



ANTIQUITY OF PHTHIRAPTERA: FOSSIL EVIDENCE

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ABSTRACT

Occurrence of the well-preserved phthirapteran insects from the Late Triassic sediments of the Satpura Basin, Central India provides the first and earliest record of such organisms in geological time scale. The antiquity of the Order Phthiraptera is discussed in view of the fossil evidence. Thus, the earliest appearance of phthirapteran insects is considered to be Late Triassic.

Key words: Phthiraptera, Chewing lice, Anoplura, Insect, India.

INTRODUCTION

The Order Phthiraptera includes chewing or biting and sucking lice, normally small to medium in size without wings and dorsoventrally flattened. The insects thrive as ectoparasites on birds and mammals. They have different types of mouthparts, three to five segmented antennae, sometimes hidden in a recess of head. The eyes are reduced, no compound eyes and no ocelli. The thorax is usually small, sometimes indistinct. The legs are short but stout. The abdomen has five-eight distinct segments (Ross, 1965).

The Order Phthiraptera consists of four distinct suborders Amblycera, Ischnocera, Rhynchophthirina and Anoplura (Price and Graham, 1997). The insects belonging to chewing lice have a simple, reduced type of chewing mouthparts and normally live on the body of host. These insects feed on scaly skin, bite of feathers, hairs, clotted blood, etc. The Anoplura (Siphunculata) includes sucking lice. The piercing and sucking stylets evolved in order to achieve blood sucking habit. These insects occur on mammalian hosts and feed on blood, which is sucked through a tube formed by an eversible set of fine stylets. A fossil chewing louse was reported from the Lower Cretaceous of Baissa, Transbaikalia (Rasnitsyn and Zherikhin, 1999).

The fossil forms incorporated in this paper were earlier recorded as phthirapteran insects by Kumar and Kumar (1999, 2001) from the Triassic of the Satpura Basin, M.P. Price, Hellenthal, Palma, Johnson and Clayton (2003) included these fossils in the world record of chewing lice, but evaded giving

their opinion on regarding them as chewing/sucking lice; however, in the same publication (p. 462), they write that these fossil specimens are "... possible recent findings" of phthirapteran insects. In order to establish affinities of fossil forms with the order Phthiraptera, the detailed study of these specimens was carried out to clarify the interpretation of morphological features and their systematic position. One of the specimens belongs to Amblycera (chewing or biting lice, Pl. I, figs. 1-8; figs. 1a-c,3) and the other to Anoplura (sucking lice, Pl. II, figs. 1-9; figs. 2a-b,4).

These two microscopic, apterous specimens are insects because they show three distinct body parts or regions of a typical insect, i.e. head, thorax and abdomen. One specimen resembles Amblycera shows thorax, bearing three pairs of legs. From this condition evolved the term Hexapoda meaning six legged and used as the class of insects (Ross, 1965). As the preparations of both insects were made after acid treatment to remove the inorganic material in which fossil insects were embedded, segmentation on abdomen may be affected. Hence, not clearly visible but this is segmented in both, as spiracles are present and there are no cerci. Another insect, which resembles Anoplura shows three distinct thoracic segments and spaces for the anteriormost pair of legs. These ectoparasitic insects probably began their life on mammalian host, as remains of early mammals were recorded from the Tiki Formation (Late Triassic) by Datta and Das (1996). Therefore, the presence of phthirapteran insects ectoparasitizing on mammals during Triassic cannot be ruled out.

The new taxon of this fossil amblyceran insect differs from living amblyceran insects in lesser number of setae on abdomen. However, arrangement of setae is on the pattern of extant Amblycera and Inchnocera (Kumar and Tandan, 1971) and minute to small, simple straight setae of this fossil specimen resembles with modern amblyceran insects. It has definite rows of setae on its abdomen (Pl. I. fig. 6). Therefore, it is being described as a new genus and new species under a new family Mammalophagidae as it is usually ectoparasitic on a mammal.

SYSTEMATIC DESCRIPTION

Order Phthiraptera Haeckel,
1896

Suborder Amblycera Clay, 1970

Family Mammalophagidae
Kumar, 2004

Genus Amblyceropsis n. gen.

(Genotype : *Amblyceropsis indica* n. gen. and n. sp.)

Etymology : Named after amblyceran insect.

Generic Dignosis: It probably shows fused pro-meso-and metathorax while in living Amblycera prothorax is free, meso-and metasterna are fused together but meso-and metanota of pterothorax may be separate. Clubbed antennae are situated on posterior portion of head while they are on anterior portion of head in extant Amblycera. Presence of comb shaped setae (Css) (Pl. I, fig. 7).

Amblyceropsis indica n. sp.

