Symposium on Evolutionary Plant Biology—an introduction to the theme

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EVOLUTIONARY tendencies, pathways and patterns in relation to form and function and climatic interaction are intricately related to environmental responses. Records of nature's experiments in these directions are entombed in sedimentary rocks. The plant fossils are part of nature's own archives and comprise a miniscule subset of a part of vegetal life that thrived in the past. These meagre remains constitute the only reliable evidence of plant life. They also provide valuable data for determining relationships among different taxonomic groups as well as for working out rates of evolution and for developing new hypotheses in systematic and evolutionary biology.

There is not only physical evolution but evolution of consciousness. All organisms have made attempts and adjustments to relate to their environment. Every organism selectively absorbs, assimilates and transforms what it receives from the environment. Ontogeny reflects phylogeny and thus evolutionary history is recapitulated.

A traverse from the origin of life itself through prokaryote-eukaryote transition, heterotrophy-autotrophy, migration of plants from sea to land, modifications/evolution of vegetative/reproductive structures, appearance of flowers and their ultimate diversification and conquering of the earth by these plants exemplify impact of plant fossil research on evolutionary botany. The complete picture is reconstructed by the plant fossil researcher like a forensic expert. Investigation, correlation, analysis and synthesis of the plant fossil scene thus provides basic data on plant evolution. Strategies adopted by plants, character diversification, evolution of leaf, tracheid, vessel, flower, seed and processes involved in controlling the ancient plant community structure, extinction and migration pattern are all reflected in sedimentary records.

Some important events in the earth's history are discussed with reference to their impact on evolution and distribution of plants.

EARLY AQUATIC LIFE

About 3.5 billion years ago erosion of terrestrial rocks and their redeposition in the oceans gave rise to the first sedimentary rocks. Life elements apparently appeared around this time. Life perhaps began at the interface of solid, liquid and gaseous surfaces where normally there was an energy influx. The dilute "broth", activated by solar energy and lightening might have first formed the amino-acids, then proteins and gradually the first organisms (Venkatachala *et al.*, 1988). The earliest organisms were chemoheterotrophs-absorbing necessary nutrients from the surrounding water. The next organisms that appeared were chemoautotrophs. They obtained their energy by degradation of chemical compounds for the synthesis of food molecules. These organisms are found even today in the Islands of Galapagos and deep ocean thermal springs. Cyanobacteria represent the highest level of evolution in kingdom Monera. They generated oxygen photosynthetically and appeared in the Archaean. When the oxygen level started rising chemical and biological strategies to cope with this new situation were adopted. Many organisms, unable to tolerate the toxicity of this gas, were permanently driven to anaerobic niches while others first developed tolerance, then facultative use and eventually the obligate use of oxygen in metabolism.

The first eukaryotes were probably primitive Protists : aerobic, aquatic, unicellular organisms whose patterns of cell division and life cycle vary extremely from one species to another. The acritarchs and vase-shaped microfossils (*Melanocyrillium*) in the Precambrian sediments (1800 million years) probably represent the earliest records of the Protista. The origin of the eukaryotic cells surely involved endosymbiosis, the engulfing

of one organism by another, giving rise to cell organelles such as the mitochondrion and chloroplast.

. The three defining properties of living system, viz., autopoesis (self maintenance), growth and reproduction can occur in total absence of sex. The evolution of sex possibly was a biological strategy to meet the vagaries of environment. At some stage in the distant past some free-living single-celled organisms might have exchanged genetic material with one another and gained advantage over those that did not. This new means of incorporating adoptive genetic changes being advantageous, helped in rapidly recombining and forming new individuals. Favourable traits, developed through mutation in different individuals, were quickly brought together in one individual. The sexual reproduction along with meiosis thus helped not only in the recombination of characters but also in developing diverse characters in the offspring (Margulis & Sagan, 1986).

Metaphytic organisms must have evolved from unicellular protists. The first stage in the evolution requires arrangement of these cells in a linear pattern. Presence of such a linear multicelled condition is quite common in several filamentous algae. If one takes the evolutionary process further, the next step could be the formation of plate-like algal bodies or algal sheets. *Vendotaenia*—a sheet alga has been recorded from 1,000 million years old Vindhyan sediments of Madhya Pradesh (Shukla & Sharma, 1970). Gradually the practice of the division of labour, delegating workload to specialized cells or group of cells, evolved. For example, the heterocyst of cyanobacteria takes up the responsibility of reproducing in adverse conditions (Sastry *et al.*, 1972).

