ACARID MITES FROM EARLY PERMIAN SEDIMENTS OF THE CHAMBA VALLEY, HIMACHAL PRADESH, INDIA

PRABHAT KUMAR*, NEER JA JHA**, D.D. BHATTACHARYA*** and A.C. PANDE***

* DEPARTMENT OF ZOOLOGY, LUCKNOW UNIVERSITY, LUCKNOW.

**BIRBAL SAHNI INSTITUTE OF PALAEOBOTANY, 53 UNIVERSITY ROAD, LUCKNOW.

***GSI, NORTHERN REGION, ALIGANJ, LUCKNOW.

neerjajha@yahoo.co.uk

ABSTRACT

Acarid mites have been described for the first time from the sediments of the Manjir Formation, Chamba Valley, Himachal Pradesh, which have yielded Early Permian palynomorphs. The reported two fossil specimens are almost well preserved, weakly sclerotised astigmatid mites, having no spiracles or stigmata and trachea, hence respiration cutaneously. These minute, microscopic acarid mites are extremely important as acarid mites are currently not recorded from the Permian. These mites are 365x180 µm and 45x200µm in size. Triangular gnathosoma (capitulum), 38x30µm and 45x35µm in size, is much smaller than idiosoma, narrowing towards the front side where it becomes pointed.

Keywords: Mites, Manjir Formation, Early Permain, Chamba valley

INTRODUCTION

Mites are the widely distributed members of Arachnida and inhibit practically all kinds of habitats available to animal life (Prasad, 1958). There are 15 Palaeozoic, 15 Mesozoic and 253 Cenozoic species of Acari: Actinotrichida (=Acariformes=Acarina). Devonian and Lower Carboniferous mite fossils are reported by Subias and Arillo (2002). Labandiera et al. (1997) noted that Oribatid mite trace- fossil record is abundant in the Carboniferous. Kellogg and Taylor (2004) also agree with this observation. Within Palaeozoic, mites are known from Devonian and Mississippian (Carboniferous), but not from Permian. Thus, there is hiatus in the fossil record until mites began to be formally recorded in the Middle Mesozoic.

The present paper communicates the record of two fossil specimens of the astigmatid mites from the sediments of the Manjir Formation, Chamba Valley, Himachal Pradesh. Presence of acarid mites from the Manjir Formation is extremely important as acarid mites have not been reported from the Permian and this is the first report from India.

The Manjir Formation was believed to represent Upper Proterozoic. Some workers considered it Mid-Palaeozoic primarily on the basis of lithological attributes and associations. Palynological studies have shown presence of Early Permian palynomorphs in the Manjir Formation of Chamba Valley which suggest that the fossil-yielding sediments of the Manjir Formation are of Early Permian age (Pande *et al.*, 2004). In these Early Permian sediments, acarid mites have been recorded. The present report of acarid mites from the study area fills the gap in mite body fossil record.

REGIONAL GEOLOGY

The Chamba Basin of Himachal Pradesh represents the Tethyan realm of northwestern Himalaya. To work out the geology of this region, McMahon (1882) traversed the area and prepared the maiden geological map. Later on, workers from GSI and other institutions carried out extensive investigations and elucidated geology and structure of the Chamba Basin in finer details.

The study area forms a part of the Lesser Himalaya and is delimited in the north by the Pir Panjal Range and in the south by the Dhauladhar Range. After McMahon (1882, 1885), Sehgal (1965) made significant contribution and classified the rocks. The study area exposes the rocks ranging in age from Precambrian to Lower Triassic, disposed in a NW-SE trending inverted syncline. The Geological map of the area north west of Chamba in Himachal Pradesh has been depicted in Fig.1 showing area of study. The geological succession in the Chamba area has been presented in table 1 (after GSI, 1995).

The rocks of the Manjir Formation have been studied and sampled in detail along the Siul River. The Manjir Formation unconformably overlying the Chamba Formation is represented by a heterogenous, poorly sorted pebbly beds separated by non-pebbly, quartzite, shale/ phyllite and carbonate fragments embedded in an argillaceous matrix, often sandy and calcareous. The rocks are foliated and metamorphosed. Four pebbly beds separated by three non-pebbly horizons have been delineated. Samples for microfloral studies were collected systematically from the dark grey to black shale/slate separating the pebbly horizons. The Manjir Formation is overlain by the Katarigali Formation with a sharp contact.