(Pl. I, figs. 1-8; figs. 1a-c, 3)

Holotype: BSIP slide No, 12051

Etymology: Named after India

Diagnosis: The Chewing mouthparts consist of three pairs of vertically arranged mandibles. They are sclerotised, cone shaped and each with anteriorly directed tooth (Pl. I, fig. 8). There is one pair of maxillary palp. These mouthparts are underside the head, but are slightly projected anteriorly outside (Pl. I, fig. 6)

Description : The head, thorax and abdomen of this amblyceran fossil species is discernible (Pl. I,

figs 1,6,8). The large, more or less rounded head is wider than long also wider than thorax and its anterior margin is flat as well as without ventral spinous head processes. The chewing mouthparts consist of three pairs of vertically arranged mandibles. They are sclerotised cone shaped and each with one anteriorly directed tooth (Pl. I, fig. 8). There is one pair of maxillary palp. These mouthparts are underside the head, but they are slightly projected anteriorly outside of head (Pl. I, fig., 6). The head gradually narrows towards front with side edges folded inside slightly arch like manner and front end of clypeus is almost straight. One pair of clubbed, many segmented exposed antennae (Pl. I, figs. 2,3,6,8) are present which arise from sockets or grooves and their three parts flagellum, pedicellus and scarpus can be clearly demarcated (Pl. I, fig. 8). The leathery thorax is with probably fused pro- meso- and metathoracic regions (Pl. I, figs. 1, 6, 8) only two broken legs are on left side and three broken legs are on right side (Pl. I, figs. 2-3,8). Ventrally located thoracic spiracle of left side has been observed (Pl. I, figs. 2-3). The segments of sac-like leathery abdomen are indistinct but four distinct abdominal segments have been observed (Pl. I, figs.4-5). The definite rows of simple short setae, although less in number, have been observed on dorsal abdominal segments (Pl. I, fig.6). Abdomen bears comb shaped lateral setae (Css) (Pl. I, fig. 7). Three pairs of spiracles are present in abdomen (Pl. I, figs. 4,5,7). The male genitalia is simple and is partially extruded posteriorly from the abdomen (Pl. I, figs. 4-5, 7-8). Head, thorax, abdomen and legs are yellowish brownish and with endoskeleton structures.

Remarks: It is included in Amblycera because of its flat shape, minute size, prognathus head which is wider than long and other characters that resembles with living Amblycera which parasitize mammals (see Emerson & Price, 1975). Presence of comb-shaped setae on this specimen is the primitive feature of Amblycera (Bedford, 1932). An extruded genitalia (Pl. I, fig. 7) as observed in this specimen is generally found in living Amblycera. Two flap-like structures present near genitalia have resemblance with living chewing lice, *Eiconolipeurus inexpectatus* (see Emerson, 1967). Due to its some primitive characters. e.g. cone-shaped mandible, simple male genitalia. it