Indian examples of early life forms are few. The possibility of extensive presence of methanogens during Archaean has been suggested (Hayes, 1983). Isotopic evidences for the methanogenic and methanotrophic bacteria are also available from the Archaean sediments. The graphites in the Dharwar Craton, India give evidences of high degree of fractionation of carbon and provide C^{13} values of −23%.. and −35%.. vs PDB respectively. Such low values of isotopic ratios of carbon are considered to have resulted by the primary organic matter with normal C values being consumed by methanogenic bacteria and the released methane ($C < -40\%$..) in turn, being taken up by methanotrophic bacteria. (Jurgen Hahns, Max Planck Institut für Chemie, Personal Communication to RS, in Venkatachala *et al.*, 1986). These graphite samples also revealed the presence of probable bacteria morphologically comparable with methanogenic and methanotrophic bacteria.

Isotopic evidence of dissimilatory sulphate reduction indicates the possibility of the appearance of sulphate respirers betwen 2.8-3.1 Ga (Schidlowski, 1979). Record of coccoid and rod-shaped bacteria morphologically comparable to members of Siderocapsaceae and *Thiobacillus*, from 2.6–3.2 old sediments of Kudremukh Iron Formation provides structural evidence for sulphate reducing bacteria (Venkatachala *et al.*, 1988). These finds predate the earlier known evidence of sulfur bacteria from the 2 billion years old Gunflint cherts.

The stratified stromatolites in the Archaean are considered to have formed by benthic, anaerobic, photosynthetic and heterotrophic bacterial community (Margulis *et al.*, 1980) and the presence of columnar stromatolites is indicative of the possible existence of filamentous photoautotrophs. The occurrence of both stratified and columnar stromatolites provide presumptive evidence of cyanobacterium dominated biocoenoses around 2.8 billion years (Srinivasan *et al.*, 1989; Vasudev *et al.*, 1989). Structural evidences of probable filamentous aerobic photoautotrophs have also been found in the Donimalai Formation of the same area in Karnataka (Venkatachala *et al.*, 1989). Evidences of anaerobic photoautotrophs in 3.5 billion year old Warrawoona Group, Australia and aerobic photoautotrophs in 2.8 billion years old Fortesque Group, Australia are already known and therefore there is a need to search for photoautotrophic biological and chemical signatures in even older sediments.

EARLY LAND LIFE

The earliest multicellular algal sheets gradually developed features like branching. They inhabited the aquatic media where nutrients were plenty and easily available to all parts of the organism. Migration to land can be explained in terms of depleting nutritional resources of the early seas. The Silurian-Devonian plant fossil records indicate differential ecological preference of early plants. The forms inhabited brackish, fresh water and terrestrial areas. The continental habitats occupied by these plants witnessed changing trophic structure and productivity. Competition demanded gradual innovation of newer strategies. Environmental factors probably played a key role during the time period between advent of eukaryotes and the invasion by early land plants. Changes in the sea level attributed to Ordovician glaciation may have stressed near shore communities leading to the

advent of stress-tolerant intertidal and subtidal algae (Pratt *et al.*, 1978).

The evolution of land plants from an algal group to a group of organisms which completed their life cycles in a subaerial environment was the first major change involved. An initial exploitation of the land environment was mediated by a number of vegetative adaptations. These probably involved protection from dessication by deposition of water impermeable substances such as cutin and probably simultaneous induction of perforations of lesser or greater morphological differentiation for the exchange of gases. A change in plant chemistry would have played a significant role at the time both for formation of the cuticle and also of lignin. Some degree of morphological differentiation into aerial portions and supporting parts would be required to stabilize the plant in its growth environment and to permit efficient photosynthesis (Tiffney, 1985).