AGE OF THE MANJIR FORMATION

The Manjir Formation has been correlated by some workers with the Blaini Formation assigning a Carboniferous age, while Rattan (1973) is of the opinion that this conglomeratic bed represents the "Mid Palaeozoic Hiatus" and is of Cambrian age. Later, the well-preserved, stratigraphically significant palynomorphs (chiefly monosaccates viz. Parasaccites, Plicatipollenites, nonstriate disaccates, viz. Scheuringipollenites, Platysaccus, and striate disaccates viz. Striatopodocarpites, Faunipollenites and Striatites) were reported in the sediments of the Manjir Formation. Presence of these texa indicates definite Early Permian age for the Manjir Formation. Thus, on the basis of palynological studies Early Permian age has been assigned to these rocks of Manjir Formation (Pande et al., 2004).

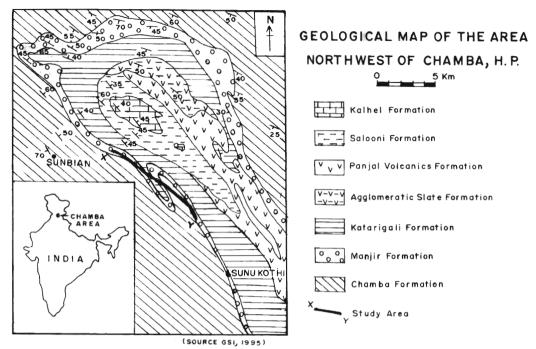


Fig.1. Map of the Chamba area, Himachal Pradesh showing area of study.

MATERIAL AND METHODS

The material for study was collected from the Manjir Formation exposed in the Bhalsu-Suni Kothi-Kundmarl section of Siul River, Chamba Valley, Himanchal Pradesh.

The rock samples were processed for the recovery of palynomorphs by usual maceration technique. The 10-15gm of material from the rock samples was first treated with conc. hydrofluoric acid for two to three days to remove silicates and then by conc. nitric acid for five to six days, followed by 10% potassium hydroxide after thorough washing with water. The macerates were then mounted in canada balsam and the slides were prepared. The mites were recovered in these slides. The slides have been deposited in the repository of BSIP museum.

A BRIEF REVIEW OF THE MITE STUDY

Mites are the widely distributed members of the class Arachnida and as such should have a segmented body with the segments organized into two tagmata, Prosoma and Opisthosoma. There is no discrete head. However, only faint traces of primary segmentation remain in mites, the prosoma and opisthosoma are insensibly fused and a region of flexible cuticle circumcapitular furrow (CCF) separates the chelicerae. (Ch) and pedipalps (Pe) from the rest of the body.

The anterior region of the body is gnathosoma or capitulum and according to some acarologist, is also found in *Ricinulei*. The remainder of the body region is known as idiosoma and is unique to mites. The mouth parts of the mites may be adapted for biting, stinging, sawing, piercing and sucking. They breathe through trachea, stigmata (small openings of the skin, spiracles), intestine and skin itself. Astigmatid mites have no stigmata or spiracles and trachea, hence, they breathe through integument. Species hunting for other mites have very acute senses but many mites are eyeless. The central eyes of arachnids are always missing or they are fused into a single eye. Thus, any number from none to five may occur.

Acarines are extremely diverse and widespread as they live in practically every habitat and include aquatic (fresh water and marine) and terrestrial species. Mites outnumber other arthropods in the soil, organic matter and detritus. Many are parasites and they affect both vertebrates and invertebrates. Most parasitic forms are external parasites, while free-living forms are generally predatory and may even be used to control undesirable arthropods. Others are detritivores which help to break down forest litter and dead organic matter such as skin cells and many still are plant feeders and may damage crops. Very small mites live inside the tracheal tubes of honey bees.

The phylogeny of Acari is disputed and many taxonomic

Table 1: The geological succession of the study area.