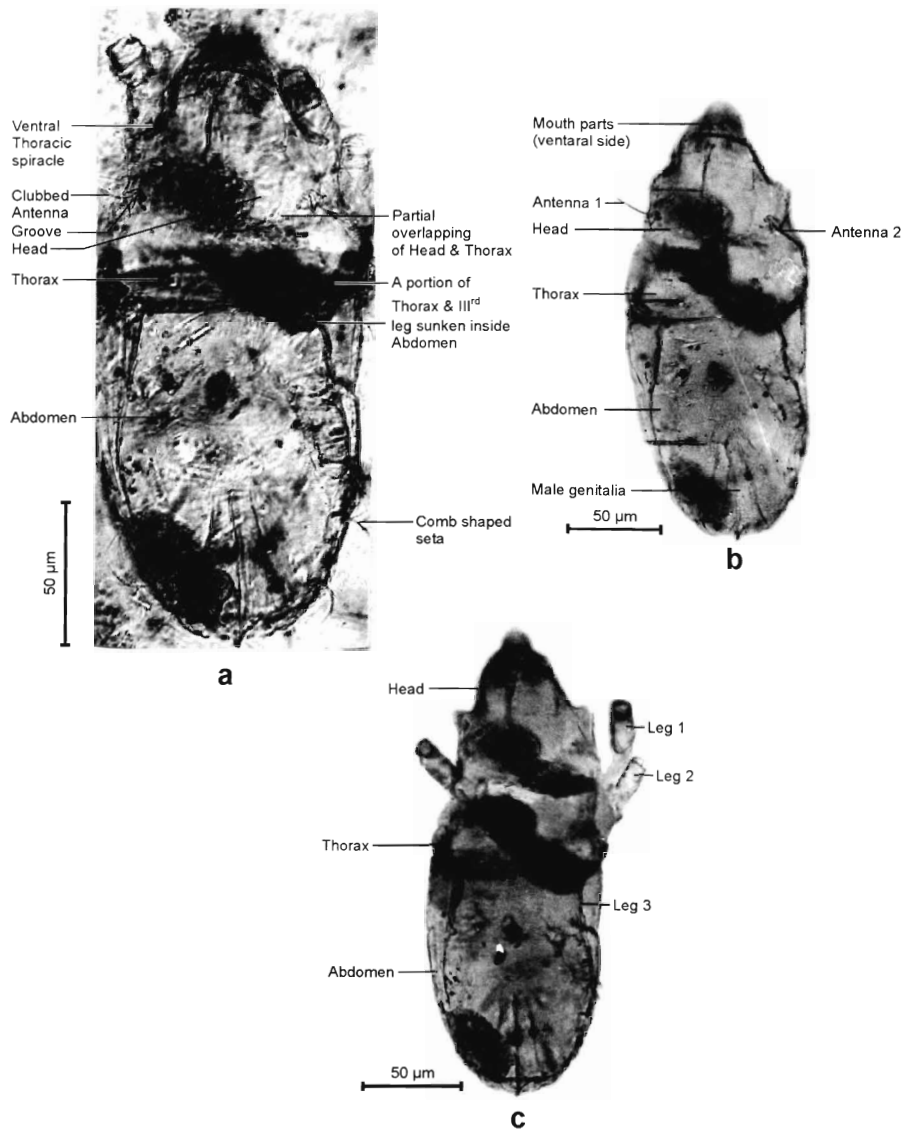


Fig. 1 a-c. Reconstruction of the fossil phthirapteran insect *Amblyceropsis indica* n. sp.

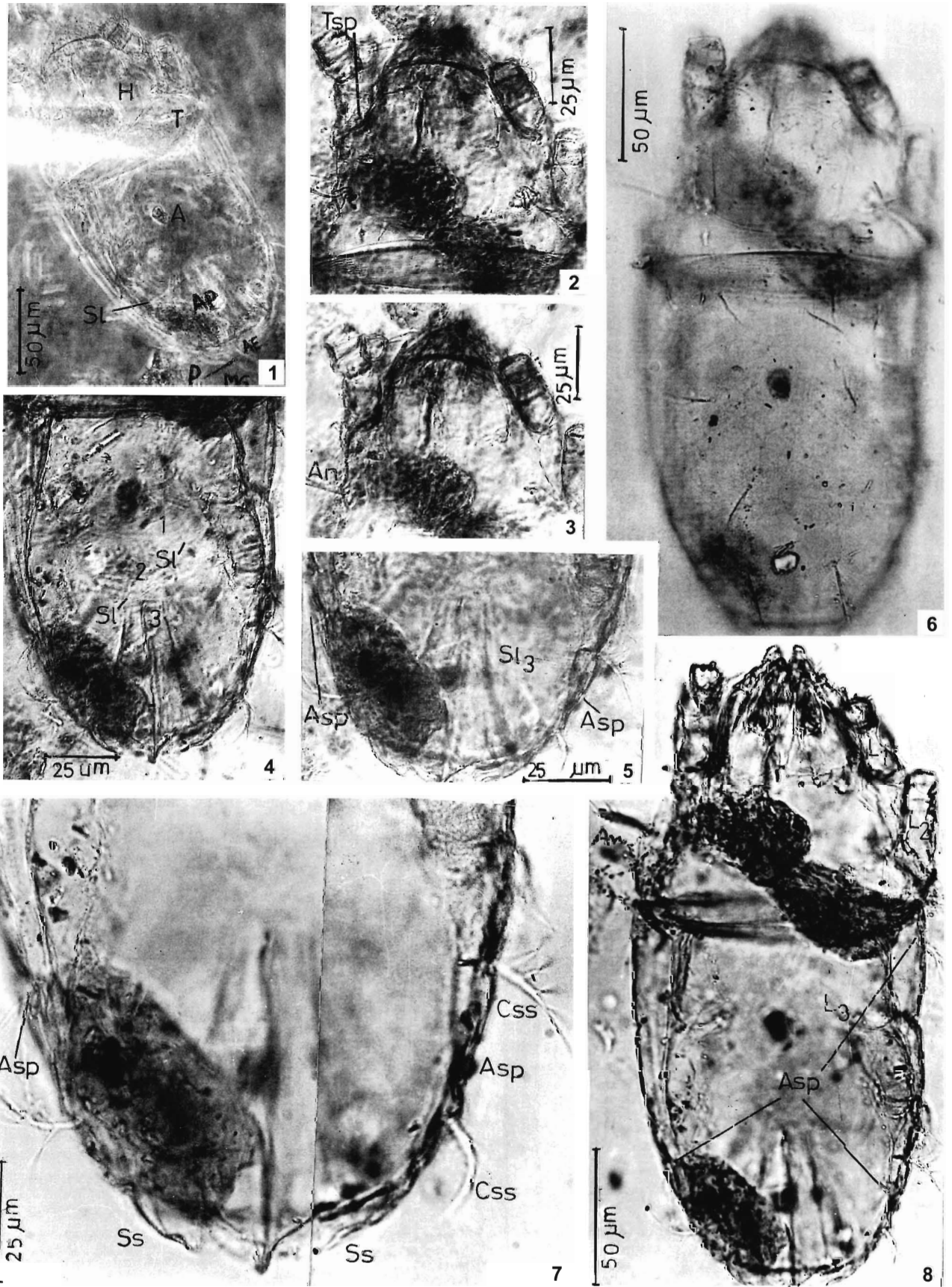
EXPLANATION OF PLATE I

Amblyceropsis indica n. gen. & n. sp.