During the course of time sexual reproduction increased in efficiency. The communities slowly became more diversified and the vegetative growth decreased in significance. This diversification was further aided by the appearance of relatively larger plants in the herbaceous component. With the increase in height appeared the shrubs and finally the trees. The effect of selective increase in verticality of the community was to permit the distinction of separate layers (herb, shrub, canopy tree) so that more organisms could be accommodated within one community. Arborescence went hand in hand with continued refinement of the vascular cambium. The energy expended originally in a lateral growth plane was redirected into a vertical one. Certain selective pressure played important role in the development of arborescence. Competition for light among the members of the community and dispersal advantage to be gained from a tall sporophyte, was a defensive move on the part of land plants against insects. This new strategy was successful until the insects discovered flight Evolutionary changes in reproductive systems other than introductions of new vegetative characters gradually contributed to significant increase in community diversity (Knoll, 1986).

Thus the initial adaptation of plants to land involved a host of characters which became integrated over a period of time and which evolved primarily in response to the relatively desiccating environment. The sporophyte and gametophyte were on an equal competitive basis during the earliest stage of this evolution. Moisture requirements eventually dictated the dominance of sporophyte. Together with conservation of energetics mega- and

micro-spores appeared and ultimately lead to the evolution of the seed habit.

The diversification process was accelerated by the Devonian appearance of seed plants to a Late Devonian peak of over 40 genera; thereafter following a slight decline diversification resumed in the Carboniferous and the number of species increased to over 200. The increase in the number of plant species occurred gradually between the Middle Carboniferous and the end of the Permian. The slight reduction of about twenty per cent in diversity at the end of Permian was followed by rapid increase to pre-Mesozoic levels. Subsequently diversity increased slowly to about 250 species in the Early Cretaceous (Signor, 1990).

Only fragmentary records of vascular plants are known from India. Definite vascular plants are known from the Lower Carboniferous of Spiti Valley (Gothan & Sahni, 1937) and Kashmir. These mostly belong to the Lycophytopsida and are represented by remains of aerial axes of the order Lepidodendrales.

ADVENT AND DECLINE OF COAL FORMING INDIAN FLORA

The land in the Late Palaeozoic was mostly populated by swampy forests. The vast swamp floras of the Carboniferous which formed the greatest coal deposits of geologic history were mostly restricted to the northern hemisphere. In the Permian the locus of the great coal swamps shifted from cool-temperate to warm-temperate regions of the Southern Hemisphere.

In India, the Upper Carboniferous was a time of the great glaciation that also covered most of the Gondwana Supercontinent. The vegetation cover must have been drastically reduced, plants surviving in protected niches. The glaciation was followed by the deposition of a great thickness of sediments.

The Gondwana vegetation probably arose from the pre-existing Carboniferous stock through saltations. The glacial episode could have acted as a catalyst for rapid genetic reorganisations in the parent populations resulting in newer morphophysiological types (Maheshwari, 1990). In the basal Permian, the plants were small and simple that could tolerate the rigours of an arid climate. During the late Early Permian, the plants had relatively thick cuticle indicating restricted availability of water. During the Middle Permian, the precipitation in India probably was very high. A temperate climate is indicated by the presence of growth rings in the trees. In the Late Permian, the climate was warm-temperate with comparatively

high wind velocities. The climate became arid during the Triassic as is indicated by reduction in leaf size and by the presence of papillae overhanging the stomatal aperture in most cases (Bose, 1974).

Likewise pollen show a significant evolutionary pattern. Striations on the central body show a definite trend of evolution in their complexity. Older elements mainly have simple horizontal striations. Progressively branched striations sometimes with vertical partitions and a reticuloid pattern came into being. By the Late Permian the striae get transformed into taeniae. The maximum diversification in striation patterns is evidently associated with maximum luxurient vegetations which produced coal. Some of the important palynotaxa include *Protohaploxypinus* (*Faunipollenites*), *Striatopodocarpites* (*Gondwanipollenites*), *Densipollenites* and *Crescentipollenites*. A warmer humid climate at this time must have favoured this proliferation (Tiwari & Tripathi, 1988). At the beginning of the Early Triassic a change is noticed in the basic composition of the palynoflora. The taeniate pollen perhaps increase consistently at the cost of striate pollen in the Triassic (Vijaya & Tiwari, 1991).

From the genus *Gangamopteris* started a great lineage of plants that dominated the vegetational scenario of India and other countries of the Gondwana Supercontinent for almost forty million years, i.e., althrough the Permian Period. The *Gangamopteris* leaf was simple, tongue-shaped, non-petiolate. A number of vascular bundles entered the base, repeatedly dichotomized and anastomosed to form a net venation pattern. In slightly younger sediments an almost similar leaf appeared. The leaf had a definite midrib instead of a central strand of vascular bundles and has been named *Glossopteris*. The leaves were borne in tight spirals almost simulating whorls.

