood in Jurassic beds, laid down long before the first known appearance of the angiosperms, would therefore be as interesting as it seemed improbable. It was Sahni's intention to follow up this matter and to settle the

question of systematic relationship more definitely by a detailed anatomical study of the modern Homoxylae, of which he had succeeded in aquiring a valuable material. After publishing a note on *Tetracentron* (1933), however, he ultimately handed over the whole material to Dr. K. M. Gupta. When the interesting paper by that author, which appeared in 1934, strongly emphasized the possibility that *Homoxylon rajmahalense* might after all be the wood of a cycadeoid rather than of a primitive angiosperm, it was characteristic that Sahni did not combat this view, which he had already considered as an alternative. In a discussion at the International Botanical Congress in Amsterdam (1935a) he remarked : "But supposing that it was a cycadeoid — and there is nothing to prove that it was not — the resemblances with *Tetracentron* and *Trochodendron* . . . remain undeniable." It can scarcely yet be decided to what extent this resemblance is an expression of phyletic relationship or is due to parallel development. Whatever the actual taxonomic position of the Indian stem may be, Sahni made important contributions to the study of a much-discussed phylogenetical problem by his exact account of the anatomical structure, by his comparative studies, and by inspiring continued work on the homoxylous woods.

Sahni's work on *Williamsonia Sewardiana* (1932f) was a valuable addition to our knowledge of the order Bennettitales. This group was already known to be represented in the Rajmahal Series by both stems, leaves and Williamsonia-"flowers" ; but with one exception the various organs only occurred detached. In 1900 Seward had found bennettitalean leaves, identified as *Ptilophyllum* cf. *cutchense*, in organic connexion with a stem which he later (1917) named *Bucklandia indica*. In 1913 Dr. Nellie Bancroft had described other petrified plant-remains from the same locality, near Amrapara in the Santal Pargana district of Bihar. A flower could be compared with *Williamsonia scotica* Sew. from the (probably Upper) Jurassic of Sutherland, but it was poorly preserved and no proof could be found of its connexion with a stem. — Sahni's own investigations were primarily concerned with two specimens, also from Amrapara, one of which bore leaf-scars, remains of rachises, bracts and a fairly well-preserved female flower. In this case it was possible to examine the structure of the various parts of the flower, including the unusually long and short-stalked ovules as well as the interseminal scales. The flower was found to be identical with that described by Dr. Bancroft ; the resemblance to *Williamsonia scotica* was confirmed and could be extended to the gynoecium. By careful comparison of the structural details Sahni could now prove that the flower belonged to the same kind of plant as the *Bucklandia indica* stems and the *Ptilophyllum* leaves. The connexion between all the subaerial organs, except the male flowers, had thus been established, and Sahni, following the prevailing custom, applied the new name *Williamsonia Sewardiana* to the whole plant. His excellent account of the structure of the female flower, added to the information that Seward and Bancroft had given on the stem and the leaves, made the new species in some respects the best known in the genus. Sahni depicted the result of the reconstruction work in the form of a well-known drawing illustrating the habit of the plant, which is so far only known from the Rajmahal Series. Incidentally the researches made it seem probable that this series, of old classified as Liassic, extends up into the Middle Jurassic.

The investigation of the structural features of Mesozoic plants has always been impeded by the scarcity of petrified material, which is only very partially compensated by the frequent preservation, and of late most successful study, of cutinized remains. It is true that a good many Mesozoic petrifactions are known; but with the exception of the stems and flowers of some bennettites, and the silicified ginkgophytes of Franz Joseph Land, they are mostly found to be very scattered and have not added much information of botanical interest. The great desideratum has always been to find accumulations of all sorts of delicate plant-remains preserved in something like the manner of the petrified peat which has made the structure of Palaeozoic plants in many respects better known than that of their Mesozoic descendants. It was, therefore, a matter of great interest when a silicified flora containing more or less well-preserved remains of many different kinds of plants was discovered in the Rajmahal Series in time to be included in Sahni's researches.

The scattered petrified stems and fructifications discovered near Amrapara caused Sahni to organize special collecting tours to this area with his students and assistants; the first, as far as the present writer is aware, in 1927. Then, in 1929, Mr. Hobson of the Geological Survey of India discovered a silicified shale rich in fairly well-preserved petrified plant-remains of the most varying kinds *in situ* at the village of Nipania in the same neighbourhood. This important event gave new impetus to the Lucknow investigations, and Sahni for some time concentrated the collecting activity on this new and promising locality. His last tour deserves to be particularly remembered as it was undertaken little more than three months before his death. From a letter, dated 2nd February 1949 and the last of many received by the present writer, the following passages may be quoted: " . . . your letter . . . which I received on the 2nd January, when I returned from Amrapara and Nipania. . . Off and on I have also been rather unwell, and unable to do much work. In fact I fell ill while at Amrapara and came back home with a fever and cold. I seem to have contracted an infection in wounds caused by the pricks of *Andropogon contortus*, a troublesome grass common in Bihar." The incident seems worth recording as it may perhaps have had some slight bearing on Sahni's last illness and premature death. In any case it will remind his foreign colleagues of the indomitable zeal which caused him to undertake this last fatiguing tour in spite of his already weakened health.