1. Complete dorsal view of fossil amblyceran insect showing three parts of a typical insect- Head (H), thorax (T) and abdomen (A) with a segmental line (Sl) indicating segments. male genitalia (MG) Basal apodeme (AP), Paramere (P), and Aedeagus (AE). BSIP slide no. 12501
2. Head dorsal view showing clubbed antennae of both sides and their origin from a socket or a groove, endoskeleton of head, ventrally located thoracic spiracle (Tsp).
3. Head as above showing head, its endoskeleton, more clear clubbed antenna (An.) and socket of one side.
4. Abdomen, ventral view showing two-three segmental line (3 segments- 1, 2, 3), two abdominal spiracles (Asp).
5. Terminal segment of abdomen showing clear, 3rd segmental

line (Sl₃) and one abdominal spiracle each on different segments of abdomen (Asp). →

6. Complete dorsal view of entire insect showing three regions of body – Head (H), thorax (T) and abdomen (A), clubbed antennae and sockets. A portion of thorax is sunken inside abdomen. Four rows of abdominal setae and one segmental line.
7. Terminalia of insect showing extruded male genitalia, two abdominal spiracles (Asp) on different abdominal segments, two spur like structures (Ss) near genitalia and comb shaped setae (CSs) a primitive feature of Amblycera
8. Complete ventral view of entire amblyceran insect showing three regions of body, mandibles, three legs (L₁, L₂, L₃), two spiracles, comb shaped setae and clubbed (Antenna (An).



is considered to be the earliest Amblycera and may be called as Protoamblycera.

Type Horizon: Bagra Formation, Mahadeva Group (Triassic).

Type Locality: Khatama caves, Hoshangabad District (Satpura Basin), M.P.

The new fossil form assigned to Anoplura differs from present-day anoplurans in having separate pro-, meso- and metathorax which are fused in extant forms of this groups.

Suborder Anoplura Hopkins, 1949;
Clay, 1970

Family Khatamammalophagidae
Kumar, 2004

Genus Anopluropsis n. gen.

(Genotype: *Anopluropsis khatamaensis*
n. gen and n. sp.)

Etymology : Named after anopluran insect.

Generic Diagnosis: All parts of thorax (pro-, meso-, and metathorax) are free.

Anopluropsis khatamaensis n. sp.

(Pl. II, figs. 1-9; figs. 2a,b, 4)

Holotype: BSIP Slide No. 12350.

Etymology Named after Khatama caves.

Diagnosis Thorax is leathery in appearance, wider than head, pro-, meso- and metathorax clearly demarcated. Metathorax larger than pro- and

mesothorax (Pl. II, figs. 1, 4-5, 7-8).

Description: As stated above the body of anopluran fossil specimen is elongated in shape and more or less dorsoventrally flattened. It is without external evidences of eyes and also without sclerotized abdominal plate. Its colour is whitish cream. The solid sharpened or pointed, free and horizontal head is longer than wide and narrower than thorax as well as more or less rounded (Pl. II, figs. 1,5,7). Antenna of one side is visible. Head has no definite postantennal and posterolateral angles but its lateral margin is strongly convex. Mouth is terminally located and mouthparts are retractile, piercing and sucking type, hence true bloodsucker. Actual mouthparts are kept retracted within head and only small circular tube, haustellum with a circle of chitinous teeth or hooks at the foremost parts of head is present (Pl. II, figs. 2,5,8). These minute teeth or hooks are used for anchoring the insect to its host during feeding but at rest they are kept inverted within tube.

Thorax is leathery in appearance, wider than head and three parts pro-, meso- and metathorax are clearly demarcated. Metathorax is larger than pro- and mesothorax (Pl. II, figs. 1, 4-5, 7-8). Probably there is one thoracic spiracle on left side. A part of coxae of fore legs are evident as rounded structures (Pl. II, figs. 4-5, 7-8). The largest part of the body abdomen is completely leathery, sac like, oval without distinct tergal, sternal plates but paratergal plates are there, a few segments (three) are discernible (Pl. II, figs. 6,9) and six spiracles lie on one lateral side of abdomen that suggests abdominal segmentation (Pl. II, fig. 6).

