NEOGENE CHAROPHYTE FOSSIL ASSEMBLAGES FROM INDIA IN THE CONTEXT OF EXTANT FORMS, PALEOBIOLOGICAL ISSUES AND GEOLOGICAL INFERENCES

A thesis submitted to the

University of Petroleum and Energy Studies

For the Award of

Doctor of Philosophy

In

Department of Petroleum Engineering and Earth Sciences

By

Nandita Tiwari

June 2022

SUPERVISORS
Dr. Uday Bhan
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Energy Cluster
(Department of Petroleum Engineering and Earth Sciences)
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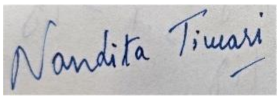
DECLARATION

I declare that the thesis entitled "NEOGENE CHAROPHYTE FOSSIL ASSEMBLAGES FROM INDIA IN THE CONTEXT OF EXTANT FORMS, PALEOBIOLOGICAL ISSUES AND GEOLOGICAL INFERENCES" has been prepared by me under the guidance of Dr Uday Bhan, *Associate Professor*, Department of Petroleum Engineering and Earth Sciences, University of Petroleum & Energy Studies and Prof. Mukund Sharma, Scientist *G*, Birbal Sahni Institute of Palaeosciences, Lucknow-226007. No part of this thesis has formed the basis for the award of any degree or fellowship previously.



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CERTIFICATE

This is to certify that the thesis entitled "NEOGENE CHAROPHYTE FOSSIL ASSAMBLAGES FROM INDIA IN THE CONTEXT OF EXTANT FORMS, PALEOBIOLOGICAL ISSUES AND GEOLOGICAL INFERENCES" is being submitted by NANDITA TIWARI in fulfillment for the Award of DOCTOR OF PHILOSOPHY in the Department of Petroleum Engineering and Earth Sciences of the University of Petroleum and Energy Studies. Thesis has been corrected as per the evaluation reports dated 26/10/2022 and all the necessary changes/modifications have been inserted /incorporated in the thesis.

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ABSTRACT

As part of a larger project on Indian fossil charophytes, this doctoral investigation was carried with the primary objective of documenting fossil Charophyta from nonmarine Neogene sequences in two geologically distinct settings: the Middle Siwalik (Sub-Himalaya) of Mohand area, near Dehradun, and the Ladakh Molasse Group occurring in the zone of collision between the Indian and Asian plates (Indus Suture Zone), Ladakh Himalaya. In addition, for purposes of comparison with the fossil counterparts, efforts were also made to discover and document extant charophyte gyrogonites from the Doon valley. The motivation for undertaking this study comes from the fact that fossil Charophyta on the whole is a relatively poorly studied group in the Indian context despite the potential importance of this group in addressing important geological issues pertaining to paleoecology, biostratigraphy and paleobiogeography of non-marine sequences. Published literature clearly shows that fossil Charophyta, their present and past dispersal, biostratigraphic utility, simple but poorly understood biological attributes of gyrogonites, environmental tolerance, chirality, and their role as the ancestral stock for land plants, present a plethora of scientific questions for contemporary researchers.

Using bulk screenwashing, an assemblage of gyrogonites was recovered for the first time from the Middle Siwalik strata of Mohand area near Dehradun. The assemblage, dated as early late Miocene (~9 Ma), is taxonomically fairly diverse (Tiwari and Bhan, 2021) and comprises thirteen species belonging to seven genera: *Chara aspera, Chara globularis*, *Chara rantzieni, Chara* sp., *Hornichara maslovi, Lychnothamnus breviotus, Nitellopsis megarensis, Nitellopsis* (*Tectochara*) *merianii, Nitellopsis* (*Tectochara*) *huangii, Sphaerochara tewarii, Lychnothamnus barbatus, Lychnothamnus* sp. and *Lamprothamnium papulosum.* The assemblage is indicative of a paleoenvironmental setting with a shallow, warm, low energy, semi-permanent to permanent lake or pond.

The second Neogene charophyte assemblage described in the dissertation was recovered from two sections of molasse deposits: Kargil Formation of Early Miocene age exposed near Kargil in western Ladakh, and the Basgo Formation of Late Oligocene/Early Miocene age exposed near Taruche in central Ladakh. Prior to this work, charophytes were described from the Ladakh Molasse Group nearly half a century ago. Five species of charopytes were identified in this study from the Ladakh Molasse Group: *Nitellopsis* (*Tectochara*) *megarensis*, *Lamprothamnium papulosum*, *Lychnothamnus barbatus*, *Hornichara maslovi* and *Chara* sp. The Basgo Formation is of particular interest since it was considered to be at the base of the Ladakh Molasse Group (e.g. Garzanti & Van Haver, 1988), directly overlying the granitoids of the Ladakh Batholith with an erosional contact. The present charophyte assemblage does not include any Cretaceous element and is consistent with a Late Oligocene/Early Miocene age assigned on the basis of ostracods and rodents. Paleoecological considerations of the Ladakh charophytic flora from Kargil and Taruche sections suggest the presence of a freshwater, cold, alkaline lacustrine environment, possibly with a depth not exceeding ~ 8m.

Study of the extant representatives of fossil taxa is of great help in paleoecological reconstructions besides tracing their antiquity and distribution. Gyrogonites of *Chara vulgaris* were discovered in the Sahastradhara area of Doon Valley and are helpful in evaluating the reported occurrence of its fossil counterparts in the Kashmir valley. It is for the first time that gyrogonites of the extant species *C. vulgaris* are documented from the state of Uttarakhand.

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It is a proud moment for me to acknowledge guidance, encouragement, help, support, probing questions, affections, and space from host of people in completing this dissertation. To begin with I thank my research guides Prof Mukund Sharma, Scientist G, BSIP, Lucknow and Dr Uday Bhan, Sr. Associate Professor, UPES, Dehradun in completing this mission and to Dr Vandana Prasad, Director, BSIP, Lucknow for laboratory facilities of the Institute required in this regard. Scientists of the Institute, namely, Dr Vivesh Vir Kapur and Dr Ansuya Bhandari were kind in giving me the benefit of their experience in charophyte studies and supported in many ways in accomplishing this task., Dr Anil K. Pokharia whose lab is currently assigned to me for my duties at BSIP, granted me space and time to move forward unhindered in carrying out my research work. Dr Rohtash Kumar, retd. Scientist G, Wadia Institute of Himalayan Geology, Dehradun guided me in field for enlarging my fossil gyrogonite collection besides giving me the benefit of his vast experience in knowing geological attributes of the fossil yielding section. I am grateful to Professor Sunil Bajpai, IIT, Roorkee for allowing me to study gyrogonites from Ladakh in his care for this dissertation. I am also grateful to SEM expert Dr. Subodh of BSIP for his support in guiding preparation of the studied samples and related crucial help in that regard. UPES officials too came forward to attend my frequent queries promptly and thus need special mention in my acknowledgments

` My husband, Mr. Abinash Ojha, being a technocrat, never allowed my laptop issues to become a problem in word processing and graphics besides being immensely supportive overall in this venture, so many thanks to him on record. My parents and in-laws helped me in negotiating difficult spells while working for this dissertation and associated field and laboratory work by encouraging and counselling me in their usual affectionate ways. My younger sister Garima and her husband Mr. Amit Gairola showered their affection by finding out and suggesting easier ways to come out of difficult spells during this tenure, particularly in corona pandemic duration.

Preliminary Part

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Chapter 1 : INTRODUCTION AND OBJECTIVES

1.1. Preamble

Indian Neogene Charophyta and their living descendants are part of the 'time table of evolution' of the Planet Earth depicting charophyte evolution from green algal lineage since their first record in the uppermost Silurian till date (Grambast, 1974; Knoll and Nowak, 2017). Charophytes (stoneworts) are macrophytes - aquatic plants large enough to be seen by the bare eye – that occur in a variety of exclusively non-marine aquatic habitats. They are found represented in microfossil assemblages through their tiny calcified oospores called 'Gyrogonites'. These reproductive organs are like seeds of the embryophytes, i.e. the land plants (Soulié-Märsche, 2004). Gyrogonites, the calcified fructifications of all living charophytes, are characterized by a distinct simple structure comprising five all-encompassing cells, which are spirally wrapped clockwise (cells ascending from right to left in lateral view with apex upward) around an inner ovoid egg cell. Unlike in the early phase of their study, charophytes are now increasingly being used in identifying fossil and living plant taxa (Soulié-Märsche and Garcia, 2015). Recent studies (Zhong et al. 2013; Delwiche and Cooper, 2015) suggest that an ancestral lineage of charophytes emerged and adapted themselves to the terrestrial conditions, survived successfully and started reproducing, with some later members evolving into proper land plants. The whole biogeochemistry of Earth was changed due to this huge biological event of "Terrestrialization", and further helped in the emergence of various diverse life forms on the planet due to favourable atmospheric changes and improvement in the soil conditions, eventually leading to the creation of agriculture and formation of modern human civilization.

In the past few decades, charophytes have gained a lot of attention from the plant biologists, due to their significant role in the evolution (Pickett-Heaps and Merchant, 1972;

Pickett-Heaps, 1975; Mattox and Stewart, 1984; Becker and Marine,2009; Harholt et al. 2016).

The fact that all the terrestrial plants with such diversities have evolved from a single streptophyte-algae which took over the land mass around 470 million years ago is truly remarkable (Timme et. al. 2012). Being an ancestral stock for the evolution of land plants, charophytes have enriched the planet with terrestrial life (Domozych et al. 2016) (Figure 1-1). Therefore, studies on fossil and living charophytes are interesting and offer opportunities for stimulating research.

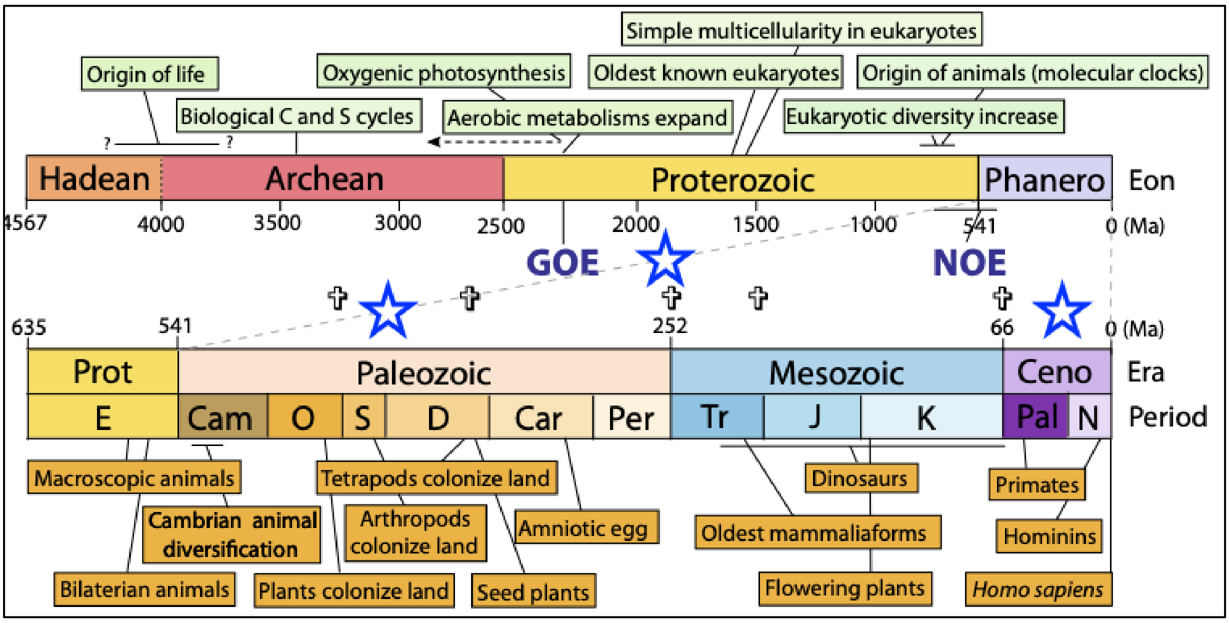

Figure 1-1 The evolutionary timetable. Phanero, Phanerozoic; Prot, Proterozoic; Ceno, Cenozoic; E, Ediacaran; Cam, Cambrian; O, Ordovician; S, Silurian; D, Devonian; Car, Carboniferous; Per, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pal, Paleogene; Neo, Neogene; GOE, Great Oxygenation Event, NOE, Neoproterozoic Oxygenation Event. Crosses and stars indicate times of major mass extinction and charophyte bioevents, respectively (modified after Knoll and Nowak, 2017).

Another aspect of charophyte gyrogonites that has attracted considerable attention is their chirality i.e. sinistral (left-handed) spiral cells since the Permian–Triassic boundary extinction datum. Prior to this extinction event, fossil charophytes of Paleozoic Eon were mostly dextral (right-handed) gyrogonites although they co-occurred with sinistral (right-handed) charophytes until the end of the Paleozoic (Soulié-Märsche, 1999) (Figure 1-2).

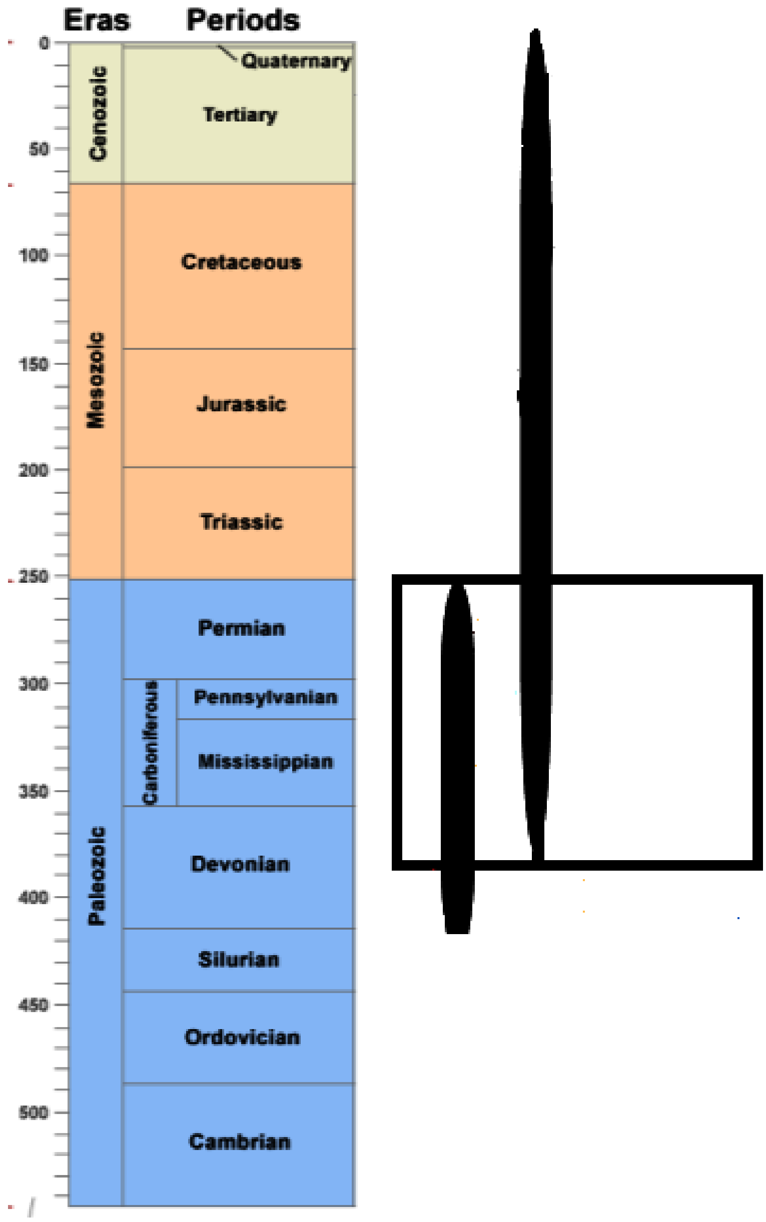

Figure 1-2 Exclusively dextral gyrogonites occurred during the period from Late Silurian to Middle Devonian; then onwards till P/T boundary they co-occur with sinistral gyrogonites, and after that till date for about 250 Ma charophyte gyrogonites are exclusively sinistral. (Based mainly on data in Shaïkin 1991).

Chiral objects are easily distinguished by the fact that their mirror images do not superimpose their own images and our hands are best chiral examples to test it.

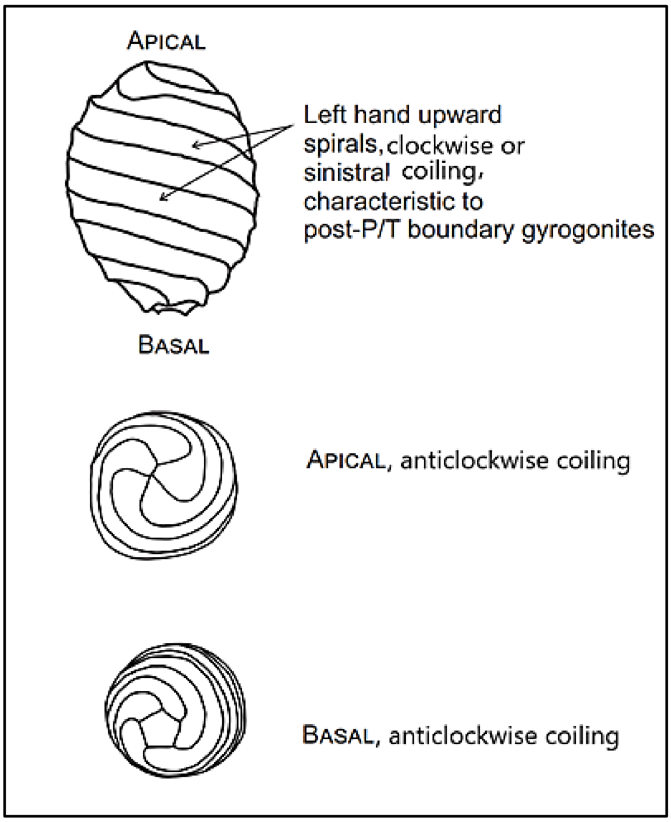

Figure 1-3 Left-handed coiling of the enveloping cells in gyrogonites since P/T boundary; basal and apical views show right-handedness in a sinistral gyrogonite. (Based on data in Soulié-Märsche 2004).

Handedness is observed in lateral view with apical and basal sides towards the upper and lower margins; in left-handed (sinistral) forms, cells take left turn towards apex (Figure 1-3) whereas in the right-handed (dextral) forms, cells move upward towards the apex, the opposite way, that is, they take right turn. Figure 1-4 showing the lateral, apical and basal views of the gyrogonite of *Nitellopsis obtusa* (living charophyte species of *Nitella*) on the left side with non-superimposable mirror images on the right side, illustrate chirality (handedness) of the object in all views used in describing the gyrogonites. Like *N. obtusa*, all extant gyrogonites are sinistrally coiled.

Figure 1-4 Gyrogonite of *Nitellopsis obtusa* with non-superimposable mirror images on the right-side illustrating chirality (handedness); photographs of *N. obtusa* in the left column are from Kropelin and Soulié-Märsche (1991) and were laterally flipped through computer-tech for their respective mirror images in the right column and do not represent any fossil or extant gyrogonite views.

1.2. Charophytes: applications in palaeosciences

In lakes, streamd and ponds, charophytes are often found in noticeable abundance and reflect an interplay of ecosystem properties particularly carbon and nutrient balance, and water clarity. Charophytes are sensitive to changes in ecosystem properties, and this makes them excellent indicators of ecosystem status. Finally, some charophyte species can produce calcified parts which are known as gyrogonites and are easily fossilizable. In non-marine deposits, the fossil record of charophytes spans the past approximately 425 million years, hence gyrogonites are of great value in paleoecological, biostratigraphic and paleobiogeographic studies (e.g. Schneider et al. 2015). As indicators of present and past ecosystems, the use of charophytes as a tool in paleoecological reconstruction similar to ostracods and diatoms is gaining ground, and there are now many examples where charophytes have been used successfully to obtain important information about the past environments, thus forming a link between the past and the present ecology (e.g., Sanjuan et al. 2021). Charophytes have been used in paleoecology as indicators of lake water levels, and paleosalinities in non-marine water bodies (Garcia and Chivas, 2006; Rodrigo et al. 2010; Garcia 1999; Soulie-Marsche et al. 2010). On the basis of geochemical, sedimentological, and taphonomical analysis, species specific paleoenvironmental restrictions for fossil charophytes have been defined (Villalba-Breva and Closas, 2011). As a part of special issue of *Aquatic Botany* entitled "Charophytes and their environmental impact: past records and modern status" (editors, Adriana García, Allan Chivas, Carles Martín-Closas, and Susanne Schneider, published in January, 2015) the results of first controlled-temperature culturing of a charophyte species indicated that (i) growth is optimum at 25 °C, (ii) the gyrogonite carbonate chemistry can provide estimates of Mg/Ca and Sr/Ca of past waters, and (iii) the $\delta^{18}O$ values of *Lamprothamnium* cf. *succinctum* display strong temperature and salinity effects (Dux et al. 2015).

Apart from paleoecological studies, charophytes have also been used extensively in biostratigraphic correlations and paleobiogeographic reconstructions (e.g. exploration for hydrocarbon fields) for both Cenozoic and pre-Cenozoic intervals (e.g. Riveline 1986; Riveline et al. 1996; Mojon et al. 2018; Li et al. 2019; Musacchio, 2000; Sanjuan et al. 2021). Integration of the charophyte data with other fossil groups (such as mammals, nannofossils) and integration with Magnetic Polarity Time Scale has greatly refined the biostratigraphic biozonation as, for example, in the Miocene deposits of the Swiss Molasse (Mojon et al. 2018) and the Cretaceous-Paleogene boundary sequences in the Songliao Basin of northeastern China (Li et al. 2019).

Besides their geological utility, charophytes are an important ecosystem services provider. Charophytes are a major component in food chain and food web, since they are a source of food for various organisms such as snails (Baker et al.2010), herbivorous fish (Lake et al.2002), Cray fish (Cirujano et al.2004), water fowl (Noordhuis et al. 2002; Schmieder et al.2006). Charophytes, by forming dense patches and giving protection from currents and predators, serve as habitat to various organisms mostly periphytic microorganisms and invertebrates and thus play a significant role in sustaining biodiversity in nonmarine water ecosystems. They enhance the water clarity by precipitating large amounts of $CaCO_3$ (Rodrigo et al. 2015) which is responsible for the decrease in the concentration of Ca^{2+} (Pelechaty et al.2014). Kufel and Kufel (2002) stated that Charophytes are involved in carbon and other nutrient storage and thus control nutrient cycle and biogeochemistry of the water body by increasing autochthonous sedimentation and preventing the resuspension of the sediment particles (Vermaat et al. 2000) by accumulating nutrients in plant biomass and indirectly co-precipitating phosphorus with calcium carbonate. Phosphorus which is insensitive to redox changes and is correlated with the $CaCO^3$ is stored in the sediment of charophyte meadows for a long time (Kufel et al. 2013). Heavy metals like Uranium, Cadmium, and Lead (Kalin et al. 2005; Sooksawat et al. 2013) and organic chemicals like Hexachlorobenzene (Schneider and Nizzetto, 2012) which can diminish cyanobacterial blooms (Pakdel et al. 2013) from the water bodies can also be efficaciously removed by the charophytes. Thus the presence of their living charophyte species in surrounding wetlands assure a clean livable aquatic environment. Interestingly, charophytes can also be used as fertilizers for vegetable fields (Schmieder, 2004) and mud bath for therapeutic applications (Zaneveld, 1940). *Chara intermedia* is used in homeopathic medicine, fish culture, water purification, food for farm stock and aquatic animals, insect control, sugar purification and in polishes (Brand and Groeger, 2012). However, although overall favourable, the presence of charophytes in an ecosystem can occasionally be damaging to human interests, such as in Munich (Germany) where overgrowth of *Chara hispida* is found clogging the reservoirs and the channels (Zaneveld, 1940).

1.3. Previous literature on fossil charophytes from India

Globally, studies on charophyte fossils date back to 1785, when the name Vortex was given to tiny fossil gyrogonites by Dufourney de Villers who believed that they were small sea urchins. Later, Lamarck (1807) considered them to be minute univalve molluscs and named them *Gyrogonites*. In 1810, Léman recognized gyrogonites as charophyte fossils (Knowlton, 1888), and then onwards the collection and studies of fossil charophytes started in other countries including India (e.g. Sowerby, 1840).

1.3.1. Pre-Neogene records: Chronologically, studies of Indian fossil charophytes began with a pre-Neogene record of silicified gyrogonite samples collected by John Grant Malcomson from fossiliferous non-marine Deccan intertrappean beds in Sichel Hills, near Nirmul in central India. The collected gyrogonites were later described as *Chara malcolmsoni* by Mr J de C Sowerby in 1840 (Sowerby, 1840). Similarly, *Chara elliptica* described by Hislop and Hunter (1855) in an important and one of the earliest papers on Indian fossil charophytes. Much later, in the 20th century, several workers published descriptive accounts, discoveries and review articles on intertrappean charophytes (Rao, 1938; Rao and Rao, 1939; Sahni and Rao, 1943; Rao and Rao, 1969; Rao, 1954; Rao, 1974, to mention a few). In an important contribution, Rao and Rao (1939) described 13 species of fossil charophytes from the intertrappean beds near Kateru, Rajahmundry, Andhra Pradesh. In a monograph on the Charophyta, Pal et al. (1962) drew attention to the intertrappean charophyte flora described by Rao and Rao (1939) and mentioned the occurrence of charophytes in Central Provinces, Rajahmundry and Hyderabad localities in the intertrappean horizons. Sahni and Rao (1943) also described an intertrappean fossil charophyte from Sausar near Chindwara (M.P.) and referred it to the modern genus *Chara*. (*C. sausari*). From the Vicarabad intertrappean beds Mahadevan and Sharma (in Sahni 1947) described oogonia attached to corticated branches and resembling those of *Chara malcolmsoni*. Intertrappean charophytes were also reported from Yellur, Belgaum in Karnataka by Rao (1954) who described them as *Chara medicaginula, C. turbinate, C. oehlerti*. Later studies on intertrappean charophytes include those by Shivarudrappa (1972a, b, 1977, 1989), Bhatia and co-workers (Bhatia and Mannikeri, 1976; Bhati and Rana, 1984; Bhatia et al. 1988), and most recently by Srinivasan et al. (1994). A total of nine charophyte genera, namely *Peckichara, Harrisichara, Nemegtichara, Stephanochara, Grambastichara, Microchara, Chara, Platychara,* and *Pseudoharrisichara* on the basis of gyrogonites have been named by different teams working on freshwater Deccan intertrappeans of Cretaceous/Paleocene age (Srinivasan et al. 1994)

Charophytic flora from horizons older than the Deccan intertrappean deposits of peninsular India have been described from the early Cretaceous, early Jurassic and Permian horizons. Vishnu-Mittre (1952) reported charophytes from the early Cretaceous Rajmahal Hills, Bihar, and referred them to the Nitelleae rather than Characeae in view of their small size, laterally compressed form and reticulated ornamentation of the oospore wall. Horn af Rantzien (1957) studied these charophyte oospores from Rajmahal and described them as two different species, including a new species *Nitellites sahnii* under the new organ genus *Nitellites*. The Jurassic occurrences are known from the Upper Gondwana Kota Formation of Early Jurassic age, which included two charophyte taxa, *Aclistochara* and *Praechara symmetrica* (Feist et al. 1991; Bhattacharya et al. 1994). These Jurassic records marked the beginning of calciphile charophytes in India. Other Jurassic records include those from the Callovian of Jaisalmer, western India (Bhatia and Mannikeri, 1974). In India, the oldest known record of charophytes is from the Permian (~300 Ma) Barakar Formation of the Talchir Gondwana Basin, Orissa (Narain et al. 2003). *Paracuneatochara*, the taxon reported by Narain et. al (2003) is now considered to be a junior synonym of *Leonardosia* De, 2003.

Amongst the other important occurrences of pre-Neogene Charophyta of India are

Eocene gyrogonites from the Subathu Group of NW Himalaya which are assigned to five genera, *Harrisichara, Gyrogona, Raskyella, Stephanochara,* and *Chara* (Bhatia, 1992). Also worth mentioning is a charophyte record of Paleocene age from the Niniyur Formation of Tamil Nadu (Nath, 1989) and the vegetative parts (thallus/filament) and the fertile organs (globule, nucule) of *Chara* from Paleocene lignite horizons of Rajasthan (Harsh and Shekhawat, 2018).

1.3.2. Neogene and younger charophyte records*:* Sporadic occurrences of Neogene Charophyta from India are known from the Siwalik succession of northwestern Himalaya (Bhatia, 1999) although Details of published Neogene and younger records of charophytes from India, including those of extant taxa, are discussed in Chapter 4 (Systematic Description). It needs to be mentioned that the contributions made by Late Professor S B Bhatia and co-workers on fossil Charophyta from India, has inspired this author to undertake such studies as part of a larger project on Indian extinct and extant charophytes of India. The review articles published on Siwalik Charophyta (Bhatia, 1999, 2003) served as base papers for the present research on Neogene and extant gyrogonites. It also needs to be mentioned that Prof Bhatia donated over fifty type specimens of fossil charophytes to the Museum of the erstwhile Birbal Sahni Institute of Palaeobotany (now Birbal Sahni Institute of Palaeosciences; acronym BSIP), as recorded in the Institute's Annual Report 2004-2005.

1.4. Brief outline of Indian Neogene history

It is widely believed that the northward movement of the Indian island subcontinent culminated in India-Asia collision and the evolution of the Himalaya, with associated faunal and floral changes. In a temporal perspective, the Cretaceous Period (~142 to 66 Ma) is known for the northward movement of the subcontinent, and the succeeding Cenozoic Era (past 66 million years) saw the collision and evolution of the Himalaya during its Paleogene (66 to 23 Ma) and Neogene (23 to 2.6 Ma) periods respectively (Chatterjee et al. 2017 and related references therein). Depiction of the northward movement of the Indian plate and stacking of thrust slabs in the Himalaya due to India-Asia collision has been done by successive workers on the basis of multidisciplinary data and field observations (Figures 1-5, 1-6 and 1-7).

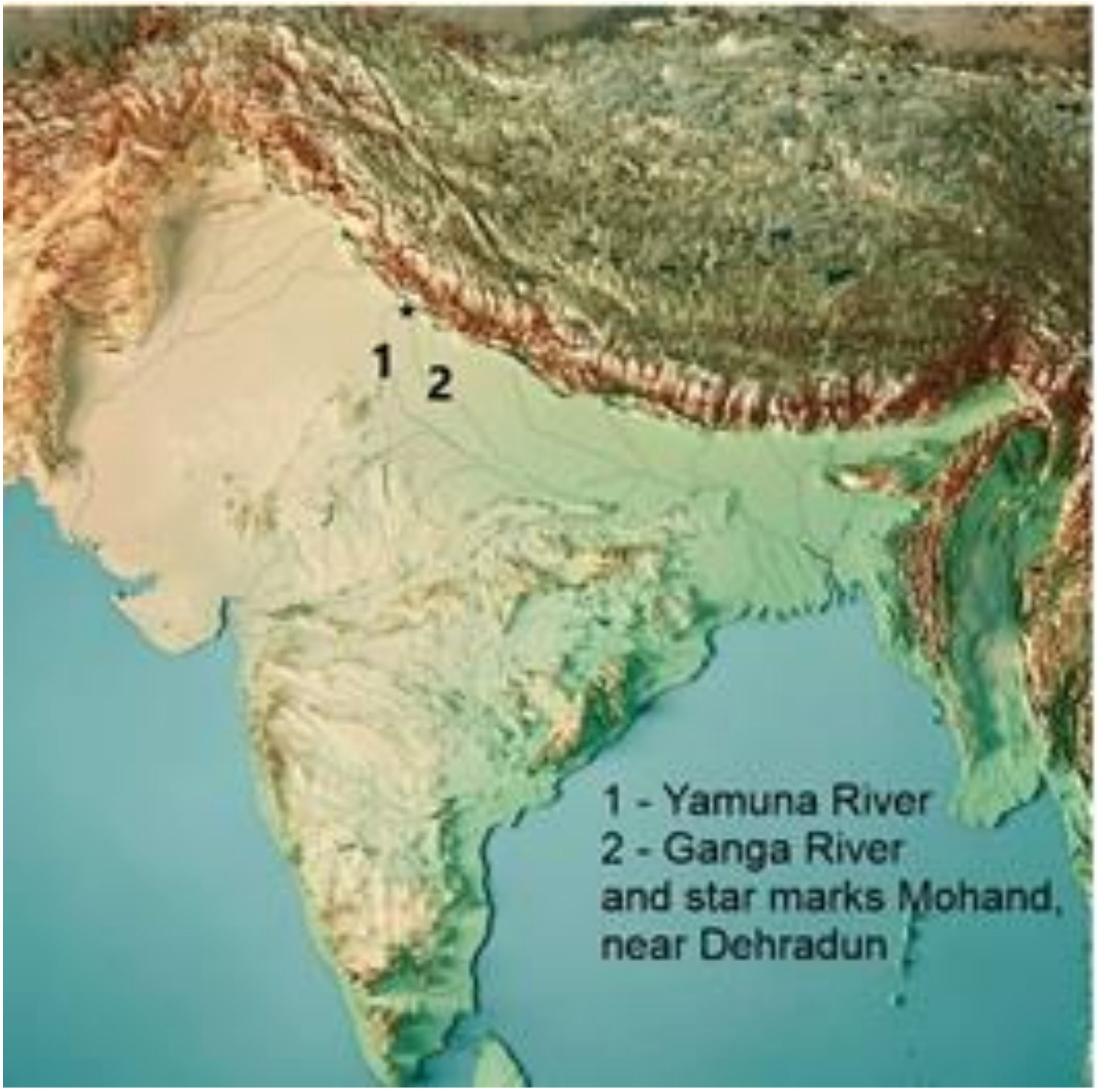

Figure 1-5 Himalayan Arc formed due to India-Asia collision in Cenozoic with syntaxial bends on either side; charophyte localities near Dehradun are between Yamuna (1) and Ganga (2) rivers.