The little village of Nipania has already become known to palaeobotanists in many countries through the interesting fossil plants described by Sahni and other Indian palaeobotanists. Several new genera indeed commemorate the very name of the village, which suggests that of a botanical genus and seems specially suited to nomenclatorial purposes. At the International Botanical Congress in Amsterdam, Sahni (1935c) briefly recorded a number of the plants that had so far been recognized and partly described. Since then many more have been discovered, and the plant-bearing bed, several feet thick, is evidently far from exhausted. A considerable number of papers by Sahni's collaborators and assistants show that he freely distributed the material among them. In addition to the work on his own papers, he directed and helped his associates in theirs, and in the case of the most interesting group of plants he gave the final synthesis and drew the most important conclusions. These combined investigations are indeed a fine example of personally directed teamwork and as such stand out as something rather unusual in palaeobotanical research.

The Pentoxyleae — Of the many remarkable fossils from Nipania and Amrapara it must suffice to mention those that were ultimately classed by Sahni in a new group, the Pentoxyleae. Not only is this group of extraordinary importance, but the progress of its investigation makes an interesting and connected story. The beginning was a paper by Sahni (1932) on the anatomical structure of the fern-like leaves then going under the name of *Taeniopteris spathulata* McCl. The form-genus *Taeniopteris* was already known to include plants belonging to the ferns, the Cycadales and the Bennettitales; but the vascular anatomy had not been satisfactorily investigated in any of its many species. Sahni found that the structure of the mesarch vascular bundles in the midrib of the Nipania leaves agrees almost exactly with that in modern cycads, and later he demonstrated a similar structure in the petiole (1938). The investigation was continued by Dr. A. R. Rao, who confirmed and added to Sahni's observations, especially in regard to the epidermal structure. In his final summary Sahni (1948a) assigned the leaves to a new organ genus, *Nipaniophyllum*, of which he distinguished two species. — Associated with the leaves were found some most peculiar stems and branches varying in diameter from several centimetres to a few millimetres. The study of this material and of a number of other plant-remains from Nipania was entrusted to the late Mr. B. P. Srivastava. At the time of the premature death of this promising young palaeobotanist only a couple of preliminary notices had appeared. His incomplete manuscript, notes and illustrations, however, were revised and rearranged by Sahni with the help of Drs. A. R. Rao and R. V. Sitholey. The results could thus be published in Srivastava's own name in an important posthumous paper of 1945. Most of the stems, including branches (short shoots), were referred to a new genus and species, *Pentoxylon Sahnii*. They proved to be of a unique and most interesting type. The cross-section showed a ring of generally five steles; in each of them the primary bundle was entirely surrounded by its own

zone of secondary wood, most strongly developed in a centripetal direction. The secondary wood was compact and its general structure that of a conifer. Sahni had early (1938) suspected that these stems bore leaves of the kind later named by him *Nipaniophyllum Raoi*. Srivastava's sections seemed to confirm this though he contented himself (p. 199) with remarking that the vascular bundles show a similar arrangement in both cases. — The blocks studied by Srivastava also contained ovule-bearing fructifications which he described as cones and assigned to a new organ genus, *Carnoconites*, under the names of *C. compactum* and *C. laxum*. The most remarkable feature of these cones was that the numerous ovules were attached directly to a central axis without any trace of megasporophylls, ovuliferous scales or interseminal scales. The integument had a well-developed hard sclerotesta and a very thick and fleshy outer layer, from which the name of the genus was derived. As the ovules were densely packed, the continuous fleshy mass with the embedded "stones" must, as Sahni remarks, have given the ripe fructification an appearance resembling that of a mulberry. The cones were borne terminally on long-branched stalks grouped together in a complex infructescence — no doubt a strange-looking habit as compared to that of recent gymnosperms. Srivastava noted that the cone-axis was frequently pentagonal in transverse section and had a ring of usually five collateral bundles. He did not, however, discuss the taxonomical relations, nor the question of the vegetative parts to which these unique inflorescences might have belonged.

In a final and most important paper (1948 a) Sahni summed up and connected the results of the previous investigations. He also added many new facts, some of which, for the sake of simplicity, have been incorporated in the descriptions given above. As regards the *Nipaniophyllum* leaves, he remarked that their peculiar combination of characters is suggestive of affinities with both the Cycadales and the Bennettitales. The most important of his new observations concerned the *Carnoconites* cones. He described, analysed and profusely illustrated the morphological and anatomical features of both species, but particularly *C. laxum*, of which Srivastava had only given a brief diagnosis. His general conclusion was that the *Carnoconites* cones, like the *Pentoxylon* stems, represent a quite unique type.

Discussing the relations between the three categories of organs, Sahni only referred lightly to his own original suggestion that the *Nipaniophyllum* leaves belong to the *Pentoxylon* stems, and scrupulously pointed out that the first actual proof had been given by Srivastava. Sahni had, probably at a comparatively early stage, conceived the idea that the *Carnoconites* cones, too, belonged to the same plant as the stem and the leaves, or rather that two closely related species of one natural genus are represented among the specimens of the three categories of organs. The evidence was in this case more circumstantial. It was based chiefly on the undoubtedly very close agreement between the stem and the cones in important morphological and anatomical features, especially the prevailing pentamerous structure or arrangement of various parts. A more indirect, but far from negligible, support was found in the unique types of both the leaf-bearing branches and the cones: if these did not belong to the same kind of plant, at least *two* hitherto unknown major groups of gymnosperms must be represented among the closely associated remains but by different kinds of organs — certainly an almost incredible coincidence. While, as Sahni repeatedly points out, absolute certainty can only be attained by demonstration of actual organic connexion, it seems scarcely possible to doubt his conclusions. In his reconstructions, however, only the leaves, but not the inflorescence, are represented as actually attached to the stem. He assigned the remains of all the three categories — the male organs are as yet unknown — to one natural genus, named *Pentoxylon* after the stem, and drew the obvious conclusion that it represents a new main group of gymnosperms. This group, the *Pentoxyleae*, combines certain features suggestive of the Coniferales, the Bennettitales and the Cycadales; but in the morphology of the inflorescences and the cones and especially in the vascular anatomy of the stem it stands entirely isolated. — It is an interesting coincidence that the investigation of the Pentoxyleae had reached its decisive stage just in time to be related in Sahni's last palaeobotanical publication. This final achievement certainly seems most aptly to crown his career as a research worker. It was thus a happy thought that a design