EXPLANATION OF PLATE II

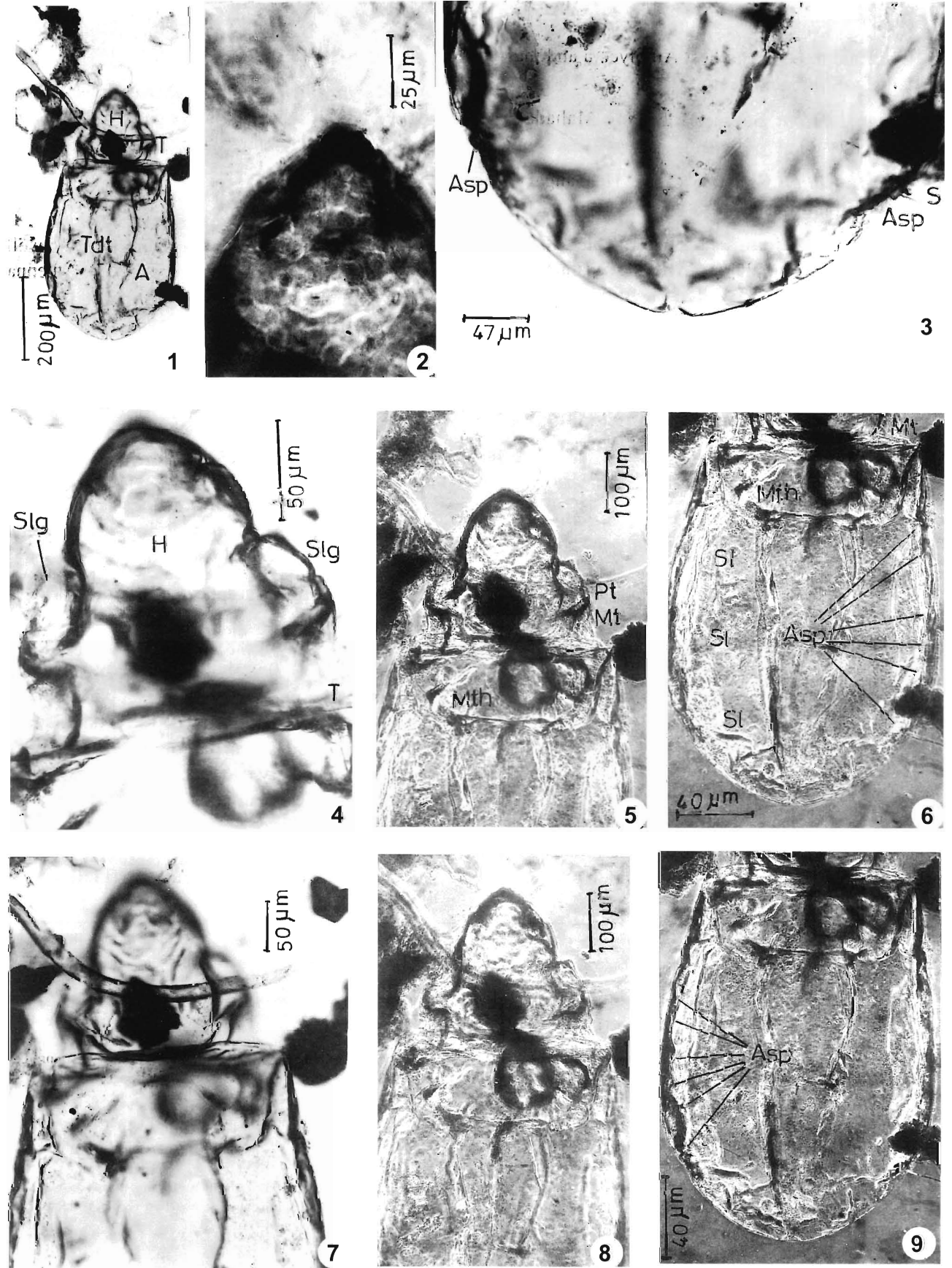


Anopluropsis khatamaensis n. gen. and n. sp.

1. Complete dorsal view of fossil anopluran insect showing three parts of a typical insect - Head (H), thorax (T) and abdomen (A) and tubular digestive tract (Tdc, a characteristic feature of an insect), BSIP slide no. 12350.
2. Anterior most part of head showing mouth, a tube (haustellum), outer rim probably with fine teeth or hooks.
3. Terminalia of insect showing two abdominal spiracles (Asp), one on each side of different abdominal segments, one seta (S) near one spiracles.
4. Head (H), and thorax (T) of insect showing two spaces for anterior most legs (Slg).
5. Same as above with some portion of abdomen and haustellum.

It shows demarcation of pro- (Pt), meso-(Mt) and metathorax (Mth) and first pair of abdominal spiracles.