Formation	Lithology	Age
Kalhel	Dominantly carbonate sequence represented by limestone, limestone and shale having crinoids	Lower Triassic
Salooni	Dark grey black shale, fossiliferous in nature with calcareous sandstone bands	Upper Permian
Panjal Volcanics	Amygdaloidal basic lava flows	Lower Permian
Agglomeratic slate	Pebbly slate, quartz arenite and conglomerate	Lower Permian to Upper Carboniferous
Katarigali	Shale, slate, quartzite and limestone	Upper Proterozoic
Manjir	Diamictite, shale, slate and limestone	Upper Proterozoic
Chamba	Slate, phyllite and quartzite	Middle Proterozoic

Fig. 2a. Acarus siro, complete specimen (dorsal side as coxa of legs are not clearly visible) showing two broken left legs on anterior side, one broken left leg on posterior side, one broken first right leg and one complete short stubby second right leg on anterior side and two broken right legs of posterior side. 10x. BSIP slide no. 13236. Coordinates M-53/3. Me-Mesopodosoma.

schemes have been proposed for the classification. Several acarologists agree that acari contain two separate lineages: Acariformis (Actinotrichida) and Parasitiformes (Anactinotrichida) but some workers treat these groups as superorders and others as orders.

Acariformes are the most diverse group of mites and include mite-like mites.

Trombidiformes are plant parasitic mites such as spider mites, gall mites, peacock mites, red-legged earth mites, snout mites, hair follicle mites, velvet mites, water mites etc.

Sarcoptiformes are oribatid endostigmatan and astigmatan mites.

- (a) Endostigmata- basal sarcoptiform lineage
- (b) Orbatida-Orbatid mites, beetle mites, armored mites also known as Cryptostigmata.
- (c) Astigmata-stored products, fur, feather, dust and human itch mites etc.

Parasitiformes is the group including ticks (larger mites) and a variety of mites

- (a) Mesostigmata-bird mites, phytoseiids mites
- (b) Ixodida-hard and soft ticks
- (c) Holothyrida-Holothyrans

Opilioacariformes is a small order or suborder of Parasitiformes mites which are superficially similar to harvestmen or daddy-long-legs (opiliones, hence their name) Three major lineages are currently recognized: Opilioacariformes, Acariformes, Parasitiformes (Krantz,1978, Evans, 1992) Here, we have followed the systematic classification given by Krantz and Walter (2009).

In most modern treatments, Acari is considered to be subclass of Arachnida and contains 2-3 superorder or orders Acariformes (or Actinotrichida) which have setae with a layer of optically active chitin, actinochitin that is birefringent under polarized light. Parasitiformes (or Anactinotrichida) where setae lacking in actinochitin are optimally isotropic and Opilioacariformes which is often considered a subgroup within Parasitiformes. The present two microscopic apterous fossil specimens are mites because they show oval compact body that consists of fused cephalothorax and abdomen; further more, they are weakly sclerotised and their tracheal system as well as true claws are absent. Empodium being claw inserted on a distinct pretarsus, Idiosoma are not covered by sclerites. The detailed study of these fossil mites was carried out to clarify the interpretation of morphological features and their systematic position.

SYSTEMATIC DESCRIPTION

Kingdom Animalia Phylum Arthropoda Subphylum Chelicerata Class Arachnida Subclass Acarina (or Acari) Leach,1817

Superorder Acariformes
Order Astigmata

Suborder Acaridia Superfamily Acaroidea

Family Acaridae (partim), Ewing and Nesbitt, 1942

Genus Acarus

Acarus siro (figs. 2,4)

The discovered organic matter includes two, almost complete specimens of fossilized minute acarid mites (not visble with naked eyes). The present specimens are delicate, soft bodied, weakly sclerotised and dorsi-ventrally flattened. The both specimens are Arachnida, as such they should have a segmented body. The segments are organized into two tagmata: Prosoma (cephalothorax-head and thorax fused) and other Opisthosoma (abdomen). The prosoma and opisthosoma are intensively fused and a region of flexible cuticle, the circumcapitular furrow (CCF), that separates mouth parts, containing chelicerae (Ch) and pedipalps (Pe), from the rest of the body. This anterior region of body is known as capitulum (C) or gnathosoma which is triangular in shape and its capitular base is faintly demarcated (fig.2a) as well as it does not contain camerstome, hence visible from above. The remainder of the body is idiosoma (I) which is unique in mites.