based on his reconstructions of *Pentoxylon* should be chosen for the seal of the Birbal Sahni Institute of Palaeobotany.

VARIOUS INVESTIGATIONS OF PALAEOZOIC AND MESOZOIC PLANTS

Sahni's researches into the structure and affinities of Palaeozoic and Mesozoic plants have been recorded here more or less in order as they progressed along two main lines, one concerned with Palaeozoic ferns, the other with Indian Gondwana plants, especially gymnosperms. For the sake of continuity, several investigations have been omitted; some of these relate to the two main themes, others are of a more isolated nature. It must suffice merely to mention the following subjects, with references to the publications: the epidermal structure of *Glossopteris* (1923 a); the interpretation of the inner root-zone in the Palaeozoic tree-fern *Psaronius* (1935 e); petrified stems and wood from the Gondwanas of India, from Burma and Australia (1920, 1925 a, 1926 a, 1933 b, 1937 a); and Mesozoic plant-impressions from the Salt Range, including specimens with beautifully preserved sporangia of the widely distributed genus *Phlebopteris*, not previously recorded from India (1945 c jointly with R. V. SITHOLEY).

While Sahni's work on Mesozoic plants was chiefly concerned with the most important Jurassic material, he made one particularly interesting contribution to the Lower Cretaceous flora of India (1936 h). Among a few specimens from Himmatnagar in Idar he recognized a new species of *Matonidium* and a few fragments of *Weichselia reticulata*. The latter species is well known as having an almost universal distribution in beds of Neocomian to Cenomanian age, but is particularly common in the lowest Cretaceous (Wealden). Though the specimens were not held to settle the exact geological age, they strongly suggest the occurrence of a typical Wealden flora. In the same paper a restoration of the frond of the new species *Matonidium indicum* was illustrated by a drawing by Mrs. Sahni.

It might seem that the various subjects mentioned above would have afforded a sufficiently wide sphere of activity even to Sahni, charged as he also was with the teaching of general botany at a great university, and with many other duties. But for one with his unbounded passion for work and compelling urge to investigate any palaeobotanical matter that came within his reach, this was not enough. While still engaged in his study of the Rajmahal flora he also carried out connected researches into the very different subject of the Tertiary plants from the cherts of the Deccan Traps.

THE SILICIFIED FLORA OF THE DECCAN INTERTRAPPEAN SERIES

This flora may in some respects be described as an Early Tertiary counterpart of the similarly preserved Jurassic flora of the Rajmahal Hills; in Sahni's researches it also came to play a somewhat similar rôle. The siliceous freshwater sediments (cherts) interstratified with the Deccan Traps contain an abundance of plant-remains of various kinds, often so well preserved that the most delicate structures can be examined. It is no wonder Sahni was attracted by this exceptional opportunity to extend his anatomical studies of fossil plants to material from the era of the angiosperms.

When he began his work, the occurrence of fossil plants in the intertrappean cherts had been known for close on a hundred years (J. G. MALCOLMSON, 1837). The first accounts of the flora were given in a few papers by S. Hislop and R. Hunter (1853-55), who had collected a large material of silicified palm stems and various seeds and fruits but had not illustrated or described them in sufficient detail. Except for a good many specimens which cannot be traced and may have been lost, the Hislop and Hunter collections are now in the British Museum. They were lent to Sahni for his researches, which were largely, and at first exclusively, based on this old material.

A new epoch in the investigation of the intertrappean flora began when Sahni himself took a hand in the collecting of new material and interested others in the task. In 1925 the Director of the Geological Survey of India sent to Sahni for examination some blocks of plant-bearing chert. In one of them Sahni identified remains of the water-fern *Azolla*, which caused him to visit the locality and collect new material, as it happened, on New Year's Day, 1926. The place was near Sausar, in the same part of the Chhindwara district where the pioneer geologists had worked. Later, in 1930, the Banaras geologist Professor K. P. Rode brought Sahni a number of petrified plants

which he had discovered at Mohgaon Kalan, in the same classical area; and in January 1931 Sahni, too, visited the place. Much new material was later brought together at these two localities, especially by Sahni, Professor Rode and Dr. V. B. Shukla.