6. Mesothorax (Mt) (a part), metathorax (mth), (largest, sunken inside abdomen), abdomen showing six abdominal spiracles (Asp) on one side and three feeble segmental line (Sl) on abdomen.
7. Insect showing Head (H), thorax (T) and abdomen (A) with first pair of abdominal spiracles.
8. Same as above with clear tube of mouth parts.
9. Mesothorax, metathorax and abdomen of insect with six abdominal spiracles on one side and two feeble segmental line on abdomen.



Pl.II, fig. 9 shows six spiracles of other side and Pl. II, fig. 3 shows two spiracles on different segments. One seta is near one spiracle. Its lateral curves are unbroken. A tubular digestive tract is clearly visible (Pl. II, figs. 1, 6, 9).

Remarks: It is included in Anoplura because of its structure, minute size, flat, terminally located mouth, piercing and sucking mouthparts (which are retractile in nature), head conical, narrower than thorax as in living Anoplura (Touleshkov, 1955) and prognathus head which is longer than wide. Due to its primitive characters, it may be termed as Protoanoplura. Tubular digestive tract (Tdt) of this specimen (Pl.II, figs. 1,6,9) is a characteristic feature of an insect (Ross, 1965). Lateral curves of the specimen are unbroken as in *Linognathus*, Ox louse, an extant (modern) insect (Roy and Brown, 1970).

Type Horizon: Denwa Formation, Mahadeva Group (Triassic).

Type Locality: Khatama caves, Hoshangabad District (Satpura Basin), M.P.

Key for amblyceran fossil insect

Extant Amblycera: Head normally broader than long and also broader than thorax, biting and chewing mouthparts sclerotised mandibles large with more than one tooth and horizontally arranged, antennae four or five segmented, short and concealed at the side of the head, usually free prothorax but fused meso- and metathorax which forms pterothorax, generally six pairs of spiracles in abdomen.

Fossil Amblycera: Sclerotized large six cone shaped mandibles with one anteriorly directed tooth in each cone and they are vertically arranged (Pl. I, fig. 8), clubbed many segmented exposed antennae, probably pro-, meso- and metathorax fused (Pl. I, figs. 1,6,8), three pairs of spiracles in abdomen (Pl. I, figs. 4-5, 7-8) ...*Amblyceropsis* n. gen. and n.sp.