Cephalothorax is broadly joined with the abdomen by a shallow groove known as sejugal furrow (SF), which is not deeply constricted. This furrow is situated in between second and third legs and dividing the idiosoma into propodosoma and hysterosoma (notogastor). External openings or spiracles as well as trachaea (respiratory tubes) are absent. These are absent in astigmata. Idiosoma is never covered with sclerites. Anal and genitel openings are situated in idiosoma but here in both the specimens these are not visible

There are four pairs of walking legs. The first and second pairs of legs are placed anteriorly and forwardly directed, while third and fourth pair of legs are placed posteriorly and backwardly directed. Both pairs of legs are widely separated, therefore there is a large space for mesopodosoma. The idiosoma (I) is divided into four parts (1) Propodosoma (P) - an area of first and second legs, (2) Mesopodosoma (Me) - an area of second and third legs. Second leg is well anterior to third leg, therefore well demarcated in these fossil forms. This area is not well marked in those mites where second and third legs are not widely separated. Due to this large mesopod@somal area, placement of coxa of second leg is considerably well anterior to third leg. (3) Metapodosoma (M) - an area of third and fourth legs. The genital opening is found in this area. (4) Opisthosoma (O) - an area posterior to fourth leg where anal opening is situated.

The propodosoma, mesopodosoma and metapodosoma all together constitute podosoma (portion of leg first to leg fourth). Gnathosoma and podosoma together form prosoma, gnathosoma and propodosoma together constitute proterosoma and in the same way metapodosoma and opisthosoma form hysterosoma (notogaster). Gnathosoma with

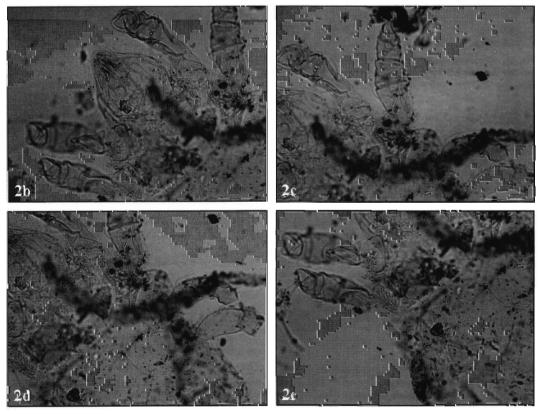


Fig. 2b. Acarus siro, mouth parts (two chaelate chelicerae, dark and two pedipalps, light) and two pairs of broken legs on anterior side. Circumcapitular furrow (CCF) faintly demarcated. 40x. c. all four legs of right side in focus, second leg of right side appears to be complete. 40x. d. Two broken anterior legs and one posterior leg of left side in focus. 40x. c. two broken left legs on anterior side, 40x.



Fig. 3a. *A. indicus* n.sp. complete specimen (ventral side as coxa of legs are clearly visible) showing two complete short stubby left legs on anterior side and two complete relatively longer simple and straight but not stubby left legs on posterior side as well as two broken legs (one anterior and one posterior) on right side. Circumcapitular furrow (CCF) clearly demarcated. 10x. Holotype,BSIP slide no. 13237. Coordinates U-46/3. Me-Mesopodosoma.

podosoma create prosoma. The entire posterior region with podosoma is pear-shaped idiosoma. In this way, there is no discrete head and head-like conical capitulum is strongly fused with the remaining portion of the body. There are two pairs of mouth appendages attached to anterior part of gnathosoma, chelicerae (the main important feeding organ placed infront of mouth) and pedipalps that lie one on either side of mouth parts. Two segmented small pedipalps are held close to the side of infracapitulum. Chelicerae are chelate type in one specimen (Fig.2a), while dentate in other specimen (new species, Fig.3a). In both the specimens, chelicerae project as a rostrum. Chelicerae are actual cutting instruments that are capable of retraction. Each consists of chitinous bar and is enclosed in separate sheath both dorsally and laterally. Both organs are used for acquiring food. Both specimens have biting type of

mouth parts. A leg has seven segments, coxa, trochanter, femur, genu, tibia, tarsus and apotale. True claws are absent but possess empodial claws. Some setae are observed on legs but not on body. Four sensory setae are visible on the tip of two anterior first and second legs of right side (Fig. 3a, Text Fig.5). Specimen of fig. 2a has two broken left legs on anterior side and one broken left leg on posterior side, one broken first right leg and one complete short stubby second right leg on anterior side, while two broken right legs of posterior side are clearly visible.