As in the case of the petrified Rajmahal flora, Sahni shared the investigation with several other Indian palaeobotanists. Except for some plants independently described by others, especially Professor Rode, the usual procedure seems to have been something like this: Sahni mostly made the preliminary identifications, the material was then described more or less in detail either by him, by his collaborators, or, frequently, in joint papers; and finally Sahni summed up the results and drew the general conclusions. A preliminary account of the early work, brief but crammed with important information, was published by Sahni in 1934, jointly with B. P. Srivastava (1934, 1934b). It was followed by a series of papers that was only cut short by Sahni's untimely death. Of the numerous interesting plants so far recognized, only a selected few may be mentioned as an illustration of the progress and scope of the work. In many cases definite descriptions have not yet appeared, and no doubt much material remains to be investigated. Sometimes a newly discovered plant was described and discussed so to speak by instalments in successive reports -- of late years especially in *Palaeobotany in India* — or was only mentioned in passing. This method of publication does not facilitate a general survey of the flora, and has the disadvantage that new names may be preliminarily introduced in such a manner that they cannot always be considered valid according to the rules of nomenclature. On the other hand, the prompt communication of results made it possible to follow the progress of the work, and no doubt had a stimulating influence on Sahni's assistants and collaborators. It is tragic that time was not granted him to coordinate the many important scattered data and make them more easily accessible in a comprehensive publication, as he doubtless intended to do. — Sahni himself and the Lucknow palaeobotanical school were almost exclusively concerned with the plant-remains in the freshwater beds of the Chhindwara district. The fossil algae from brackish-water or marine beds, especially in the Rajahmundry district, were studied by Professor L. Rama Rao and his associates, Professor S. R. Narayana Rao, Mr. K. Sripada Rao, and others.

Petrified remains of *Angiosperms*, apart from stems, are exceedingly rare in all fossil floras, and Sahni naturally recognized the great importance that attached especially to the numerous silicified fruits and seeds. These also invited comparison with the rich carbonized material of similar fossils from the Lower Tertiary of Europe, which has been found to contain a large percentage of modern Indo-Malayan elements. The *Dicotyledons* are unfortunately comparatively scarce in the intertrappean beds. Several specimens of a capsule with normally eight loculi had been described, though not named, by Rode. The definite classification of this fruit, to which Sahni gave the generic name *Enigmocarpon*, came about in a curious way which seems worth recording. Though its excellently preserved structure was studied and described in detail by Sahni (especially 1943b, with references) the exact affinities long remained obscure. Finally Dr. V. B. Shukla discovered in the same locality, at Mohgaon Kalan, numerous specimens of a flower for which he proposed the name *Sahnianthus*; these were so completely preserved that he could construct a floral diagram. One of the two families to which this flower could possibly belong was the Lythraceae. On renewed studies in the light of this clue it was found that both the *Sahnianthus* flower and the *Enigmocarpon* fruit belong to that family and represent different stages in the development of the same plant.

The *Monocotyledons* of the intertrappean beds offered Sahni and his associates much interesting material. The dominant group is the palms, known since the days of Hislop and Hunter to be represented by both stems and fruits. The petrified palm stems were included in a comprehensive study of similar material which Sahni had acquired from various parts of India and Burma. It is convenient here to consider the whole of this subject, which Sahni dealt with in many separate publications (especially 1928, 1931b, 1932a, 1938, 1943a, 1947a). As early as 1934 he had distinguished no less than 45 species, most of them new to science. These species, like practically all fossil palm stems, are known under the provisional generic name *Palmoxylon*, which denotes a wholly artificial and provisional genus. The

attempt to distinguish natural taxonomic units obviously required intensive comparative studies of recent palm stems with a view to discovering whether their anatomical structure presents characters on which a classification could be based in the absence of reproductive organs. On Sahni's suggestion this laborious task was undertaken by his then research assistant Mr. K. N. Kaul. The results did not confirm J. C. Schoute's sceptical views of the possibilities, but rather the somewhat vague and tentative general ideas previously expressed by F. H. Knowlton and K. G. Stenzel: genera founded on the morphological features of flowers and fruits could largely be distinguished by corresponding differences in the anatomy of the stem. Criteria of generic affinity were found not only in the form and distribution of the fibro-vascular bundles — extensively studied by H. von Mohl nearly a hundred years earlier — but especially, under certain conditions, in the structure of the ground tissue, the " parenchyma pattern ", as it was called by Sahni. As could be expected, *Palmoxylon* was found to contain species belonging to several different natural genera, such as *Borassus*, *Bactris* and *Cocos*. The particular species referred to these genera, and many more, were described by Sahni, others chiefly by Rode and Kaul; but here again Sahni's most important rôle was that of an inspiring leader of research. It is desirable that the results of these researches be made accessible by full publication both of Kaul's work on recent palm stems and of the investigation of the fossil material, which has so far only been described in separate papers and scattered notes. Among the palm fruits in the intertrappean flora Sahni often referred to a species described by Rode as *Nipadites Hindi* and later transferred by Sahni to the recent monotypical genus *Nipa*; it is in fact closely similar to *N. fruticans*, the well-known " stemless " palm of the mangrove swamps. The species is chiefly of ecological, geological and geographical interest, more or less similar " Nipadites " fruits being widely distributed in the early Tertiary as far north as north-western Europe. Other palm fruits, too, have been discovered but as yet only briefly described or recorded in passing.

A most unexpected discovery was made when Sahni (1944, jointly with Dr. K. R. SURANGE; also *Palaeobotany in India*, V) identified a peculiar type of silicified palm-like stem as belonging to the South American family *Cyclanthaceae*. This stem, first described by Rode and later named *Cyclanthodendron* by Sahni, represents the only satisfactory fossil record of the family. Sahni also observed that a monocotyledonous infructescence in the Hislop and Hunter collection, to which he had given the new generic name *Viracarpon*, suggested comparison with the same family, though no definite conclusion could be drawn (1934 a; *Palaeobotany in India*, V). Later on, some other associated remains — leaves, and a floral axis — were discovered, which are thought to belong either to the same species, *Cyclanthodendron Sahnii*, or at least to the same family (SAHNI & SURANGE, *Palaeobotany in India*, 1950; T. S. MAHABALE, ibid.).