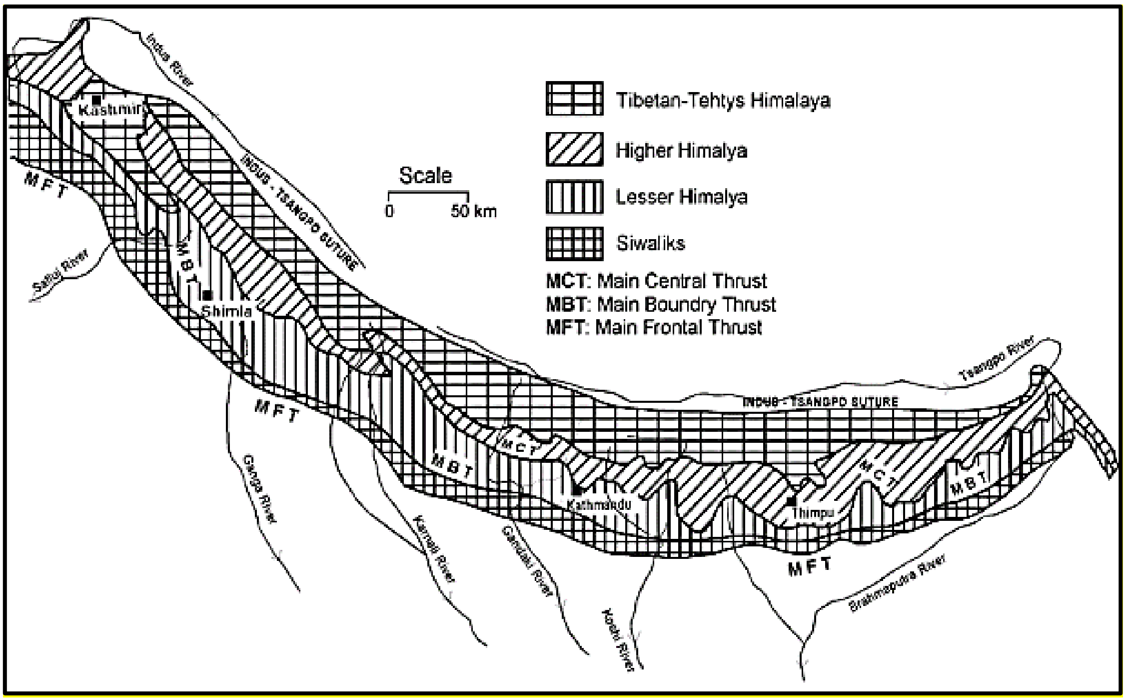

Figure 1-6 Himalayan longitudinal tectonic subdivisions defined by the Main Frontal Thrust (MFT) between the Sub-Himalayan (Siwalik) Zone and Gangetic Plains, the Main Boundary Thrust (MBT) between the Lesser Himalayan Zone and Siwalik, the Main Central Thrust (MCT) separating the Higher Himalayan Zone and the Lesser Himalayan Zone, and the South Tibetan Detachment System (STDS) divides the Higher Himalayan Zone and the fossiliferous Tibetan-Tethys Himalayan Zone, the Indo-Tsangpo Suture Zone juxtaposes Indian and Tibetan (Eurasian) Plate (modified after Gansser, 1964).

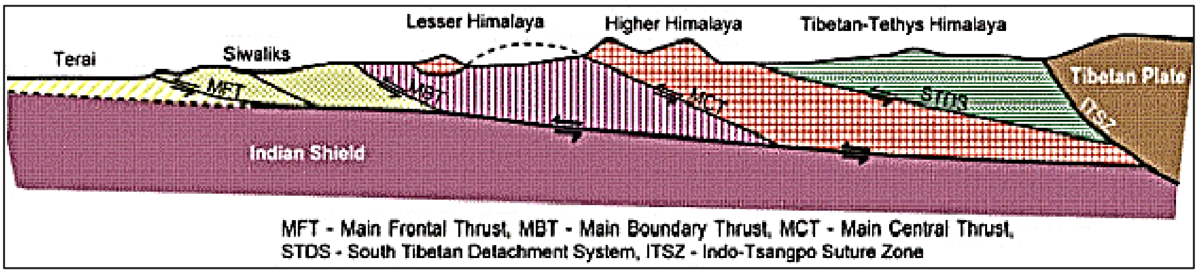

Figure 1-7 Generalized oft-repeated geological cross-section depicting stacking of tectonic slices. (From Dahal, 2006).

Before commencing its northward journey for the northern hemisphere, the Indian island subcontinent, off the Australian coast, was separated from the Asian continent by the Tethys Sea. The northward journey started about 200 Ma with the break-up of Pangaea

(Figure 1-8). Studies reveal that about 140 Ma, the subcontinent was located as south as 50° S latitude, and the Tibetan block was a part of the Asiatic landmass. India collided with Asia about 50 Ma causing rapid uplift of the Himalaya.

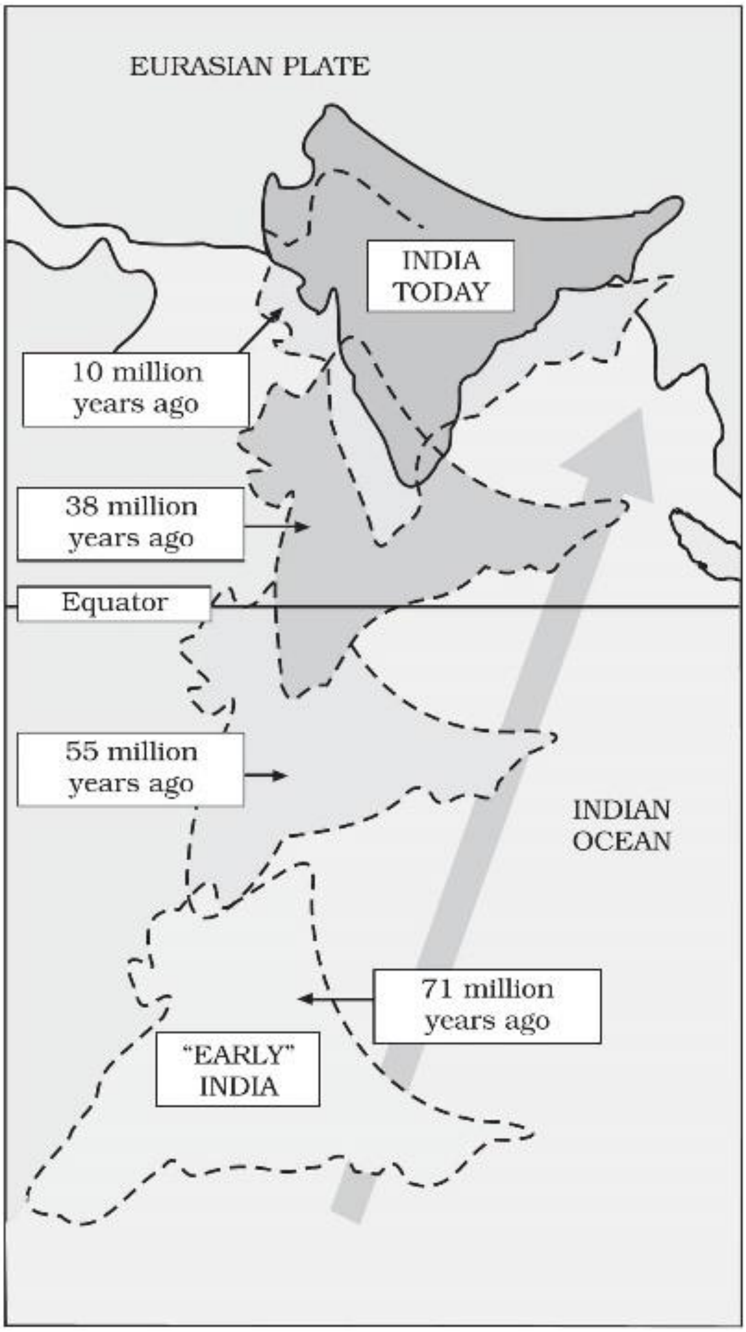

Figure 1-8 Simplified palaeogeographic reconstruction of northward journey of the Indian Island subcontinent to be a part of Eurasia after crossing equator and India/Asia collision ~50 Ma and consequent Himalayan evolution (modified after Molnar & Tapponnier, 1977).

By the Neogene, India was firmly sutured with the Asia and the Tethys had completely disappeared. The history of India's northward movement, which saw a gradual withdrawal of the Tethys sea, is preserved in the Himalayan sedimentary successions exposed in the foreland basin and the Trans-Himalaya. These sequences show a change from shallow marine to fluvio-deltaic conditions which is well documented in the Subathu-Dagshai/Murree/Dharamsala deposits in the foreland basin of Himachal Pradesh and Jammu & Kashmir (e.g. Sahni et al. 1981; Patnaik 2016), and in the Trans-Himalaya by the molassic sequences of Kargil Formation and correlative deposits (e.g., Garzanti and van Haver, 1985). The Miocene rise of the Himalaya has been attributed to the development of two south-vergent thrust faults, the Main Central Thrust (MCT) and the Main Boundary Thrust (MBT), which accommodated N-S compression, thus increasing the elevation of the Himalaya and thickening the crust (Chatterjee et al. 2017).

During the Miocene, around 20 Ma, due to the continued rise of the Himalaya and the resultant uplift of Tibetan Plateau, large rivers (e.g. Ganges, Indus) as well as their tributaries deposited thick molassic sediments (the Siwalik Group) into their foreland basins (Patnaik 2016). The Siwalik horizons are exposed in foothills as a part of the Sub-Himalaya, stretching east-west for nearly 2000 km (Figure 1-6). The Siwalik formations consist of 5–8 km thick accumulations of fluvial sediments (Table 1), and hosts some of the most impressive continental vertebrate faunal successions in the world (e.g., Barry et al. 2013).

Table 1.1. Neogene Siwalik formations of Indian subcontinent and the major tectonic and climatic events (adopted from Chatterjee et al. 2017).

Period	Epoch	Group	Formation	Age range (Ma)	Neohimalayan events	Paleoclimate
Quaternary	Pleistocene	Upper Siwalik	Boulder Pinjor Tatrot	0.9–0.2 3.3–0.9 3.5–3.3	Morphogenic phase; extreme surface uplift; Main Frontal thrust; rapid exhumation and high erosion rate	Pleistocene glaciation in Higher Himalaya; global cooling Intensification of summer monsoon
Neogene Period	Pliocene					
	Late Miocene	Middle Siwalik	Dhok Pathan Nagri	9.8–3.5 11.4–9.8	Reactivation of Main Central thrust; Main Boundary fault; high topography; tectonic upheaval; Tibetan Plateau reached a height of 2 to 3 km	Intense monsoon; increased aridity; major changes in vegetation from C3 (forest) to C4 (grass)
	Middle Miocene	Lower Siwalik	Chinji Kamlial	14.0–11.4 18.0–14.0	Rapid erosion and exhumation; high topography along Higher Himalaya; Siwalik River in the foreland	Warm and humid climate with monsoon; major faunal change
	Early Miocene	Murree		20.0–18.0	Foreland basin; Greater Himalaya uplift, channel flow; extrusion of leucogranites	Warm and humid climate with monsoon

2.6 Ma

23.0 Ma

The Middle Miocene saw the accumulation of thick piles of sediments in the foreland basins due to India’s continued northward movement which resulted in further crustal shortening, uplift of the Himalayas and the continued development of the foreland basins. This led to the development of extensive floodplains in a warm and humid climate as evident from the occurrence of thick paleosols and a rainforest vegetation (e.g. Srivastava et al. 2014; Patnaik, 2016). The overbank facies are abundant in the sedimentary succession, suggesting the dominant presence of meandering rivers. Subsequently, he Late Miocene saw a further rise of the Himalayas and the intensified development of the Asian monsoon (Amano and Taira, 1992; Harrison et al. 1993). The fluvial successions in northern India document a transition Around 10 Ma from minor to major bodies of sandstone, and the deposition predominantly took place in large braided rivers, although this marked change from mudstone to sandstone dominated facies in the Siwalik succession is considered to be time-transgressive. For instance, this change is known to occur at ~10 Ma in Kangra area of Himachal Pradesh in India, ~11 Ma in the Potwar Plateau in Pakistan, and ~9 Ma in Nepal (Kumar et al. 2003; Patnaik, 2016). The period from 11–9 Ma witnessed a reactivation of Main Central Thrust (MCT) and increased sedimentation rates in the foreland basin and in the western and central Himalayas around 6 Ma (Catlos et al. 2002). Data from palynological and mammalian enamel studies, as well as stable oxygen and carbon isotopes of soil concretions, suggest that the grasslands replaced forests during this period (Cerling et al. 1997; Hoorn et al. 2000; Patnaik, 2016).

During the Early Pliocene interval, thickly bedded conglomerate facies with lensoid bodies of sandstone and mudstones was extensively deposited. Around 5 Ma, the conglomerate facies dominated in the western Himalaya including the Dehradun sub-basin and is indicative of river reorganization (Kumar et al. 2003; Clift and Blusztajn, 2005). Subsequently, movement along the Main Boundary Thrust (MBT) in the Himalayan foothills in the beginning of the Pleistocene resulted in an intensified tectonic activity leading to an increase in sedimentation rates in the Subathu sub-basin between 3 and 2 Ma (Kumar et al. 2003). This led to significant changes in the riverine system due to increased fan deposits in the piedmont regions and decreased flood plain deposits. It is believed that the interfluve flood plain areas supported a diverse flora and fauna, while fan deposits provided a preferred habitat for large mammals (Patnaik, 2016). Data on paleosols suggest that warm and humid climate in the Early Pleistocene was followed by cool and dry conditions during the Middle Pleistocene (Sangode et al. 2001). Stable carbon and oxygen isotope data from the Siwalik palaeosols also suggest indicate monsoon intensification at 11, 6 and 3 Ma (Sanyal et al. 2010).

1.5 Indian Neogene vegetation and the charophyte-yielding horizons

Studies on plant megaflora indicate the dominant presence of tropical evergreen to moist deciduous taxa in the Early Miocene Kasauli Formation (Srivastava et al. 2014 and references therein), although several taxa such as *Acrostichum, Garcinia* and *Gluta* suggest coastal conditions (Arya and Awasthi, 1995). Further, it is important to note that *Dipterocarpus* (*Saal* tree) in the Kasauli Formation is considered to be an immigrant from Southeast Asia in the

Early Miocene and that it arrived in Asia after the final suturing of India and Asia (Shukla et al. 2013; Tiwari et al. 2012; Patnaik, 2016).

Paleobotanical investigations of the Oligo-Miocene Kargil molasse of Ladakh have yielded palms (e.g., Sabal) and the temperate Prunnus of the family Rosaceae Guleria et al. (1983); Lakhanpal et al. (1984); Mehrotra et al. (2014). The palm genus *Trachycarpus* was described by Lakhanpal et al. (1984) from the molassic beds of Ladakh. Abies, a conifer pollen, was also recorded from the molassic deposits of western Ladakh, and this record indicates warm sub-tropical to temperate conditions. (Mehrotra et al. (2014) suggested that these conditions were caused by northward moving Indian plate into the sub-tropical temperate zone together with the rise of the Himalayas in the early Miocene It is likely that these temperate elements migrated in to the Ladakh from neighbouring China region.

In India, marine Neogene horizons are in the eastern and western coastal regions as per map by Ramnathan and Pandey (1988). However Indian Neogene nonmarine horizons yielding macro- and microfossils are known from numerous exposures enumerated by Patnaik and Prasad (2016) in their review article on Indian Neogene terrestrial climate and biota (Figure1-9).

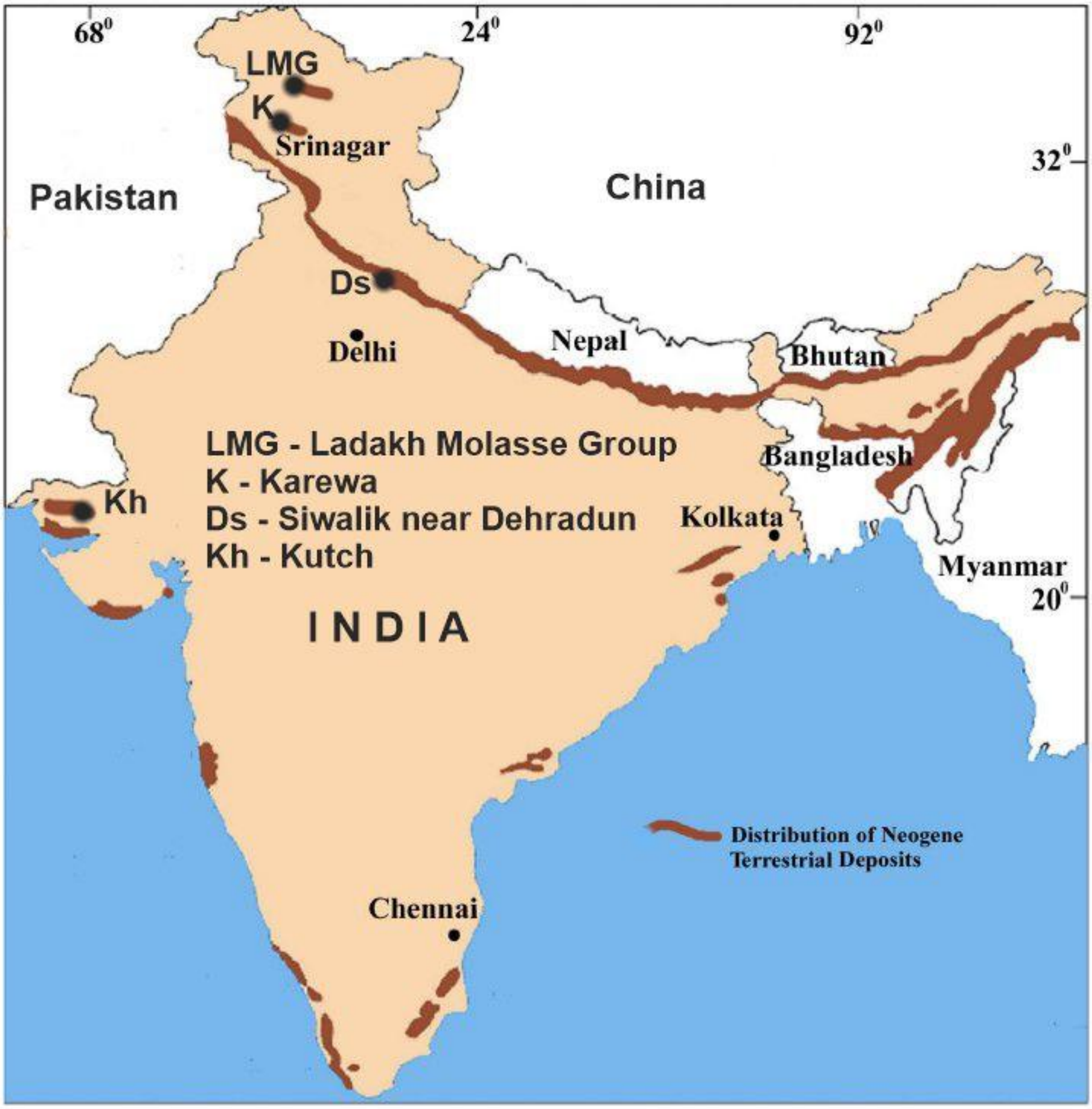

Figure 1-9 Distribution of Neogene terrestrial biota yielding horizons in India (modified after Patnaik and Prasad, 2016).

Horizons on the southern flank of the Himalayan foreland basin and the Ladakh Molasse Group in the India-Asia collision zone (Indus Suture Zone) are known to yield fossils of terrestrial fauna and flora including charophytes (Bhatia and Mathur, 1970 and 1978; Bhatia et al. 1985, 1998; Tewari and Sharma, 1972a and b; Bhatia, 1982, 1992, 1999, 2003; Kapur et al. and myself, 2019 etc.). Nonmarine Neogene microfossils containing charophytes have also been recorded from Kutch (Bhandari et al. 2018, 2021; Kapur et al. 2020; Wazir et al. 2019).

1.6 Objectives

It is clear from the above account that the occurrences of Neogene fossil charophytes from India are known from many localities in the Himalayan and adjacent plain and shield regions. However, the potential of charophyte-yielding sections in India, both in a temporal and spatial sense, is yet to be fully achieved. Ongoing investigations being carried out by this author are aimed at documenting the fossil Charophyta of India to the extent possible. As part of this project, the charophyte flora from two widely separated horizons, the Middle Siwalik beds of the Outer Himalaya and the Ladakh Molasse Group of Trans-Himalaya, were chosen for this doctoral dissertation. In addition, extant charophyte forms are also included in this study because they help in inferring the geological past of the territory through recovery of their fossil counterparts and in better understanding the aquatic life of the past freshwater ecosystems. To this end, a collection of fossil and extant charophytes was made from the Middle Siwalik sediments of Mohand area near Dehradun, and Sahastradhara area of Dehradun for a detailed study (Figure 1-10).

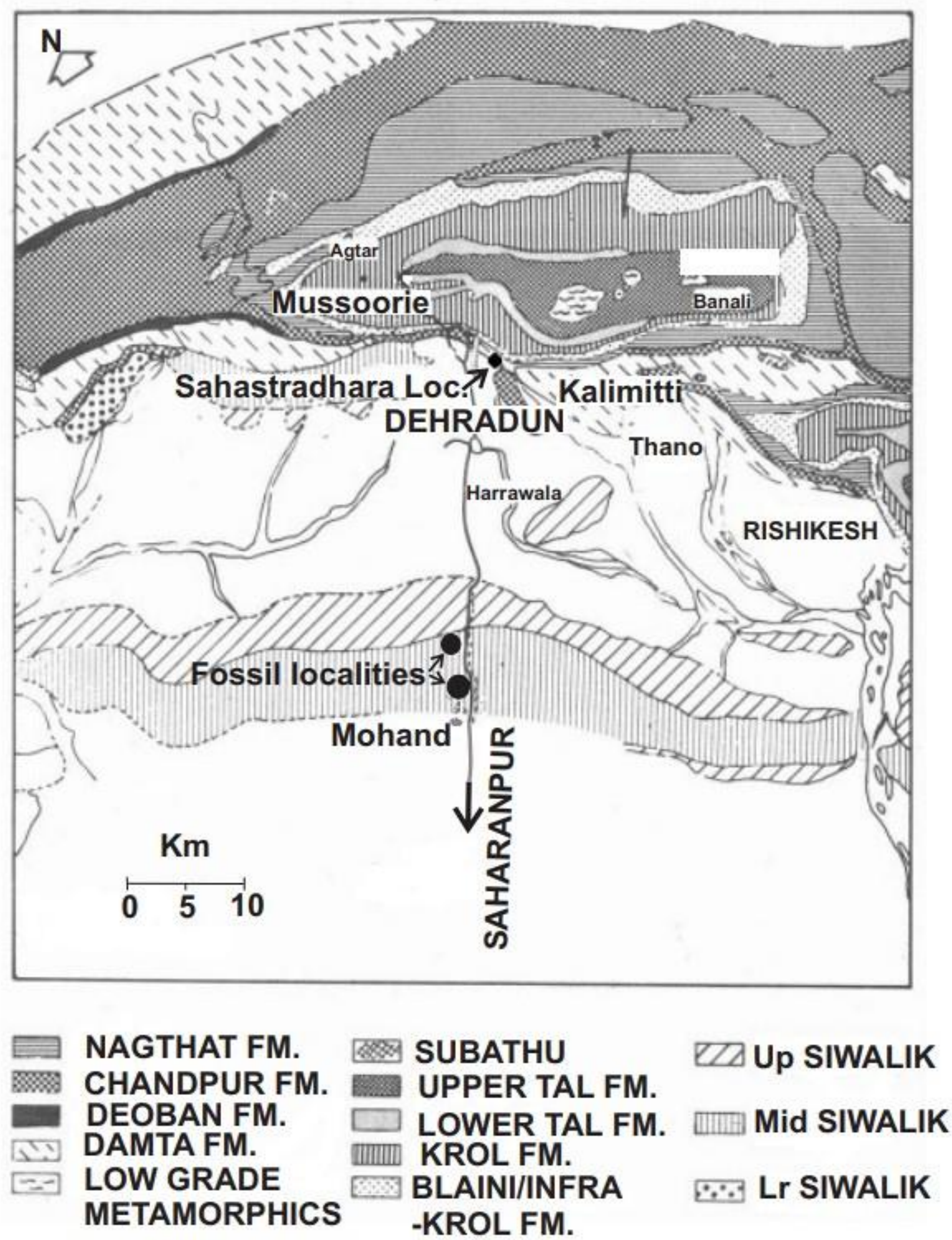

Figure 1-10 Localities of fossil and extant charophyte gyrogonites amidst exposed geological horizons (after Rupke, 1974).

In addition, a coeval charophyte assemblage from two sections of the Ladakh Molasse Group was obtained from Prof. Sunil Bajpai, IIT Roorkee, who kindly made this small collection available for study. Thus, this systematic study deals with the Neogene charophytes from Middle Siwalik strata of Mohand area near Dehradun, and from Kargil and Taruche localities of Ladakh Molasse Group, Ladakh, along with an extant charophyte assemblage from Sahastradhara locality in Doon Valley. The objectives sought to be achieved are summarized as follows:

i. To document the charophyte taxa from the nonmarine Neogene Siwalik sediments of Mohand area, near Dehradun
ii. To document the charophyte taxa from the Ladakh Molasse Group exposed near Taruche (Leh District) and Kargil District, Ladakh.
iii. To document the extant charophytes from the Sahastradhara area, Dehradun
iv. To ascertain the biostratigraphic implications of the studied fossil charophytes
v. To ascertain biogeographic aspects of the recovered fossil charophytes

Chapter 2 : GEOLOGICAL AND TECTONIC BACKGROUND OF THE INVESTIGATED CHAROPHYTE-YIELDING SECTIONS

2.1 General Geology and Tectonics

The charophyte-yielding Neogene molassic sections investigated for this dissertation are located in the Sub-Himalayan and the Indus Suture Zone, north of the High Himalaya. The Himalaya, a characteristic orographic feature on the northern part of the Indian Subcontinent, is the classic example of collision-type of orogenic belt (e.g. Searl et al. 1987; Valdiya, 2015). It was formed in the early Paleogene (around 50 ma ago), after the Indian plate was separated from the Gondwanaland, moved northward to reach the northern hemisphere, and collided with Eurasian plate by consuming the intervening oceanic crust below the Neotethys. The collision resulted in crustal shortening of the northern margin of India till southern margin of Tibet and there was an upliftment and upward thrust of Higher Himalayan Crystallines over the sediments of Lesser Himalayas, which paved the way for continental nonmarine deposition.

The Himalayan orogen is strongly asymmetric and is made up of four units, which are designated from north to south as the Tethyan (or Tibetan) Himalaya, the Greater Himalaya, the Lesser Himalaya, and the Sub-Himalaya. Tectonics has played prime role in the Himalayan evolution through three major thrust faults namely, MCT (Main Central Thrust) which separates Higher from Lesser Himalaya; MBT (Main Boundary Thrust) which divides the Nappes of the Lesser Himalayas from the Sub-Himalaya, and MFT (Main Frontal Thrust), the southernmost Himalayan thrust juxtaposing the upheaved Siwalik/Sub-Himalaya and the Indo-Gangetic Plain Foreland Basin. Of these subdivisions, the Sub-Himalaya and the Indus Suture Zone (Trans-Himalaya) are particularly relevant to this investigation because of the localities yielding the studied Neogene fossil charophytes located in these zones. The Himalayan lithotectonic zones have been described in detail by numerous workers (e.g. Searl et al. 1987, Valdiya, 2015). The salient features of these zones are briefly presented here:

***Sub-Himalaya**:* The Sub-Himalaya or the Outer Himalaya is a continuous belt of foothills. This longitudinal subdivision is rather synonym to Siwalik Hills and occurs all along the southernmost part of the Himalaya, delineated to the south by the vast Indo-Gangetic alluvial plain. To the north, the Sub-Himalayan subdivision is demarcated by an extensive orogen scale tectonic contact which is known as the Main Boundary Thrust (MBT) (Figure 2-1). The Sub-Himalaya has an average elevation of 900 m to 1200 m and a width ranging from 8 km to 100 km. Sedimentary sequences of the Sub-Himalaya consist of shallow-marine Late Cretaceous to Early Eocene beds, followed by thick coastal/continental sediments of the Subathu Formation, succeeded further by the Dharamsala/Dagshai/Murree (?Upper Eocene–Lower Miocene) and the Neogene and Quaternary molasse deposits of the Siwalik Group. The transition from marine to continental regime in the Eocene Subathu Formation indicates the initiation of India-Asia collision (Chatterjee et al. 2017). The Siwalik Hills consists of clastic sediments that were produced by the uplift and the subsequent erosion of the Lesser Himalaya.

***Lesser Himalaya**:* They consist of metamorphic rocks and fossiliferous sediments which are older towards the north and of the interval of between early Proterozoic to lower Palaeozoic.

***Higher Himalaya**:* This is the main Himalayan range representing the greatest uplift and which consists mainly of metamorphic rocks and is demarcated from the Lesser Himalayas by MCT.

***Tethys (Tibetan) Tethys Himalaya**:* This is a sedimentary sequence ranging in age from upper Proterozoic to middle Eocene. The sequence is richly fossiliferous from Cambrian onwards.

Indus Suture Zone: It is the zone of collision between India and Asia and comprises Indus Suture, Karakoram-Tethys zone, and Shyok Suture. It was designated as Indus Suture Zone by Gansser (1977). The Indus Suture Zone consists of ophiolites, plutonic-volcanic rocks of Cretaceous to Tertiary age, the Shyok Suture represents a back arc basin, and Karakoram-

Tethyan zone consists of upper Palaeozoic to Cretaceous sediments. Occurrence of assorted rocks representing deep-sea sediments of thrust slices of Indian passive margin, island-arc and fore-arc associated igneous and sedimentary rocks with ophiolite melanges, Mesozoic exotic limestones define the Indus Suture Zone with signatures of suturing.

Within the zone of India-Asia collision (i.e. Indus-Tsangpo Suture Zone or ITSZ), freshwater molasse deposits are extensively developed in the northwestern Himalaya of Ladakh region (Tewari, 1964; Searl et al. 1990). These molassic sequences document the continent-continent collision between India and Asia which probably started between 55 and 60 Ma (e.g. Hu et al. 2016; Verma et al. 2021). The molasse sequences are exposed to the north of the Higher Himalaya along the stretch of the Indus Suture Zone and were first described from South Tibet with a thickness of approximately 1000 m of conglomerate facies (Heim and Gansser, 1939) with an eastward lateral continuation along the Tsangpo Valley in the south of L

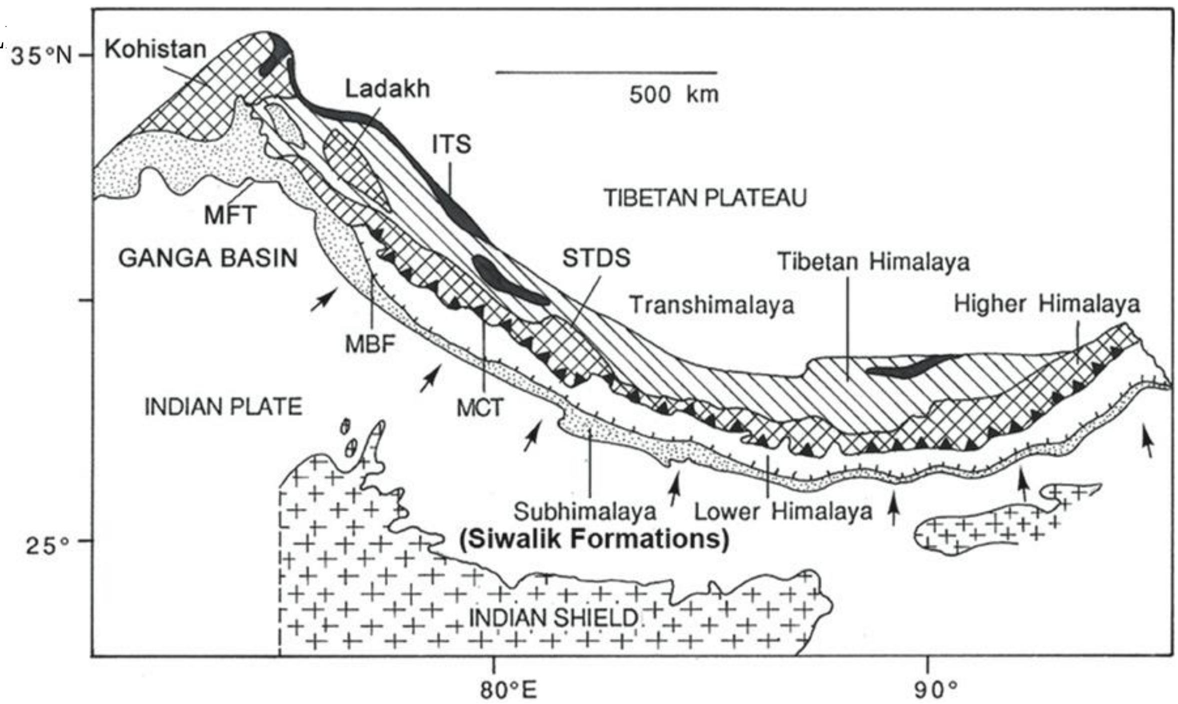

Figure 2-1 Himalayan orogen and deposition of Siwalik sediments. ITS—Indus- Tsangpo Suture; STDS—South Tibetan detachment system; MCT—Main Central thrust; MBF—Main Boundary fault; MFT—Main Frontal thrust. Siwalik sediments were deposited in the foreland basin of the Lesser Himalaya and are represented by the Sub-Himalaya (modified after Gansser, 1964).