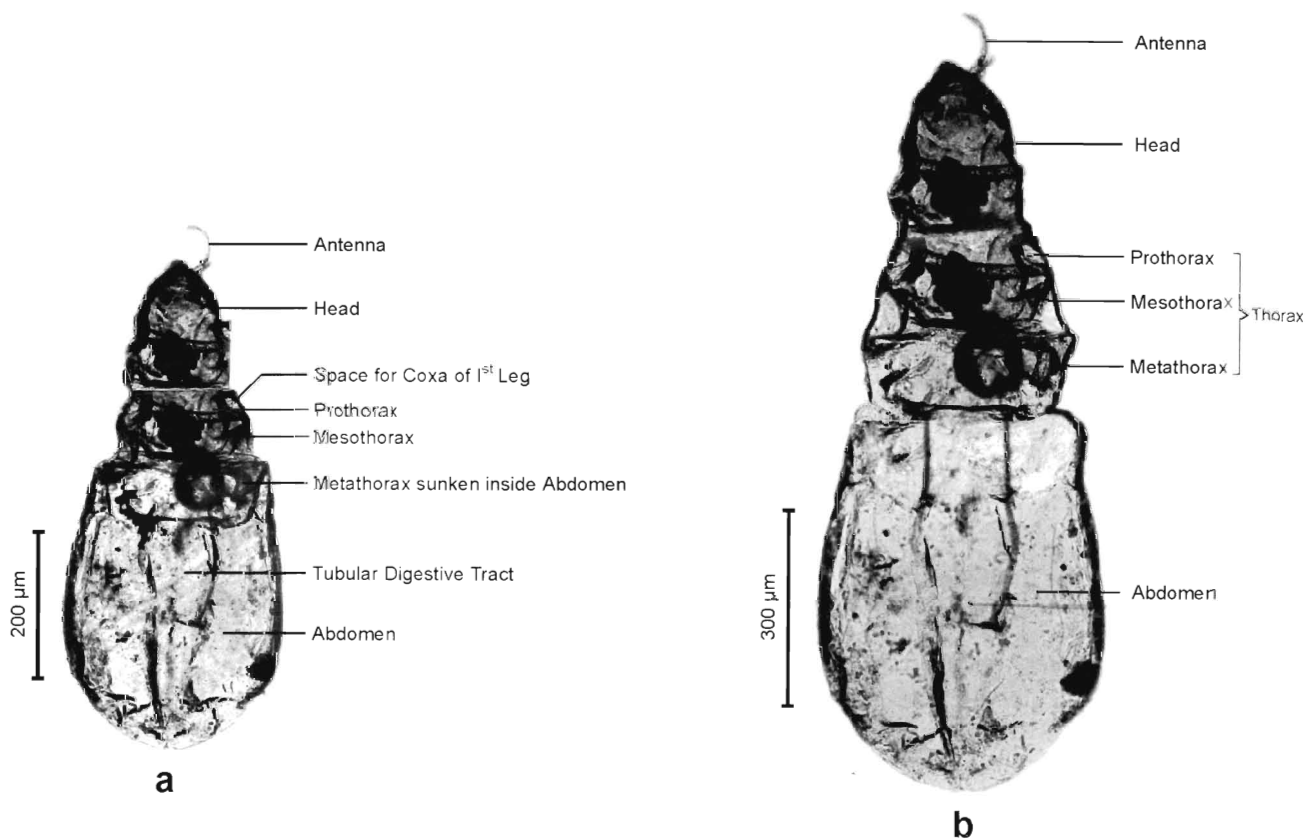


Fig. 2 a-b. Reconstruction of the fossil phthirapteran insect *Anopluropsis khatamaensis* n. sp.

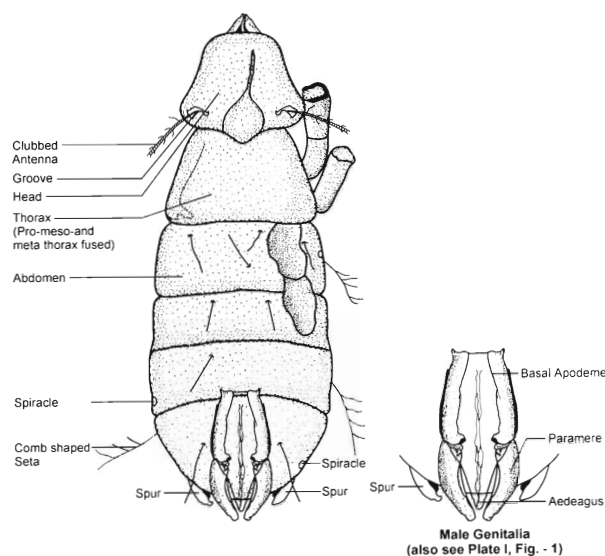


Fig. 3. Line drawing of *Amblyceropsis indica* n. sp. (not to scale)

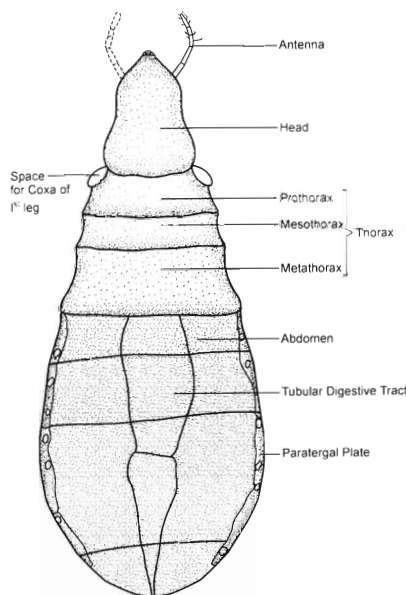


Fig. 4. Line diagram of *Anopluopsis khatamaensis* n. sp. (not to scale).

Key for anopluran fossil insect

Extant Anoplura: Head conical, usually longer than broad, mandibles apparently absent, retractile piercing and sucking mouthparts, pro-, meso- and metathorax completely fused in a mass.

Fossil Anoplura: Free pro-, meso- and metathorax; metathorax, larger than pro- and mesothorax (Pl. II, figs. 4-5, 7-8) ... *Anopluopsis* n. gen. and n. sp.

Figs. 1a-c, 2 a-b, 3 and 4 show insect character of the present fossil forms, as three parts of typical insects, head, thorax and abdomen are clearly discernible in them and antennae are present in both the specimens. As the head and thorax in both these specimens overlap each other and a portion of thorax is sunken inside the abdomen, these are reconstructed to show clearly their different parts of the body. Figs. 1 a-c and 3 represent an amblyceran insect because this apterous insect is very much flattened dorsoventrally. It has mandibles and its ventral thoracic spiracle is visible. Head and thorax bear endoskeleton and segmented abdomen with three pairs of spiracles. The arrangement of setae is of amblyceran type. Comb-shaped setae are also there which were found in early Amblycera. Head capsule is large and horizontal in position and temple and gula are present (Price *et al.*, 2003). Antennae arise from groove. Male genitalia (MG) is represented by a median eversible aedeagus (AE), parameres (P) are traceable (Pl. I, fig. 1) and two spur-like structures at the end of abdomen. Cerci absent. It is Protoamblycera as it differs in some characters from recent Amblycera and due to evolutionary processes it may evolve in the present forms of Amblycera as for example size of cat like horses evolve in the present form of horses. The head of this fossil insect somewhat resembles the head of *Gyropus ovalis* (see Price and Graham, 1997).