Sahni's work on the intertrappean *Gymnosperms* was chiefly concerned with silicified cones of conifers. The most interesting of these belong to the two genera *Indostrobus* and *Takliostrobus*, already mentioned as described in the " Revisions of Indian Fossil Plants " (1931 c).

The *Hydropterideae* proved to be of extraordinary interest. Sahni's discovery of *Azolla* has already been mentioned. The delicate plants of this genus are known from other areas to be surprisingly well preserved in Tertiary beds when the conditions are favourable, so for instance in the Oligocene of Bembridge (Isle of Wight). The Bembridge specimens, which had been investigated shortly before Sahni began his work, are either mere impressions or else carbonized, not petrified. The Deccan material is more fragmentary, but even the most delicate tissues are beautifully preserved in a silicified state. Most parts of the plants seem to be represented, though it has not always been possible to establish the connexion between them. The species was named *Azolla intertrappea* in a preliminary report in 1934 by Sahni and H. S. Rao and was later most carefully studied and described by Sahni (1941 b, with references). One specimen may be particularly mentioned, because the beautiful photographs cannot fail to give pleasure to any palaeobotanist. Pl. XXVI shows a detached megasporocarp which appears as if it were still floating in the silica. Not only the floats and the megaspore are preserved, but even the felt of delicate fibrils investing the megaspore wall. And to these fibrils two massulae containing microspores are attached

by the anchor-like tips of their glochidia, apparently in preparation for future fertilization. The photograph almost gives the impression of a lucky snapshot of an actual happening some fifty million years ago. *Azolla intertrappea* was found to differ from all other living and fossil species; Sahni remarks that it is probably the geologically oldest known representative of the genus, and seems to some extent to connect its two sections.— Another water-fern that Sahni himself both discovered and investigated proved, for different reasons, to be even more interesting. In sections of the chert blocks collected on his first visit to Sausar in 1926 he observed scattered micro- and megaspores which he compared to those of the modern South American genus *Regnellidium* (1943c, with H. S. Rao). Fifteen years later he discovered in the same locality a stalked, rounded bisporangial sporocarp in which the same kinds of spores were still enclosed. The sporocarp resembled *Regnellidium diphyllum* so strongly that Sahni at first considered placing it in the same monotypical genus as another species. It was only because some important features were unknown that he made a new, provisional organ genus which he named *Rodeites* (1943). The plant, Sahni remarks, is interesting also because it seems to represent the first undoubted fossil record of the Marsiliaceae.

The only *Thallophytes* in Deccan Intertrappean that have so far been extensively studied are various kinds of calcareous algae. These plants, as already remarked, were chiefly investigated by other botanists and geologists. But it may be mentioned that Sahni, in addition to showing his interest in this work in other ways, took active part in the study of the Characeae and, in collaboration with Professor S. R. Narayan Rao (1943d), described a new typical species of *Chara* which he had himself discovered on his first visit to Sausar.

Sahni's interest in the intertrappean flora was not confined to the structure and affinities of the plants. On many occasions he took up such general questions as the ecology, the geographical relations and the geological age of the flora (especially 1934f, 1937g, 1938, 1940, 1943c). Observations and discussions concerning these and related matters are in fact scattered throughout most of his publications on the various plants or localities. In his General Presidential Address to the 27th Indian Science Congress, Madras (1940), he drew a vivid picture of the landscape and the dramatic happenings at the time when the intertrappean beds were laid down. He described how the lava flows dammed up the watercourses into temporary lakes, how plants, growing in these or in sluggish rivers, became embedded in sediments containing volcanic ash, and how these beds were in their turn buried under new sheets of lava. Without discussing the details of the diagenetic processes, which are indeed imperfectly known, he pointed out that the water-plants must have been speedily killed and their tissue penetrated by rapidly solidifying colloidal silica. In several papers he discussed the evidence of a lacustrine origin afforded by the plants themselves. The water-ferns, the characeous remains and other aquatic forms were of course decisive in this respect. But he also noted that the occurrence of air-chambers or spongy tissues in, for instance, palm fruits and the capsules of *Enigmocarpon* suggests dispersal by water in the case of plants which may not have been strictly aquatic. Estuarine conditions were indicated not only by the marine or brackish-water algae in the Rajahmundry area but also by the fruits of *Nipa Hindi* from Mohgaon Kalan, though it is of course conceivable that different species of the genus may have lived under somewhat other conditions than the halophilous *Nipa fruticans*, for instance in freshwater swamps.

Passing to *the geographical relations* and *the geological age* of the intertrappean flora, reference may first be made to the discovery of certain links with the present-day flora of South America, exemplified by the new genera *Cyclanthodendron* and *Rodeites* mentioned above. Sahni wisely refrained from making these discoveries the basis of any theories about migrations. He no doubt realized that the groups concerned have every appearance of being strongly reduced, and may once have had a wide distribution in the tropics though they happen to have survived only in South America.