The glossopterids, as this group is informally known, were mostly trees. A number of fossil genera are recognised on the basis of characters of pith, primary xylem and secondary wood (Kräusel, Maithy & Maheshwari, 1962). Similar fossil woods have also been reported from the Permian sediments of Antarctica (Maheshwari, 1972). A very characteristic form of woody axis is *Vertebraria* which is known from all the Permian sediments of the Gondwana Supercontinent. This axis, which has now been proved to·be a root, comprised 5-7 vertical wedges of secondary xylem interconnected by horizontal septae, also made up of tracheids (Schopf, 1965).

Two groups of ovule-bearing fructifications have been assigned to the glossopterids. In one the

ovules were arranged in a regular array on the adaxial surface. In the other group the stalk was branched, each branch terminating in an ovule-bearing capitulum. Both types apparently arose from the midrib; but there is a distinct possibility that the fructification were axial to the leaf and hence modifications· of a shoot. Polliniferous structures also seem to be axial. Other fructification types reported may be variations or belong to other orders. The capitula of some of the Ottokariales are incurved at the margins to varied extents as seen in thin sections or transfer preparations (e.g., *Satsangia*). Was it an experiment to enclose the ovules? (Maheshwari, 1990). Recently an unique branched fructification has been reported in which the ovules are not associated with a capitulum. The leaf/plant that bore this fructification is not known (Bajpai & Maheshwari, 1991). Other gymnospermous leaves associated with the glossopterids have been referred to Cordaitales (*Noeggerathiopsis*), Cycadales (*Pseudoctenis, Pterophyllum*), Coniferales (*Paranocladus, Buriadia, Walkomiella*) and Ginkgophytopsida (*Saportaea, Psygmophyllum, Rhipidopsis, Ginkgoites*). The glossopterids that dominated the Permian vegetational scenario started declining during the uppermost Permian, though the genus *Glossopteris* continued atleast into the basal Triassic. There are reports of occurrence of this genus even in the Late Triassic (Lele, 1962).

Basically though the Gondwana flora of India has a characteristic composition, yet several northern forms have been identified from time to time. The question whether they are real migrants or are the result of parallel evolution/homoplasy is still vexing the minds of palaeobotanists. Many of the ferns have been shown to be indigenous to Gondwana (Lele, 1976), but due to lack of fertile structures, the exact status of other remains is as yet not clear, e.g., *Schizoneura, Sphenophyllum* and *Lobatannularia*. The recent report of ginkgopsid *Saportaea* from the Lower Permian of Rajmahal Hills (Maheshwari & Bajpai, 1992) has added another aspect, because of its occurrence in both Cathaysian and Euramerican floras. If the palynotaxa are also taken into account, a close similarity will be found between different floristic provinces which will be difficult to explain with our present understanding of palaeopositions of the continents. Sahni (1936) discussed the implication of homopositious floras and continental drift, and opined that detailed critical comparative studies will help to understand floristic provincialism.

AGE OF CYCADS

The Mesozoic Era—the age of cycads and

dinosaurs—was the point of time where major diversification of plant groups took place. Marine and terrestrial biotas were impoverished at the beginning of the era. There was a floral diversification. Ferns, pteridosperms, cycads, Bennittitales, Coniferales, Ginkgoales flourished at various levels in the middle of this era. Near the end of the era flowering plants replaced conifers and their relatives as the dominant forms of terrestrial vegetation. Large scale extinctions punctuated the Mesozoic history of life.

Scanty information is available about plant life of the Triassic Period in India. The vegetation possibly comprised Pteridosperm-like plants. These leaves have been referred to the genera *Dicroidium* and *Lepidopteris*. The Late Triassic records show presence of coniferous foliage, such as, *Elatocladus* and *Pagiophyllum* (Pal, 1986). Pteridophytic micro- and mega-spores reflect the occurrence of a fairly varied pteridophytic undergrowth during this period. The change in plant forms indicate that there was a marked upheaval in the edaphic factors influencing the vegetation. Possibly there was a major climatic change bringing about extinction of the early vegetation which is replaced by an entirely new one. There was a decrease in diversity of lycopods and sphenopsids.