The Neogene geological history of the Indian subcontinent saw i) a progressive continentality in sedimentation; ii) changing climatic patterns from warm, tropical rain-forest settings throughout the Miocene up to the Early Pliocene, with a drier climate in the Pliocene, followed by glacial conditions in the Middle Pleistocene; iii) shifting of climatic zones towards south and east; and iv) emergence of Himalayan terrain as a huge, perennial source of sediments from the Miocene onwards (Sahni and Mitra, 1980). By the start of the Neogene, the Tethys Sea had finally disappeared and the Indian plate was firmly sutured to the Asia. Extensive exhumation around this time was caused by tectonic activity along the Main Central Thrust (MCT) in the central Himalayas and along South Tibet Detachment System (STDS) in the western and eastern Himalayas (Catlos et al. 2001; Grujic et al. 2002; Yin, 2006(Clift et al. 2008; Patnaik 2016). These records are preserved in the Himalayan sedimentary sequences and document a a transition from shallow marine depositional conditions to an essentially fluvio-deltaic environment in the Indus Suture Zone (e.g. Ladakh Molasse deposits), Himalayan foreland basin (e.g. Murrees/Dagshi/Kasauli formations and correlative deposits) in northwestern India and in the Sulaiman Province of Pakistan. This transition is considered by some workers to be abrupt and representing a major unconformity encompassing the Oligocene interval in large parts of the foreland basin (e.g. Najman et al. 2004). However, some noticeable Oligocene fluvio-deltaic deposits are also known to occur (e.g. Lower Chitarwata Formation, Pakistan), and contain a diverse fauna of fossil mammals, including possible precursors to some of the Siwalik lineages (Antoine et al. 2013; Lindsay et al. 2005; Marivaux et al. 2005; Métais et al. 2009; Welcomme et al. 2001; Patnail 2016).

Recently, Patnaik and Prasad (2016) asserted that the terrestrial connections between Africa and Eurasia played a key role in the Neogene climatic and paleobiogeographic aspects of the Indian subcontinent. According to them, the fossil data suggest a warm, humid climate in the early Neogene, which was followed by cooler and drier conditions in the late Neogene.

This climatic shift led to a noticeable change in vegetation in India with Early and Middle Miocene having C3 vegetation with warm and humid tropical flora in low land areas, whereas the Late Miocene and Pliocene had characteristics of C4 grasslands. This regional reconstruction is based on studies in sedimentary deposits narrating a transition from a shallow marine condition to an essentially fluvio-deltaic environment in Ladakh Molasse Group in the Trans Himalaya, pre-Siwalik (Dharmsala, Dagshai/Kasauli, etc.) and Siwalik Group in the Himalayan foreland basin on the southern flank.

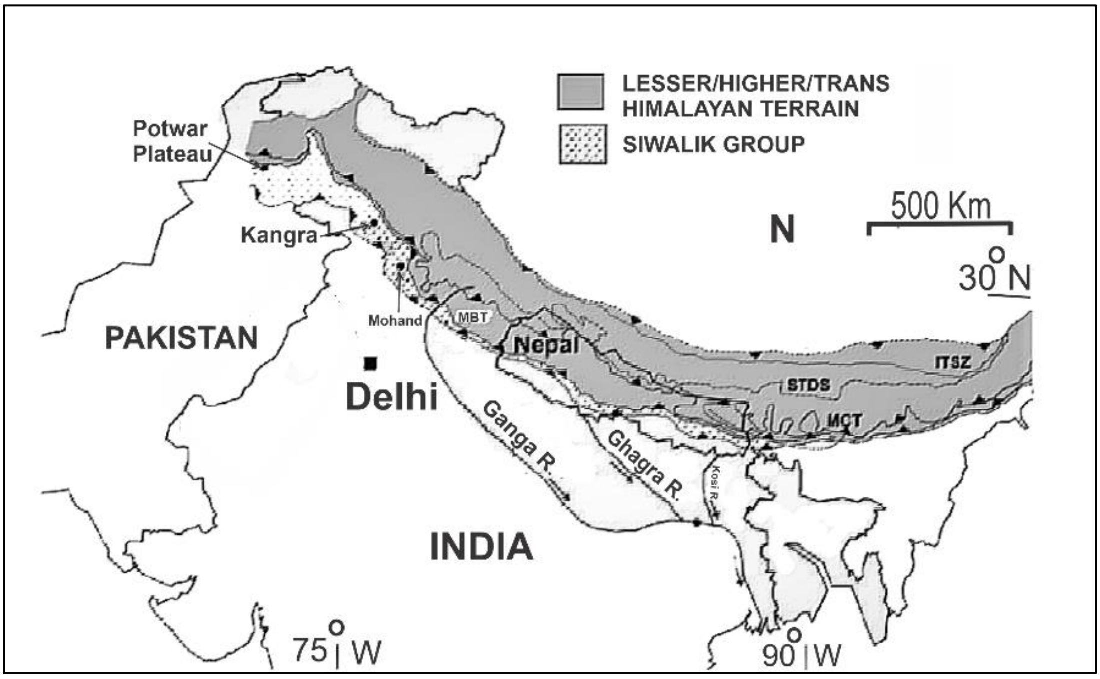

Figure 2-2 Siwalik Group exposed all along the southern flank of the Himalaya comprising Lesser, Higher and Trans-Himalayan ranges (modified after Gansser, 1964).

2.2 Siwalik Group

The Siwalik Group embodies one of the world's thickest pile of sediments that were deposited by rivers in a continental environment (Opdyke, et al. 1982, Tandon et al. 1988; Kumar et al, 1991). The Siwalik Group is ~6 km thick and exposed along the Himalayan foothills from the Potwar Plateau in the west to the Brahmputra Valley in the east (Krishnan, 1982). The width of the Siwalik Hills ranges from 10 to 50 km, and their average elevation is 1,500 to 2,000 m. Updated stratigraphy of the Siwalik Group takes into account radiometric dating of the zircons from the volcanic ashes horizons along with rigorous application of the magnetic reversal stratigraphy. Classification of the Siwalik Group in a table with inputs of ages from the well constrained magnetic polarity stratigraphy was compiled by Tandon et al. (1988) and Kumar et al. (1991). The Siwalik basin on the southern side of the rising Himalaya started receiving sediments in early Miocene around 19 Ma (Johnson et al. 1985). Preceding the Siwalik, extensive nonmarine sediments of extending in age up to earliest Neogene accumulated in a pre-Siwalik basin setting and are known as Dharamsala Group; these pre-Siwalik beds are known by local names such as Dagshai and Kasauli formations in the Simla Hills of Himachal Pradesh, and the Murree Group in Jammu region and farther west in Pakistan.

The Siwalik Group comprises nearly 6000 m thick succession consisting mainly of mudstones, sandstones and conglomerates. These lithological units, considerably varying in their thickness in space and time, were deposited by complex channel and fan systems. The Lower Siwalik Subgroup characteristically consists dominantly of red mudstone with subordinate mostly fine-grained sandstone horizons which may be taken as transient stream deposits. With the advent of big river system around 10 Ma in the basin, the style of sedimentation changed significantly. Multi-storied sandstones with reddish-brown and orange clays are a dominant feature of lower Middle Siwalik that are referred to as Nagri Formation.

Mudstones horizons of Nagri Formation of Haritalyangar, famous for hominoid fossils, are ferruginous low grade oxisols of typical flood plain (Johnson, 1977). Sedimentary sequences deposited by isochronous fluvial system have been identified in the Siwalik horizons of Pakistan (Behrensmeyer and Tauxe, 1982). Sedimentological investigations of the Upper Siwalik Subgroup suggest increasing proximity of the source terrain and a successive change from trunk river system through multi-channel river system to distal alluvial fan and finally proximal alluvial fan deposits (Kumar and Tandon, 1985). Prakash et al. (1980) through their systematic sedimentological studies found that the Siwalik Group was deposited in two coarsening up megacycles comprising i) sandstone clay alternations in the older horizons, passing gradually into, and ii) coarse sandstones and/or conglomerates towards the youngest level. Temporal changes in source terrain rocks resulting in consequent changes reflected in detritus deposited have formed the basis of the Siwalik Group rocks being divided into 3 subgroups:

Lower Siwalik Subgroup: It is dominated by red mudstone besides subordinate fine to medium grained, grey sandstone and siltstone. The sandstone is indurated and tough to wearing down.

Middle Siwalik Subgroup: The sedimentary rocks in this subgroup include medium grained bright grey sandstone of coarser material and grey-black mudstone. The deposition of the subgroup commenced and culminated from around 10.5 to 2.5 Ma, respectively.

Upper Siwalik Subgroup: The subgroup predominantly consists of pebbles, cobbles and boulders and coarse grained loose sandstone.

Figure 2-3 Mohand locality pinpoints Middle Siwalik localities in Mohand area in the vast stretch of Siwalik Group exposures (after Sanyal et al. 2005).

Table 2.1 Characteristic sedimentological features of the Siwalik Group in Dun Valley, Mohand area (after Kumar et al. 1991).

Stratigraphic unit	Lithological details; Contact information	Age
Doon Gravel (~600 m)	Thickly bedded massive conglomerate embedded in sandy silly matrix; Lower contact is erosional with angular unconformity, at places with conformable contact.	Quaternary
Upper Siwalik Subgroup (-2000 m)	Thickly bedded massive conglomerate embedded in sandy matrix and interbedded with trough cross-stratified sandstone; Lower contact with Middle Siwalik Subgroup is transitional and erosional.	Middle Pleistocene to Middle Miocene
Middle Siwalik Subgroup (-1800 m)	Upper Unit (~400 m): Grey, fine-to coarse-grained multistoried sandstone with pebbles and brown to grey mudstone-siltstone.	
	Middle Unit 2 (~1100 m): Thickly bedded, grey, multistoried trough and planar cross- stratified sandstone complex with occasional mudstone lenses.	
	Lower Unit 1(~300 m): Grey, fine-to coarse-grained sandstone & brown to grey mudstone; Lower contact is thrusted over recent alluvium along Himalayan Frontal Thrust.	

2.2.1. The Middle Siwalik charophyte-yielding sections

Two Middle Siwalik sections in Mohand area are now known for their fossil bearing mudstone horizons (Figures 2-3; 2-4 and 2-5). One is Mohand Rao section, around 500 meters from iron bridge towards upstream side and the other stratigraphically younger section, with mudstone unit yielding fossil fish otoliths besides other microfossils, is in Bhang Sot, a tributary of Mohand Rao meeting around two kilometers upstream on the right bank from the iron bridge. In Bhang Sot fossil bearing mudstone unit is exposed around 1.5 kilometer upstream from its confluence with the Mohand Rao (Figure 2-4). As per details available in the published account of the Mohand Rao section, an 8 m thick fining upward cycle consisting of large scale trough cross-bedding sandstone is overlain by grey medium- to fine-grained sandstone. This medium- to fine-grained unit is succeeded by a mudstone unit. Quartzite and older sedimentary clasts, interpreted as extraformational and intraformational clasts respectively, are conspicuous in this section, particularly in the fine to medium-grained sandstone unit overlying the mudstone. The mudstone at the youngest levels of the <10 m thick sequence consists of an indurated siltstone bed and is succeeded by a 10 cm thick brown colour mudstone bed.

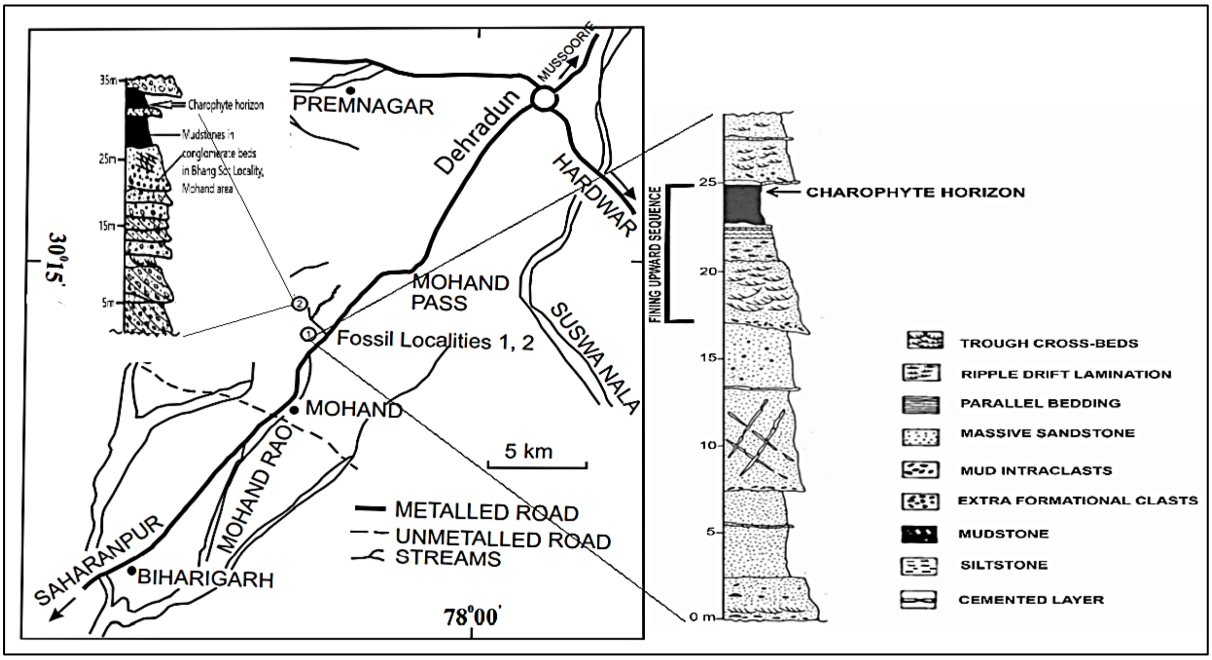

Figure 2-4 Mohand Rao (1) and Bhang Sot (2) localities in Mohand area with the sedimentary log of the fossiliferous section; charophyte horizons are lithologically light to dark grey mudstones (modified after Tiwari & Bhandari, 2014).

In the Middle Siwalik Subgroup at Mohand, a fining upward cycle with fossiliferous mudstone is observed on the right bank of Mohand Rao (mentioned as Stop 3 by Tandon et al. 1988 and Stop 2 by Kumar et al. 1991) and accessible from Mohand-Dehradun Road (Figure 2-4). The fining-upward cycle of 8 m thickness with fossiliferous mudstone at its top is of particular interest insofar as fossils are concerned (Bhandari et al. 2014; Bhandari and Tiwari, 2003; Tiwari and Bhandari, 2014). The grey sandstones are medium- to fine-grained with occasional quartzite pebbles and are multistoried in nature. Each sandstone body (trough cross-stratified with thickness varying from of 2 to more than 5 m) is demarcated by distinct erosional surfaces along with intraformational, grey mud balls and a few extraformational clasts of quartzite. In the exposed section, a prominent erosional surface exhibiting scouring with grey mud clasts of up to 15 cm size marks the initiation of the fining upward cycle. Coarse- to fine-grained grey sandstone in its lower part shows trough cross-stratification, passing upward at times into ripple drift lamination and finally ending in parallel laminations. The grain size characteristically decreases in the successive horizons of the cycle and the sedimentary structures change from large-scale trough cross-bedding to small scale ripple drift and parallel lamination, finally ending in mudstone with a gradational contact (Tandon et al. 1988, Kumar et al. 1991).

The fossil bearing mudstone horizons in the Mohand area localities are more vulnerable to natural calamities resulting in washing away or covering of mudstone units with burden of rock debris (e.g., Figure 2-5, Figure 2-6).

Figure 2-5 Field photographs: a) Mohand Rao locality showing microfossil bearing horizon in the succession of beds, b) Slump material covering the fossiliferous horizon, c) Close-up of the thinly bedded gray mudstone marked by arrow, d) Hammer head pointing at the fossiliferous horizon (hammer as scale).

2.3 Ladakh Molasse Group

The molassic deposits in the Indus Suture Zone occur discontinuously in an arcuate belt along the southern margin of the Transhimalayan magmatic arc. These molassic outcrops extend from Kargil township in western Ladakh through Basgo in central Ladakh to Nyoma in eastern Ladakh. Correlative deposits are also found in Pakistan and Tibet. These continental deposits, which provide important clues for understanding the early collisional history including exhumation, erosion and deposition along the southern margin of Asia (Brookfield and Andrews-Speed, 1984; Searle et al. 1990; Zhou et al. 2020), are variously referred to as Ladakh Molasse Group/ Indus Molasse/ Indus Group/ Kargil Formation/ Hemis Conglomerate/Karu Molasse/ Wakka Chu Group etc. (Frank et al. 1977; Srikantia and Razdan, 1980, 1985; Brookfield, 1994). In central Ladakh, a molasse sequence near Taruche in central Ladakh, designated as Basgo Formation, is considered by some workers to be the basal continental deposit overlying the Ladakh Batholith in the Indus Suture Zone (Garzanti and Van Haver, 1988).

Molasse horizons in the high altitude late Cenozoic intermontane basin in Indus Suture Zone of Ladakh were first recognized as distinct stratigraphic entity and mapped by differentiating them from 'Indus Flysch' (=Indus Formation, see Thakur and Virdi, 1979) by Tewari (1964). This study (Tewari, 1964) led to increased interest in the various aspects of Ladakh molasse deposits in different parts of the region. Tiwari (2003) took note of the multiplicity of stratigraphic names for high altitude molasse horizons and proposed a provisional stratigraphic scheme of classification which divides the Ladakh Molasse Group comprising northern and southern belts (for details see Frank et al. 1977; Shankar et al. 1982) extending from Kargil in the west to Hanle in the east, into two units: the older Liyan Formation and the younger Kargil Formations. The Liyan Formation, already in use for molasse succession near Liyan Gompa on the left bank of Indus River (Shankar et al. 1982; Verma et al. 2021), includes almost entire southern molasse package resting on the volcano-sedimentary Sumdo Formation. The younger Kargil Formation includes most of the northern molasse horizons overlying unconformable on the Indus Formation and/or Ladakh Granitoids. In this stratigraphic classification of Ladakh Molasse Group subdivisions of Kargil Formation proposed by Bhandari et al. (1977) and Srikantia and Razdan (1980).

2.3.1. Charophyte-yielding section in Ladakh Molasse Group

The sections and localities that have yielded microfossils including fossil gyrogonites (kindly loaned to me by Prof. Sunil Bajpai, IIT Roorkee for their systematic study for this Ph.D. project) are on Kargil- Batalik Road, Kargil and near Taruche village, District Leh in Ladakh. These localities have been prospected by a number of teams from different institutions during the last more than two decades for their macro and microfossil content (Sahni and Nanda, 1990,1998; Kumar et al. 1996; Bajpai et al. 2004; Prasad et al. 2005; Parmar et al. 2013). The fossils have been published by these workers in a series of papers with an appropriate account of sectional details and geological attributes, and the fossil groups published by them include mammals, fishes, ostracods, molluscs, plant fossils including palynomorphs and charophytes.

The presently described charophyte material from Ladakh comes from two localities: Kargil in western Ladakh and Taruche in central Ladakh (Figure 2-7). The Kargil Formation is exposed about 4 km east of Kargil town along the road from Kargil to Batalik on the left bank of Wakka Chu river. It is a sequence of purple, brown and grey shales, green sandstones and siltstones and conglomerates unconformably overlying the Ladakh Batholith. The section consists of buff maroon coloured outcrops at the base. The grey shales yielded several charophytes in association with a few fish and molluscan remains. This is roughly the same level (K/4b) which yielded the Oligo-Miocene rodents described by Kumar et al. (1996).

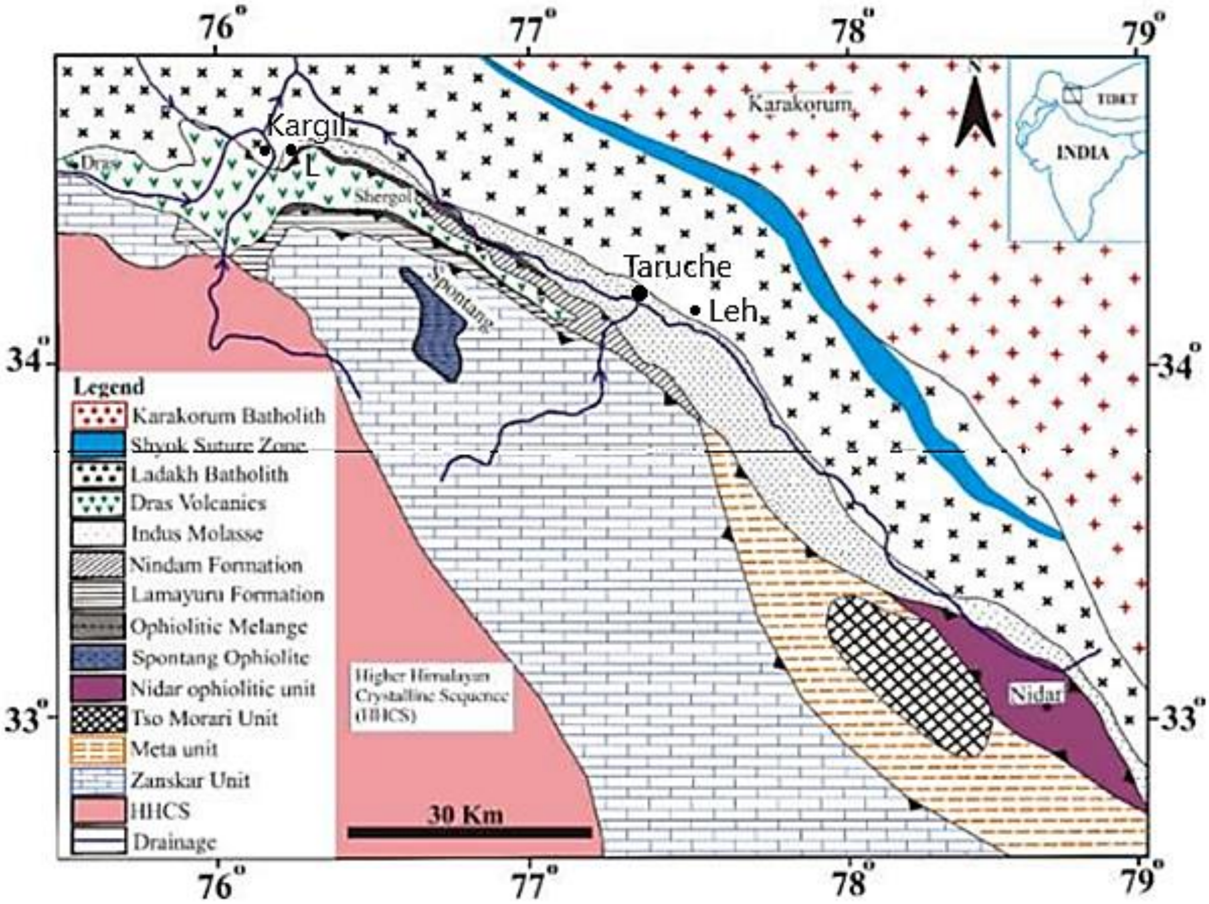

Figure 2-6 Kargil and Taruche Gyrogonite Localities in Ladakh Molasse Group in geological map of Kargil-Leh-Nidar region, Ladakh (after Bhat et al. 2018).

The second locality which yielded the charophytes described in this dissertation is located 3 km west of the village on an unmetalled track between Yangthang and Taruche. Grey shales at this locality form part of the Basgo Formation of Garzanti and van Haver (1988). The Basgo Formation in this section consists mainly of sandstone and conglomeratic sandstone with intercalated hard, fossiliferous mudstone and siltstone beds. This locality was designated as Tr2 by Bajpai et al. (2004, see Fig. 2), who described a small assemblage of freshwater ostracods including the late Oligocene Chinese genus *Dongyingia*. Associated fossils also include cyprinid fishes and gastropod opercula. Fossils are reported to occur at least at ten levels in this section and include freshwater gastropods, cyprinid fishes and fragmentary bones. The charophyte-yielding level is situated about 130 m above the contact of the Basgo Formation molasse with the underlying granites.

Chapter 3 : Material and Methodology

3.1. Charophyte-yielding sediment samples from Siwalik beds of Mohand

The Mohand Range is located on the southern side of the Dehradun re-entrant and, unlike in other sectors, is separated from the Lesser Himalaya by the Doon valley. The Mohand Range has the Middle and Upper Siwalik horizons exposed in numerous approximately north-south trending streams. The charophyte-yielding mudstone samples were collected from the Middle Siwalik subgroup which is exposed along the Mohand Rao stream. Overall, the Siwalik sequence in the area is a coarsening upward succession. A massive, 30-45 cm thick, dark grey charophyte-yielding mudstone unit occurs near the top of the youngest level of fining upward cycle beginning from a conspicuous erosional surface. This fossiliferous unit shows the presence of black-coloured fish remains, and white specks of gastropod shell fragments on the exposed surface. With a hand lens it is possible to see the presence of microfossils in the matrix. After ascertaining the presence of traces of fossil remains, promising samples from this horizon were collected for bulk processing in the laboratory.

3.2. Samples for extant charophytes from Doon Valley and adjoining plains

Lotic and lentic water bodies in Doon Valley and adjoining plains were visited but apparently because of pollution and industrial chemical effluents, aquatic domains bearing charophytes have ceased to thrive. However, attempts to locate extant charophytes succeeded in the Sahastradhara area as this area is relatively free from industrial pollution and population pressure. Field work was undertaken after winter but before the start of the tourist season in the month of April, when the calcium concentrations are found to reach their maximum values after their lowest calcium concentrations in January (Khanna and Singh, 2000). The charophyte plants were located in clear, very shallow, hard spring water streamlets through boulders on their way to join the main north-south trending Sahastradhara stream. This locality is around

200 m upstream of the sulfur springs in the Sahastradhara picnic area situated around 15 km north of Dehradun (Figure 3-1). The N-S trending main stream in the area is a tributary of river Song. The submerged charophyte plants along with a few other underwater floral taxa formed sparse monospecific population on a thin clay layer on the rocky substrate. The collected charophyte samples were dried in order to recover extant gyrogonites that were studied under a binocular microscope and SEM.

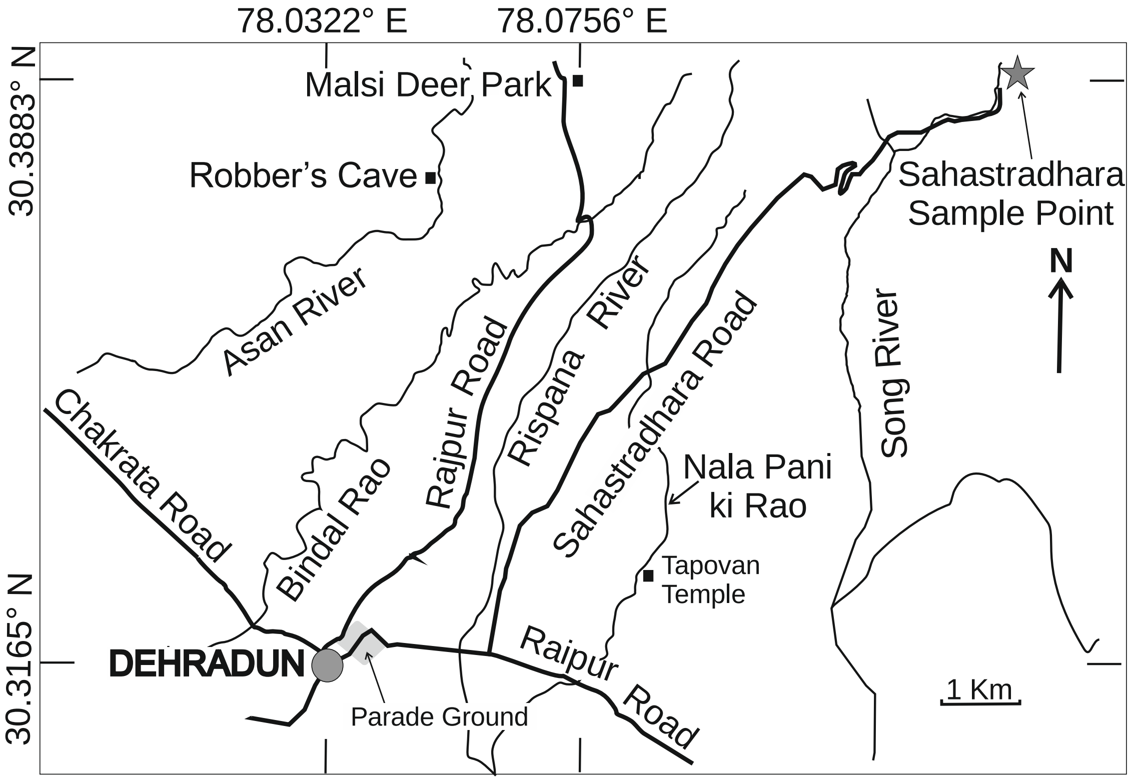

Figure 3-1 Sample point in Sahastradhara amidst the north-south trending streams in Doon Valley: Bindal Rao and easterly streams go to Ganga River whereas Asan River and associated streams are part of Yamuna River with a water divide between them.

3.3. Charophyte samples from Ladakh Molasse Group

Gyrogonites from Ladakh, used in this investigation, were provided by Prof. Sunil Bajpai, Head, Department of Earth Sciences, Indian Institute of Technology Roorkee (IITR). These will be returned to IITR after the study is over.

3.4. Bulk maceration of fossiliferous sediment samples from Mohand

Extraction techniques of calcareous microfossils from modestly to slightly indurated rock samples are basic, using non-destructive, pulverizing methods. Detailed account of other techniques (some of them were given a try for faster processing and cleaner microfossils) are given in many publications (Green, 1995 and 2001).

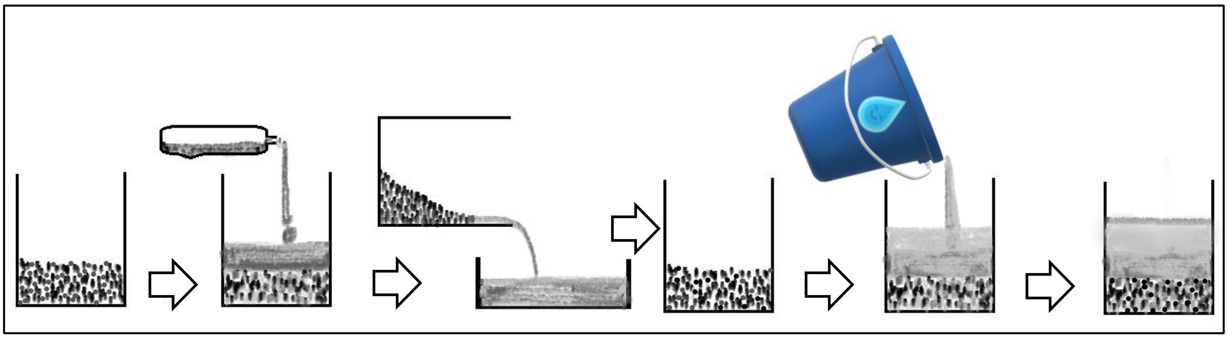

Figure 3-2 Maceration of charophyte-yielding rock samples.

Conventional use of acid in this regard was avoided as because of its non-suitability for fossils composed of calcium carbonate. Around 70 kg sample from fossiliferous horizon of the Mohand section was brought to laboratory and macerated. For the Mohand samples, maceration was done in three simple steps after reducing the larger chunks into pieces of around 2 cm diameter using an iron mortar and pestle of modest size. As the first step, these small samples were dried in sun for 1-2 days to free them from moisture. After drying them completely, the sample was shifted in a dried bucket to soak it in the kerosene by pouring the same to immerse all the pieces completely. After about 5-6 hours, kerosene was decanted or drained out and then water was poured in the bucket to immerse the samples completely. The sample was left in water overnight (Figure 3-2). The sample then became disintegrated and ready for wet sieving through a set of ASTM sieves of mesh size 60, 40, 25, and 10, with the smallest size sieve placed at the bottom. While dried 60+ and 40+ residues were ideal for charaophytes, ostracods, fish teeth, and other tiny fossils or their fragments, 25+ and 10+ was dominated by gastropod shells and undigested rock pieces occasionally with embedded washed fossils. Experienced workers on this section helped me in perfecting this simple yet effective technique for encouraging and successful results. Using this technique, a total of more than 65 kg of the mudstone unit was macerated and a charophyte assemblage was recovered from the +40 and +60 mesh residues

3.5. Optical microscopy and Scanning Electron Microscopy

Optical microscopes are suitable good for picking the microfossil specimens of around 1 mm size but are of limited use in the study of morphological features since such a tiny object cannot be characterized satisfactorily with an optical microscope. A Scanning Electron Microscope (SEM) generates images of an object with a focused beam of electrons by scanning the surface. Interaction of the electrons of the beam with atoms of the sample surface produces signals containing information about surface morphology and relief features under examination (Figure 3-3).