Specimen shown in fig.3a has two complete short stubby left legs on anterior side and two complete relatively longer simple and straight but not stubby left legs on posterior side. Two broken legs, one anterior and one posterior of right side, are present. Length of leg segments of all available legs (in μ m)

Table 2: Length of leg segments in specimen I Acarus siro (Fig.2a and 4)

Leg no. Co Tr Fe Ge Ti Ta 19.35 23.74 15.57 1 14.46 24.30 21.08 2 14.64 26.11 18.70 14.08 8.50 3 27.77 ? ? 15.38 11.83 13.75 28.42 11.92

in both the specimens of one side (right in *Acarus siro* and left in *A. indicus* n. sp.) are presented in the following tables 2 and 3.

Acarus indicus n.sp. (Fig. 3a and 5)

Holotype: Slide No. 13237.

Discription and Comparison: Acarus siro (fig. 2a) resembles the extant Astigmatid mite, A. siro but the fossil specimen shown in fig. 3a differs from A. siro in some important characters of mouth parts and body size. Therefore, it is considered as a new species and named after India as Acarus indicus n. sp. (figs. 3,5) This new species bears dentate chelicerae. Body size, capitulum size and size of Mesopodosoma (space in between second and third legs) are more elongated and wider than A. siro (see table 2, 3). Anterior pair of legs are short and stubby but posterior pair of legs are relatively longer, simple and straight (not stubby) in this new species, while all legs are apparently short and stubby in A. siro. In A. siro posterior pair of legs are situated at the proximal end of idiosoma due to which there is less space between second and third leg (Fig. 2a), while in A. indicus the case is

Table 3:Length of leg segments in specimen II.

Leg no.	Co	Tr	Fe	Ge	Ti	Ta
1	21.14	18.03	19.86	19.58	10.36	14.55
2	22.70	17.24	19.39	18.86	11.23	15.09
3	20.81	17.10	18.81	19.27	12.30	16.09
4	21.10	17.95	19.10	19.56	11.95	15.95

reverse where the posterior legs are situated distally on idiosoma in comparison to *A.siro*; therefore, posterior legs are away from anterior legs and this causes more space in between second and third leg (Fig.3a). It shows prominent capitular base.

The body size, capitulum size and size of Mesopodosoma (space in between second and third legs) of both specimens are given in the table 4.

Type locality: Bhalsu-Suni Kothi-Kundmarl Section along Siul River, Chamba Valley, Himachal Pradesh.

Horizon and age: Manjir Formation, Early Permian.

DISCUSSION

The mites and ticks are the closest relatives of spiders because abdomen of mites and ticks are broadly joined with cephalothorax forming idiosoma but lack a pedicel which is characteristic of spiders. Fossil mites have been described from the Lower and Middle Devonian deposits (Hirst, 1923 and Norton et al., 1988). Despite some controversial opinions on their family appurtenance (Dubinin, 1962 and Norton et al.,

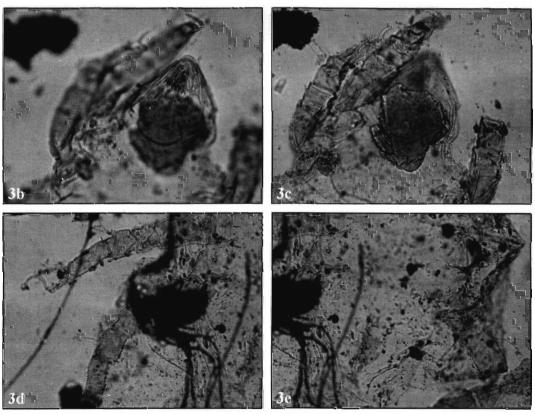


Fig. 3b. A. indicus n.sp. mouth parts (two dentate chelicerae (dark) and two pedipalps (light). 40x. c. First and second complete legs of left side and second broken leg of right side in focus showing two claws and four sensory setae on the tip of first and second legs of left side. 40x d. two (third and fourth) broken legs right side in focus. 40x. e. one broken right leg of posterior side. 40x.

Table 4: Showing size of body, capitulum and Mesopodosoma of both specimens.