Figs. 2 a-b and 4 represent an anopluran insect as this elongated apterous insect is dorsoventrally flattened. Its head resembles the head of *Pediculus* or other sucking lice. Mouthparts are piercing and sucking type. Abdomen has six pairs of spiracles. Cerci absent. Paratergal plates are also visible. These structures resemble *Pediculus* or other sucking lice, though there is some difference in structure; therefore, it is Protoanoplura and it may evolve to present-day Anoplura due to evolutionary process. The visibility of particular organ or a part of body mainly depends on preservation during fossilisation.

DISCUSSION

According to Packard (1887), lice are related to free-living book or bark lice (Psocids) of the Order Psocoptera. It is generally accepted that both chewing and sucking lice descended from Psocid-like ancestors

(Price and Graham, 1997). Osborn (1891) explains that development of parasitic habit of chewing lice and Anoplura progressed from a free living state through a semiparasitic form (which sometimes fed both on plants and vertebrate hosts) to a modern parasite mode. Modern taxa are derived from a common ancestral stock. Due to scarcity of food and other factors in environment, these insects changed their free life and adopted parasitic mode of life in which problem of food was solved. Therefore, morphological and other isolation for better adaptation occurred in these insects. Both groups of lice are highly host specific and parasitize only a single animal species or a small group of closely related animals (Kim and Ludwig, 1978a; Emerson and Price, 1985). It is hypothesized that primitive ancestor of parasitic lice of today invaded new habitat (animal skin and deposit of skin debris) in the geological past and gradually adapted to parasitic mode of the life (Kim and Ludwig, 1978a).

Anatomy of recent anopluran lice is most clearly related to Ischnocera and Rhynchophthirina; this suggests that Anoplura arose from Ischnocera Trichodectid like stock, living on early mammals and undergoing considerable specialization of their own in the structure of mouthparts and fusion of thoracic segments as well as loss of tentorium (Richards and Davies, 1983). Clay (1970) also opined that Anoplura were derived from Ischnocera but this plea was rejected by Kim and Ludwig (1978b) who suggested that Anoplura arose from a single ancestor, a primitive Psocodean, and similarities between Anoplura and Amblycera and other chewing lice could be explained as the result of parallel or co-evolution (which occurred due to similar habits and adaptive roles). Clay (1970) placed all ectoparasitic lice in the Order Phthiraptera and Haub (1980) supported it.

Insects of amblycerans are most primitive and ischnocerans are less primitive as they evolved later (Clay, 1970; Butler, 1985). Some genera of amblycerans have patches of setae on ventral surface of legs and abdomen (Bedford, 1932). Similar comb-like setae are also visible in the present fossil insect (Pl. I, figs. 7-8). Insects of amblycerans are closer in their habits and morphological characters to their free-

living Psocid-like ancestors than other members of chewing lice (Hopkins, 1949). The species from mammals are found only on more primitive living mammals (Emerson and Price, 1985).

It is believed that anoplurans are a monophyletic group, which achieved a major change in their feeding habits when they began to ingest blood during the Late Cretaceous or early Palaeocene (Kim and Ludwig, 1982). Anoplura must have existed in Mid Cretaceous Period (Hopkins, 1949). A phylogeny of Anoplura was prepared by Kim and Ludwig (1978a) on the basis of study of evolution of mammalian hosts, because anopluran fossil was not recorded at that time. As both specimens have been found in the same area, parallel or co-evolution is evident. This view is also supported by Kim and Ludwig (1978b).

Chewing lice and Psocoptera share specializations in sitophore sclerite, sclerotized filament hypopharynx, etc. These indicate that chewing lice have arisen from Psocoptera-like stock and it is also clear that they share several specialized features with sucking lice which include reduced antennae, eye, spiracular arrangements and small number of nymphal instars in their life history (Konigsmann, 1960). Insects of amblycerans are markedly more primitive than a group comprising Ischnocera, Rhynchophthirina and Anoplura, hence it has been advocated that phylogenetic relationship of these groups would be better expressed by a classification in which a single order Phthiraptera is divided into four subordinate groups: Amblycera, Ischnocera, Rhynchophthirina and Anoplura (Keler, 1957).

The modern insect fauna is the result of eons of change and evolution as well as a struggle for existence among them. Both fossil species resemble those that are ectoparasite more on mammals than birds (see Emerson and Price, 1975). The morphological characters present in these two fossils described here may represent the primitive features of early insects during the Triassic time, and hence they may be termed the Protoamblycera and Protoanoplura, respectively.

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