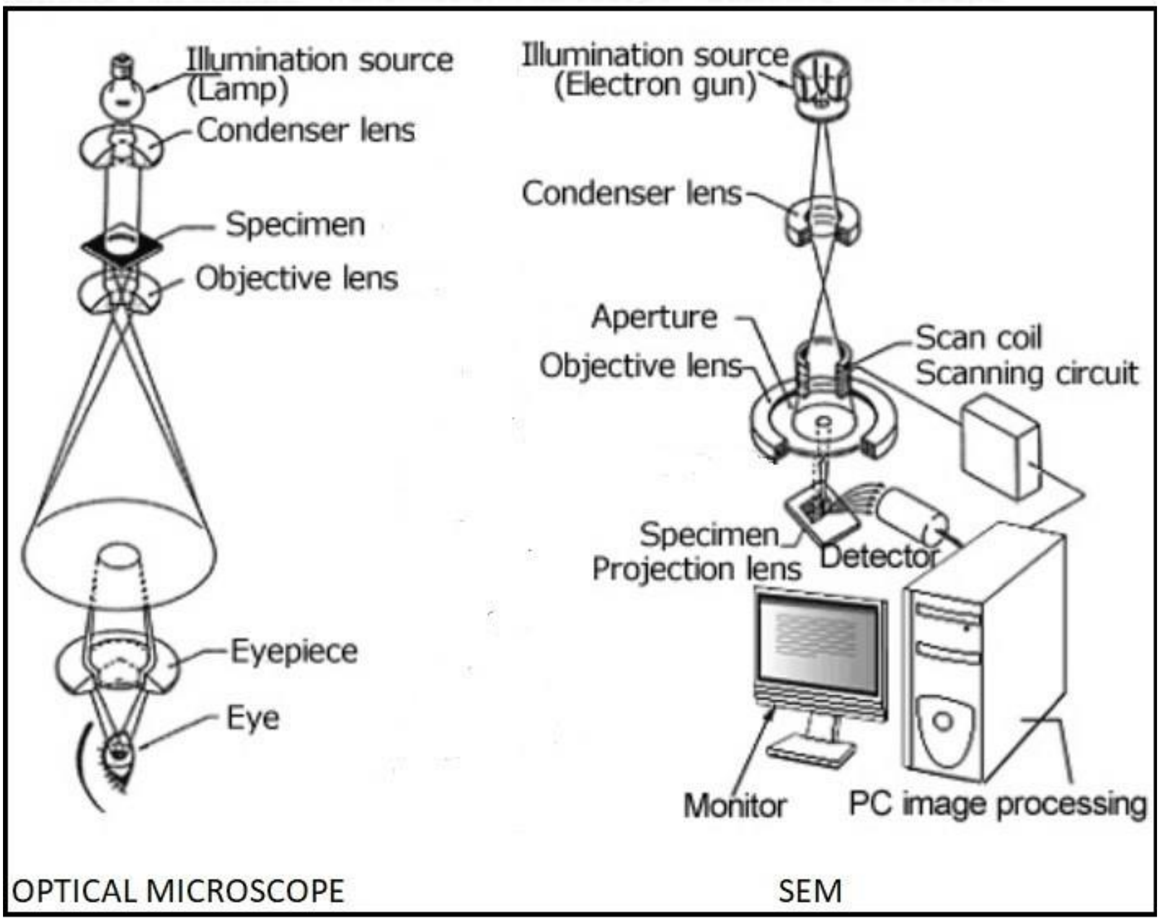

Figure 3-3 Essential components of Optical Microscope and Scanning Electron Microscope, a schematic representation.

In microscopy, the resolving power is the smallest ‘detail’ observed using the microscope and it is directly influenced by wavelength of the imaging beam of the microscope. In Optical Microscopy the wavelength of the beam is 400-700 nanometers, limiting resolving power to 200 nm or above, and can offer up to 1,500 x magnification. In contrast, the comparatively very high energy electron (light) beam used by a SEM, the depth of focus and resolving power is much greater, providing an enormous advantage. Both optical binocular microscope and SEM are greatly useful in microfossil studies.

3.6. Image analysis

Image analysis involves gaining important information mainly from digital images by employing digital image processing techniques; digital images are composed of picture elements, known as pixels, each with finite, discrete quantities of numeric representation for its intensity or gray level. Without resorting to any available software, the basic information was obtained from SEM digital photographs of charophyte gyrogonites for tabulation and calculation of biometric parameters. A custom-made program was developed to make calculations of linear measurements with the scale given in the SEM photographs easier with the help of my husband Abinash. Measuring litholog from photographs of the section with good sized scale placed on the outcrop also proved helpful; known measurements of the section confirmed that this simple image analysis technique can save a lot of time and effort.

Chapter 4 : SYSTEMATIC DESCRIPTION OF THE CHAROPHYTE COLLECTION

The collection of samples studied during the present doctoral investigation comprises Neogene fossil gyrogonites from geological archives and extant gyrogonites from living plants. Samples of fossil gyrogonites representing Neogene charophyte fossil assemblages from India were obtained from two stratigraphic units: Middle Siwalik Subgroup (Middle Miocene) exposed in Outer Himalaya of the Mohand area near Dehradun (Uttarakhand) and the Ladakh Molasse Group in the India-Asia collision zone of Ladakh, Tran-Himalaya. Extant gyrogonites were obtained from the living charophyte plants occurring in submerged vegetation in one of the several shallow, clear-water, transient/ephemeral mildly flowing streamlets in the Sahastradhara area of Doon valley, Dehradun (Uttarakhand).

4.1. Classification of charophytes

Charophytes, which represent basal streptophytes, comprise a diverse taxonomic collection of unicellular, filamentous, and parenchymatous terrestrial green algae and extant fresh water algae (Graham, 1993; Lewis and McCourt, 2004; Becker and Marin, 2009; Leliaert et al. 2012). The members of this group have very complicated and highly evolved sex organs. However, the structure of charophytes is relatively simple in vegetative organs with no vascular bundle. These algae not only share a close evolutionary history with land plants but also have a rich fossil record which is unique among the charophyte algae. (Fiest and Grambast-Fessard,1991; Grambast,1974; Peck 1953; Tappan, 1980). Currently, Charales contains one extant family in two tribes with a total of six genera. Out of the 6 extant charophyte genera distinguished on the basis of morphological characters, 4 belong to the tribe Chareae (*Chara*, *Lamprothamnium*, *Lychnothamnus*, *Nitellopsis*) and 2 to the tribe Nitelleae (*Nitella*, *Tolypella*) (Wood & Imahori, 1965; Wood, 1965). *Chara* and *Nitella* are relatively species rich, while the remaining genera (*Lamprothamnium* and *Tolypella*) are represented by only a few or a single species (*Lychnothamnus* and *Nitellopsis*). *Lamprothamnium papulosum* is rare and known to be extraordinarily forbearing to salinity, living in brackish, saline and hyper saline water bodies (Wood & Imahori, 1965; García & Chivas, 2004, 2006; Noedoost et al. 2015).

Until recently, the classification of fossil and extant charophytes was unrelated as they were based exclusively on gyrogonite characters (defining organ-genera of fossil forms) and on soft tissue structures, respectively. Since the latter are commonly not preserved in fossil records, this disconnect prevented the use of vast information available on extant charophyte taxa in realizing the full potential of fossil gyrogonites in the reconstruction of past ecosystems. Charophyte specialists noticed this hindrance of disconnect in taking forward their fossil charophyte research and focused on gyrogonite features in living forms to characterize their genera as fossil/living. Now it has been found that even without taking into account the soft tissue features, distinctive gyrogonite features can lead to determination of the living taxon (Soulié-Märsche, 1989 and 2005). However, species determination on the basis of gyrogonite features continue to be challenging: It is because of host of variations in putative nongeneric feature of gyrogonites of a species credited to hosting environmental/abiotic (physico-chemical) parameters. This interesting aspect of phenotypic plasticity has been discussed in the light of published literature with own observations and perceptions in a subsequent chapter of Discussion.

Further, over the years, the colloquial use of the term ‘Chara’ or ‘chara’ in regular font, for charophytes got entrenched in scientific parlance. This is because the single charophyte genus *Chara* (including all living genera) was used almost as a synonym to the Charophyta in the earliest phase of their study. Agardh (1824) divided *Chara* into two genera *Chara* and *Nitella*. Currently, *Chara*, exclusively in italic font, is one of the six living charophyte genera and is also one of the four living gyrogonite producing genera having a fossil record.

4.2. Gyrogonites: defining features and parameters

Gyrogonites are subjected to measurement of distinct morphological parameters defined and used in several publications (Peck, 1937; Mädler, 1952; Horn af Rantzien, 1956; Bonnet & Soulié-Märsche, 1971; Soulié-Märsche *et al.* 1991; Soulié-Märsche & Joseph, 1991). Out of many parameters proposed for fossil gyrogonite studies by the previous workers, the following designated measurements and their ratios have been used in this study (Figure 4-1):

- LPA, Length of polar axis i.e. length;
- LED, Length of equatorial distance i.e. width;
- AND (Anisopolarity distance) i.e. distance of the apical pole to the LED as measured along the polar axis;
- ISI, Isopolarity Index (sphericity; LPA/LED*100) i.e. length/width*100;
- ANI, Anisopolarity Index (AND/LPA*100) i.e. Anisopolarity distance/length *100;
- Lsp or ECD, width of the lime spiral at the equatorial level or Equatorial Cell diameter;
- CN, Convolution Number i.e. number of spiral cells in lateral view.
- CS, spiral index as calculated from gyrogonite length to width of the spiral cell

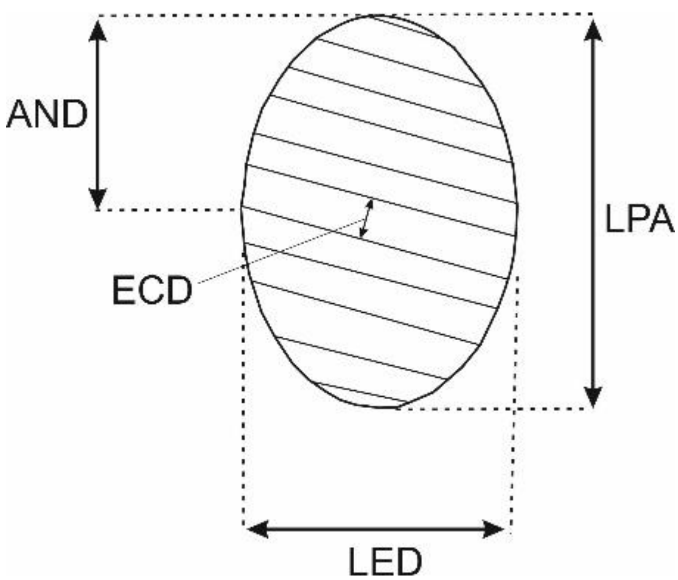

Figure 4-1 Schematic of a gyrogonite showing LPA, LED, AND, and ECD described in the text.

4.3. Abbreviations and Repository

Studied specimens from Mohand area and Sahastradhara are catalogued as BSIP numbers for UB and NT's charophyte collection in the repository of the Birbal Sahni Institute of Palaeosciences, Lucknow 226007. Specimens from Ladakh are housed in the Paleontology Laboratory at Department of Earth Sciences, Indian Institute of Technology, Roorkee and catalogued as IITR/SB/LCH numbers.

4.4. Previous studies on Neogene fossil charophytes in India

***Siwalik and Dharmsala Groups**:* The Siwalik charophytes of India are fairly well recorded from the Upper Siwalik Subgroup. Bhatia and Mathur (1970) recorded some charophytes at the generic level from the Upper Siwalik near Pinjor. Tewari and Sharma (1972a) described 6 taxa of Charophyta, namely *Charites indica*, *Charites surajpurica*, *Grambastichara rantzienii*, *Grambastichara bhatiai*, *Tectochara pinjorica*, and *Tectochara* cf. *diluviana* from the Upper Siwalik beds near Chandigarh. Subsequently, Bhatia and Mathur (1978) revised the earlier work and described a rich assemblage consisting of 13 species. Bhatia (1982) also put forward a Siwalik biostratigraphic zonation based on charophytes and reviewed a previous report on charophytes from the Lower Siwalik Subgroup of Tanakpur by Lakhanpal et al. (1976). Subsequently, Bhatia (1999) presented a detailed review of Siwalik Charophyta and also discussed its age implications. The assemblage was described by Bhatia (1999) as consisting of an admixture of taxa that are endemic, cosmopolitan and those confined to southern Europe and southern hemisphere. The Middle Miocene Chinji Formation and the Late Miocene Dhokpathan Formation are considered to be dominated by palearctic taxa such as *Nitellopsis (Tectochara*) and *Lychnothamnus breviovatus* (Bhatia (1996, 1999). The Upper Siwalik (Tatrot and Pinjor formations), on the other hand, yields an admixed assemblage of palearctic and cosmopolitan taxa (e.g. *Chara globularis* and *Sphaerochara prolifera*. Another significant work on charophytes is by Liu (1989) on the Siwalik Group of Nepal. Scant occurrences of charophytes are also known from the Dharmsala Group sediments which stratigraphically underlie the Siwalik. Mathur et al. (1994, 1996) recorded the genera *Harrisichara*, *Nitellopsis* (*Tectochara*) and *Chara* from Lower Dharmsala.

Ladakh Molasse Group: The Ladakh Molasse Group represents the initiation of continental sedimentation in the trans-Himalayan Indus Tsangpo Suture Zone (ITSZ). Fossils from these molasse horizons document the consequences of India-Asia collision and the resultant changes in ecology and environment in the region. Tewari and Sharma (1972b) discovered charophyte from Wakka River Formation (Kargil Formation) in Kargil (Ladakh), in the then Jammu and Kashmir state. These charophytes are found associated with fresh water gastropods and angiosperm leaf impressions. Tewari and Sharma (1972b) identified these charophytes as *Grambastichara* cf. *tornata* (Ried and Groves) Horn of Rantizien and *Harrisichara* cf. v*asiformis* (Ried and Groves), L. Grambast. The organ species *Grambastichara* cf. *tornata* and *Grambastichara* cf. *cylindrica* range in age from Eocene to Lower Miocene in the beds of U.K., Switzerland and Germany. Tewari (1964) assigned an Oligocene–Miocene age for the Wakka River Formation. Recently, charophyte gyrogonites from Kargil Formation of Ladakh Molasse Group were studied and presented by a team of workers including the present author (in Kapur et al, 2019). Their fossil prospecting in these sedimentary horizons yielded leaf impressions, fossil woods, pollen spores, charophytes, ostracods, molluscs, fishes, and mammals indicating presence of a terrestrial-freshwater regime. Kapur et al. (2019) recorded charophytes including *Grambastichara*, *Lamprothamnium, Lychnothamnus* and *Sphaerochara* from the Kargil Formation. Recorded fossils from the Ladakh Molasse Group suggest a terrestrial-freshwater ecosystem during Oligocene-Miocene transition.

Kutch Miocene: Recently, charophytes from a Miocene (~11-10 Ma) locality have been brought to notice from Kutch, Gujarat, India for the first time (Wazir et al. 2021). Though their sample size is small, the authors have identified four species, three of *Chara* and one of

Nitellopsis. The assemblage, which comprises *Chara globularis* cf. *aspera, C. globularis* cf. *globularis, C. sp.* indet. and *Nitellopsis (Tectochara) merianii*, was interpreted as indicative of a lacustrine environment of deposition with palaeosalinity less than 5 ‰.

***Karewa Group**:* Charophytes of the Hirpur Formation of the Kashmir intermontane basin of India have been described by Bhatia et al. (1985). The assemblage comprisees four species: *Nitellopsis megarensis, Lychnothamnus barbatus, Chara globularis* and *Chara vulgaris*. The basal pore morphology of *N. megarensis*, which is in between the Oligocene-Miocene *Nitellopsis merianii* and the Late Pleistocene-Holocene *N. obtusa* led Bhatia et al. (1985) to suggest that these three taxa represent an anagenetic lineage ending up with *N. obtusa* which still inhabits lakes in Kashmir. Karewa Group charophytes corroborate sedimentological studies concluding that horizons of the Hirpur Formation are shallow water lacustrine deposits.

***Indo-Gangetic Plains**:* Charophytes have also been described from the Holocene deposits of southern Haryana and Uttar Pradesh (Bhatia and Singh, 1988,1989). Taxa recorded by these authors from Haryana include *Chara aspera* and *Lamprothamnium papulosum*, both of which were considered to be indicative of brackish water habitats. Based on these charophytes and associated ostracods and foraminifers, Bhatia and Singh (1988) postulated mesohaline conditions during the Middle Holocene. The charophytic flora from Uttar Pradesh was found to be more diverse but did not include the species *Lamprothamnium papulosum*.

4.5. Studies on extant charophytes in India

The usefulness of fossil charophytes in the reconstruction of ecosystems of the past stems from an understanding of the attributes of extant (living) forms. This is particularly obvious in the case of Neogene charophytes as some of them are represented in modern habitats. Studies on extant charophyte reveal that charophytes are a kind of complex structured algae that grow in freshwater or brackish water. These studies have increasingly updated our understanding of charophytes and their utility in palaeosciences on issues like their hosting habitats, physico-chemical attributes, classification and evolution.

Living Indian charophytes have drawn the attention of workers since as early as 1920s, and continue to remain important objects of research on contemporary lines (Groves, 1924; Mukherji, 1935; Allen, 1942; Sundaralingam, 1959; Pal et al. 1962; Mukherji and Ray, 1966; Chatterjee, 1976). Considerable amount of work has been done on e extant forms of charophytes in India. Sunderlingam (1962), who is credited with significant contributions on charophytes found in the southern part of India, reported several species of *Nitella* and *Chara* from Chennai and its neighborhood, Tirupati hills, Kurnool district, Ooty, Mahabalipuram, Rameshwaram, Banglore, and Nandi Hills. Mandal and Ray (2004) described the ornamentation of extant forms and also reported *C. corallina* Klien. Ex. Willdenow from India. Balakrishnan and Rani (2015) published the SEM studies on *Nitella* and *Chara* species from South India, and the various patterns like granular, pusticular, reticulate, rough and spongy ornamentation were seen in these specimens. Earlier, much work on the morphological characters of the Charophytes was done, among others, by Allen (1942), Iyengar (1958), Barathan (1983, 1987) and Groves (1924). Charophytes have also been studied extensively in Maharashtra, mainly in the Western Ghats area (Dixit, 1931, 1935, 1940a, 1940b, 1942; Vaidya and Gonsalves, 1963; Karande and Chaugule, 1998; Karande and Karande, 2000; Desai and Karande, 2009; Kamat, 1965, 1967; Vaidya, 1967; Patil and Chaugule, 1998). In addition, Ingawale et al. (2019) described the ecological and geographical aspects of six species of *Chara* i.e., *Chara vulgaris*, *Chara setosa*, *Chara zeylanica*, *Chara braunii*, *Chara socotrensis*, *Chara globularis*, and two species of *Nitella* i.e., *Nitella gracilis*, and *Nitella stuartii* from Satara District Maharashtra.

Habib and Pandey (1990) described hitherto unknown six charophyte species from Nakatia River, approx. 4 km from Bareilly (U.P.). The recorded species included *Nitella batrachosperma, N. furcata f. mucronata, Chara braunii, C. corallina, C. flaccida* and *C. vulgaris*.

4.6. Systematic descriptions

This section is subdivided into i) Systematic Palaeontology of fossil gyrogonites from the Neogene and ii) Systematic description of extant Indian species represented by gyrogonites from living plants of charophyte in Sahastradhara area, near Dehradun.

4.6.1. Systematic paleontology of Neogene gyrogonites

The fossil gyrogonite collection from Siwalik Group horizons of Mohand area comprises 7 genera represented by 13 species, that have been described recently by Tiwari and Bhan (2021). The recorded species are as follows:

- *Chara aspera*
- *Chara globularis*
- *Chara rantzieni*
- *Chara sp.*
- *Hornichara maslovi*
- *Lychnothamnus breviotus*
- *Lychnothamnus barbatus*
- *Lychnothamnus* sp.
- *Nitellopsis (Nitellopsis) megarensis*
- *Nitellopsis (Tectochara) merianii*
- *Nitellopsis (Tectochara) huangii*
- *Sphaerochara tewarii*
- *Lamprothamnium papulosum*

4.7. Systematic Palaeontology

Division	Charophyta Migula 1890
Class	Charophyceae Smith 1938
Order	Charales Lindley 1836
Family	Characeae L Ci Richard 1815
Genus	*Chara* Linnaeus, 1753

Lectotype species: *Chara vulgaris* Linnaeus

Chara aspera (Deth. ex Willd.) Wood, 1962

(Plate I. figs.1-3)

Chara aspera Wildenow, Mag. Ges. Natur. Freunde. Berlin 3: 298 (1809)

Chara contraria Bhatia & Mathur (non Braun ex Kuetzing), Geophytology 8 (1): 91–92, pl. 3, fig. 4a–c (1978)

Chara globularis var. aspera Deth. ex Willd. Soulié-Märsche, Tilleuls Millau 137: pl. 20, figs 1–9: pl. 25, figs 1–8 (1989)

Chara aspera Deth. ex Willd, Soulié-Märsche, Jour. Afr. Earth Sci. 12: 344, fig. 1c–d (1991)

Referred specimens*: 3 gyrogonites* (BSIP41931/UB/NTC/101-103*) and more than 125 gyrogonites in collection*

Locality and Horizon: Mohand Rao Locality, Mudstone horizon

Description**:** Lime shells prolate and ellipsoidal in shape with the apical pole rounded and the basal part truncate; lime spirals show around 14-16 convolutions, which become flat at the equator; apical junction is formed in a very short zigzagged line; basal pore with an outer opening and a distinct pentagonal shape, and surrounded by prolonged basal tips of the lime spirals.

Table 4.1 Measurements (in µm) of *Chara aspera*.

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41931/UB/NTC/101	862.2	535.5	442.3	161	51.2	55	16
BSIP41931/UB/NTC/103/1	866.7	609.2	396.8	142.3	45.8	68.9	13
BSIP41931/UB/NTC/103/2	851	598.6	397.1	142.2	46.7	67.3	14
BSIP41931/UB/NTC/103/5	862.2	649.7	420.1	132.7	48.7	72.3	14
BSIP41931/UB/NTC/103/6	874.8	667.5	389	131	44.5	73.9	13

***Remarks**:* The present collection consists of over 125 gyrogonites of this species. The range of variation in this species is: LPA 800-900; LED 525-675; Lsp 53-75. It represents the dioecious form of the monoecious *Chara globularis* (Proctor, 1980). This species was described as a Quaternary lacustrine biomarker in North Africa (Soulié-Märsche 1989) and is also known from the Quaternary marls of the Indo-Gangetic Plains (Bhatia and Singh 1989) and later also from the Tarot and Pinjor formations of Upper Siwalik (Bhatia, 1999). This is the oldest record from the Siwalik Group. In LPA-LED graph of the Mohand charophytes the gyrogonites of the taxon are larger than more than those of five associated taxa as per Figure 4-2 below.

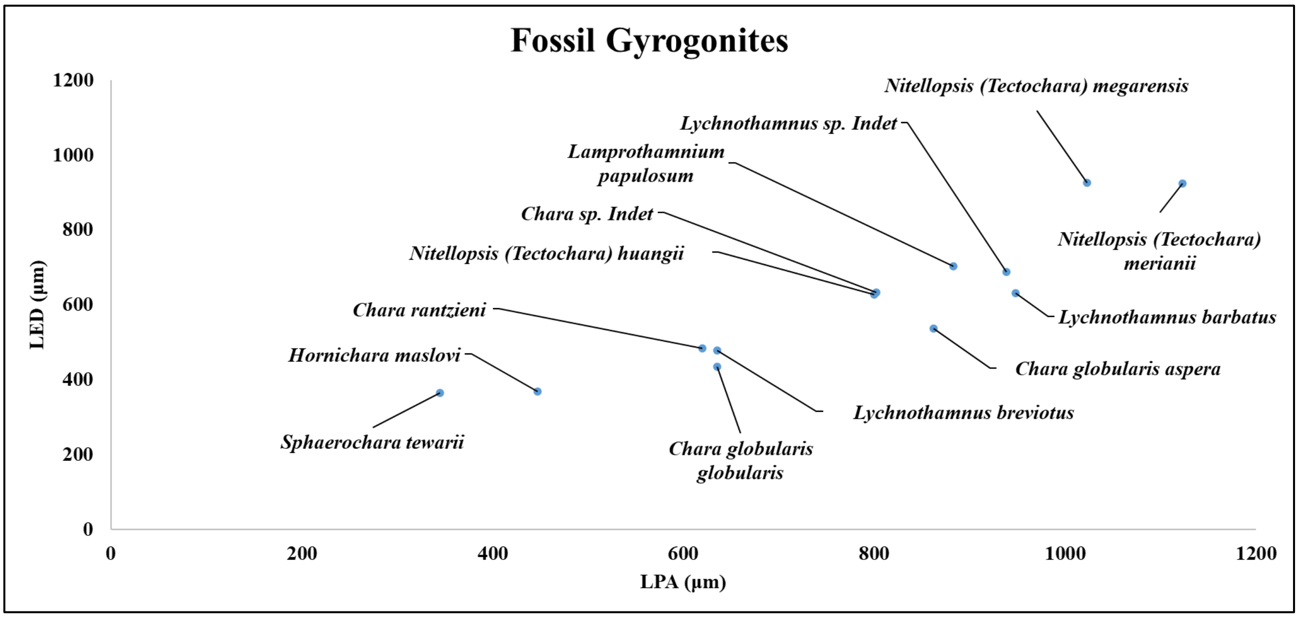

Figure 4-2 LPA-LED graph of the Mohand charophytes species.

Chara globularis Thuillier,1799

(Plate I. figs. 4-6)

Chara *globularis* cf. *globularis* Thuillier, Soulié-Märsche, Tilleuls Millau 137: pl. 24, figs 18 (1989)

Charites indica Tewari & Sharma, Bull. Ind. Geol. Assoc. 5: 67, pl. 1, fig. 2ac; text fig. 2ac (1972)

Chara rantzieni sivalensis Bhatia & Mathur, Geophytology 8 (1): 95, pl. 3. fig. 3ac (1978)

Chara surajpurica (Tewari & Sharma) Bhatia & Mathur, Geophytology 8 (1): 95, pl. 3. fig. 5ac (1978)

Referred specimens: 3 gyrogonites (BSIP41931/UB/NTC/104-106)

Locality and Horizon: Mohand Rao Locality, mudstone horizon

Description: Lime shells sub prolate to prolate spheroidal in shape; apical portion of the gyrogonites rounded; basal portion subtruncated; apical periphery looks truncated when viewed laterally; 9-15 thick convex convolutions which become thinner towards the apical periphery; 5 spiral cells make a moderate spiral rosette joined by a zig zag line; basal pore circular to pentagonal in shape.

Table 4.2 Measurements (in µm) of *Chara globularis*.

C. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41931/UB/NTC/104	635	435	306.8	145.9	48.3	53.4	14

Remarks: Nearly 175 gyrogonites in the present collection pertain to this species. *Chara globularis* is an extant and cosmopolitan species with the following variation in dimensions: LPA 620-850; LED 420-600; Lsp 50-60. It is also from Siwalik and younger Karewa horizons (Bhatia, 1999 and Bhatia et al. 1998); it is a widespread species of fresh- and brackish-water environments. Tewari and Sharma (1972a) previously described this species as *Chara indica*, while Bhatia and Mathur (1978) initially reported it as *Chara surajpurica.* Subsequently, Bhatia (1999) referred it to *Chara globularis*.

Chara rantzieni (Tewari & Sharma, 1972) Bhatia & Mathur 1978

(Plate I. figs.7-9)

Grambastichara rantzieni Tewari & Sharma, Bull. Ind. Geol. Assoc. 5: 79, pl. 1, fig. 3ac; Text fig. 2, fig. 3ac (1972)

Chara rantzieni (Tewari & Sharma) Bhatia & Mathur, Geophytology 8 (1): 9394, pl. 3, fig. 1ac, 2ac (et syn.) (1978)

Chara pappii Soulié-Märsche, Ann. Geol. Des Pays Hellen 3: 1130 -1131, pl. 2, figs 18 (1979); Kröpelin & Soulié-Märsche, Quat. Res. 36 (2): 218-219, fig. 7a-f (1991)

Referred specimens: 3 gyrogonites (BSIP41931/UB/NTC/107-109)

Locality and Horizon: Mohand Rao Locality, mudstone horizon

Description: Gyrogonites small to medium-sized; shape prolate spheroidal to subprolate, ellipsoidal to subovoidal; apically rounded and sometimes subtruncate; basally mostly rounded; apical periphery somewhat truncated in the lateral view; 8-10, flat to convex, moderately thick to wide convolutions; moderately developed apical rosette present, joined along by a short zigzagged line; intercellular ridges seen in thinly calcified gyrogonites; basal pore cone-shaped, pentagonal to subcircular, without outer basal depressions; LPA 550-650: LED 450-500; Lsp 75-85.

Table 4. 3 Measurements (in µm) of *Chara rantzieni*..

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41931/UB/NTC/107	620	484	303.9	128	49	81.4	9

***Remarks**: Chara rantzieni* is rare in the present collection. It ranges in age from Pliocene to the Recent and is known from the Upper Siwalik (Tatrot Formation) of India (Tewari and Sharma, 1972a; Bhatia and Mathur, 1978; Bhatia,1999). The species is characterized by a well developed apical rosette and, interstingly, a basal opening similar to that of the genus *Chara*. *C. rantzieni* is considered to be correlative with *C. pappi* that was reported from the Pliocene and Quaternary of Greece and the Indo-Gangetic plains, respectively (Soulié-Märsche, 1979; Bhatia and Singh, 1989). *C. pappi* is described as a younger representative of *C. rantzieni* (Bhatia, 1999).

***Chara* sp**. indet.

(Plate I. figs.10-12; Plate IV. figs. 1-3)

Referred specimens: 3 gyrogonites from Mohand area (BSIP41931/UB/NTC/110-112) and three from Taruche, Ladakh (IITR/SB/LCH101-103)

Locality and Horizon: Mohand Rao Locality, mudstone horizon and Taruche Locality, Ladakh

Description: Gyrogonites small to medium-sized: subprolate to prolate, rarely prolate spheroidal and ellipsoidal, rarely subovoidal; apically slightly protruding to broadly rounded; basally, broadly rounded; 9-11, moderately thick concave convolutions; apical cells wide and joined along a short straight line; basal pore pentagonal, wide and conical.

Table 4.4 Measurements (in µm) of *Chara* sp. indet.

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41931/UB/NTC/110	802.3	633.3	431.4	126.6	53	94	11
IITR/SB/LCH101	882.5	673.75	451.6	130.9	51.2	113.3	9
IITR/SB/LCH102	823.6	658.3	375.1	125.1	45.5	102.5	9
IITR/SB/LCH103	862.9	636.8	402.2	135.5	46.6	102.9	10

Remarks*:* Three gyrogonites in the collection are similar to those described as *Chara* sp. from the Upper Siwalik by Bhatia and Mathur (1978). Additional specimens are needed for a precise identification. The specimens also bear some resemblance with *Charites angusta* described by Maslov (1966).

Genus Hornichara Maslov, 1963

Type species *Hornichara kazakstanica* Maslov.

Hornichara maslovi Bhatia and Mathur, 1978

(Plate II. figs.1-3: Plate V. figs. 1-7)

Referred specimens: three specimens from Mohand area (BSIP41931/UB/NTC/113-115) and four from Kargil, Ladakh (IITR/SB/LCH109-115), more than ten uncatalogued gyrogonites in collection

Locality and Horizon: mudstone horizons of Mohand Rao Localities and Kargil Locality, Ladakh

Description: Gyrogonites small-sized, predominantly subprolate, and occassionaly prolate spheroidal and rarely prolate and ellipsoidal; apically broadly rounded; conically protruded at the base; 9-12 moderately wide, concave convolutions; intercellular ridges sharp; apical cells join at a point; basal pore pentagonal, moderately wide.

Table 4.5 Measurements (in μm) of *Hornichara maslovi*.

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41931/UB/NTC/113	447.1	368.2	245.8	121.4	54.9	49.4	11
IITR/SB/LCH109	449.5	396.6	218.5	113.3	48.6	51.8	10
IITR/SB/LCH110	553.9	429.9	270.4	128.8	48.8	61.8	10
IITR/SB/LCH113	495.4	381.1	235.7	129.9	47.6	59.7	11
IITR/SB/LCH114	482.3	408.5	209.3	118.1	43.4	56.2	11
IITR/SB/LCH115	512.7	431.1	247.7	118.9	48.3	60.2	10

***Remarks**:* Over 10 gyrogonites in the present collection pertain to *Hornichara maslovi* which is being recorded for the first time from the Middle Siwaliks. Bhatia and Mathur (1978) described this species from the Upper Siwaliks (Pliocene). Its range of variation is as follows: LPA 400-650; LED 300-550; widths between the convolutions 48-65.

Genus Lychnothamnus (Ruprecht) A. Braun, 1856

Type species *Lychnothamnus breviotus* (Meyen) Leonhardi

Lychnothamnus breviotus Lu & Luo, 1990

(Plate II, figs. 4-6; Plate VI, figs. 1-5; Plate IX, figs. 1-5)

Referred specimens: Three catalogued specimens (BSIP41932/UB/NTC/116-118 a, b, c, d, e e) and 20 more specimens referred to this taxon in collection. Five catalogued specimens collected from Kargil, Ladakh (IITR/SB/LCH 117-121).

Locality and Horizon: Mohand Rao Locality, mudstone horizon

Description: Oval-elongated gyrogonites of medium size; wide and generally flattened apex lacking apical nodules; basal funnel well developed, short; spiral cells smooth, broad and slightly concave to flat with 8–10 convolutions and a faintly developed double suture.

Table 4.6 Measurements (in µm) of *Lychnothamnus breviotus.*

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41932/UB/NTC/116	635.5	476.9	316.9	133.2	53.6	74	11
BSIP41932/UB/NTC/118/1	721.5	579.8	373.2	124.4	51.7	96.5	10
IITR/SB/LCH117	565.0	485.2	290.9	116.4	51.5	63.3	11
IITR/SB/LCH118	632.1	519.1	320.1	121.8	50.6	71.6	9
IITR/SB/LCH119	596.5	482.8	294.9	123.5	49.4	68.4	10
IITR/SB/LCH120	681.7	573.1	313.1	118.9	45.9	73.2	10

Remarks*:* More than 20 gyrogonites in the present collection are identified as *Lychnothamnus breviovatus*, a species which was first recorded in India from the Karewa deposits of Kashmir (Bhatia, 1985), and was subsequently also reported by Bhatia (1999) from the Siwalik Group (Dhok Pathan and Pinjor formations). The species occurs quite abundantly in the Pinjor Formation but was found to be rare in the Dhok Pathan Formation (Bhatia, 1999). *L. breviotus* was originally described from the Late Oligocene and Neogene deposits of Tarim Basin, Xinjiang, China (Lu and Luo, 1990). It is known to range from middle Middle Miocene to Quaternary in Europe (Mojon et al. 2018). Known variation in the dimensions of this species are: LPA 550-700; LED 450-580; Lsp 65-75. Compared to the type species *L. barbatus,* L. *breviotus* is much smaller in size and ovoidal to nearly spheroidal in shape. The present record extends the geographic range of L. *breviotus*.

