

Article

Discovery of the Puparia of a Whitefly Species Found on Malvaceae in the Pliocene Rajdanda Formation, Jharkhand, Eastern India

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Abstract: A new genus and species of fossil whitefly, *Praealeurolobus indicus* gen. et sp. nov., is described and illustrated based on puparia found on leaves of a malvaceous plant from the Pliocene Rajdanda Formation in Eastern India. It is the first record of whitefly puparia on leaves from the Neogene deposits of Asia and the second taxon formally named and described from such adpression fossils. The cephalothorax of some of the puparia has a large, irregularly shaped hole with jagged edges, typical of the emergence holes of parasitoids of modern-day whiteflies and represents the earliest record of parasitism on whiteflies. This finding enriches our knowledge of the fossil record of Aleyrodidae in connection with allied fossils and provides new insight into the ecological interactions of the palaeobiota and taphonomy of fossils preserved in the Pliocene Rajdanda Formation.

Keywords: whiteflies; aleyrodidae; sternorrhyncha; hemiptera; *Praealeurolobus indicus* gen. et sp. nov.; new genus; new species; puparium; parasitism; Malvaceae; host plant relationships; Pliocene; Indian subcontinent; *Aleurolobus*



Citation: Drohojowska, J.; Evans, G.A.; Khan, M.A.; Hazra, T.; Szewdo, J. Discovery of the Puparia of a Whitefly Species Found on Malvaceae in the Pliocene Rajdanda Formation, Jharkhand, Eastern India. *Diversity* **2023**, *15*, 564. <https://doi.org/10.3390/d15040564>

Academic Editors: Uwe. Kaulfuss and Michael Wink

Received: 9 March 2023

Revised: 30 March 2023

Accepted: 13 April 2023

Published: 17 April 2023



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1. Introduction

Hemiptera represent the only order of hemimetabolous insects among the five largest insect orders; the remaining ones, the Coleoptera, Diptera, Hymenoptera, and Lepidoptera, are holometabolous. Among the Hemimetabola, it is the most species-rich insect order and is comprised of 330 extinct or extant families, which is the highest number of families known among the orders of insects. The evolutionary success of the Hemiptera is indicated by its diversity (number of included species) and its disparity (extent of morphospace occupied by its members). The diversification in the life history of species of Hemiptera began during the Carboniferous period, yielding specialized morphological adaptations that enabled these insects to occupy various terrestrial and aquatic habitats and to exploit various food sources. In Hemiptera, the mouth part is uniquely formed into an elongated rostrum. The mandibles and maxillae are modified into long, pointed shafts, while the palps are completely absent; the labium forms an almost complete tube containing the stems, and the labrum closes the remaining gap in the rostrum. The latter, most often, is directed backwards under the head. Apart from a few exception species, all Hemiptera pierce and suck fluids from plant tissues, mainly vascular plants. These extreme modifications of the mouthparts are an adaptation to feeding on liquid plant or animal food [1,2]. The order is divided into six suborders: extinct Paleorrhyncha, and extant Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha, and Heteroptera. Hemipteran insects are ophiophagous, feeding on plant phloem, xylem, and cell content, members of several lineages such as whiteflies, psyllids, and aphids, belong to the most destructive agricultural

insects known worldwide; at the other end of the hemipteran trophic spectrum, some heteropterans are predatory or hematophagous, being notorious medical pests, e.g., bed bugs and kissing bugs [2–4]. The sedentary lifestyle of sternorrhynchs, coupled with their phloem-feeding behavior, has driven morphological reductions and losses, neoteny females, extreme sexual dimorphism, convergently derived morphological characters, and neoteny (the retention of immature characters in the adult stage).