On several occasions Sahni pointed out the close analogy between the Deccan Intertrappean flora and that of the Eocene London Clay (1937i, 1940, 1943a, 1947a). While the old geologists had noted this resemblance in a general way, Sahni's researches made it clear that in the Deccan Trap period Peninsular India had a vegeta-

tion of the same general character as that of Western Europe in early Tertiary times. This matter is one of considerable general interest. Reid and Chandler and others had accounted for the preponderance of recent Indo-Malayan elements in the London Clay flora by assuming an actual advance of tropical plants from southern Asia towards the north-west along the shores of the Tethys sea. This, however, is not the only conceivable explanation. Any discussion of the problem obviously required information on the composition of the flora of southern Asia at, or before, the time when the northward migration was supposed to have begun.

The problem of the geographical relations of the flora thus gave the old controversy about the geological age of the Deccan Traps added significance. The geologists of a hundred years ago had placed the traps in the early Tertiary, but about 1870-80 a late Cretaceous age came to be generally accepted. This view was still officially held by the Indian Geological Survey when Sahni's investigations of the intertrappean flora caused him to look into this important problem of Indian geology from the point of view of a palaeobotanist. At first taking a late Cretaceous age for granted, he soon became convinced that the flora dated from the Eocene (1934f, 1937g, 1940, 1943, 1943c). The chief grounds for his opposition to the prevailing opinion were the great preponderance of palms, especially forms belonging or closely related to modern genera such as *Nipa* and *Cocos*, further, the occurrence of *Azolla*, and the general resemblance of the flora to that of the European Eocene. The problem was somewhat complicated by the fact that floras of tropical aspect seem to be rather less well represented in the uppermost Cretaceous than in the Eocene, especially as far as petrified material or fossil fruits are concerned. However, Sahni's convincing arguments, added to other palaeontological evidence, prevailed, and in one of his latest contributions on the subject (1947a) he could state that the doubts concerning the Tertiary age of the Deccan Traps and their flora had then been " practically laid at rest ".

WORK ON THE RELATIONS OF FOSSIL FLORAS — OTHER ACTIVITIES

A good deal of Sahni's work on the distribution and relations of fossil floras has already been touched upon, especially in connexion with the revision of the Gondwana plants and the investigation of the Deccan Intertrappean flora. It may, therefore, suffice to add here a cursory sketch of Sahni's work and views on some particularly interesting matters.

Purely floristic studies, aiming at complete inventories and detailed comparisons of local floras, played no very great part in his researches. He was more concerned with the important unsolved problems that are still attached to the distribution of extinct floras in time and space. Especially the complex relations between the great botanical provinces of the late Palaeozoic offered him congenial subjects for discussion and ample scope for his analytical mind and dialectic gifts.

He was naturally much interested in the problems connected with the relations of the *Glossopteris* flora to the contemporaneous northern floras and to the Gondwana Ice Age. In a joint publication (1937b) W. Gothan and Sahni described a few but important Lower Carboniferous plants from the Po Series of Spiti, which had been provisionally identified by Zeiller (in HAYDEN, 1904). The authors confirmed Zeiller's conclusions, which implied that the fossils are remains of the preglacial flora which has been recorded from other parts of Gondwanaland and seems to have been more or less uniformly spread over the whole globe. On various occasions Sahni expressed his agreement with the idea that the Ice Age not only broke the dominion of this cosmopolitan flora, but was also somehow causally connected with the origin and rise of the *Glossopteris* flora. At the same time he fully considered the objections against assuming a direct influence of climatic changes on the evolution of new groups of plants, and discussed the problem of causation from the angle of modern genetics (especially 1937f).

In the controversy over the geological age of the Gondwana glaciation he decidedly opposed those palaeontologists and geologists — notably the late Ch. Schuchert — who still persisted in placing this revolution well up in the Permian. In agreement with most geologists and probably all palaeobotanists he maintained that the Ice Age must have set in long before the close of the Carboniferous period. Among the palaeobotanical arguments he quoted especially J. Walton's discovery of typical northern

species of Stephanian age associated with *Glossopteris* in Rhodesia. In discussing the general problem of the occurrence of European elements in the Lower Gondwana floras, he was not inclined to accept the idea of a late immigration from the north as an all-sufficient explanation. He believed that at least in some cases these species had survived the glaciation in refuge areas in Gondwanaland, just as some plants are generally held to have " wintered " in peripheral parts of Scandinavia during the Quaternary Ice Age.

Several well-known objections had been raised against the old view that the *Glossopteris* flora was more or less adapted to a glacial climate. It had been pointed out, of late especially by Sir Cyril Fox, that the Indian Gondwana flora had not been found associated with the glacial boulder beds, but only appeared in the topmost part of the Talchir Series; the climate of the glacial epoch was thus thought to be unfavourable to this flora. While Sahni did not regard the presence of *Glossopteris* as indicating glacial but rather cold temperate conditions, he drew attention (especially 1938, 1939 a, 1946) to discoveries in Australia and South Africa — in the latter continent especially by T. N. Leslie and A. L. du Toit — which prove that the Gondwana flora sometimes flourished in close vicinity of the ice. But he also conceived the idea of a direct search for early remains of *Glossopteris* by new means in order to find out how far down into the Gondwanas this flora could be traced. He thus suggested to Miss C. Virkki (now Mrs. K. Jacob) to look for microfossils in the lowermost, supposedly barren shales of the Indian Talchirs and, later, in samples of the tillites themselves from both India, Australia and South Africa. The now well-known result was that spores of a type elsewhere found associated with *Glossopteris* were discovered in horizons immediately above the Talchir boulder bed in India and even in the matrix of the Bacchus Marsh tillite of Australia.