Genus *Lychnothamnus* (Ruprecht) v. Leonhardi 1863 emend A. Braun, 1882

Lychnothamnus barbatus (Meyen) v. Leonhardi 1864

Lychnothamnus barbatus (Meyen) Leonhardi 1863

(Plate III, figs. 8,9; Plate V. figs. 8)

Referred specimens: two from Mohand Locality (BSIP41932/UB/NTC/122-123) and four from Kargil Locality Ladakh (IITR/SB/LCH 116) besides two more gyrogonites in collection

Locality and Horizon*:* the fossiliferous mudstone horizons of the Mohand Rao Locality and the Kargil locality, Ladakh

Description*:* The lime shells are medium sized, elongated oval and in shape. Wide and flattened apex without any apical nodule, 8-10 flat to concave convolutions, with moderately prominent double sutures, well developed and a protruding basal funnel is present.

Table 4.7 Measurements (in µm) of *Lychnothamnus barbatus.*

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41932/UB/NTC/122	948.4	631.3	500.1	150.2	52.7	113	10
IITR/SB/LCH 116	993.2	627.5	475.9	158.3	47.9	98.8	11

Remarks*: L. barbatus* is the single extant species of the genus *Lychnothamnus*, which was earlier reported from some localities of Europe, Asia and Australia and recently it was discovered in North America also. This is a fresh water species; it has been reported from the Ganga plain in India by Bhatia (2006). The range of variation of this species is: LPA 900-1000; LED 620-650; Lsp 95-115.

Lychnothamnus sp. indet.

(Plate III, figs. 4-6; Plate IX, figs. 6-9; Plate X, figs. 1-9)

Referred specimens: BSIP41932/UB/NTC/119-121 and BSIP41932/UB/NTC/121/6-9, BSIP41932/UB/NTC/121/1-9

Locality and Horizon*:* The fossiliferous mudstone horizons of the Mohand Rao Locality and the Taruche locality, Ladakh

Description: Gyrogonites subprolate and ellipsoidal to subovoidal; basally slightly prolonged but truncate in the basal centre; apically truncate; 9-10 mature concave lime spirals; weakly calcified and a brittle apical plate that is depressed below the peripheral zone; apical junction at a point or forms a short line; basal pore with an outer opening in the bottom of a pentagonal depression; pore cone-shaped.

Table 4.8 Measurements (in µm) of *Lychnothamnus* sp. indet.

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41932/UB/NTC/121	938.7	688.2	520.7	136.3	55	132.4	9
BSIP41932/UB/NTC/12/6	1160.2	1003.7	532.5	115.6	45.9	176.2	8
BSIP41932/UB/NTC/121/7	1062.1	905.7	482.7	117.3	45.4	163.1	8
BSIP41932/UB/NTC/121/1	1073.4	862.2	505.9	124.5	47.1	155.6	9
BSIP41932/UB/NTC/121/2	1142.7	773.4	503.2	147.7	44	136.8	9
BSIP41932/UB/NTC/121/3	1108.9	772.9	525.0	143.5	47.3	137.9	8
BSIP41932/UB/NTC/121/4	1094.4	993.7	495.8	110.1	45.3	181.8	9

Remarks*:* The affinities of these gyrogonites with known species of *Lychnothamnus* can be currently ascertained due to their sufficient numbers. This species is recorded for the first time from the Siwalik Group.

Genus Sphaerochara Mädler, 1952

Type species *Sphaerochara hirmeri* (Rásky) Mädler

Sphaerochara tewarii Bhatia and Mathur, 1978

(Plate III, fig. 7)

Referred specimens: rare, one specimen, BSIP41933/UB/NTC/124

Locality and Horizon*:* Mohand Rao Locality, mudstone horizon

Description: Gyrogonite small-sized, broadly prolate spheroidal to narrowly oblate spheroidal or ellipsoidal to subovoidal; lime shells apically rounded to subtruncate, and basally rounded or slightly protruding conically; truncated in apical peripheral zone in lateral view; 8-10 flat to convex moderately thick convolutions; apical junction punctiform or forms a short line; basal pore opening pentagonal to subcircular, present at the same level or slightly below the surface of the surrounding spiral cells.

Table 4.9 Measurements (in µm) of *Sphaerochara tewarii.*

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41933/UB/NTC/124	344.9	365.1	203	94.4	58.8	57.4	9

Remarks*:* Identification of *Sphaeochara tewarii* in the present collection is based on a single gyrogonite. The range of variation of this species is: LPA 310-400; LED 330-380; Lsp 55-58. The species was first described from the Middle Siwalik (Dhok Pathan Formation) of Himanchal Pradesh by Bhatia and Mathur (1978). It has been reported from the Lower Siwalik horizons of Trilokpur, near Kotla, Himachal Pradesh by Bhatia and Mathur (1978).

Bhatia (1999) also described *S. prolifera* from the Middle Siwalik. The Mohand specimens differ from *S. prolifera* in having a rounded apex and their smaller size. *Sphaeochara* (*S.* sp. indet.) has also been reported from the Lower Siwalik Chinji Formation

(Bhatia and Mathur, 1978). Outside India, at the generic level, *Sphaerochara* is widely known from the Tertiary sequences of Europe and North Africa (e.g. Feist-Castel, 1977; Feist et al. 1994; Sanjuan and Martín-Closas, 2014). *Sphaerochara* is known from the Quaternary of North Africa (Soulié-Märsche, 1989).

Genus Lamprothamnium (Wallr.) J. Grove, 1916

Type species: *Lamprothamnium papulosum* (Wallroth) J. Groves

Lamprothamnium papulosum (Wallr.) Groves, 1924

(Plate III, figs. 10-12; Plate IV. figs. 4-8)

Referred specimens: three specimens from Mohand (BSIP41934/UB/NTC/125-127) and five from Taruche, near Leh, Ladakh (IITR/SB/LCH104-108)

Locality and Horizon*:* Mohand Rao and Taruche Localities, the mudstone horizons of Siwalik and Ladakh Molasse groups.

Description*:* The gyrogonites are medium to small in size; subprolate to prolate spheroidal; 10-12 concave to flat convolutions; no ornamentation present; characteristic thin apical portion is rarely preserved; basal pore wide and pentagonal in shape.

Table 4.10. Measurements (in µm) of *Lamprothamnium papulosum.*

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41934/UB/NTC/125	847.4	732.1	393.5	115.7	46.4	90.3	10
BSIP41932/UB/NTC/126	917.6	674.1	471	136.1	51.3	95.2	10
IITR/SB/LCH104	878.3	520.5	416.2	168.8	47.4	93.1	10
IITR/SB/LCH105	732.2	527.9	338.8	138.7	46.3	85.7	10
IITR/SB/LCH106	738.9	506.2	331.2	146.0	44.8	80.5	11
IITR/SB/LCH107	847.3	501.4	389.2	169.0	45.9	91.4	11

Remarks*:* Bhatia (1999) reported *Lamprothamnium papulosum* and *Lamprothamnium succintum* from Pinjor beds of Upper Siwalik for the very first time, and it was suggested that the species must have flourished in an oligo to mesohaline environment. However, the taxaon is euryhaline and grows abundantly in brackish water with increased growth during periods of reduced salinity (Soulie-Marsche, 1991). Later it was reported by Sharma et al. (2015) from Dhok Pathan beds exposed near Polian Prohita, extending its range from Middle Siwalik to Upper Siwalik. The range of variation of this species is: LPA 790-950; LED 630-750; Lsp 85-95.

Genus *Nitellopsis* Hy, 1889

Type species *Nitellopsis stelligera (Bauer) Hy*

Nitellopsis is an important charophyte genus with geological history since Oligocene and has two subgenera, *Tectochara* and *Nitellopsis.* It is represented by *Nitellopsis (Nitellopsis) obtusa* in Recent charophytes continuing since Quaternary. Gyrogonites of the subgenera *Tectochara* and *Nitellopsis* are distinct in their basal morphology details. In former subgenus the basal pentagonal depression is with sharp boundaries or star shaped where as in other, that is, subgenus *Nitellopsis* the basal depression is reduced to absent in most of the recorded and studied gyrogonites referred to this subgenus of the genus *Nitellopsis.* These progressive basal morphology trend of the two subgenera of the *Nitellopsis* lineage runs from the *Tectochara* type to *Nitellopsis* type culminating in predominance of latter type in Quaternary. Thus as, observed by previous workers (Grambast and Soulié-Märsche, 1972; Soulié-Märsche, 1972; Soulié-Märsche et al. 1997) these two *Nitellopsis* subgenera represent chronological sequence of biostratigraphical importance.

Subgenus *Nitellopsis*

Type-species *Nitellopsis* (*Nitellopsis*) *obtusa*

Nitellopsis (Tectochara) megarensis Soulié-Märsche, 1979

(Plate II, figs. 7-9; Plate XI, figs. 1-7)

Referred specimens: seven catalogued specimens (BSIP41935/UB/NTC/128-130), (BSIP41935/UB/NTC/130/1-7) and more than 25 gyrogonites in collection.

Locality and Horizon: The mudstone horizons of Mohand Rao Locality.

Description: Gyrogonites broadly rounded to ovoidal; heavy calcification in some lime shells; 6-8 convolutions, flat to convex; apical pole slightly protruding with distinct apical nodes; basal pole truncates to rounded; lime shells having truncate basal pole have a broad basal funnel that surrounds the basal opening; unususal "stomata-shaped" protrusions present at the sutures of lime spirals.

Table 4.11 Measurements (in µm) of *Nitellopsis (Tectochara) megarensis.*

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41935/UB/NTC/128	1022.8	925	537.5	110.5	52.5	162.5	7
BSIP41935/UB/NTC/130/1	1170.6	1019	539.8	114.9	46.1	144.1	9
BSIP41935/UB/NTC/130/2	1039.9	933.2	482.3	111.4	46.4	134.6	9

Remarks*:* The morphological characters of over 25 gyrogonites in the collection are generally similar to those of other species of *Nitellopsis* (*Tectochara)*, but the Mohand specimens closely resemble *T. merianii diluviana* reported by Tewari and Sharma (1972a) from the Upper Siwalik sediments exposed near Chandigarh. The known variation of this species is as follows: LPA 1000-1180; LED 900-1025; Lsp 140-165.The reason for the presence of stomata-shaped protrusions is unclear, but this phenomenon is possibly related to a difference in calcification pattern and process resulting from external disturbances (Bhatia et al. 1998). This species is also known from the Hirpur Formation of the Karewa Group of Kashmir (Bhatia et al. 1998).

In Europe, it characterizes the Charophyte zone *Megarensis* for the entire Pliocene from 5.333 to 1.8 Ma (Mojon et al. 2018).

Subgenus *Tectochara* L. & N. Grambast

Type species of subgenus *Nitellopsis (Tectochara) merianii* (Al. Brown ex Unger) Gramblast and Soulie Marsche 1972

Nitellopsis (Tectochara) huangii (Lu, 1945) Grambast & Soulié-Märsche, 1972

(Plate II, figs.10-12)

Referred specimens: three catalogued specimens (BSIP41935/UB/NTC/131-133) and ten specimens in the collection.

Locality and Horizon: Mohand Rao Locality, mudstone horizon.

Description: Gyrogonites range in shape from prolate spheroidal to sub prolate, subovoidal or ellipsoidal, predominantly subovoidal; apically rounded to subtruncate, basally protruding and generally conically prolonged; lime shells strongly calcified, and the lime spirals are mature and are flat to strongly convex; lime spirals thick in the apical periphery forming a distinct apical rossete with inflated spiral tips, joining each other at a zigzagged line; basal pore characteristically protruding and wide, with its shape varying from pentagonal to subcircular.

Table 4.12. Measurements (in µm) of *Nitellopsis (Tectochara) huangii*.

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41935/UB/NTC/131	800.1	626	417	127.8	92	52	11

Remarks*:* Ten gyrogonites in the collection are referable to this species. It was initially described from the Lower Siwalik (Bhatia and Mathur, 1978) but was later also reported from the Pliocene Tatrot Formation of the Upper Siwalik (Bhatia, 1999). The known variation of this species is as follows: LPA 800-950; LED 600-750.The present find is the first such record from the Middle Siwalik. Its characteristic, protruding basal pore, which is wide and pentagonal to subcircular in shape, distinguishes this species from other species of *Nitellopsis*. Lu (1945a, b) and Horn af Rantzien (1959) initially described this species from the Kuchar Group of Sinkiang Province, China. It was widely distributed in Europe and Asia (Wang, 1961,1965; Castel, 1967).

Nitellopsis (Tectochara) merianii

(Al. Braun & Unger, 1850) Grambast & Soulié-Märsche, 1972

(Plate III, figs.1-3)

Referred specimens: three catalogued specimens (BSIP41935/UB/NTC/134-136) and seven more in collection

Locality and Horizon*:* Mohand Rao Localities, mudstone horizon

Description: Lime shells range in shape from prolate spheroidal to sub prolate, subovoidal or ellipsoidal, but predominantly subovoidal; apically rounded to subtruncate; protruding at the base, and generally conically prolonged; lime shells strongly calcified; spirals flat to strongly convex; lime spirals thick in the apical periphery, forming a distinct apical rosette with inflated spiral tips, joining each other at a zigzagged line; basal pore situated in the bottom of a large, regularly pentagonal depression, with a narrow pore opening.

Table 4.13 Measurements (in µm) of *Nitellopsis (Tectochara) merianii*.

Cat. No.	LPA	LED	AND	ISI	ANI	Lsp	CN
BSIP41935/UB/NTC/134	1122.6	922.8	592	121.5	52.7	136	10

Remarks*:* This rare species in the present collection (7 gyrogonites) is widely distributed in the European Oligocene to Pliocene including southern Germany, Austria, Switzerland and France and in the Asian Miocene basins of Northern Thailand (Soulie Marsche et al. 1997; Mojon et al. 2018). Originally, this long ranging species was described from

Oligocene/Miocene of Switzerland (Horn af Rantzien, 1959). The size and morphological variation of this species are as follows: LPA 1190-1330; LED 900-1190; number of convolutions 8-10; widths between the convolutions ranges from 130 to 180.

In India, *Nitellopsis merianii* was first recorded from the Lower (Chinji Formation) and Middle (Dhok Pathan Formation) Siwalik by Bhatia and Mathur (1978). Subsequently, Bhatia (1999) extended the range of this species to the Upper Siwalik Tatrot Formation (Pliocene). The oldest global record of *Nitellopsis merianii* (A. Braun ex Unger) is from uppermost Eocene horizons of Iberian Peninsula implying that later the taxon spread the entire Eurasia during the Oligocene and Miocene, i.e., 5.3 to 33.9 million years ago (Soulié-Märsche et al. 1997; Sanjuan and Martín-Closas, 2015) with a remarkable find in North Africa (Soulié-Märsche et al. 2002). In a review paper on long record of Iberian fossil charophytes Martin-Closas et al. (2016) observed that "the isolation of Iberia represented not only a source of endemism, but also a factory of new species that later could enrich the Eurasian charophyte floras".

4.8. ASSOCIATED BIOTA

A few freshwater molluscs (gastropods) and ostracods were recovered together with the charophytes. Gastropods include a planorbid (*Gyraulus* sp.), characterised by a planispiral shell with 3-4 whorls separated by deep sutures. Similar specimens are known from the Miocene and Pliocene of the Churia Group of Nepal (Gurung et al. 1997). Another taxon, characterised by a turreted spire and up to 7 whorls divided by shallow sutures, is referable to a cerithioidean *Plotia* cf. *P. scabra* described by Bhandari et al. (2014) from the Mohand area. Ostracods are represented by carapaces of a single species referable to *Stenocypris* sp. (family Candonidae). Diagnostic characters of these carapaces include rounded anterior and the posterior margins; left valve larger than right valve, with complete overlap and the greatest height more or less in the middle. Similar ostracods have been reported from the Upper and

Middle Siwalik deposits (Sharma et al. 2015).

4.9. Systematic description of gyrogonites of extant Indian species

Division	Charophyta Migula 1890
Class	Charophyceae Smith 1938
Order	Charales Lindley 1836
Family	Characeae Agardh 1824
Genus	*Chara* Vaillant 1719
Type species	*Chara vulgaris* Linnaeus

Chara vulgaris Linnaeus 1753

(Plate VII figs. 1-16)

Locality*:* Sahastradhara picnic area, Dehradun

Referred material*:* 51 catalogued gyrogonites (BSIP 41936/UB/NTC/137-188)

Description: The recovered terete and charoid type gyrogonites of monoecious *Chara vulgaris* are small in size, varying from 569 to 472 µm in length, 320 to 413 µm in width and have concave lime spirals. The gyrogonites are prolate (LPA > LED), ellipsoidal, and apically protruding, and have 10 to 12 (but often 11) sharp convolutions with distinct intercellular ridges. At the base, the gyrogonites have often truncate basal column. In the apical region, the lime spirals tend to get wider towards the apical periphery while becoming narrower in the equatorial region, and do not culminate as an apical rosette. The lime spirals are wider in the basal region also. The basal pore is protruding, cone shaped, wide and distinctly pentagonal in shape. Measures of spherecity (ISI) and asymmetry (ANI) of gyrogonites, range from 160-128 and 50-56 respectively (Fig 4-5).

The gyrogonite features (morphology) of living charophytes are essential in to the identification of fossil species in recent sedimentary sequences e.g. Garcia and Chivas (2006). The here-studied gyrogonite population recovered from living plants in Sahastradhara area (Doon Valley, Uttarakhand) is attributed to the well-known and cosmopolitan species Chara vulgaris on the basis of its distinctive morphological parameters. The morphometrical parameters of the studied population can be compared with the parameters obtained by Sanjuan et al (2017) from gyrogonite of C. vulgaris of living plants exposed at different light irradiances and water temperatures.This study provides significant information about the diagnostic features characterizing the gyrogonites of this taxon which are are small to medium in size with a prolate ellipsoidal shape displaying concave spiral cells and commonly 11 convolutions in lateral view and distinctly pentagonal shape of the protruding basal pore. Based on comaprison with the study of Sanjuan et al. (2017), C. vulgaris from the Sahastradhara area is considered to have thrived in shallow waters at temperatures ranging between 12 and 18° C. A similar paleoecological setting is likely for the fossil occurrence of C. vulgaris in the Pleistocene of Kashmir Valley.

Remarks*:* In view of the reported polymorphism of *Chara vulgaris* (e.g. Sanjuan et al. 2017), morphological observations on a number of gyrogonites of *Chara vulgaris* in the present collection were taken into account for identifying the diagnostic features. These observations suggest that the arrangement of enveloping cells, putatively governed by genetics (Casanova, 1997), resulting in the consistent presence of 10-12 convolutions of small to medium charoid type gyrogonites, represents a diagnostic feature of the species.

The gyrogonites of *C. vulgaris* from Sahastradhara show a striking resemblance with *Chara strobilocarpa*, but are smaller than the latter. Published fossil records of *C. vulgaris* from the Hirpur Formation (late Pliocene-Early Pleistocene) of the Karewa Group in the Kashmir valley of northern India suggests the antiquity of this species in the late Pliocene. Gyrogonites from Sahastradhara are morphologically comparable with the fossil records of *Chara vulgaris* from the Karewa Group in which LPA and LED range from 500-575 µm and 300-400 µm, respectively (Bhatia et al. 1998). Published lateral view of the Karewa *C. vulgaris* reveals that the number of convolutions (CN) is 11. The estimated ISI and ANI of the fossil species are 166 and 44, respectively. Closer comparison indicates that the sphericity measure (ISI) of the Karewa gyrogonite is similar to that of the presently studied gyrogonites. However, the asymmetry measure or ANI (= 44) is distinctly less than the ANI value of 50 or more in the studied gyrogonites. If the ANI is 50, the LED passes through the mid-point of LPA in lateral view, and if it is less or more than 50, then the LED cuts in apical or basal half of the polar axis. A more detailed comparison based on additional specimens of fossil *C. vulgaris* from Kashmir Valley will possibly allow a critical evaluation of the taxonomic identification of the fossil species.

Significantly, high resolution SEM photographs of the gyrogonites collected from Sahastradhara showed clusters of epiphytic freshwater diatoms like *Cymbella* and *Gomphonema (Class: Bacillariophyceae Order: Bacillariales)* on the lime spirals of gyrogonites (Figures 4-3 and 4-4; personal communication from Dr Sunil Shukla, BSIP, Lucknow). These diatoms are indicative of pristine freshwaters environments.

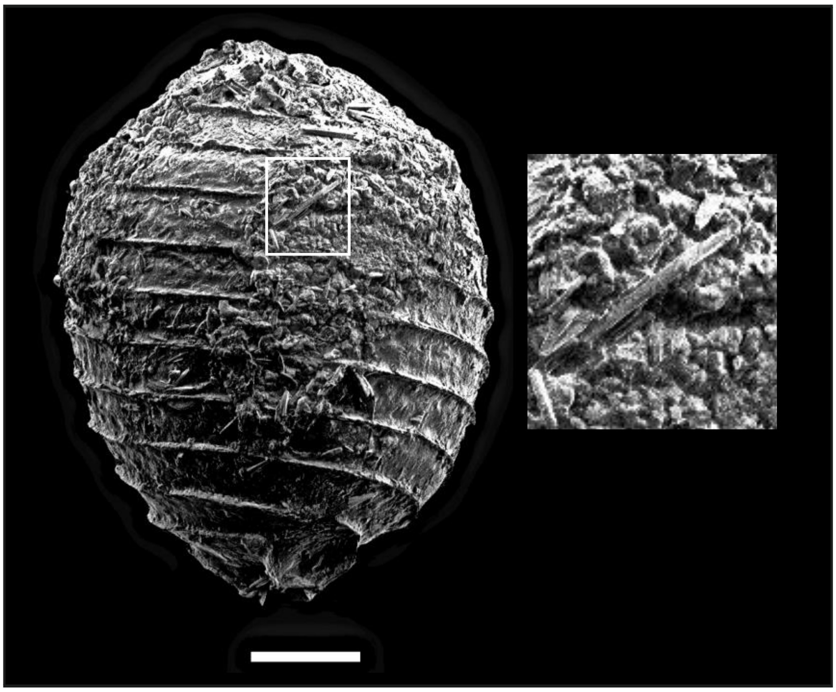

Figure 4-3 Diatoms on the spirals of gyrogonite BSIP 41936/UB/NTC/143; boxed area enlarged in the adjacent photograph.

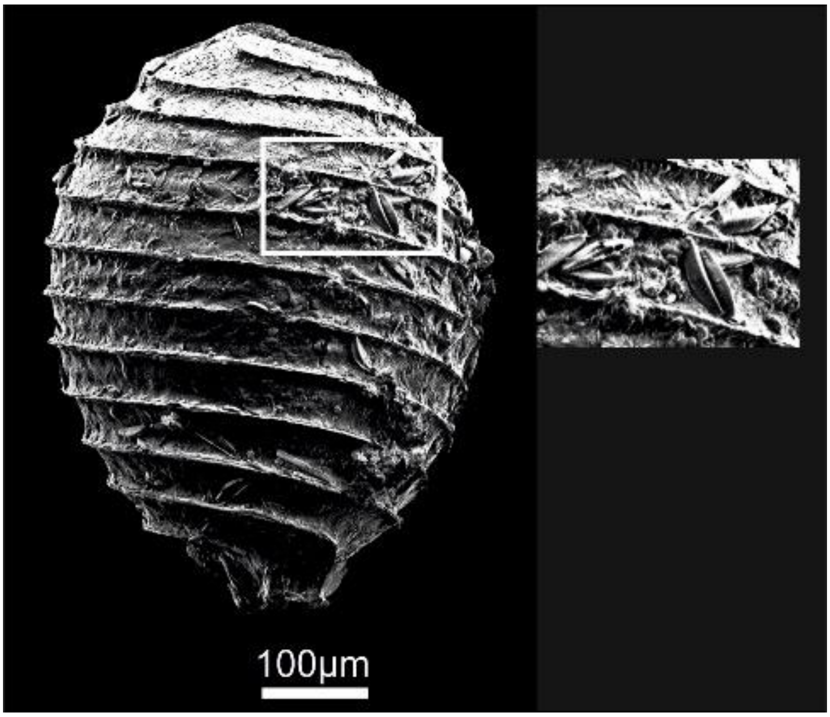

Figure 4-4 Diatoms on the spirals of gyrogonite BSIP 41936/UB/NTC/144; boxed area enlarged in the adjacent photograph.

Regarding habitat**,** *Chara vulgaris,* though also found in slightly brackish water, is a freshwater species. The *Chara* species thrives in a large variety of habitats including ponds, puddles, ditches, rivers, littoral pools and periodical waters but exceptionally in lakes. *Chara vulgaris,* often richly fertile, occurs as annual and perennial forms. It is found both in soft and alkaline water (around 8 or 9 on the pH scale) and it grows down to 1 m.

The pH of natural water in the Sahastradhara stream is apparently controlled exclusively by the interaction of hydroxyl ions arising from the hydrolysis of bicarbonate of surrounding limestone (Sharma, 1986). The pH of Sahastradhara stream ranges from 7.2-8.1 and is thus slightly alkaline. This hardness is due to calcium and magnesium salts of bicarbonates, carbonates, sulphates and chlorides but alkalinity is due to presence of bicarbonates. (Bharti, 2014).

Table 4.14 Measurements of gyrogonite parameters of the catalogued specimens of *Chara vulgaris,* from Sahastradhara, Doon Valley, Uttarakhand. lengths are in µm.

Catalogue No.	**LPA** (µm)	**LED** (µm)	**AND** (µm)	**ISI**	**ANI**	**ECD** (µm)	**CN**
BSIP41936/UB/NTC/137	552	387	287	143	51	59	11
BSIP41936/UB/NTC/138	472	320	239	148	51	50	11
BSIP41936/UB/NTC/139	501	391	248	128	50	51	10
BSIP41936/UB/NTC/140	521	326	264	160	51	48	11
BSIP41936/UB/NTC/141	492	371	269	133	55	55	11
BSIP41936/UB/NTC/142	569	413	319	138	56	54	11
BSIP41936/UB/NTC/143	517	394	258	131	50	49	11
BSIP41936/UB/NTC/144	544	395	284	138	52	50	12
BSIP41936/UB/NTC/145	547	355	274	154	50	50	11
BSIP41936/UB/NTC/146	530	393	265	135	50	50	11
BSIP41936/UB/NTC/147	584	383	303	152	52	47	10
BSIP41936/UB/NTC/148	522	399	276	130	53	49	11
BSIP41936/UB/NTC/149	507	399	253	127	50	50	11
BSIP41936/UB/NTC/150	601	416	306	144	51	48	11
BSIP41936/UB/NTC/151	554	403	277	137	55	50	11
BSIP41936/UB/NTC/152	555	347	278	160	51	50	12
BSIP41936/UB/NTC/153	583	384	309	152	53	50	11
BSIP41936/UB/NTC/154	587	401	294	146	50	49	11
BSIP41936/UB/NTC/155	506	397	253	127	50	51	11

BSIP41936/UB/NTC/156	590	400	312	147	53	50	10
BSIP41936/UB/NTC/157	557	377	279	148	50	48	11
BSIP41936/UB/NTC/158	539	354	275	152	51	51	12
BSIP41936/UB/NTC/159	574	387	310	148	54	50	11
BSIP41936/UB/NTC/160	562	379	281	149	50	47	11
BSIP41936/UB/NTC/161	543	406	277	134	51	50	10
BSIP41936/UB/NTC/162	586	411	293	143	52	50	12
BSIP41936/UB/NTC/163	557	393	279	142	50	50	11
BSIP41936/UB/NTC/164	585	384	293	152	50	49	11
BSIP41936/UB/NTC/165	548	376	285	146	52	50	11
BSIP41936/UB/NTC/166	548	353	274	155	50	49	12
BSIP41936/UB/NTC/167	593	343	297	173	51	50	11
BSIP41936/UB/NTC/168	574	390	287	147	55	50	11
BSIP41936/UB/NTC/169	554	385	243	144	44	50	11
BSIP41936/UB/NTC/170	523	329	278	159	53	49	11
BSIP41936/UB/NTC/171	482	384	293	126	61	50	12
BSIP41936/UB/NTC/172	579	412	285	141	49	48	11
BSIP41936/UB/NTC/173	543	384	244	141	45	50	11
BSIP41936/UB/NTC/174	585	349	288	168	49	50	11
BSIP41936/UB/NTC/175	581	407	248	143	43	51	11
BSIP41936/UB/NTC/176	527	332	285	159	54	50	11
BSIP41936/UB/NTC/177	540	392	278	138	51	50	11
BSIP41936/UB/NTC/178	556	381	262	146	47	50	12
BSIP41936/UB/NTC/179	582	366	241	159	41	48	11
BSIP41936/UB/NTC/180	579	395	253	147	44	51	11
BSIP41936/UB/NTC/181	496	361	294	137	59	50	11
BSIP41936/UB/NTC/182	591	388	279	152	47	51	11
BSIP41936/UB/NTC/183	600	397	286	151	48	49	10
BSIP41936/UB/NTC/184	498	353	254	141	51	50	11
BSIP41936/UB/NTC/185	532	379	263	140	49	50	11
BSIP41936/UB/NTC/186	571	411	280	139	49	51	11
BSIP41936/UB/NTC/187	549	386	310	142	56	48	11
BSIP41936/UB/NTC/188	597	407	265	147	44	50	11
Max	601	416	319	173	61	59	12
Min	472	320	239	126	41	47	10
Median	554	387	279	145	51	50	11

Interestingly, small sized gyrogonites found in high numbers are known to characterize shallow and temporary ponds and interpreted as a manifestation of opportunistic strategy by the charophyte living and fossil taxa (Vicente et al. 2016, Böhme et al. 2021). Small gyrogonites of *Chara vulgaris* from a shallow temporary pond in Sahastradhara locality obviously supports this contention. Further, co-occurrence of smaller gyrogonites referred to *Chara vulgaris* and *Chara globularis* from Soknag Section in Kashmir Valley in contrast to the bigger gyrogonites from younger levels of the Karewa package reported by Bhatia et al. (1998) indicate shallow temporary ponding was succeeded by the perineal water bodies sustaining charophyte taxa producing medium to larger gyrogonites.

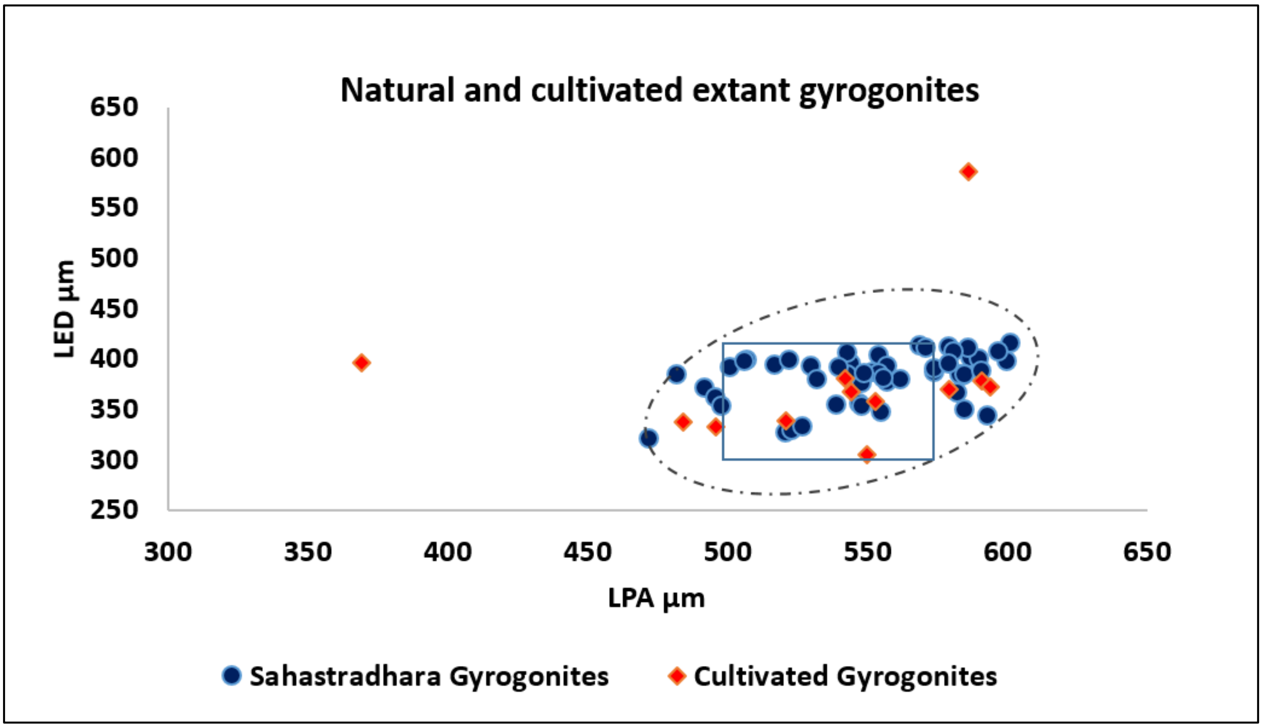

Figure 4-5 Dispersion graphic of the LED (gyrogonite height) and LPA (gyrogonite width) parameters of the studied Chara vulgaris gyrogonites from Sahastradhara (BSIP 41936/UB/NTC/137-188). See LED and LPA parameters (mean average) of the gyrogonite population of Chara vulgaris studied by Sanjuan et al. (2017: tab.1) extracted from cultivated plants under controlled light and temperature conditions. Rectangle represents the LED and LPA ranges of fossil gyrogonites from Karewa Group studied by Bhatia et al. (1998).