The consensus opinion treats the Sternorrhyncha as monophyletic lineage consisting of about 19,000 nominal species in 4 extant lineages: infraorders Aphidomorpha—the aphids, Coccidomorpha—the scale insects, Aleyrodomorpha—the whiteflies, and the superfamily Psylloidea—the psyllids. The fossil record of Sternorrhyncha can be traced back to the Permian [5], but the early stages of their evolution and diversification are poorly understood. In addition to these four extant lineages, three extinct infraorders have been distinguished. The Pincombeomorpha and Naibiomorpha are placed variously in classifications and are hypothesized to be more related to aphids and scale insect lineages; the Dinglomorpha are a sister group to Aleyrodomorpha; and the relationship of the extinct superfamily, Protopsyllidoidea, is debatable [5–7].

Whiteflies belong to the infraorder Aleyrodomorpha Chou, 1963 [8], which consists of a single family, the Aleyrodidae Westwood, 1840 [9]. Currently, the family is subdivided into four subfamilies: the Bernaeinae Shcherbakov, 2000 [10] which are only known from the fossil record, and the Aleyrodinae Westwood, 1840 [9], Aleurodicinae Quaintance et Baker, 1913 [11], and Udamoselinae Enderlein, 1909 [12], which contain both extant and fossil species. The Udamoselinae contain two South American species in a single genus and are of dubious taxonomic status [13] because of their similarity to the species of Aleurodicinae. Aleyrodids are commonly called whiteflies due to the presence of powdery secretion, which is often white and preened over the bodies and wings of the adults of almost all species. As in other sternorrhynchs, whiteflies use plant sap (phloem) as their diet and most of them are closely associated with particular host plants [1,13,14]. If the numbers of the described species are an accurate guide, then whiteflies are by far the least speciose of the four infraorders of sternorrhynchs, with around 1707 currently valid species [13]. The fossil record of the family Aleyrodidae reaches back to the Late Jurassic [10,15]. Other fossils (but only a few formally described species) have been reported from the sedimentary deposits and fossil resins aged as Lower Cretaceous, Upper Cretaceous, Paleogene, and Neogene [10,15–29]. Findings of the puparia of fossil whiteflies on their fossil host plants are very rare [17,26,30–32], and only solitary specimens have been found so far. *Aleurochiton Petri* Rietschel, 1983 [17] is the only fossil whitefly described from the puparial stage, whereas the other species are described from the adult stage, with the possible exception of *Aleurochiton eozaneticus* Weigelt, 1940 [30], which Weigelt [30] mentioned as being a puparium found on the leaf surface, from the Middle Eocene Fossil Lagerstätte Geiseltal in Germany. Unfortunately, he gave no diagnosis or other features allowing a recognition of the identity of this fossil; therefore, the name was recognized as a *nomen nudum* by Drohojowska et al. [25].

2. Material and Methods

Insect impressions were collected from an outcrop of upper Neogene (Rajdanda Formation) sediments exposed on the left bank of the Birha River in the Mahuadanr Valley (23.3965° N, 84.1066° E; 353 m a.s.l.), Jharkhand, Eastern India (Figure 1). The fossil specimens (Figures 2–5) were extracted manually from the shale layer. The overburden was removed using hand tools (hammers, chisels, small picks, awls, and brushes) until their edges were clear, revealing the extent of the fossil specimens. The impressions were then washed in water, followed by scrubbing with a brush and rinsing with clear water. Photographs were taken using a digital camera (Canon EOS 1500D; Canon Inc., Tokyo, Japan). Close-up views of the specimens were taken using an incident light (Zeiss Stemi Stereo SV 11) and transmitted light compound microscope (Zeiss Axioskop 40; Carl Zeiss AG, Oberkochen, Germany). In addition, we used Carl Zeiss's inverted fluorescence