In numerous original publications, presidential addresses and lectures Sahni discussed with his customary clearness various important problems concerning the relations of Indian pre-angiosperm floras to those of similar age from other parts of Asia and from the continents of the Southern Hemisphere. General comparisons between southern floras are found especially in his Presidential Adresses to the Indian Science Congresses of 1921 c (Botany) and 1926 (Geology). Though some matters now appear in a different light in consequence of later discoveries, these surveys are still indispensable to all students of the same subjects. — Later on Sahni turned his attention more especially to the carboniferous and Permian floras of Asia.

In no other part of the world does the distribution of the late Palaeozoic floras present so many puzzling features as in Asia. At the time when Sahni was studying the plants of the Lower Gondwanas, much new work was being done by others on the roughly contemporaneous floras of Siberia, China, Korea and Sumatra. Sahni's interest in these investigations, which raised more problems than they solved, seems to have been much stimulated by his participation in the Sixth International Botanical Congress in Amsterdam in 1935. The late Palaeozoic floras were one of the outstanding items on the programme of the Section of Palaeobotany of this congress, and also at the immediately following Heerlen Congress of Carboniferous Stratigraphy. On both occasions Sahni took a prominent part in the discussions which, as it happened, largely concerned conditions in Asia (1935 b, 1937 c). Several special publications, mostly of a later date, deal more or less with similar matters (1935 f, 1936 f, 1937, 1937 h, 1939 a, 1939 b). His presidential Address to the Botany Section of the 25th Indian Science Congress (1938) contained a particularly interesting and useful summary of his ideas. He was especially attracted by two analogous problems: the relations of the Lower Gondwana flora of India to the Siberian Palaeozoic Angara flora and to those of China and Sumatra. His contributions were all the more interesting and valuable because, unlike most other authors, he looked at the problems from the angle of India.

With some reservations Sahni accepted the current idea that the Gondwana elements in the Permian flora of Siberia can only be accounted for by assuming immigration from India. In discussing the question how the invaders could have crossed the intervening Tethys sea, he referred, among other possibilities, to evidence from Indian geological explorations in Kashmir. According to Dr. D. N. Wadia, continental conditions prevailed in this region during the greater part of the Carboniferous period, and as late as in the Permian an archipelago of volcanic islands

encroached upon the Tethys. Sahni pointed out that these islands might have served as a kind of bridge and found some support of this idea in certain Russian observations north of the Pamir. The present writer, who had the privilege of discussing these and other related matters with Sahni, did not always see eye to eye with him, but could not fail to be impressed with his ingenuity in introducing new ideas or suggesting modifications of old ones.

Another, even more difficult and important question to which Sahni gave much thought was the abnormal geographical relation between the Indian Gondwana flora and the almost entirely different Permo-Carboniferous flora which extended from northern China and Korea to Sumatra. This flora — which in its entirety, should be named the Cathaysia flora — is essentially of Arcto-Carboniferous type though it gradually developed some peculiar features and is known in its later phase as the *Gigantopteris* flora. The northern Arcto-Carboniferous botanical province thus reached far southward into the realm of the southern or Gondwana flora. Along part of the frontier, here running north-south instead of normally east-west, the two provinces, moreover, approach each other so closely that the well-known contrast between their floras, and presumably their climates, seems to present an inexplicable anomaly. Sahni's interest in these problems was, of course, primarily that of a palaeobotanist; but in discussing them he applied the results of recent work on the geology of the critical region. He called attention especially to the sharp southward bend of the Himalayan geosyncline round the Assam corner, on which new evidence had lately been brought forward by Wadia and P. Evans. In the sea of this geosyncline and its southern continuation through farther India Sahni saw a barrier which might help to explain the difference between the floras. The subsequent horizontal compression of the geosyncline, estimated by Evans at something like 3: 1 would naturally have reduced the original distance. But Sahni, apparently, did not think that this compression alone could have brought the floras of two different climatic zones to their present close proximity on the same latitude Horizontal crust movements of greater magnitude seemed indicated, and he logically turned to the theory of continental drift. Like many other palaeobotanists and geologists he had from the first been much attracted by Wegener's ideas, but he was at the same time duly impressed with the manifold objections against the theory. In his later publications he took a decidedly positive view of the possibility of continental displacements. He thus believed, with Jongmans and others, that Sumatra — and presumably other parts of the old Cathaysia land mass — had drifted to the vicinity of Gondwanaland from an original position more to the north and east. — The problem of the Sumatra flora was no doubt the most notable case in which Sahni adduced arguments based on continental drift. But he looked on the relations between some other Palaeozoic floras from the same angle, and it seems that like some other prominent palaeobotanists, notably W. Jongmans and A. du Toit, he is to be counted among the more or less firm supporters of what is generally called the Wegener theory.

Reference has already been made to the most important of Sahni's contributions on the subject of Mesozoic and Tertiary floras. On floras of still younger Pleistocene age he did not do much original work, but he inspired and helped in that of others. A paper in *Current Science* on the lacustrine Karewa Series of Kashmir (1936 b) contains both an account of his own brief field-work and an interesting discussion of the fossil floras, which have long been held to indicate a comparatively recent uplift of the Himalayas. The palaeobotanical work on the Karewa floras was later continued especially by Dr. G. S. Puri, who did his early work at Lucknow and on more than one occasion expressed his indebtedness to his teacher.