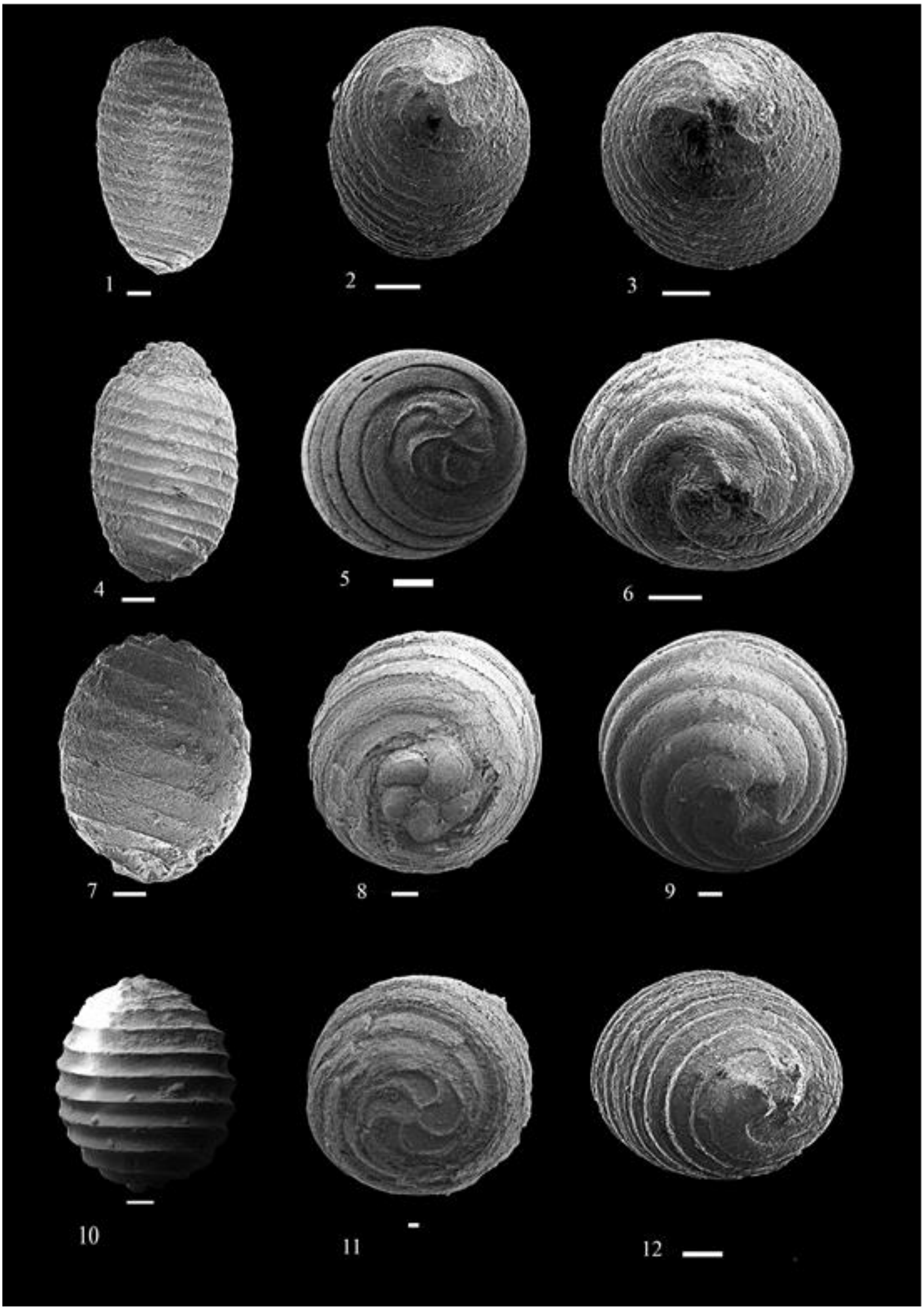

Plate I:1-3, *Chara aspera*: (BSIP41931/UB/NTC/101-103)1, lateral view; 2, apical view; 3, basal view. 4-6, *Chara globularis;* (BSIP41931/UB/NTC/104-106) 4, lateral view, 5. Apical view, 6. Basal view.7-9, *Chara rantzieni*: (BSIP41931/UB/NTC/107-109)7, lateral view; 8, apical view; 9, basal view. 10-12, *Chara* sp. Indet. (BSIP41931/UB/NTC/110-112): 10, lateral view; 11, apical view; 12, basal view. Scale bar = 100µm.

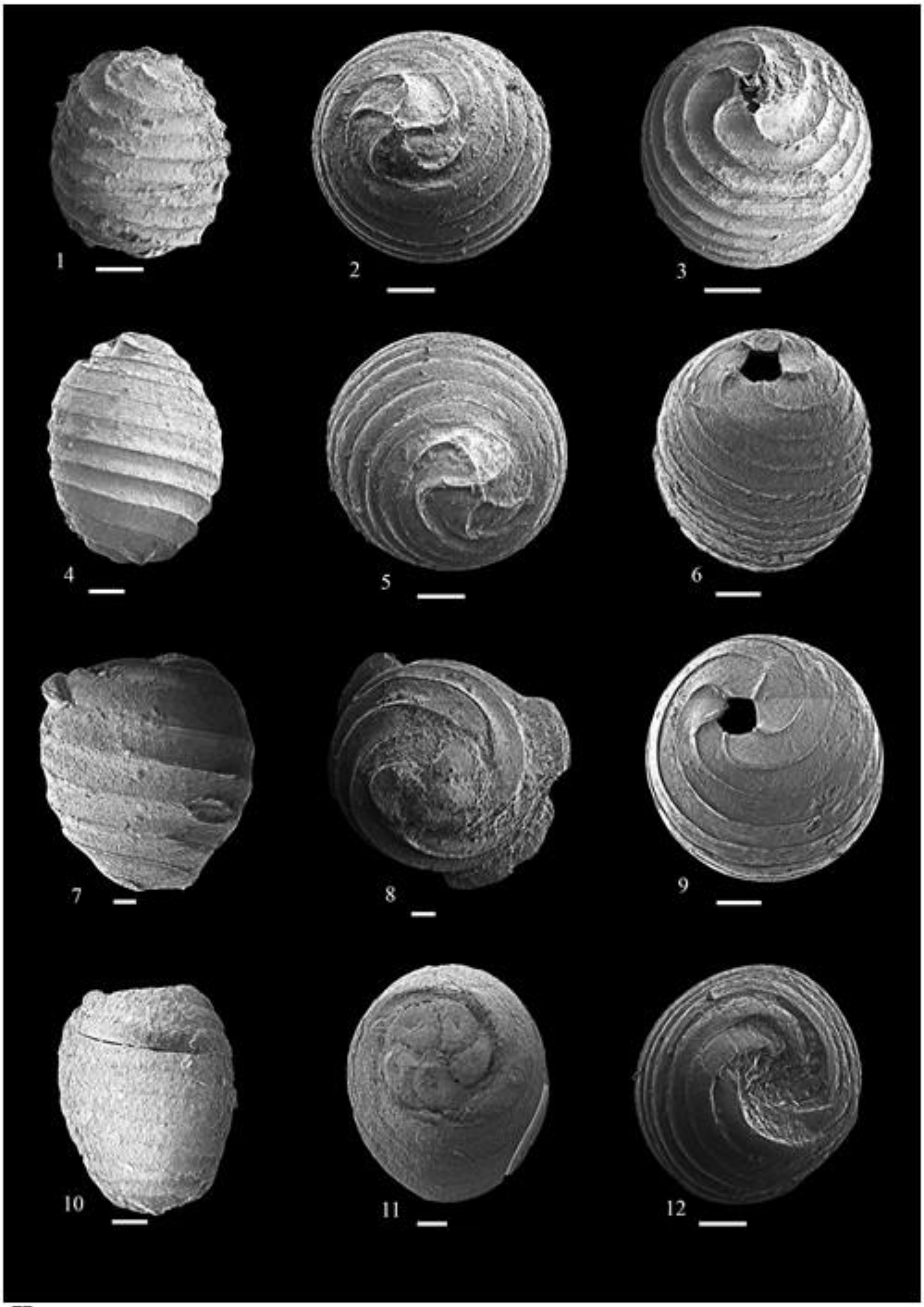

Plate II:1-3, *Hornichara maslovi:* (BSIP41931/UB/NTC/113-115) 1, lateral view; 2, apical view; 3, basal view. 4-6, *Lychnothamnus breviotus*: (BSIP41932/UB/NTC/116-118) 4, lateral view, 5. Apical view, 6. Basal view.7-9, *Nitellopsis Tectochara) megarensis*:7(BSIP41935/UB/NTC/128-130), lateral view; 8, apical view; 9, basal view. 10-12, *Nitellopsis (Tectochara) huangii*: (BSIP41935/UB/NTC/131-133) 10, lateral view; 11, apical view; 12, basal view. Scale bar = 100µm.

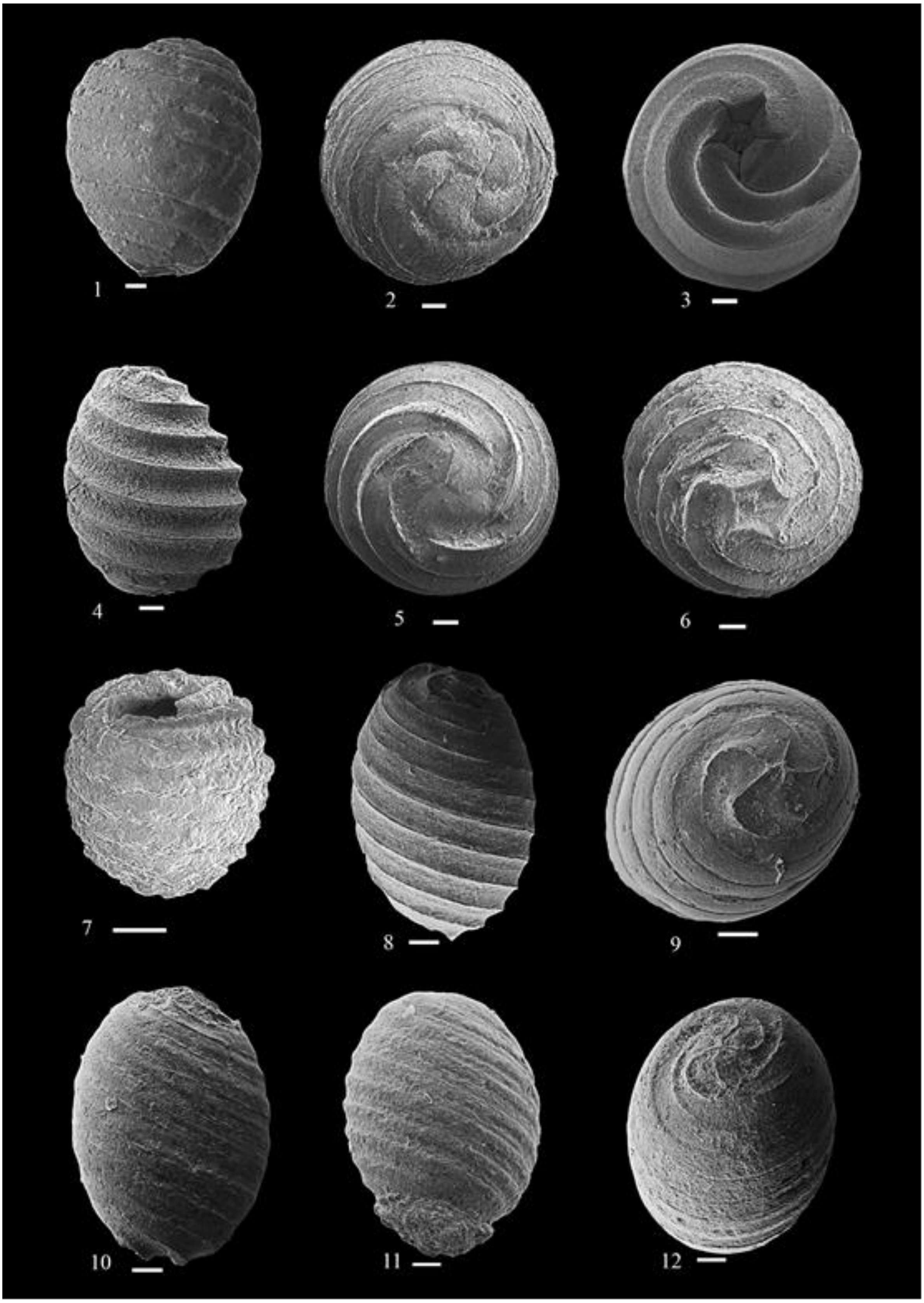

Plate III:1-3, *Nitellopsis(Tectochara) merianii:* (BSIP41935/UB/NTC/134-136) 1, lateral view; 2, apical view; 3, basal view. 4-6, *Lychnothamnus* sp: BSIP41932/UB/NTC/119-121 4, lateral view, 5. Apical view, 6. Basal view.7 *papulosum*, BSIP41933/UB/NTC/124 lateral view; 8-9 *Lychnothamnus barbatus*: (BSIP41932/UB/NTC/122-123) 8, lateral view; 9, apical view. 10-12, *Lamprothamnium papulosum*: (BSIP41934/UB/NTC/125-127) 10, lateral view; 11, lateral view; 12, apical view. Scale bar = 100µm.

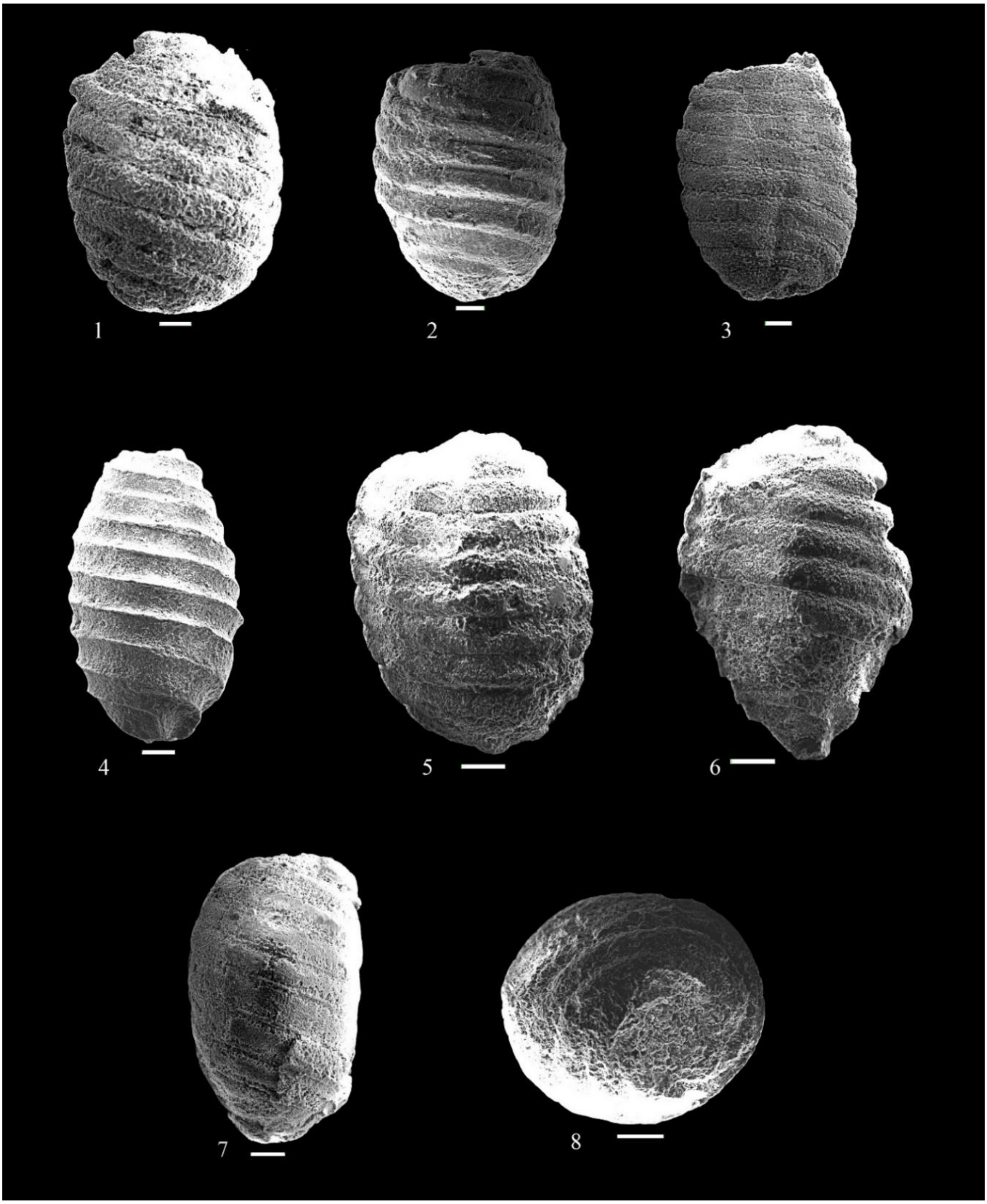

Plate IV: Ladakh Molasse Gyrogonites: *Chara* sp. (IITR/SB/LCH101-103) :1-3 lateral views; *Lamprothamnium papulosum* (IITR/SB/LCH104-107) :4-7 lateral views;*L. papulosum* (IITR/SB/LCH108):8 basal view. Scale bar = 100µm.

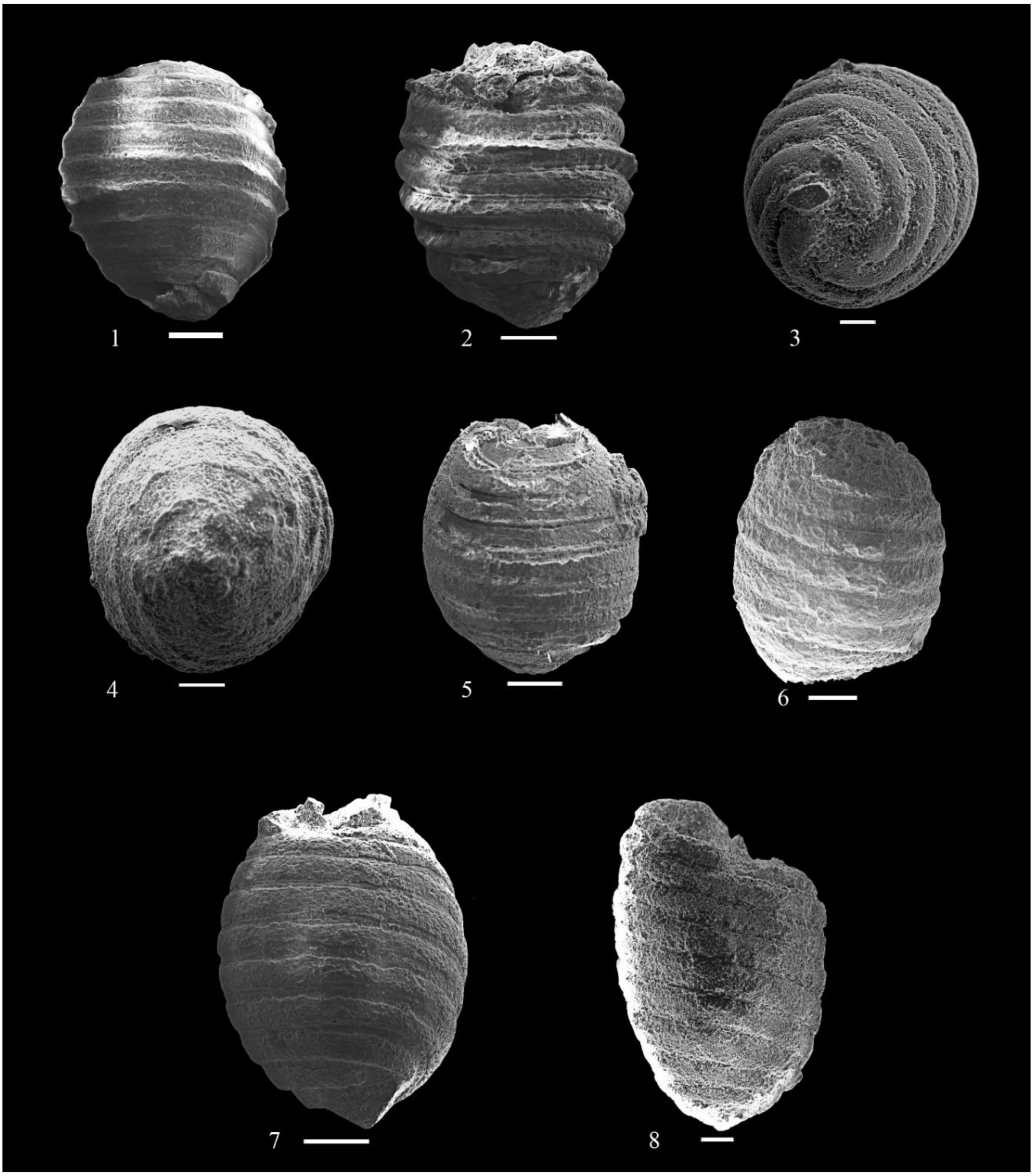

Plate V: Ladakh Molasse Gyrogonites: *Hornichara maslovi* (IITR/SB/LCH109-115):1-7, 1,2,5-7 lateral views; 3- apical view 4-basal view; *Lychnothamnus barbatus* (IITR/SB/LCH 116): lateral view. Scale bar = 100µm.

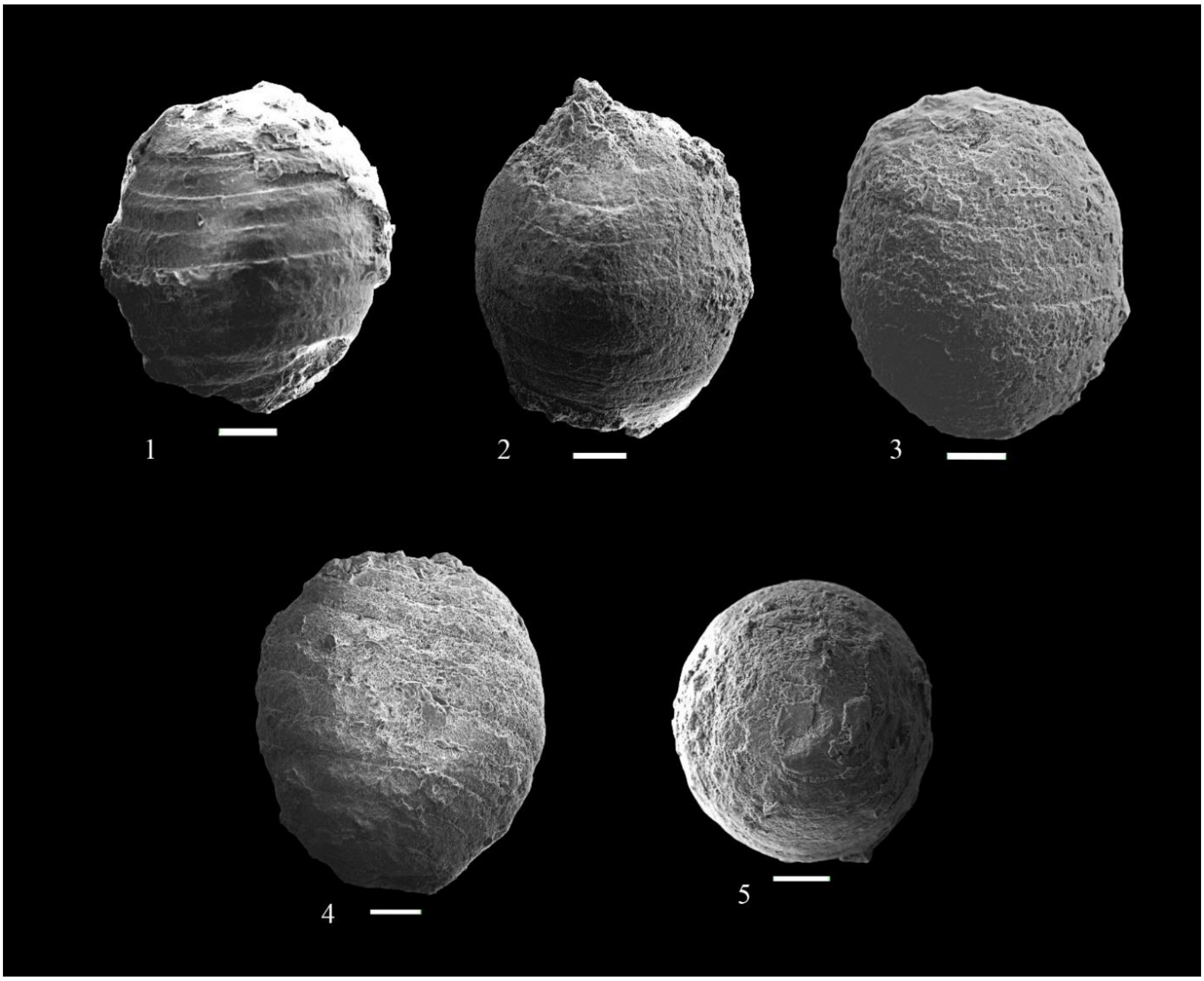

Plate VI: Ladakh Molasse gyrogonites: *Lychnothamnus breviotus* (IITR/SB/LCH 117-120)1-4 lateral views; *L. breviotus* (IITR/SB/LCH- 121):5 ,*basal* view. Scale bar = 100µm.

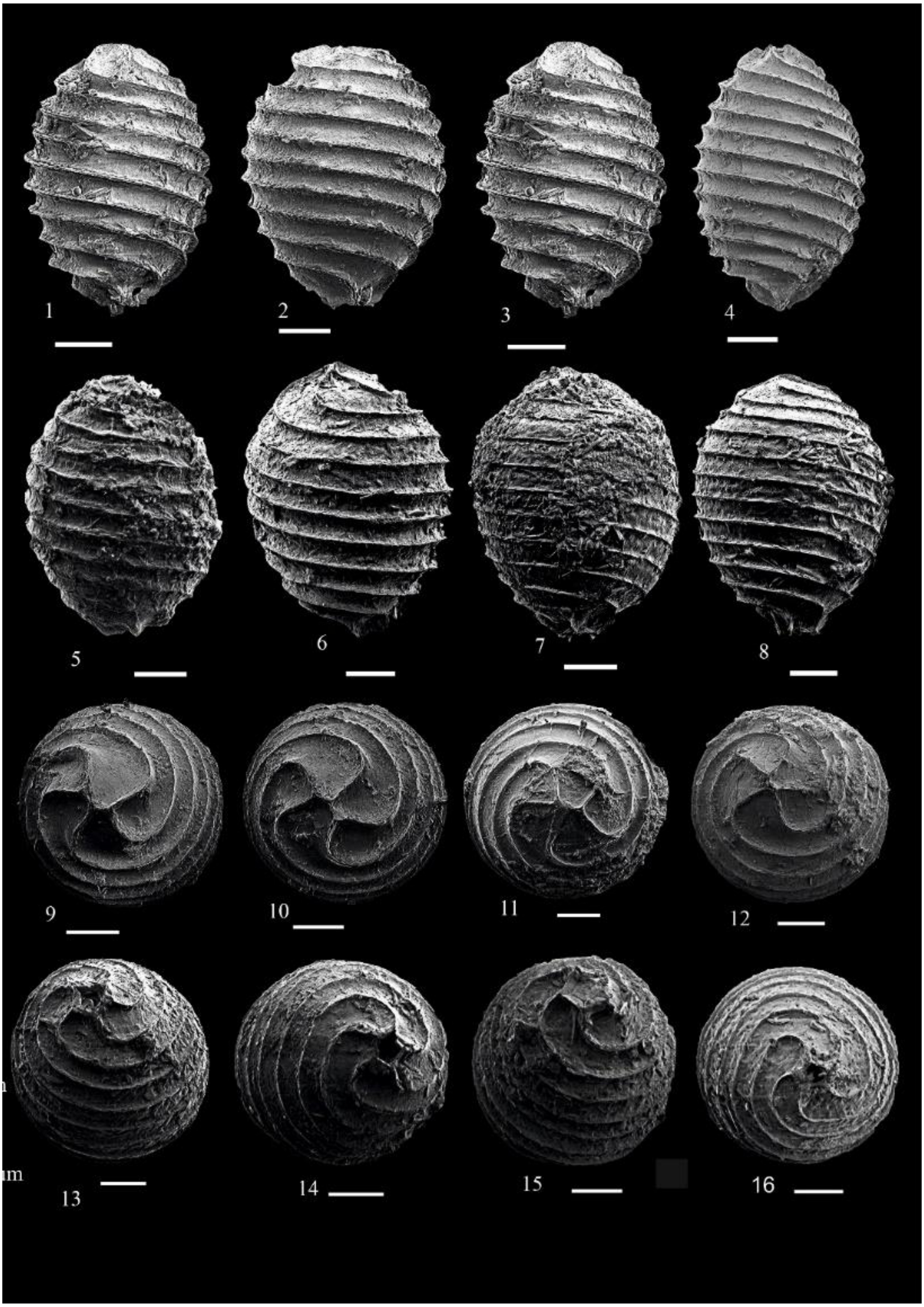

Plate VII: Gyrogonites (BSIP 41936/UB/NTC/137-152) of living *Chara vulgaris* from Sahastradhara, Doon Valley; 1-8 lateral views of BSIP 41936/UB/NTC/137-144; 9-12 apical views of BSIP 41936/UB/NTC/145-148; 13-16 basal views of BSIP 41936/UB/NTC/149-152. Scale bar = 100µm.

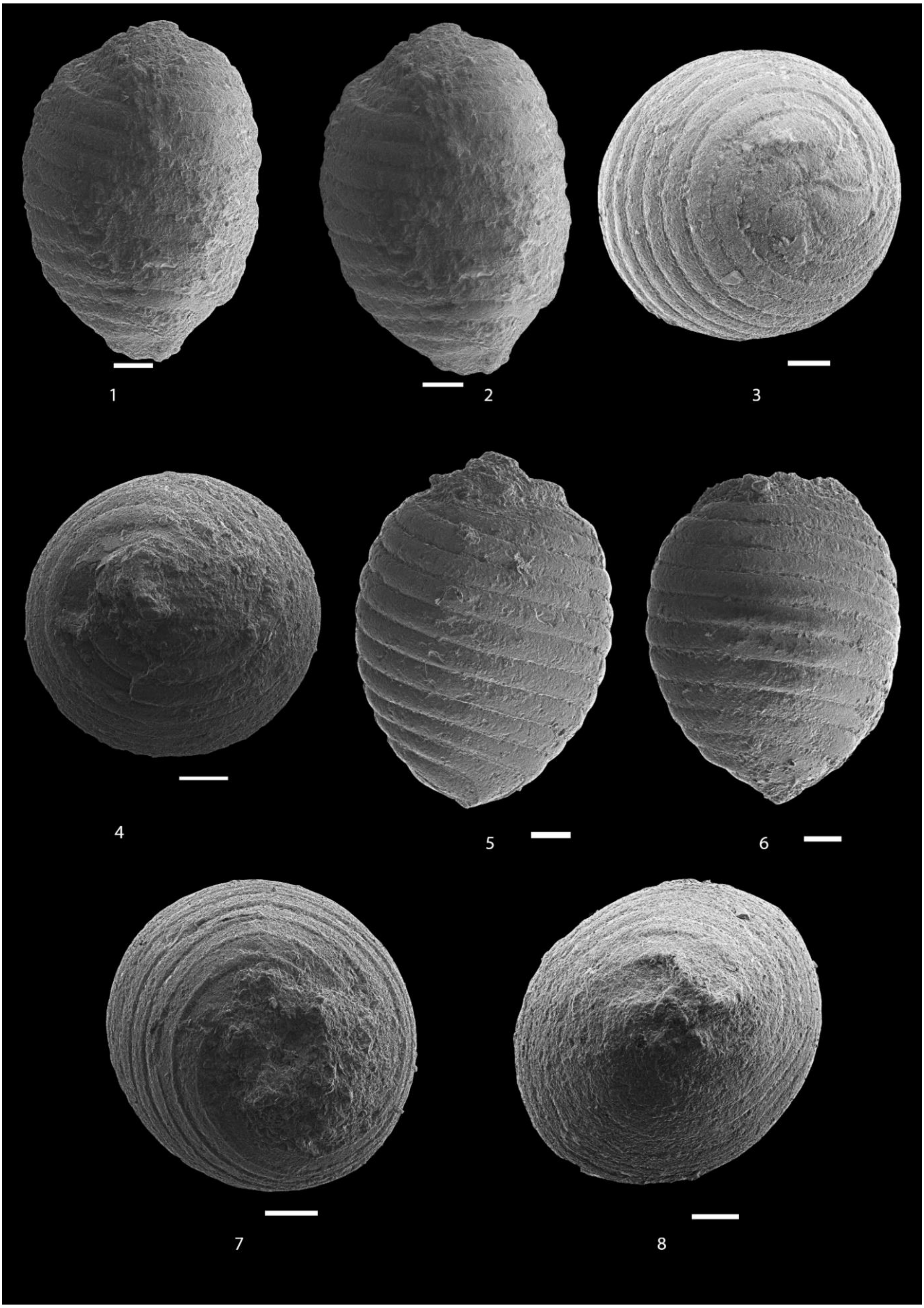

PLATE VIII: 1-4, *Chara aspera*: (BSIP41931/UB/NTC/103/1-8 1,2,5,6, lateral view; 3,4 apical view;7,8; basal view, Scale bar = 100µm.