microscope (Zeiss Axio Vert 40C; Carl Zeiss AG, Oberkochen, Germany) with a green filter cube (510–530 nm excitation band) to better investigate the detailed morphological characters of the recovered fossil specimens. We used a Zeiss microscope with transmitted light: halogen lamp, LED (wavelength 400 to 700 nm, peak at 460 nm); reflected light: HBO 50, HBO 100, HXP 120 C, LED modules (Carl Zeiss AG, Oberkochen, Germany) (wavelength, nm): 365, 385, 420, 445, 455, 470, 505, 530, 590, 615, and 625 or neutral white: 540–580 nm. Adobe Photoshop 2022 ver. 23.5.3. (Adobe Inc., San Jose, CA, USA) was used to adjust the brightness, contrast, saturation, and sharpness of the images. Corel Draw ver. 21 was used to illustrate the details of the morphological characteristics of the specimens (Figure 4A) and create a hypothetical reconstruction of the whitefly puparia on the leaf of the Malvaceae plant (Figure 6). The whitefly type specimens (SKBUH/PPL/JH/I2–holotype and paratypes) (Figures 2A, 3 and 4A) and additional specimens (SKBUH/PPL/JH/I3, which are probably dipteran species) (Figures 2B and 5A–F) were examined. All specimens are housed in the Museum of the Palaeobotany and Palynology Laboratory, Department of Botany, Sidho-Kanho-Birsha University, Purulia in West Bengal, India.