	Acarus siro	Acarus indicus n. sp.
Body length	365 μ	450μ
Body width	180 μ	200 μ
Capitulum length	38 μ	45 μ
Capitulum width	30 μ	35 μ
Mesopodosoma length	40.19 μ	70.47 μ
Mesopodosoma width	118.47 μ	171.86 μ

1989), all early Devonian species certainly belonged to superorder Actinotrichida. Several actinotrichid mites have been recorded from the Palaeozoic and Mesozoic deposits (Magowski, 1995). Superorder Anactinotrichida is extremely scarce in the fossil material. The oldest findings are known from Tertiary amber. Both superorders Actinotrichida and

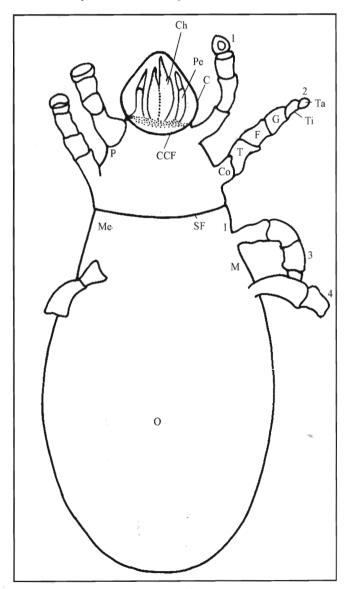


Fig. 4. Reconstruction of the mite specimen *Acarus siro*. I-Idiosoma, P-Propodosoma, Me-Mesopodosoma, M-Metapodosoma, SF-Sejugal furrow, CCF-Circumcapitular furrow (CCF), Ch-Chelicerae (Ch), Pe-Pedipalp, C-Capitulum-or gnathosoma, O-Opisthosoma, Co-Coxa, T-Trochanter, F-Femur, G-Genu, Ti-Tibia, Ta-Tarsus, 1-4 legs.

Anactinotrichida from subclass Acari show a large gap of occurrence in the oldest fossil records. No Actinotrichid mites are known from the Devonian, whereas earlier Anactinotrichid are known from Tertiary (Witalinski, 2000). The majority of the fossil mites are best known from the Oligocene Baltic amber (Norton *et al.*, 1988).

Astgmatids are fairly homogenous assemblage of free living, slow moving, weakly sclerotised forms without propodosomal sensory structures and have evolved to nonpredaceous existence, may be a highly advanced group but lowest of the free-living forms (Shipley, 1904). These fossil mites seem to be free living and slow movers because of the presence of claw-like empodia on pretarsus. They are the characteristic features of non-parasitic mite members but are absent in parasitic mites (Roy and Brown, 1970). Tarsus is short. The fossil history of Astigmata is known from a single species that was described from the late Oligocene to early Miocene (O'Connor, 1982). Acari are the most diverse and abundant of all arachnids and are among the oldest of all terrestrial animals with fossils known from Early Devonian (Norton et al., 1988: Kethley et al., 1989). 136 fossil species are known mainly in Actinedida and Oribatida (Bernini, 1991). Mites inhabit all kinds of habitats and embrace an exceedingly large number of species (Davis, 1989).

Mites are important detritivores in the modern terrestrial ecosystem. Modern Oribatid mites are abundant in temperate forest ecosystem, where they are responsible for plant litter and wood conversion to organic residues in terrestrial decomposers food chain (Wallwork, 1967). Although mites were widespread wood borers during Carboniferous, but the insects appear to have taken over as the dominant wood borers during the Late Triassic. Insect wood borers are believed to have evolved in Early Permian and continued as dominant agent in this syndrome in modern ecosystem (Labandiera and Phillips, 1996 and 2002).

Arthropod detritivores in Palaeozoic terrestrial ecosystems have been observed from the Late Silurian through the Early Permian (Labandiera, 1998). From early Permian to Late Triassic, however, there are no reports of wood borers. A growing number of Devonian fossils of mites, spiders and others show that arachnids made transition to land life. The fossil record of land cheliecerate is sparse, but nearly all terrestrial lineages had evolved by the end of the Carboniferous including land scorpions, etc. (Norton *et al.*, 1988)

Wood-boring forms from the Palaeozoic are primarily known from the coal ball carbonate permineralization and silicified peat that were deposited in wetland environments (Labandiera,1998) similar to modern Oribatid mites. Mesozoic wood-boring insects mostly occur in silicified petrifactions, most of which were deposited in drier, more riparian habitats (Tidwell and Ash, 1990). Based on borings and coprolites from Antarctica, Kellogg and Taylor (2004) concluded that insects are more prolific wood borers in dry environments and Oribatid mites are dominant in moist environments.