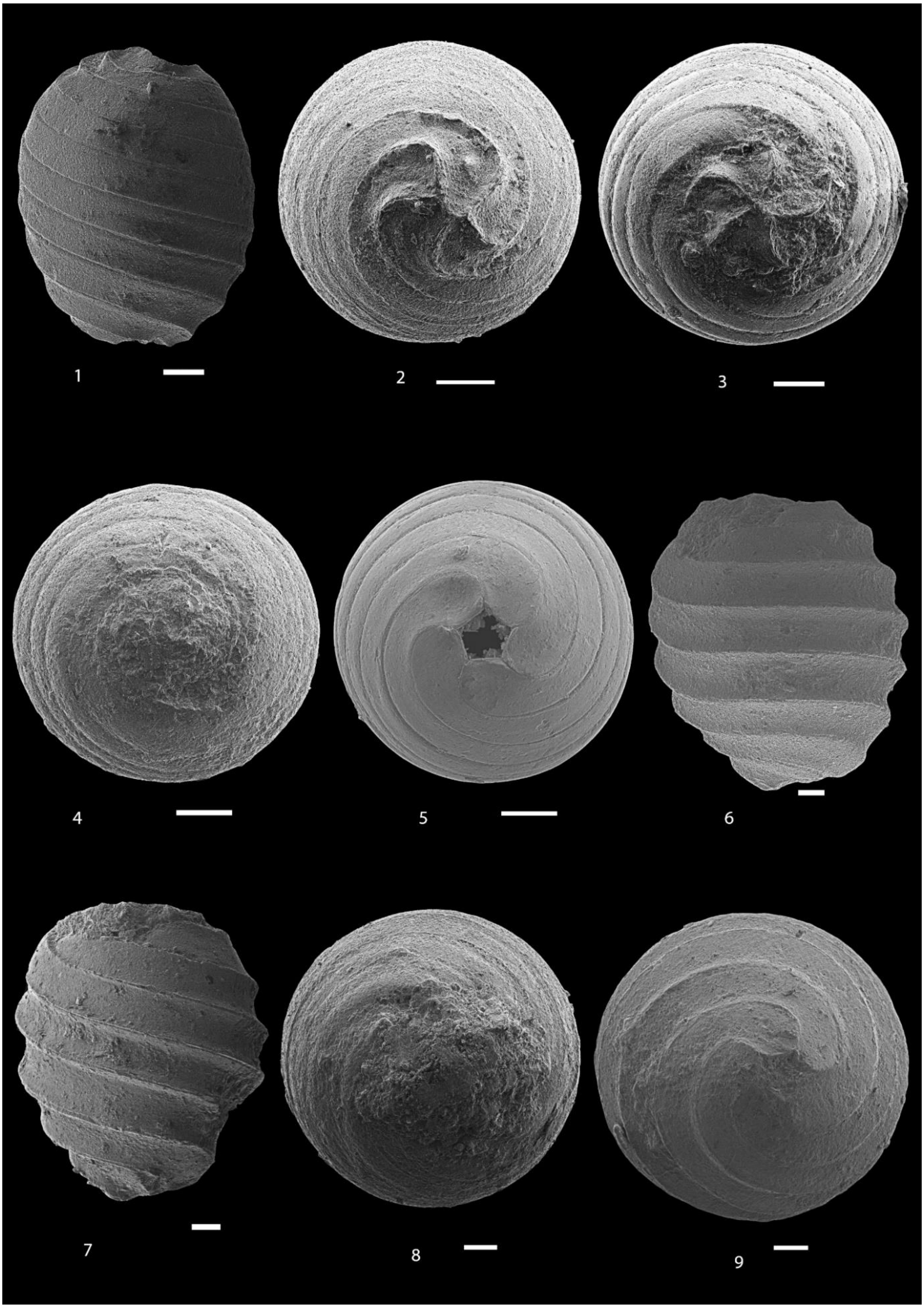

PLATE IX: *Lychnothamnus breviotus*: (BSIP41932/UB/NTC/118/1-5) 1, lateral view, 2-3, apical view, 4-5, basal view; *Lychnothamnus* sp. (BSIP41932/UB/NTC/121/6-9), 6-7, lateral view, 8, apical view, 9, basal view. Scale bar = 100µm.

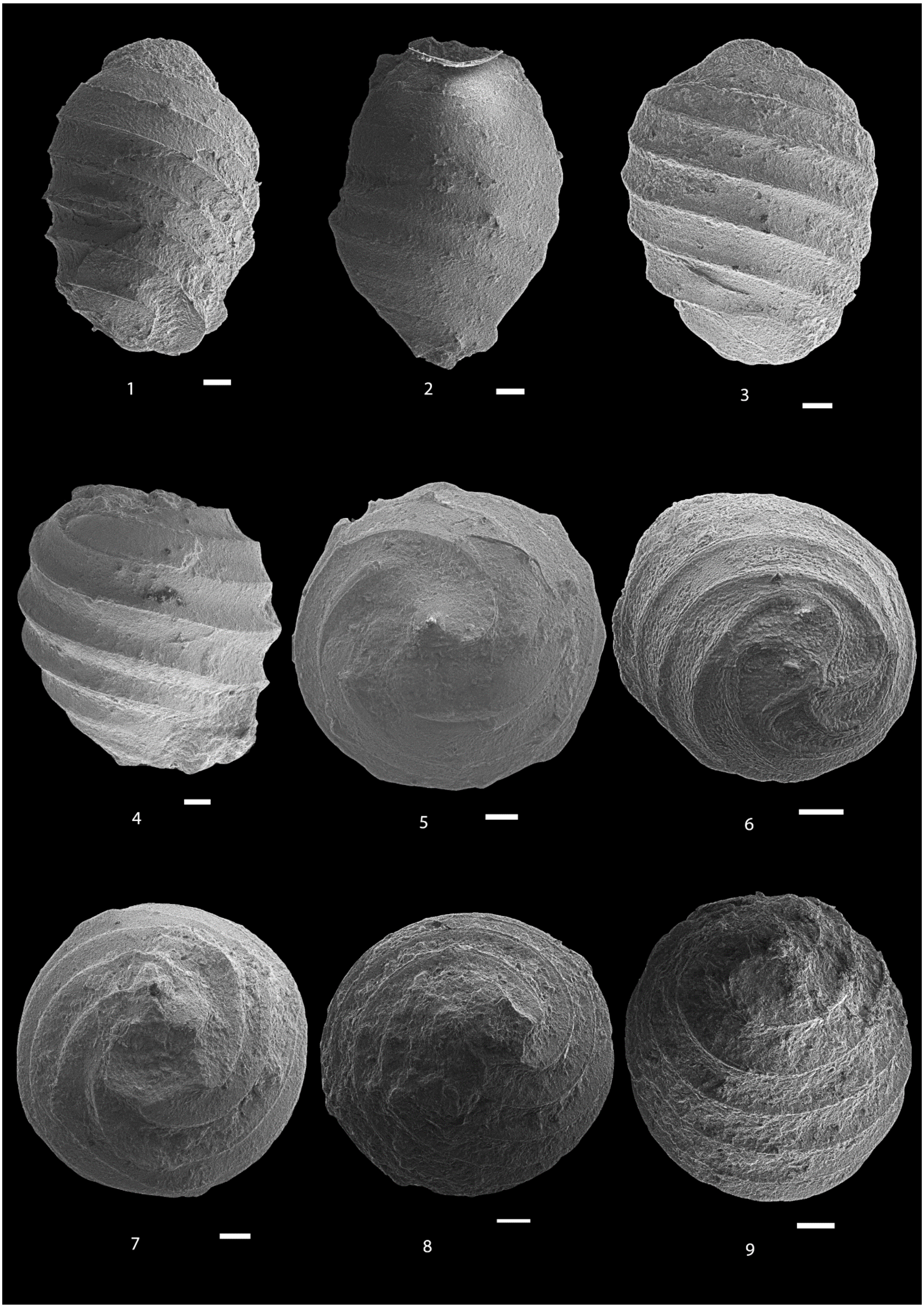

PLATE X:1-9, *Lychnothamnus* sp (BSIP41932/UB/NTC/121/1-9) :1-4, lateral view, 5-6, apical view, 7-9, basal view. Scale bar=100µm.

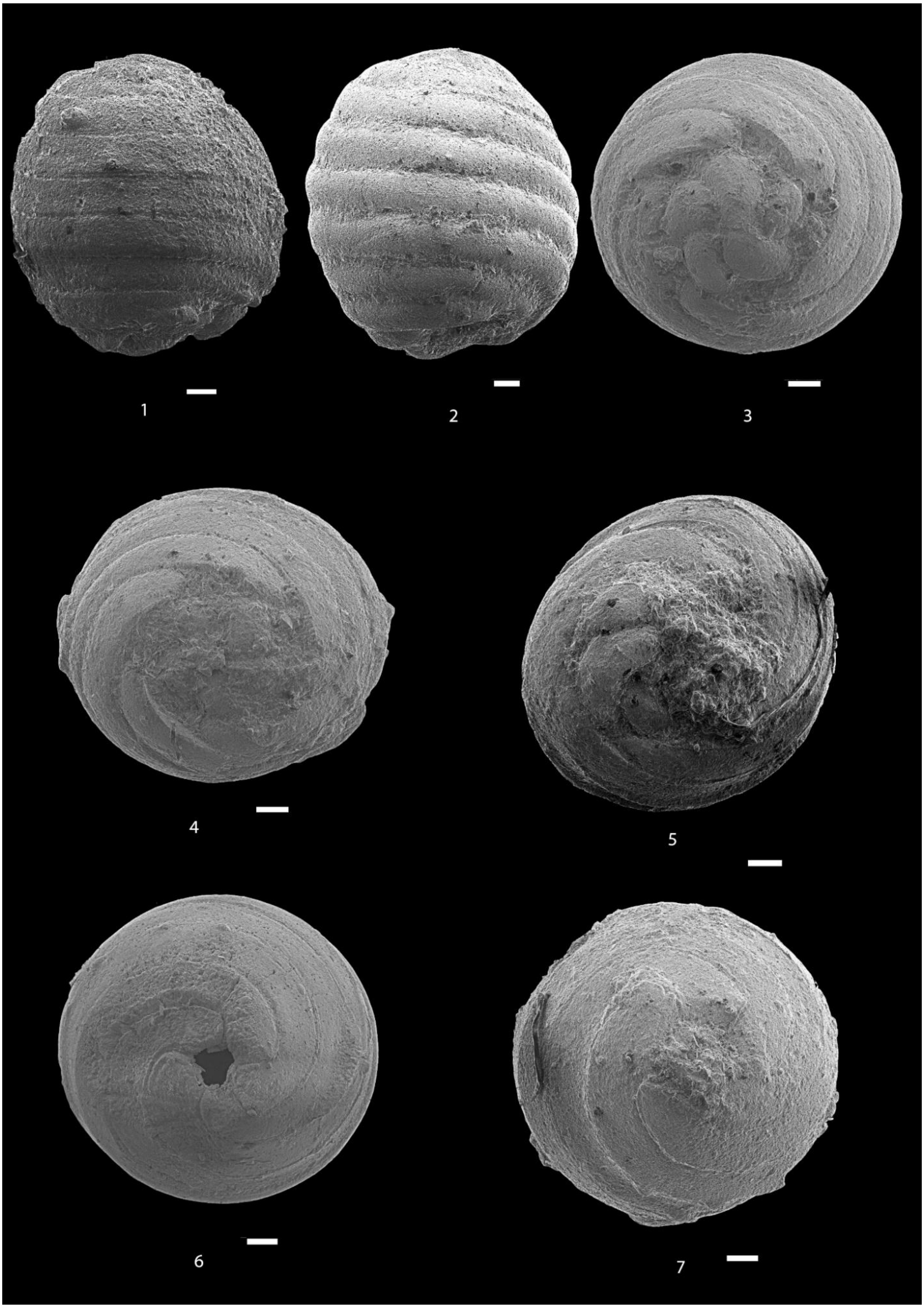

PLATE XI: 1-7, Nitellopsis (Tectochara) megarensis: (BSIP41935/UB/NTC/130/1-7); 1-2, lateral view, 3-5 apical view, 6-7, basal view. Scale bar = 100µm.

4.10. CONCLUDING REMARKS

The proven utility of gyrogonite features in characterizing extant charophyte species links them to fossil charophytes whose study is exclusively based on gyrogonite morphology (e.g. Garcia and Chivas, 2006). Comparative studies of gyrogonites of extant and fossil charophytes of Soulié-Märsche amongst authors led Bhatia et al. (1998) to record *Chara vulgaris* from the Karewa Group, Kashmir Valley. This record suggested regional geological antiquity of the extant charophyte species. The presently recorded gyrogonites from living plants from Sahastradhara area of Doon Valley, Uttarakhand are attributed to *Chara vulgaris* on the basis of their distinctive morphological parameters. The study adds significantly to our knowledge of the species by identifying their diagnostic combination of features. Further, this record of *C. vulgaris* in Sahastradhara serves as a current analogue to its reported fossil occurrence in the Karewa deposits of Kashmir Valley (Bhatia et al. 1998). Published records, exclusively based on their vegetative parts but without gyrogonite details (e.g. Saber et al. 2018), reveal that *Chara vulgaris* is a cosmopolitan living taxon and is also known from the Indian shield region, Bangladesh, and Tibet (Fan et al. 1995). Incidentally, the utility of the recorded Sahastradhara species, *Chara vulgaris*, includes its potential application in phytoremediation for treating toxic effluents (Mahajan et al. 2019, Fereshteh et al. 2007), and in antibacterial, mosquito repelling, and pesticide (Zhang et al. 2010; Snehalatha and Rao, 2017), and nitrogen fixation, soil fertility maintaining and enhancing potential by recycling and immobilizing the nutrients (Ariosa et al. 2004).

Chapter 5 : DISCUSSION

This chapter deals with the paleobiological issues and geological inferences as part of the stated objectives of this dissertation. Here it is appropriate to make a distinction between ‘Paleobiology’ and ‘Paleontology’ since the two terms are often used interchangeably with fossils as common objects of study, although they are not synonyms (e.g., Lazarus, 2014). While Paleobiology focusses predominantly on biological aspects of an extinct organism based on fossils, such as origin, evolution and stucture, Paleontology (also spelled Palaeontology or Palæontology) is concerned dominantly with aspects such as biostratigraphy, correlation, reconstruction of the past environments and other geological objectives.

5.1. Paleobiological aspects

For a better appreciation of the fossil charophyte flora described in this dissertation, this section includes a brief overview of some selected aspects of charophytes that have attracted considerable attention in the past. It is widely held that algal ancestors of land plants are charophytes. In a review of the fossil record and evolution of freshwater plants Martin-Closas (2003) mentioned that calcified fructifications of Silurian charophytes say around 425 Ma are the oldest recorded fossils of land plant ancestors.

Charophytes are known to have kept pace with continuously changing environments throughout the Neogene, particularly since the Mid-Miocene Climatic Optimum (MMCO) which is Earth's latest prolonged warming event recorded in mid- to high-latitude continents besides the deep oceans (Song et al. 2018). Charophytes are known from all continents including Antarctica where a specimen of *Nitella* sp. was collected by T.E. Berg in 1964 at Marble Point, which is close to the McMurdo station (Schubert, et al. 2018); It is also remarkable that the entire evolutionary history of the Charophyta since its deep beginning over 400 million years ago is closely tied to environmental changes including nonmarine mass extinction events rather than marine mass extinction events on earth (e.g. Vicente et al. 2019, Lucas, 2018, 2021 and references therein).

5.1.1. Change in gyrogonite asymmetry from dextral to sinistral

Gyrogonites, which exclusively represent the charophytes in the fossil record, offer an instance of biological chirality or handedness and show a phylogenetic transformation from dextral to sinistral, i.e. from one way of asymmetry to the opposite way (Figure 5-1).

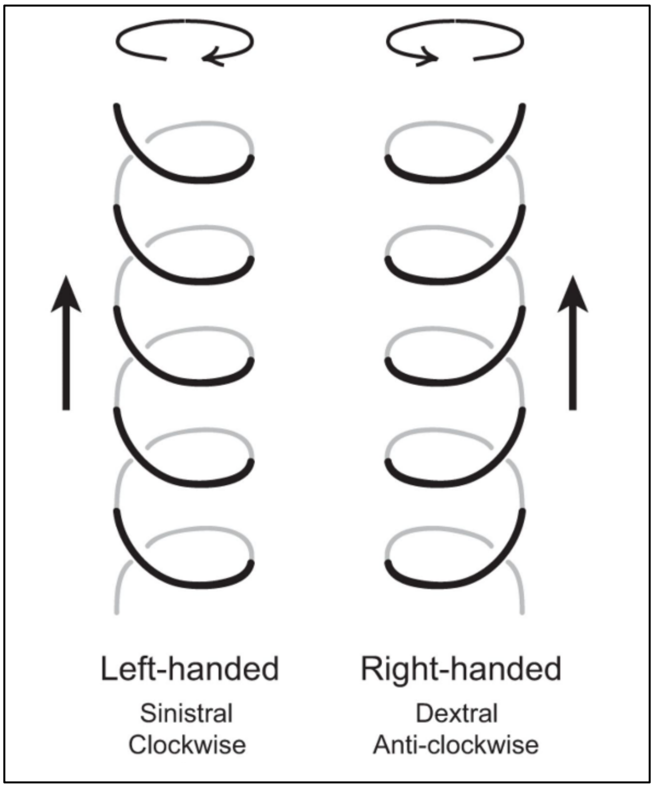

Figure 5-1 Sinistral and dextral coiling.

The change in handedness began during the Palaeozoic and, as observed in the charophyte fossil record, it occurred in several steps. In the initial phase of charophyte evolution since their origin, only dextral gyrogonites are known from Late Silurian to Middle Devonian global microfossil records. Sinistral gyrogonites, characterizing all the extant charophytes, began with only one species at a locality yielding Devonian microfossils. Fossil records reveal that the number of species with sinistrally coiled gyrogonites multiplied from Carboniferous period. Sinistrally coiled gyrogonites became generally dominant in the Permian and only a single species with dextral gyrogonites has been recorded from the Late Permian. For reasons which remain unknown, the Permian/Triassic (P/T) mass extinction wiped out the dextrally coiled gyrogonites resulting in their absence from global microfossil assemblages from the Triassic onwards(Figure5-2).

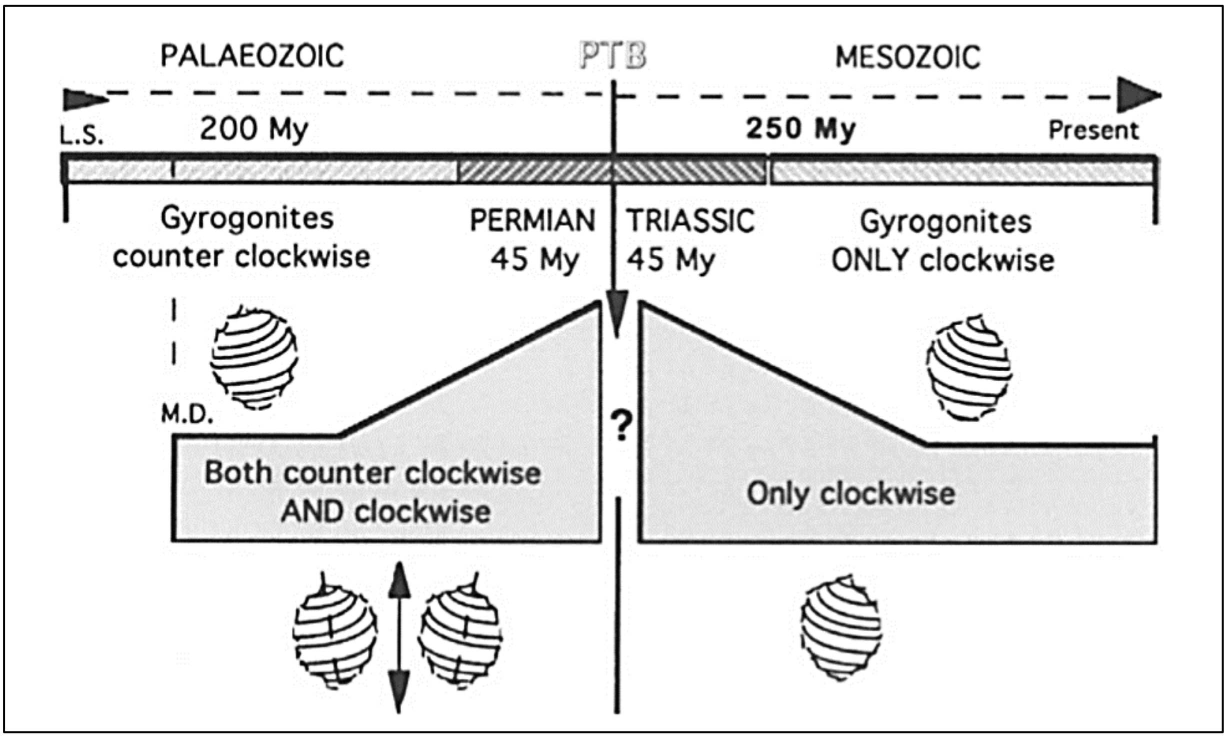

Figure 5-2 Elimination of clockwise (dextral) chirality in gyrogonites by the end of Palaeozoic (after Soulié-Märsche, 2004*)*.

Thus, the sinistrally coiled gyrogonites represented the only asymmetry that survived the P/T mass extinction event around 250 million years ago. This change in chirality observed in the evolutionary history of charophytes presents a major question which needs to be addressed using a multidisciplinary approach so that the parameters and mechanism causing extinction of dextral forms and the continuation of sinistral forms up to now are understood. This issue is discussed in detail in two edited volumes on Advances in Biochirality (Soulié-Märsche, 1999, 2004).

5.1.2. Dispersal mechanism

In the Indian context, the Neogene charophyte dispersal is an interesting aspect that needs to be seen in the context of the intensifying south Asian monsoon around Miocene (Gupta et al. 2015) and the development of inland water bodies. Passive dispersal of gyrogonites as plant seeds led to the spread of charophytes in to these water bodies. The zoochory of gyrogonites by migratory birds and immigrating cyprinid fishes presumably played a significant role role in this dispersal. Passive dispersal by migratory birds is by eating, carrying and egesting seeds (endozoochory) or less likely by carrying seeds attached to their plumage or body (epizoochory) (van Leeuwen et al. 2020). Occurrences of fossils of migratory birds further corroborates passive dispersal of gyrogonites from their native or stopover waterbodies of these flying visitors to populate non-marine water bodies in the Indian subcontinent (Stidham et al. 2014 and references therein).

5.1.3. Charophytes as permanent pioneers and ecosystem engineers: paleobiological perspectives

Charophytes, inhabiting freshwater or brackish waterbodies rather than open marine realm, are known to occur in almost all varieties of standing and sluggish waters (Martin et al. 2003). Some of the charophytes (e.g. *Chara globularis* Thuill, 1799) are very common but many are of limited spatial distribution. Charophytes are usually the first macrophytes to appear in newly formed ponds and lakes, where they are commonly referred to as “permanent pioneers” (Krause and Walter, 1985). They are also termed as an ancient group of permanent pioneers and ecosystem engineers. Owing to different life strategies, charophytes comprise both extreme R-strategists (“permanent pioneers”) and extreme K-strategists with a strong impact on the whole ecosystem (“ecosystem engineers”) (Schubert et al. 2018). Besides academic interests, current trends in ecological research often focus on applied purposes such as lake restoration, bioremediation and bioindication of water quality and water regime.

5.1.4. Ecological factors influencing/limiting the distribution of Charophytes

Of the various factors that influence the geographical distribution of charophytes, salinity is one of the most important controls. The distribution of species varies from oligohaline water, where there is very low salinity, to hypersaline waters. Also, there are cosmopolitan species like *Chara contraria,* which can tolerate changes in salinity (Adriana Garcia, 1993).

Temperature is another important factor, and the temperature changes can be due to altitude, latitude or the depth of the water body. Some species prefer temperate climates and some are found in circumtropical zones. Temperature in the water bodies is controlled by the movements of the water, deep waters have lower temperatures as compared to shallow and littoral waters. So some taxa are found in warmer and shallow waters and some are found in deep and colder waters. Some taxa are found to live above 4000 m (Adriana Garcia, 1993), but then there are certain cosmopolitan species like *Chara globularis* and *Chara contraria*, that can withstand all ranges of depths, latitudes and altitudes, they can even tolerate freezing temperatures.

Energy can also be a limiting factor for the growth of Charophytes, water energy in the form of turbulence caused by winds or by ships etc. can curb the growth of Charophytes. Charophytes prefer quiet waters or with light unidirectional waves. Species like *C. vulgaris, C. contraria*, *C. globularis* which calcify are only found in alkaline waters, the Charas and the Nitellas that do not calcify e.g., *Chara braunii* and *Nitella opaca* can withstand slightly acidic waters. Charophytes can grow over gravel, slimy clays, with organic matter and with calcareous remains, but they usually prefer fine sediments to grow upon. Charophytes are either calciphilic i.e., they form gyrogonites by calcification or are calciphobes, that do not form gyrogonites. But there are certain cosmopolitan taxa eg. *Chara contraria, C. globularis, C. vulgaris,* that are flexible enough to live and survive in all continents except Antarctica (Garcia,1993). However, recent work has shown that the notion that extant forms are found everywhere except in Antarctica (Wood and Imahori, 1965) stands modified in view of record of charophyte taxon from Antarctica too (Schubert et al. 2018). Charophytes can be found in extreme cold regions in Arctic and in Chilean Andes (Langangen, 2000; Schubert et.al, 2014), and are known from all types of non-marine habitats ranging from fresh water to hypersaline waters comprising streams, lakes, ponds, lagoons, and newly created artificial ponds (Rodrigo et.al. 2015). Charophytes flourish well submerged in water up to the depths of around 18 meters in quiet, clear water rich in calcium and little oxygen, and oligotrophic (alkalinity $CaCO^3$ 0-10 mg/l and pH 6-7, Ratcliff, 1977) conditions; these are sensitive to eutrophication (Stross, 1979; Spence, 1982; Blindow, 1992) leading them to be amongst rare and endangered species (Auderset Joye and Rey-Boissezon, 2014). Because of this character, charophyte species tend to differ from each other, depending upon the water chemistry, habitat size, ecosystem status in context of eutrophication, and the ecological status. Further, charophyte species are sensitive to the light accimilation capabilities (Rubio et al. 2015) which determines whether they are found in small ponds or large lakes (Rey-Boissenzon and Auderset Joye, 2014). Garcia and Chivas (2006) stated that Charophytes can tolerate salinities up to 58g/l. There are exceptions like the genus *Lamprothamnium* Groves, which can survive in highly saline conditions, although it completes its life cycle in brackish water (DeDeckker and Geddles, 1980). This shows that the charophytes might have existed in the fully marine environments in the early Paleozoic, but there is no such evidence at present to confirm it. They are calcareous in nature and are rough in touch, because of the calcium deposition on their body, which is the reason why they are also called “Stoneworts” or “Brittleworts”.

Extant charophytes thrive in hard waters and this is of use in inferring depositional water chemistry in studies of fossil gyrogonite. Further, the widely known fact that *Chara* species prefer Ca-rich water for unhindered growth is explained by elaborating interaction between Ca^{2+} with pectin constituting cell walls of green plants including charophytes (Proseus and Boyer, 2012).

5.1.5. Phenotypic Plasticity in charophytes

Phenotypic plasticity is an oft repeated phrase in contemporary charophyte literature with 'phenotypic responsiveness', 'flexibility', as synonyms. It is best understood as the capability of a taxon to change in response to inputs from the environment. This key mechanism assumes importance as it has often led to indistinctness in species description in charophytes, the benthic algae with an intricate morphology and high phenotypic plasticity (Schneider et al. 2016). Phenotype is the set of observable characteristics of an individual taxon resulting from the interaction of the environment with its genotype. The observable characteristics include the taxon's physical form and structure or morphology, developmental processes, biochemical and physiological properties, and behaviour and the behaviour's products. Thus, phenotypic plasticity allows individuals to respond to change in climate within their lifetime and thus is a key mechanism with which organisms can cope with a changing climate.

5.2. Paleoenvironmental constraints from Neogene charophyte assemblage from Mohand

The charophytes described in the present work were found associated with gastropods, ostracods, fish remains, and small mammals which too have been considered here for constraining the the environment of deposition of the fossiliferous horizons. The gastropods include a planorbid (*Gyraulus* sp.), characterised by a planispiral shell with 3-4 whorls with intervening deep sutures, which is known from Neogene Churia group of Nepal (Gurung et al. 1997). Another Mohand gastropod species referable to a cerithioidean *Plotia* cf. *P. scabra* with turreted spire of up to 7 whorls with shallow sutures has been recorded previously (Bhandari et al. 2014). Ostracod carapaces are identified as *Stenocypris* sp. (family Candonidae) based on diagnostic characters including rounded anterior and posterior margins, left valve larger than right valve with complete overlap, and the greatest height is more or less in the middle. Identifiable fish remains include the teeth of common cyprinids.

The abundance of *C. globularis* indicates multiple types of water bodies with their optimum occurrence in meso-eutrophic and eutrophic waters, on the shallow, organic and organic-mineral habitats (Pelechaty et al. 2004). The ostracod *Stenocypris* is usually found in warm, shallow water ponds and lakes (Bhatia, 1996), thereby corroborating the shallow and warm environment deduced from charophytes. These microfossils (charophytes, gastropods, ostracods from Mohand Rao locality suggest a paleoenvironmental setting of a shallow, warm, low energy, semi-permanent to permanent lake or pond. Furthermore, the Mohand charophyte assemblage comprises mixed- sized gyrogonites referred to various taxa and species on the basis of their morphological features. However, numerous small-sized (<500 μm) gyrogonite-producing charophyte plants are known to inhabit seasonal/temporary shallow ponds. Conversely, medium to large-sized (500-750 and >750 μm, respectively) gyrogonites come in adequate numbers from charophyte plants living in permanent, clear water bodies of appropriate photic depth. Therefore, the mixed assemblage of gyrogonites from Mohand compring both small and large forms, suggests that shallow and temporary/seasonal aquatic habitats co-occurred with permanent aquatic habitats of adequate photic depth in the Siwalik foreland basin almost all along the southern flank of the evolving Himalayan terrain. However, this paleoenvironmental setting is somewhat inconsistent with the occurrence of *Nitellopsis* (*Tectochara*) *merianii* in the present assemblage, since the single living representative of this genus (*N. 92harac*) thrives in permanent, cold, alkaline waters at a depth range of 4-11 m (Krause, 1985; Soulié-Märsche et al. 2002). The presence of *N. merianii* in the Mohand assemblage is attributed to migratory birds which feed on this gyrogonite (Guiral Pellegrin, 1981).

The scenario suggested by the Mohand charophytes is apparently at variance with that for the Ganga Basin where permanent, clear waterbodies with adequate photic depth are evident from the medium to large-sized gyrogonites (Bhatia, 2006), from Lower Siwalik Subgroup of Tanakpur (Lakhanpal et al. 1974), and from the type section of Upper Dharmsala Formation at Dharmsala, Himachal Pradesh (Bhandari, 2009). The Mohand charophyte assemblage is more akin to the intertrappean gyrogonites which are characteristically small to large-sized (Srinivasan et al. 1994) suggest that the Deccan basalt terrain harbored conducive clearwater bodies that were shallow and temporary to permanent with adequate water volume. Pertinently, exclusively small-sized charophytes from India are from Jurassic horizons of Kota Formation indicating prevalence of temporary shallow, clear water ponds in the basin of sedimentation (Feist et al. 1991).

As presently known, the Mohand Middle Siwalik fauna (~9-5 Ma) comprises small mammals (Rodentia), fishes and invertebrates (gastropods, ostracods), whereas floral remains include angiospermous pollen grains, pteridophytic spores along with charophytes. Based on the recovered microfossil assemblage, the general paleoenvironmental scenario of the Mohand region can be visualised as a shallow, warm, low energy, semi-permanent to permanent lake or pond.

The charophyte assemblage (~9 Ma) described in this dissertation adds significantly to the fossil biota from this reasonably well dated section (Tiwari and Bhandari, 2014). The assemblage comprises *Chara aspera, Chara globularis, Chara rantzieni, Chara* sp., *Hornichara maslovi*, *Lychnothamnus breviotus, Lychnothamnus barbatus*, *Lychnothamnus sp. Nitellopsis (Nitellopsis) megarensis, Nitellopsis (Tectochara) merianii, Nitellopsis (Tectochara) huangii, Sphaerochara tewarii,* and *Lamprothamnium papulosum*.

The composition and relative abundance of the Mohand charophyte assemblage is depicted in Figure 5-3.

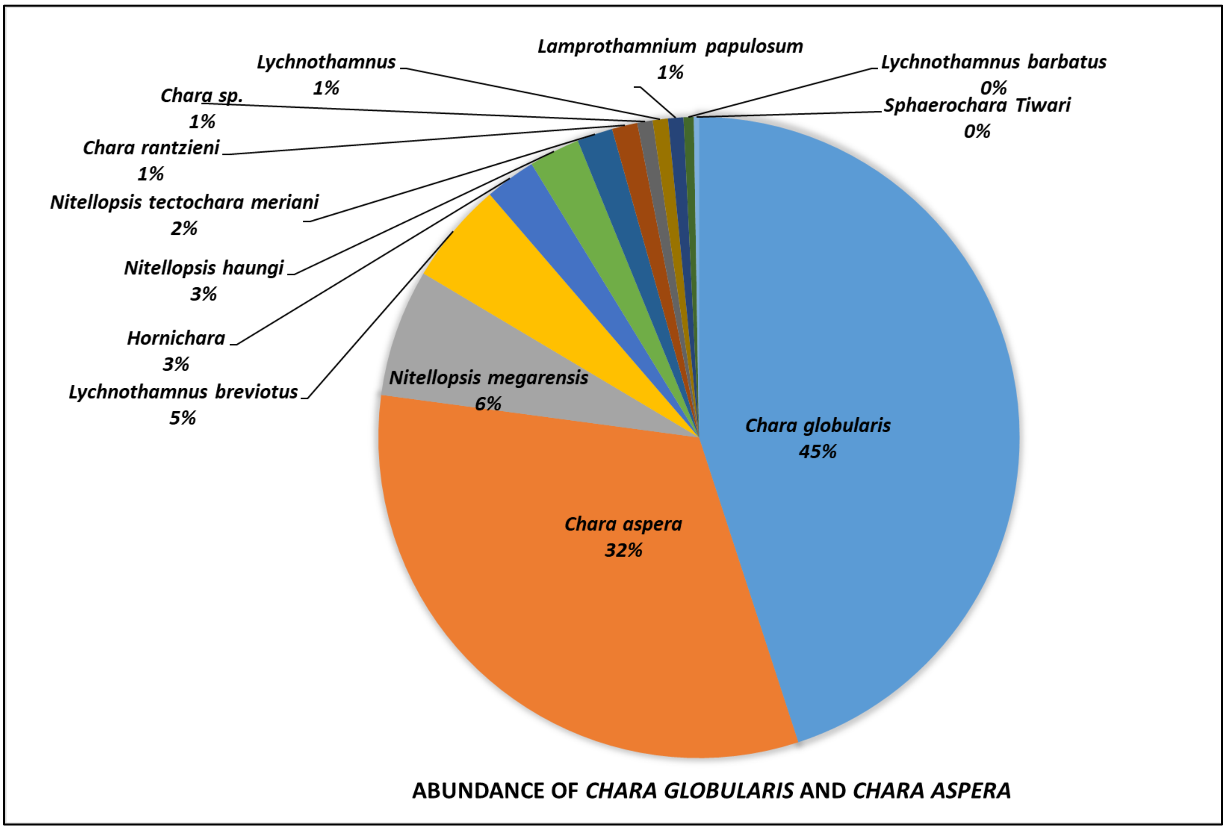

Figure 5-3 Composition and relative abundance of Mohand charophyte taxa .