When, in 1944, Sahni announced the discovery of microfossils in the Saline Series of the Punjab Salt Range, he caused a discussion which was to claim a considerable share of his few remaining years. He had probably long been interested in the study of microfloras as an aid to stratigraphy. Reference has already been made to the work on fossil spores that he had done or inspired in connexion with the search for early traces of the *Glossopteris* flora; part of this material he had himself collected in the Salt Range. It was thus a natural step to attack the problem of the Saline Series by means of similar micropalaeontological methods. The plant fragments, especially

the wood elements, recovered by Sahni and his collaborators, clearly indicated that the Saline Series cannot be of Cambrian age, as believed by a majority of geologists at the time, but is post-Jurassic and probably Eocene. This meant that the whole packet of Palaeozoic-Mesozoic beds making up the bulk of the Salt Range must have been pushed over the underlying salt formation by an immense overthrust. A discussion of the stratigraphy and tectonics of the Salt Range — one of the outstanding problems of Indian geology — falls outside the scope of this article. From a palaeobotanical point of view the matter is simple: the plant-remains, of course, cannot be Cambrian but are much younger than the beds now overlying the Saline Series. Sahni certainly proved that their presence in the samples is not due to recent contaminations, for instance in the laboratory ; they actually occur in the rocks. The crucial question is thus whether they can have been secondarily introduced through fissures in the matrix or in some other way ; and this matter does not exactly fall within the province of palaeobotany. The present writer has, from personal experience, long looked with considerable scepticism on evidence from microfossils in cases where it conflicts with other well-established facts — always remembering that a certain interpretation of stratigraphic or tectonic features need not always represent an objective fact. But, while the microfossils in the salt may be open to doubt, he fails to see how, for instance, the manner of occurrence of the wood-elements in the Fatehpur Maira oil shale, as described and depicted by Sahni, can be explained by secondary introduction. However, the subject will not be further pursued here, especially since, so to speak, the case is held by many to be still *sub judice*. Whatever the upshot of the complicated " Salt Range controversy ", Sahni undoubtedly did a great service to Indian geology by introducing a quite novel factor. The records of the two symposia where his discovery was the principal theme of the debate clearly reveal how greatly it stimulated research by forcing a reconsideration of opinions and inspiring new field-work.

While Sahni devoted much time and thought to fossil floras and their relations to geological and palaeogeographical problems, he always carried on his anatomical and taxonomical work with undiminished interest. He had a very remarkable capacity to keep various separate researches going at the same time. Thus, it frequently happened that in one year he published important contributions to both of the two main branches of study which correspond to the roughly twofold aim of palaeobotany.

Fellow-palaeobotanists, reviewing in their minds Sahni's great services to their science, might well find it difficult to decide which of these should be regarded as the most outstanding. According to personal bias and the nature of their own studies they may think in the first place of his work on one or another of several subjects: the anatomical and morphological investigations of Palaeozoic fern-like plants, highly praised by the great authority Paul Bertrand; the somewhat analogous studies of the silicified plants of the Rajmahal Jurassic, culminating in the discovery of the Pentoxyleae; or the researches on the relations of fossil floras. Any of these achievements would alone have sufficed to give Sahni's name a prominent place in the history of palaeobotany. It may perhaps be agreed that some such common heading as " Researches on the fossil plants and floras of India " would cover the most important part of his activity as an author of original publications. — But his services to palaeobotany were not confined to his own researches. An exceptionally inspiring teacher and leader, he created in Lucknow a most flourishing palaeobotanical school, and he revived and stimulated interest in this science all through India. He also promptly spread the results of the current work by means of useful reports, of late years issued annually under the well-known title *Palaeobotany in India*.— It has probably rarely, if ever, been given to one man to play so absolutely dominant a rôle in the development of palaeobotanical science in so great a country.

Many ties connected Sahni and his institute with palaeobotanists all over the world. He was, among all other things, a great letter-writer and traveller. His genial personality and charming manner, added to the high esteem in which he was held as a palaeobotanist, made his international relations unusually cordial and extensive. Though widely isolated from his foreign colleagues in a geographical sense, his standing and connexions made it natural for him to take a leading part in furthering international co-operation and the general progress of

palaeobotany by practical measures. Research in this science had been going on for about a hundred years when Sahni founded the first palaeobotanical society and gave it a wide international scope. Palaeobotanists had long felt the need of a special journal for the publication of news and reviews as well as original papers. An abortive attempt to supply this want had been made in Germany some forty years ago; but since then no one had dared to embark on so difficult an enterprise. Sahni, however, took the matter in hand with his customary optimism and energy. He did not live to see the fruit of his endeavours, but the present volume testifies to their success.

When Sahni decided to found a special palaeobotanical institute and make it an international research centre, this important project met with universal understanding and sympathy. His fellow workers in other countries are no doubt unanimous in hoping that his plans will be fully realized to the undoubted great benefit of both Indian and international science.

Sahni surely had all the essential qualities that go to the making of a great man, and would doubtless have come to the front almost in any other career as well as in science. It would not be surprising if he had been urged to transfer his activity to some wider sphere than a special branch of science. Tempting opportunities in various directions, in any case, cannot have been wanting; but he remained steadfast in his devotion to palaeobotany. His achievements in this field won him much honour in his lifetime; the unselfish and successful service that he gave to his science will certainly also be remembered with gratitude by the future generations of palaeobotanists.