Because of virtual non-deposition of continental fresh-water Jurassic deposits in India, palaeofloristics of this period are relatively less known. However, spores and pollen of land plants have been recovered from marine sediments of Rajasthan and Kutch. These reflect the occurrence of gymnosperm families Cheirolepidiaceae, Podocarpaceae and Araucariaceae besides the pteridophytic families Cyatheaceae and Osmundaceae (Venkatachala, 1969).

During the Early Cretaceous cycads, Pentoxylales, conifers, Ginkgoales dominated the vegetational scene in India. Fossil floras known from the west coast, east coast, central India reflect the diversity of plant groups that existed. An enigmatic group Pentoxylales thrived more or less in seclusion in the Rajmahal Hills of Bihar. This plant has been recorded from some parts of the Gondwana Supercontinent. Another group Bennettitales attained its acme during this time. A model of reconstruction of *Williamsonia sewardiana*, a Bennettitalean plant, reconstructed by Professor Birbal Sahni now adorns the main foyer of the Sahni Institute.

The araucarioid conifers were represented by *Araucarioxylon* (wood), *Brachyphyllum*, *Pagiophyllum* (leaves), *Araucarites* (seed scale) and *Araucariacites* (pollen). The podocarpaceous conifers were represented by *Podocarpoxylon* (wood), *Elatocladus* (leaves), *Stachyotaxus*, *Nipaniostrobus* (ovuliferous scale), *Podostrobus* (pollen producing organ), *Callialasporites*, *Podosporites* and *Microcachryidites* (pollen).

ORIGIN AND SPREAD OF ANGIOSPERMS

The flowering plants consist of about 12,000 genera and over 2,00,000 species. When the first flower opened or what flower it was—a palm or perhaps *Magnolia* or some species now extinct—is not known. But by the Cretaceous Period a hundred million years ago, flowering plants were fully established. Their spread was assisted by insects, whose evolution curiously runs parallel to their own. The innovation of the nourishing ovary for the embryos helped quick spread across the globe, leading to a clan of a quarter of a million species and occupying the landscape in a great mosaic of shapes and colours. Only a few million years after this advent most wild flowers we know were established.

The earliest and clearly accepted record of angiosperms is from the Barremian sediments in England, eastern Africa, and the Middle East represented by infrequently occurring monosulcate columellate pollen (Hughes & McDougall, 1990). Possibility exists that this group developed in dry or mountaneous areas with little chance of fossilization. One school of thought believes that angiosperm origins and initial radiations were centred near the Equator along the margins of rift valley system as the ancient land masses of Laurasia and Gondwana split into the several continental units recognised today. Pollen recovered from Albian sediments resemble extant pollen of Winteraceae which is now considered as the oldest modern angiosperm family.

A seemingly chloranthoid flower (with Clavatipollenites-type pollen) from the Late Albian of Maryland is a strong contender for early flower record. *Sarcandra chloranthoides*—flower about 3 mm long and consisting of a single stamen and a single carpel—is one such example. Another group represented by Magnoliaceae, Degeneriaceae, Austrobailiaceae, Himantandraceae, Eupomatiaceae, Annonaceae and Winteraceae with the much larger flower consisting of a perianth, many stamens and carpels is also considered to have primitive flowers (Endress, 1987). Taylor and Hickey (1990) have reported a flowering plant from the Aptian of Koonwara site in Victoria, Australia which consists of a small axis bearing two leaves and an attached flower. It suggests that some of the earliest

angiosperms were small perennial plants and the separation of dicots and monocots took place before the Early Cretaceous.

The developmental variability of angiosperms is remarkable. Angiosperms carried special features such as absence of free-living gametophyte, morphological adaptations coupled with reproductive/life cycle modifications, dormancy of seeds, clear dispersal mechanism. Each one of these characters is a response to an evolutionary need or an adjustment to changing environmental conditions. The ultimate aim of the experimentation by nature is to make the group a success and to make it succeed in balancing with other conditions. The development of exine stratification, apertural fractures of pollen, development of land habit, deposition of cuticle and lignin, the change from an herbaceous habitat to an arborescent habit, the development of the seed ultimately leading to angiospermy are only few examples. Recent SEM and TEM interpretations on the *Classopollis* group of pollen show that as far back as the Triassic, this group of pollen had developed an exine comparable to that of some modern angiosperms (Vasanthy *et al.*, 1989). One of the principal driving forces in angiosperm evolution is pollination mechanism. The sudden population explosion in the Mesozoic Era may be attributed to the appearance of primitive mammals, birds and primitive insects, like beetles.