The paleoecological implications of the representative charophyte taxa from Mohand can only be approximated by comparing them with their extant taxa. *C. globularis*, which occurs abundantly in the present collection, is known for its relatively wide ecological tolerance. In different kinds of water bodies, *C. globularis* has its optimum occurrence in meso-eutrophic and eutrophic waters, on the shallow, organic and organic-mineral habitats (Pelechaty et al. 2004). Today, *C. globularis* is found in waters up to a depth of 4m with particular preference to quiet bodies of water though it has been found in swiftly flowing waters. However, in the swiftly flowing water, the species, though well-developed vegetatively, was completely sterile (Tindall, 1966). *C. globularis* has been found to be particularly closely associated with sandy-bottomed areas of cool water bodies. It has been noticed that *Chara globularis* plants are usually seen in association with various algae, vascular plants, and with one or more of the *Chara* species namely, charophytes, namely, *C. braunii, C. contraria, C. vulgaris,* etc. The abundance and dispersal of *Chara globularis* vary greatly in the various habitats.

Chara aspera occurs abundantly in calcareous waters in the present-day. Its abundance is also attributed to the capability of producing a large number of oospores, which remain fertile for a long period of time (Auderset Joye & Boissezon, 2015). The ostracod *Stenocypris* is usually found in warm, shallow water ponds and lakes (Bhatia, 1996), thereby corroborating the shallow and warm environment deduced from charophytes.

The paleoecology of *Nitellopsis (Nitellopsis) megarensis*, *Nitellopsis (Tectochara) merianii.* And *Nitellopsis* (*Tectochara*) *huangii* can be cautiously proposed through comparison with the only living species of *Nitellopsis, N. obtusa*. This species needs permanent cold water of about 4-12 m depth for best growth. The extant *Nitellopsis* species occurs in northern Eurasian fresh and nonmarine waterbodies in well as in high-altitude lakes at about 1500 m in Kashmir and Japan (Kasaki 1962, Soulié-Märsche et al. 1997). Assuming that the overall ecologic requirements of *Nitellopsis* have persisted since the Miocene, the paleoenvironment constraint provided by the Mohand *Nitellopsis* is inconsistent with the tropical conditions suggested by the Middle and Upper Siwalik mammalian fauna (Flynn et al. 2016: Patnaik, 2016).). The presence of *N. merianii* in the Mohand assemblage may possibly be due to migratory birds which feed on this gyrogonite, a mode of dispersal similar to waterfowl from Laguna de Gallocanta, whose stomach content was found to have 95% of charophyte material (Guiral Pellegrin, 1981).

Another important paleoecological constraint comes from the mixed-sized fossil gyrogonites from Mohand. The assorted assemblage of fossil gyrogonites from Mohand area ranges in size from less than 0.5 mm to over one millimeter in size. Small sized gyrogonites

(<500 μm) are known to be produced by a few charophyte species in large numbers in non-permanent or seasonal ponds, whereas medium-sized (500-750 μm), to large-sized (>750 μm) gyrogonites are characteristic to permanent clear-water charophyte habitats.

Summing up, the Mohand fossil gyrogonites suggest the presence of permanent and temporary/seasonal ponds in the basin in close vicinity to each other. This inference is particularly relevant in the context of observations made by Vicente et al. (2016) and Böhme et al. (2021) who suggested that small-sized gyrogonites found in high numbers in shallow and temporary ponds plausibly reflect an opportunistic strategy of charophyte taxa. Field observations while sampling living *Chara vulgaris* with small gyrogonites from a shallow pond with thin veneer of sediment on a rocky substrate with in-and out-flow of sluggishly flowing clear water in Sahastradhara locality, lend support to the idea of opportunistic strategy of charophytes.

5.3. Paleoenvironments of the Ladakh Molasse deposit

The Ladakakh Molasse has long been considered to be a fluvio-lacustrine deposit (Brookfield and Andrews-Speed 1984; Garzanti and van Haver 1988). Based on fossil vertebrates including land mammals (Nanda and Sahni 1990) and cyprinid fishes (Parmar et al. 2013), a fluvio-lacustrine environment of deposition was inferred for the molassic sections around Kargil in the western part of the Indus Suture Zone and around Taruche in the central part of the suture zone. Similar cyprinid fishes have also been described from the Nyoma section in eastern Ladakh (Sahni et al. 1984). A non-marine depositional environment was also suggested by Bajpai et al. (2004) based on cypridacean freshwater ostracods recovered from the same locality as one of the charophyte-yielding sections (i.e. Taruche) described herein. Freshwater molluscs including gastropods such as *Melania* and *Viviparus*, unionid bivalves and fossil palms from the molassic deposits exposed in the various localities also suggest a fluvial environment (Sahni and Bhatnagar, 1962; Tewari and Dixit, 1971; Mehrotra et al. 2007, 2014).

The composition and relative abundance of the charophyte assemblage from Ladakh molasse is indicative. The presence of *Lychnothamnus barbatus* is particularly interesting from the paleoecological standpoint its living representatives in Europe have a typical depth range of 2 to 8 m, and it forms dense meadows of up to 1m high plants (Krause 1986). This species suggests cold and oligotrophic freshwaters usually associated to phreatic origin (Krause, 1997; Soulié-Märsche & Martín-Closas, 2003). Studies on Miocene lacustrine deposits of Catalonia (Spain) demonstrate that the fossil *L. barbatus* had similar ecological requirements as the living representative of this species studied by botanists (Martín-Closas *et al.* 2006).

5.4. Environment of extant gyrogonites of *Chara vulgaris* recovered from Sahastradhara stream, Dehradun

Calciphile charophytes represented in Neogene fossil record through their gyrogonites are a potential source of information on pH range of the depositional environment of the fossil bearing horizon. Such inferences are based on data on the living analogues of charophytes. Interaction of hydroxyl ions added through the hydrolysis of bicarbonate determines the pH value of spring waters (Sharma, 1986).

Published records of extant charophytes are based on their vegetative parts or thalli. Little attention has been paid so far to their calcified fructifications or gyrogonites (Saber et al. 2018). Chara vulgaris is a common and cosmopolitan taxon living in all continents, especially in the northern hemisphere (Corillion 1972). In India, Fan et al. (1995) reported living meadows of C. vulgaris in ponds at the Indian shield region (Bangladesh and Tibet). According to Ghetti et al. (2002) this species probably originated in the Mediterranean area during the Late Miocene and expanded worldwide during the Quaternary. Among living species, gyrogonites of *C. vulgaris* display the widest intraspecific polymorphism. This intraspecific gyrogonite polymorphism was described in detail by Soulié-Märsche (1989) and recently by Sanjuan et al. (2017). These authors concluded that the gyrogonite polymorphism of Chara vulgaris is related to environmental factors such as the light irradiance and water temperature. The morphometric parameters of the studied population from Sahastradhara are consistent with those from previous studies i.e. small to medium (472-601 μm) prolate gyrogonite, psilocharoid apex, and presence of 10-12 non-ornamented and concave spiral cells observed in lateral view oreover, gyrogonites of *Chara vulgaris* from Sahastradhara are morphologically comparable with their fossil counterparts from the late Pliocene-Early Pleistocene Hirpur Formation of the Karewa Group (Kashmir valley, NW Himalaya. The LPA and LED of the fossil specimens from Kashmir range between 500–575 μm and 300–400 μm, respectively (Bhatia et al. 1998). Published lateral views of the Karewa C. vulgaris reveals that the number of convolutions (CN) is 11. The estimated ISI and ANA of the fossil species are 166 and 44, respectively (Table 1). Closecomparison also reveals that the sphericity parameter or Isopolarity Index (ISI) of the fossil gyrogonite population from the Karewa group is similar to that of the here-studied living population. However, the asymmetry parameter or ANI (= 44) has a lower value than the ANI of the living gyrogonite population (ANI = 50). The comparison between living and fossil populations of C. vulgaris from the Kashmir valley indicates that this species already thrived in the lakes of India during the late Pliocene.

The pH of the Sahastradhara stream which yielded the specimens of *Chara vulgaris* is known to range between 7.2 and 8.1, i.e. slightly alkaline (Bharti, 2014). Here, the hardness and alkalinity are not to be used interchangeably as the hardness of water is due to presence of calcium and magnesium salts of bicarbonates, carbonates, sulphates and chlorides whereas alkalinity occurs due to dissolved bicarbonates. However, both are covariant as it has been recorded that there is positive relationship between hardness and alkalinity in Ganga waters of Rishikesh (Chopra and Patric, 1994).

Finally, this study also helps to document the wide distribution of *Chara vulgaris* in India through time (Fig. 4-6)

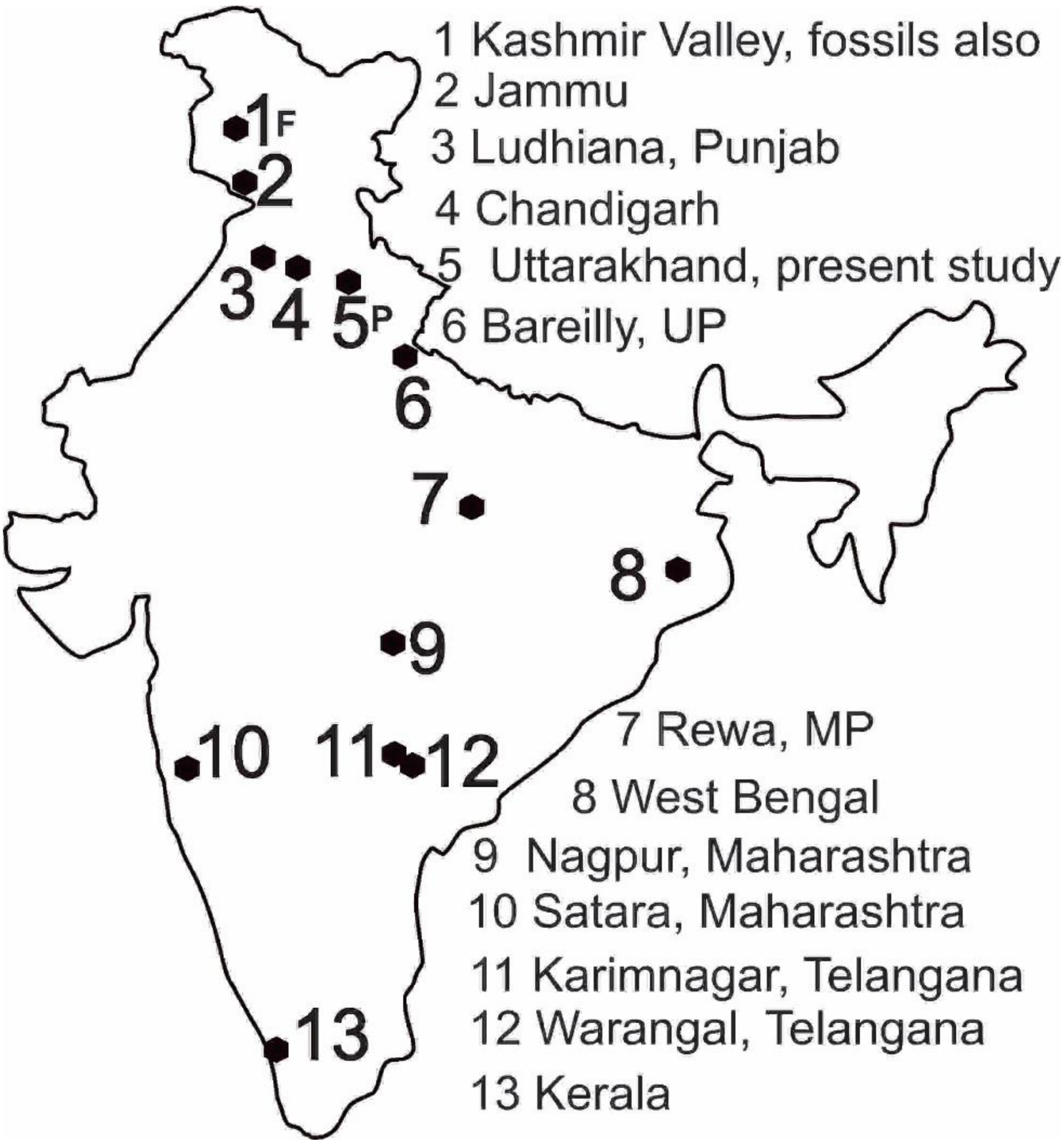

Figure 5-4 Dispersion graphic of the LED (gyrogonite height) and LPA (gyrogonite width) parameters of the studied Chara vulgaris gyrogonites from Sahastradhara (BSIP 41936/UB/NTC/137-188). See LED and LPA parameters (mean average) of the gyrogonite population of Chara vulgaris studied by Sanjuan et al. (2017: tab.1) extracted from cultivated plants under controlled light and temperature conditions. Rectangle represents the LED and LPA ranges of fossil gyrogonites from Karewa Group studied by Bhatia et al. (1998).

5.5. Biostratigraphic implications of Mohand and Ladakh charophytes

Biostratigraphic consideration of the recovered charophyte assemblages from the Mohand and Ladakh sections suggests that a majority of the species are long ranging and therefore not age-diagnostic. Two species in the Mohand assemblage are broadly consistent with the previously assigned age (~ 9.2 Ma) on the basis of rodents and paleomagnetic data (Tiwari and Bhan 2021). *Nitellopsis* (*Tectochara*) *merianii*, and *N*. (*T*.) *huangi*, which are somewhat uncommon species in the present collection, are well known from the Oligocene to Pliocene of Europe including southern Germany, Austria, Switzerland and France and in the Asian Miocene basins of Northern Thailand (Soulie Marsche *et al.* 1997). Originally, *N.* (*T.*) *merianii* was described from Oligocene/ Miocene of Switzerland (Horn af Rantzien, 1959). In India, *N.* (*T.*) *merianii* was first recorded from the Lower and Middle Siwalik (Chinji and Dhok Pathan Formations) by Bhatia and Mathur (1978). Subsequently, Bhatia (1999) extended the range of *N.* (*T.*) *merianii* to the Tatrot Formation of the Upper Siwalik. According to Bhatia (1999), the Chinji Formation (13.1-10.1Ma) shows the dominant occurrence of *N*. (*T*.) *huangi* and *N*. (*T*.) *merianii*. On the basis of fission track dating and magnetic polarity stratigraphy, the Tatrot-Pinjor boundary (2.5 Ma) is marked by the Last Appearance Datum (LAD) of *N.* (*T.*) *huangi* and *N.* (*T.*) *merianii*.

Lychnothamnus barbatus is also widely known from the Miocene of southern France (Soulié-Märsche 1989). The distribution of *Lychnothamnus barbatus* extends through the Pliocene up to recent times (Bhatia et al. 1998).

Chapter 6 : SUMMARY AND CONCLUSIONS

This dissertation primarily deals with a group of microfossils (i. e. charophytes) which remains one the neglected components of microfossils in the Indian context despite stimulating research opportunities that this group offers, especially on ancient non-marine ecosystems. This situation is in complete contrast to that in European and Asian sequences which continue to be extensively studied for their charophyte content. Published literature clearly shows that fossil Charophyta, their present and past dispersal, biostratigraphic utility, simple but poorly understood biological attributes of gyrogonites, environmental tolerance, sphenotypic plasticity, chirality, ecological services in non-marine aquatic realms, and their role as the ancestral stock for land plants, present a plethora of challenges for contemporary researchers. Hence, the documentation of extinct and extant charophytes presents ample scope to researchers to address a wide variety of questions.

Against this background, the main contributions emerging from this doctoral investigation are highlighted below:

6.1. Diversity and paleoecological significance of fossil Charophyta from Middle Siwalik Group of Mohand area, Dehradun

Using bulk screenwashing, a collection of charophyte gyrogonites was recovered from the Middle Siwalik strata of Mohand area near Dehradun. These microfossils, dated as early late Miocene (~9 Ma), are taxonomically fairly diverse (Tiwari and Bhan 2021). The collection comprises 12 species belonging to 7 genera: *Chara aspera*, *Chara globularis, Chara rantzieni, Chara* sp.*, Hornichara maslovi, Lychnothamnus breviotus, Nitellopsis megarensis, Nitellopsis* (*Tectochara*) *merianii, Nitellopsis* (*Tectochara*) *huangii, Sphaerochara tewarii, Lychnothamnus barbatus*, *Lychnothamnus* sp. And *Lamprothamnium papulosum*. Associated fossils include freshwater ostracods, gastropods and fishes. Palaeoecological contemplations of the recovered charophyte assemblage suggest a shallow, warm, low energy, semi-permanent to permanent lake or pond.

Chara aspera, represented by over 125 gyrogonites in the present collection, represents the dioecious form of the monoecious *Chara globularis* (Proctor 1980). Soulié-Märsche (1989) described it as a Quaternary lacustrine biomarker in North Africa. This taxon was also reported from the Quaternary marls of the Indo-Gangetic Plains (Bhatia and Singh 1989) and later also from the Upper Siwalik Tarot and Pinjor formations (Bhatia 1999).

Chara globularis, with more than 175 gyrogonites in the collection, is an extant and cosmopolitan species with ~ 20% variation in LPA, LED, and Lsp. Tewari and Sharma (1972a) previously described this species as *Chara indica,* while Bhatia and Mathur (1978) initially reported it as *Chara surjpurica.* Subsequently, Bhatia (1999) referred it to *Chara globularis*.

Hornichara maslovi is represented by more than 10 gyrogonites in the collection, and it is for the first time that the species is being recorded from the Middle Siwalik. Bhatia and Mathur (1978) described this species from the Upper Siwalik (Pliocene). Its range of variation, as noted in a limited number of gyrogonites, is 400-650 and 300-550 microns for LPA and LED, respectively.

Lychnothamnus breviotus, is represented by over 20 gyrogonites in the collection. *Lychnothamnus breviovatus* was first recorded from the Karewa deposits of Kashmir (Bhatia, 1985), and was subsequently also recorded from the Dhok Pathan (as rare) and Pinjor (as quite abundant) formations of the Siwalik Group (Bhatia, 1999). *L. breviovatus* was originally reported from the Late Oligocene and Neogene strata of Tarim Basin in the Xinjiang region of China (Lu and Luo, 1990). Compared to the type species *L. barbatus,* L. *breviovatus* is a smaller species and is ovoidal to nearly spheroidal. The record from the Mohand area extends the geographic range of L. *breviovatus*.

Lychnothamnus barbatus is the single extant species of the genus *Lychnothamnus*, which was earlier reported from some localities of Europe, Asia, Australia and more recently in North America also. This is a fresh water species; it has been reported from the Ganga plain in India by Bhatia (2006).

Also present in the collection is another species of *Lychnothamnus* whose affinities with any known species of *Lychnothamnus* cannot be currently ascertained due to insufficient number of specimens.

Sphaerochara tewarii, represented in the collection is by a single gyrogonite. This species was first described from the Middle Siwalik (Dhok Pathan Formation) of Himachal Pradesh by Bhatia and Mathur (1978). Another species, *S. prolifera* is known from the Middle Siwalik (Bhatia, 1999). *Sphaeochara* (*S*. sp. Indet.) has also been reported from the Lower Siwalik Chinji Formation (Bhatia and Mathur, 1978). Further, *Sphaerochara* is widely known from the Tertiary sequences of Europe and North Africa and from the Quaternary of North Africa (Feist-Castel, 1977; Soulié-Märsche, 1989; Feist et al. 1994; Sanjuan and Martín-Closas, 2014).

Lamprothamnium papulosum recorded in this work was first recorded from Pinjor beds of the Upper Siwalik where it was reported to occur together with *Lamprothamnium succintum* (Bhatia, 1999). Although *Lamprothamnium papulosum* is thought to have flourished in an oligo- to mesohaline environment, the genus is euryhaline and grows profusely in brackish water with increased growth in phases of reduced salinity (Soulié-Märsche, 1991). The species is also known from the Dhok Pathan beds exposed near Polian Prohita (H.P.) suggesting that its range extended from Middle to Upper Siwalik (Sharma et al. 2015). *Nitellopsis* (*Tectochara*) *megarensis* in the present collection is represented by over 25 gyrogonites which are generally similar to other species of *Nitellopsis* (*Tectochara),* but closely comparable to *T. merianii* *diluviana* reported by Tewari and Sharma (1972a) from the Upper Siwalik beds near Chandigarh. The reason for the presence of stomata-shaped protrusions is unclear, but this phenomenon is possibly related to differences in calcification pattern and process resulting from external disturbances (Bhatia et al. 1998). This species is also known from the Hirpur Formation of the Karewa Group of Kashmir (Bhatia et al. 1998).

Nitellopsis (Tectochara) huangii, is represented by 10 gyrogonites in the collection. The species was initially described from the Lower Siwalik (Bhatia and Mathur, 1978) and later from the Pliocene Tatrot Formation of the Upper Siwalik (Bhatia, 1999). The present find is the first such record from the Middle Siwalik. Lu (1945) and Horn af Rantzien (1959) originally described this species from Sinkiang Province, China. It was widely distributed in Europe and Asia (Wang, 1961,1965; Castel, 1967).

Nitellopsis (Tectochara) merianii, a rare species in the collection represented by 7 gyrogonites, is widely distributed in the Oligocene to Pliocene horizons of Europe including southern Germany, Austria, Switzerland and France and in the Asian Miocene basins of Northern Thailand (Soulié-Märsche et al. 1997). Originally, this species was described from Oligocene/Miocene of Switzerland (Horn af Rantzien, 1959). In India, *Nitellopsis merianii* was first recorded from the Lower and Middle Siwalik and subsequently from the Tatrot Formation of the Pliocene Upper Siwalik (Bhatia and Mathur (1978; Bhatia, 1999).

Gyrogonites of *Chara* sp. Indet. Represented by 3 gyrogonites in the collection are similar to those described as *Chara* sp. From the Upper Siwalik (Bhatia and Mathur, 1978). More specimens are needed for a precise identification, though, the specimens bear some resemblance with *Charites angusta*.

Thus, paleoecologically, the Mohand fossil gyrogonites suggest the presence of permanent and temporary/seasonal ponds in the basin in close vicinity to each other.

6.2. Diversity and paleoecological implications of charophyte assemblage from Ladakh Molasse, Northwest Himalaya

Based on the specimens kindly provided by Prof Sunil Bajpai (IIT Roorkee), five species of charopytes were identified in this study from the Ladakh Molasse Group: *Lamprothamnium papulosum*, *Lychnothamnus barbatus*, *Lychnothamnus breviotus*, *Hornichara maslovi* and *Chara* sp. The only report on charophytes from Ladakh Molasse Grouop prior to this study was by by Tewari and Sharma (1972b) who identified three species namely, *Grambastichara* cf. *tornata*, *G.* cf. *cylindrica*, *Harrisichara* cf. *vasiformis* from the Kargil molasse. The presently identified assemblage comes from two different molasse horizons: the Kargil Formation exposed in the Wakka Chu section near Kargil and the Basgo Formation exposed near the village Taruche, about 25 km west of the Leh city. The taxa from Kargil molasse are *Lychnothamnus barbatus*, *Lychnothamnus breviotus* and *Hornichara maslovi*, and the Basgo forms are *Lamprothamnium papulosum* and *Chara* cf. *C. tornata.* The Basgo Formation is of particular interest since it is considered to be at the base of the Ladakh Molasse Group (e.g., Garzanti & Van Haver 1988), directly overlying the granitoids of the Ladakh Batholith with an erosional contact. Sedimentological investigations interpret the Basgo Formation as alluvial fan conglomerates, braid plain sandstones and lacustrine marls and limestones (Garzanti & Van Haver, 1988; Singh et al. 2015). Palaeontological investigations of the Basgo Formation) suggested somewhat conjectural ages, especially the latest Cretaceous (Maastrichtian) age based on an unpublished ostracod assemblage (Garzanti & Van Haver, 1988). Later work (Bajpai et al. 2004), however, assigned a late Oligocene age based on non-marine ostracods, especially the Chinese genus *Dongyingia* (*D. sannionis*). The present charophyte assemblage from the Basgo Formation does not include any Cretaceous element and the presence of *Chara* cf. *C. tornata* is consistent with a Late Oligocene/Early Miocene age (Bajpai et al. 2004; Parmar et al. 2020) and freshwater depositional environment without any brackish water influence. The present assemblage of charophytes from Basgo and Kargil formations are consistent with a late Oligocene / early Miocene age, previously assigned based on ostracods and mammal faunas (Bajpai et al. 2004; Kumar et al. 1995).

Paleoecological considerations of the Ladakh charophytic flora from Kargil and Taruche sections suggest the presence of a freshwater, cold, alkaline lacustrine environment, possibly with a depth not exceeding ~ 8m.

6.3. Extant charophytes of Sahastradhara area, Doon Valley

As part of the larger project on fossil and extant charophytes from India, gyrogonites from living plants in the Sahastradhara area of Doon Valley have been studied for this dissertation. As stated above, the study of gyrogonites of extant charophyte taxa helps in tracing their geological antiquity and distribution besides providing valuable paleoecological information. Gyrogonites of *Chara vulgaris* were collected from Sahastradhara area in Doon Valley along with pertinent details of water chemistry. The extant gyrogonite sample was collected from a spring water streamlet joining Sahastradhara stream (a tributary of the river Song) in a picnic area, around 15 km from Dehradun; The Pre-Tertiary limestone and Tal phosphorite horizons in higher reaches to the north modulate the water chemistry but spring water joining the trunk stream remains pristine hard water with little or no nutrients added. Dried specimens of the recovered gyrogonites allowed their detailed morphological examination under a binocular microscope and their taxonomic identification as *Chara vulgaris* Linnaeus. Detailed morphological and ecological 106haracterization of *C. vulgaris* gyrogonites is helpful in evaluating the reported occurrence of its fossil counterparts in Kashmir valley. It is for the first time that gyrogonites of the extant species *C. vulgaris* are documented from Uttarakhand.

Significantly, the charophyte assemblage from nearby Middle Siwalik strata of Mohand does not include *Chara vulgaris*, which is attributable to their much older age. Published records, exclusively based on their vegetative parts but not on gyrogonite details, reveal that *Chara vulgaris* is a cosmopolitan living taxon is known from Indian shield region, Bangladesh, and Tibet (Fan et al. 1995). It is noted that the record of extant species in fossil records is potentially useful in discriminating families, genera and species, and such studies have gained momentum during the last few decades (e.g. Mädler, 1952).

6.4. Future prospects

Fossil Charophyta continues to be a highly neglected field of research in India as compared to several European countries, North America and China. The present work marks the beginning of a larger project dealing with the fossil and living Charophyta of India. Of particular interest to the present is the fossil Charophyta of Mesozoic-Cenozoic age. To this end, late Cretaceous charophytes from the Deccan intertrappean beds of peninsular India and the Neogene charophytes from the Middle Siwalik deposits of the Sub-Himalaya were recently described (Tiwari and Bhan, 2021), whereas the documentation of the extant species *Chara vulgaris* is expected to be published shortly. Some of the potential charophyte-yielding horizons proposed to be investigated in the future are: Gondwana continental deposits of Mesozoic age in the Pranhita-Godavari valley and Rewa Basin; Paleogene horizons of Kutch and Cambay basins of Gujarat; Bikaner and Barmer basins of Rajasthan; and the Neogene of Kutch and Siwaliks. It is expected that these studies will greatly augment our knowledge of the stratigraphic distribution and diversity changes in fossil Charophyta of India. Studies on the Gondwana charophytes are also expected to provide significant insights in to the challenging question concerning the evolutionary disappearance of the most primitive gyrogonites belonging to the family Trochiliscaceae (D-chirals, right-handed) at the onset of Mesozoic era and the continued survival of L-chirals (i.e., left-handed).

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Middle Siwalik Charophyta from Mohand area, Dehradun Sub-Basin, NW Himalaya, India

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ARTICLE HISTORY

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This paper describes a taxonomically diverse assemblage of charophytes recovered from the Middle Siwalik strata of Mohand area, Dehradun sub-basin, NW Himalaya. Recovered from a horizon dated ~9 Ma, early late Miocene, the collection comprises 13 species belonging to 7 genera: *Chara aspera, Chara globularis, Chara rantziene, Chara* sp., *Hornichara maslovi, Lychnothamnus breviotus, Nitellopsis megarensis, Nitellopsis tectochara merianii, Nitellopsis tectochara haungii, Sphaerochara tewarii, Lychnothamnus barbatus, Lychnothamnus* sp. and *Lamprothamnium papulosum*. Associated fossils include freshwater ostracods, gastropods and fishes. Palaeoecological considerations of the recovered charophyte assemblage suggest a shallow, warm, low energy, semi-permanent to permanent lake or pond.

Keywords: Charophyta, Siwalik, Miocene, Himalaya

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INTRODUCTION

The Siwalik succession comprises a thick pile of about 6000 m mudstone, sandstone and conglomerate which was deposited by a fluvial system in the foreland basin along the southern edge of the evolving Himalaya and now comprising Outer Himalaya/Sub-Himalaya (Kumar and Tandon, 1985 a, b; Prakash *et al*., 1980). These molasse deposits are widely considered to be excellent archives for Neogene and Quaternary biota and continue to provide extremely valuable insights into the Neogene orogenic evolution of the Himalaya besides the paleoecologic, paleoclimatic and paleobiogeographic evolution during this period (e.g. Bajpai *et al*., 2020).

Compared to other fossil groups, records of Siwalik Charophyta are scarce, and only a few sporadic occurrences have been reported (Tewari and Sharma,1972; Bhatia and Mathur, 1978; Bhatia, 1999; Sharma *et al*., 2015). Here we describe a diverse assemblage of charophytes for the first time from the Middle Siwalik strata of the Mohand section. The assemblage was found in association with freshwater gastropods, ostracods and fish remains. The palaeoecological implications of the charophyte assemblage are also discussed.

STUDY AREA

The Mohand Range is present on the southern side of the Dehradun re-entrant and is separated by Lesser Himalaya by the Doon valley. It exposes the Middle and Upper Siwalik sediments deposited mainly by braided rivers, and the succession consists of sandstone-mudstone, sandstone and conglomerate-sandstone (Kumar and Nanda, 198; Kumar 1993; Kumar *et al*. 2004) (Fig.1). A detailed geological account of the section is available in the excursion guides (Tandon *et al*., 1988; and Kumar *et al*., 1991). Magnetopolarity studies by Sangode *et al*. (1999) suggest an age from 9.73 Ma to 4.86 Ma (Late Miocene - Early Pliocene). Kumaravel

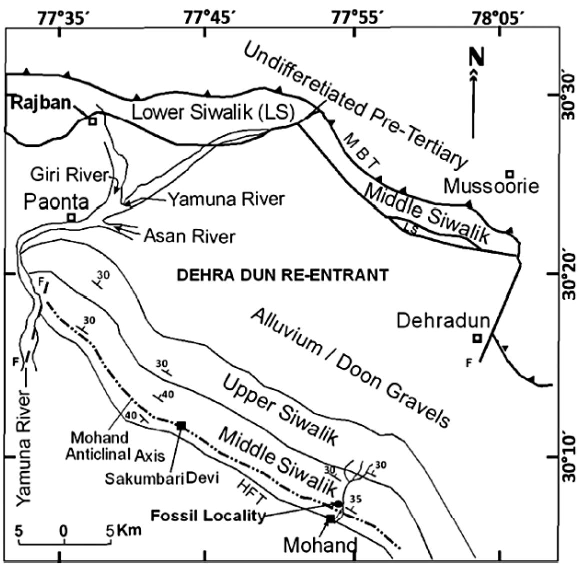

Fig. 1. Geological map of Siwalik Group in the Sub-Himalaya of Mohand-Dehradun area showing fossil locality

Acceptance for **publication** of the manuscript entititled "*Chara vulgaris* gyrogonites (charophytes) from the Doon Valley (Uttarakhand): links between living and Plio-Pleistocene fossils in the Kashmir Valley" by Nandita Tiwari & Uday Bhan.

Acceptance for publication in 'Himalayan Geology' journal (MS#726-21)

Inbox ×

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to me

Dear Authors,

On behalf of the Editor-in-Chief of the 'Himalayan Geology' journal, I am pleased to inform you that your manuscript entitled "Chara vulgaris gyrogonites (charophytes) from the Doon Valley (Uttarakhand): links between living and Plio-Pleistocene fossils in the Kashmir Valley" by Nandita Tiwari, Uday Bhan has been accepted for publication in the 'Himalayan Geology' journal (Scheduled for July 2022 issue).

Best wishes,
Rambir Kaushik
Editorial Manager

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