Oribatid mite trace records are abundant in the Carboniferous. Wood boring reflects a typical plant arthropod interaction which is fairly common in fossil records. For the first time, Feng *et al.* (2010) reported Oribatid mite borings and coprolites from the Palaeozoic terrestrial deposits in Cathaysian flora that provides an important plant mite association bridging a major time gap in this palaeogeographic area between Carboniferous and early Mesozoic deposits. Oribatida and

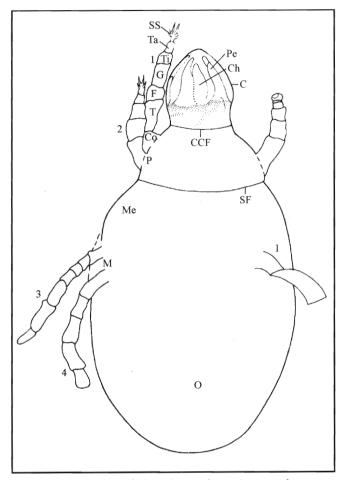


Fig. 5. Reconstruction of the mite specimen *Acarus indicus n.sp.*, I-Idiosoma, P-Propodosoma, Me-Mesopodosoma, M- Metapodosoma, SF-Sejugal furrow, CCF-Circumcapitular furrow (CCF), Ch-Chelicerae (Ch), Pe-Pedipalp, C-Capitulum - or gnathosoma, O-Opisthosoma, Co-Coxa, T-Trochanter, F-Femur, G-Genu, Ti-Tibia, Ta-Tarsus, SS-Sensory setae, 1-4 legs.

Astigmata show close phylogenetic relationship. According to Norton *et al.* (1998), it is the general hypothesis that Astigmata originated within oribatids and suggests Malaconothridae as a possible sister group. The hypothesis brings to light evolutionary questions which were previously obscured by inappropriate classifications. The nomenclatural problems that arise from this hypothesis are best solved by considering Astigmata as a subgroup within Oribatida. It is quite apparent that Astigmata are derived from within Oribatida making the latter taxon paraphyletic (O'Connar, 1984 and Norton *et al.*, 1993).

Three major lineages are currently recognized Opilioacariformes, Aariformes and Parasitiformes (Krantz and Walter, 2009; Krantz,1978; Johnston,1982 and Evans, 1992). Two major lineages are recognized in Acariformes, the Sarcoptiformes (Astigmata and Oribatida, both taxa are of equal rank) and Trombidiformes (Prostigmata). About 45,000 species of mites have been described. Mites are truly ubiquitous.

CONCLUSIONS

This paper aims to present a broad picture about the organic matter remains of acarid mites from the Early Permian sediments of Chamba Valley, Himachal Pradesh, India. This finding is specially important as Acarids are currently not reported from the Permian. The present specimens are recovered from the sediments of the Manjir Formation, Chamba Valley, Himachal Pradesh, India and is the first report of Acarid mites from Early Permian age. The present report on Permian mites from the Manjir Formation is very significant in filling the information gap in fossil record of mites. Mites are closely related to Arachnid order Ricinulei (Evans, 1992). Ricinulei and Acari (taxon name Acarinomorpha) have sister group relationship (Weygoldt and Paulus, 1979). Schultz (1990) supported the above and assumed that Acari are monophyletic but van der Hammen (1989) considered Acari as diphyletic and Acariformes and Parasitiformes are at most distally related. Mites are important detritivores in the modern terrestrial ecosystem. Arthropod detritivores in the Palaeozoic terrestrial ecosystem were reported from the Late Silurian through to the Early Permian (Labandiera, 1998). Oribatid mite detritivory in the Late Permian wood has been provided from Antarctica (Kellogg and Taylor, 2004).

ACKNOWLEDGEMENTS

We (NJ & PK) are thankful to Dr. N.C. Mehrotra, Director, Birbal Sahni Institute of Palaeobotany, Lucknow for providing facilities to carry out the research work and granting permission to publish the paper. The authors (DDB & ACP) express gratitude to Dy. Director General, GSI, Northern Region for allowing its publication. Thanks are due to Dr. Savyasachi Saxena, Er. Pranay Prabhat and Smt. Neha Srivastava for their help in literature information. We thankfully acknowledge the encouragement given by Dr. Suresh C. Srivastava, former Scientist F, BSIP, during the preparation of the manuscript. Last, but not the least, we thank the reviewer Dr. Roy J. Beckmeyer for suggesting literature related to fossil mites and giving useful suggestions.

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Manuscript Accepted September 2011

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