In India, definite angiospermic pollen have been recorded only in Albian sediments of Cauvery Basin (Venkatachala & Sharma, 1974a, 1974b). Pollen with angiospermoid characters have been recorded from the upper part of first intertrappean sediments of Rajmahal Formation which are Early Cretaceous in age (Tiwari & Tripathi, 1991). The pre-Cretaceous origin of angiosperms still remains a possibility. The group was well established by the Late Cretaceous and evolved rapidly.

The C4 and CAM (Crassulacean Acid Metabolism) system plants probably evolved during the Cretaceous Period as a response to atmospheric changes. Cretaceous atmosphere, more rich in oxygen, could have favoured the evolution of C4 systems because average global temperatures were higher and more equitable than at present. Palaeobotanical evidences are required to exemplify C3, C4 and CAM system plant evolution. Adaptations of plants to arid environments may not be well-preserved in fossil records due to preferential preservation. Isotope analysis may suggest changing relative frequencies of photosynthetic pathways through time in relation to atmospheric composition and temperature (Spicer, 1989). Pre-Eocene fossils belonging to grasses would help to understand changes in plant physiognomy.

EXTINCTIONS AND MIGRATION PATTERNS

Globally simultaneous mass extinctions have reset the clock repeatedly in animal evolution but their influence on the course of Tracheophyte evolution may have been minimal. To the extent that global simultaneity in extinction proves to be a consequence of ecological catastrophy, it may be the capacities for dormancy and vegetative regeneration exhibited by many plants that give them a higher probability of survival.

The terminal Cretaceous extinction is a much talked about phenomenon. In oceans, ecologically diverse groups including calcareous nannoplankton either died or were reduced to a fraction of their former diversity. On land, dinosaurs are most widely recognised victims of the terminal Cretaceous extinctions. Indian plant fossil records mostly drawn from Deccan trap sediments do not support the mass extinction during terminal Cretaceous—Early Tertiary sediments of central India as there was a floral continuity (Bande *et al.*, 1987).

On the contrary the extinction pattern at the terminal Eocene in India can be understood through palynological data (Venkatachala *et al.*, 1988). Many palynofossil genera which are recorded from Palaeocene-Eocene sediments in India migrated or faced extinction. *Lakiapollis* (= *Durio*, Bombacaceae) is found in Palaeocene and Eocene sediments in several regions. There is no post-Eocene record of this pollen from India but pollen comparable to *Durio* have been recorded in Miocene and post-Miocene sediments of Malaysia, where the genus is now well settled. Similar examples of taxa which inhabited India during Eocene, became extinct in the post-Eocene period but are found in other continents even today are many.

CONCLUSIONS

The continuous diversification of the green world both in quality as well as quantity reflects their success in developing appropriate strategies to face new challenges posed by change of physical conditions. The organisms that adapt to changing conditions flourish and diversify while those that fail to adapt leave fewer and fewer replicas and eventually become extinct. Thus it is the successful organism that leaves more progeny which ultimately dominates the biosphere. Evolution is continuous, newer innovations continue to appear. The Quaternary Era witnessed evolution of newer forms

and possible extermination of others through anthropogenic activities.

To sum up, the science of palaeobotany has contributed greatly to understand the evolution of life on earth, which include recognition of aspects of the early history of life and the formation of the present day atmosphere, timing and rate of biological evolution in the first four-fifth of the earth's history; biological theories on transition from prokaryotic to eukaryotic cell types; discovery of the earliest and most primitive land plants, reproductive aspects of land plants, origin and diversification of cycadophyta and coniferophyta, rate and morphological nature of the contemporaneous diversification of angiosperm leaves and pollen and chronological sequence of evolutionary events. The current "Interpretative" phase of palaeobotanical research will augment well during the coming years in generating relevant data on different aspects of plant evolution which will greatly contribute to plant and earth sciences.

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