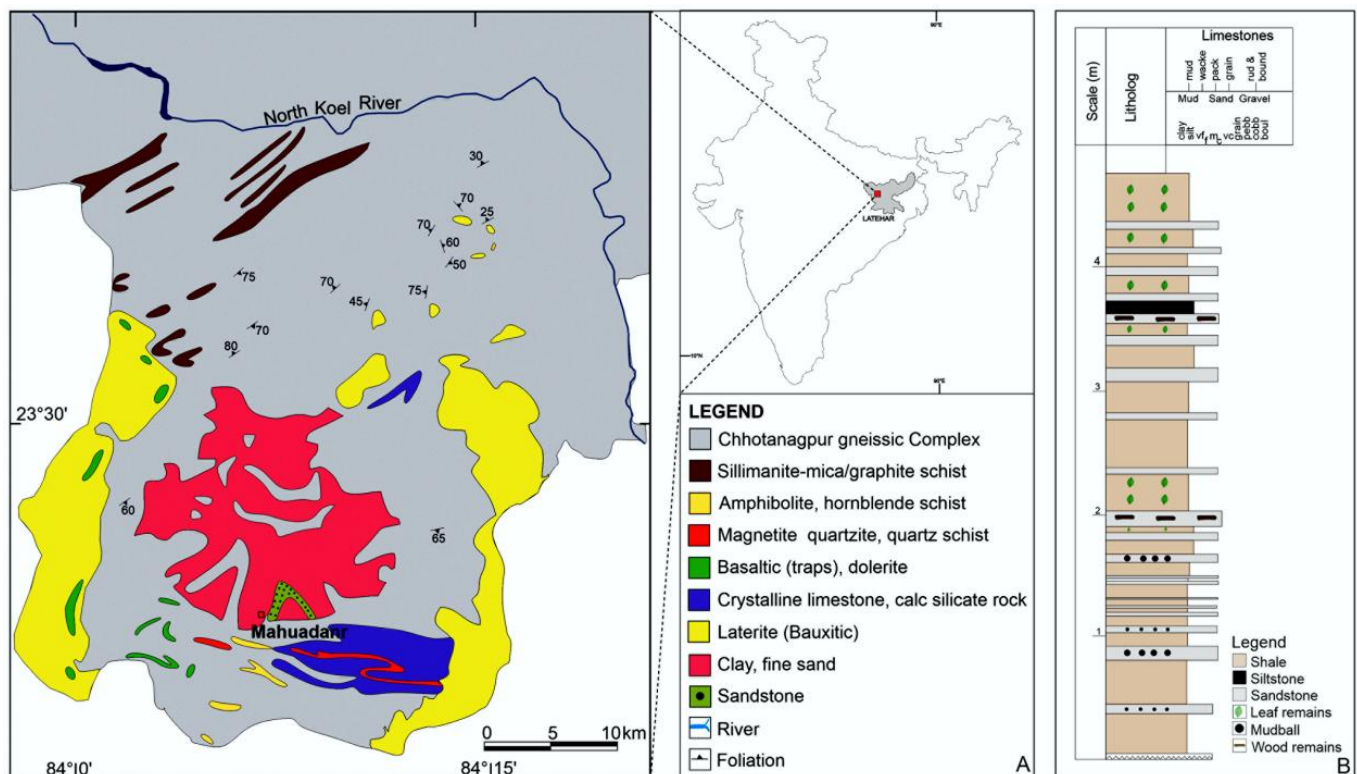




Figure 2. (A) *Praealeurolobus indicus* gen. et sp. nov. Type specimens. A fossil leaf showing well-preserved young puparia of whiteflies (SKBUH/PPL/JH/I2). An asterisk denotes the position of the holotype. (B) A fossil leaf showing probably pupal cases of Diptera (Cecidomyiidae?) (SKBUH/PPL/JH/I3)—position denoted by dotted box. Scale bar = 1 cm.

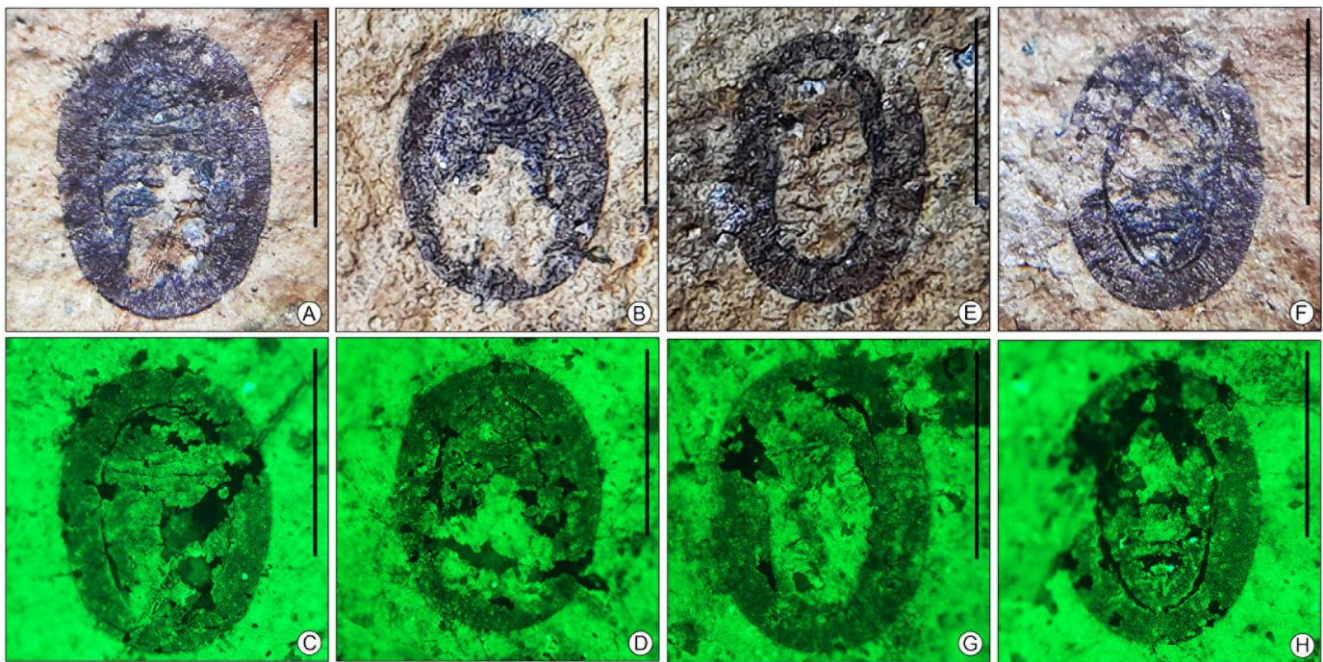


Figure 3. *Praealeurolobus indicus* gen. et sp. nov. Close-up view of specimen SKBUH/PPL/JH/I2. (A,B) and (E,F) stereo-zoom microscopic images of young puparia of whitefly. (C,D) and (G,H) fluorescence microscopy images of young puparia of whitefly. Scale bar = 1 mm.

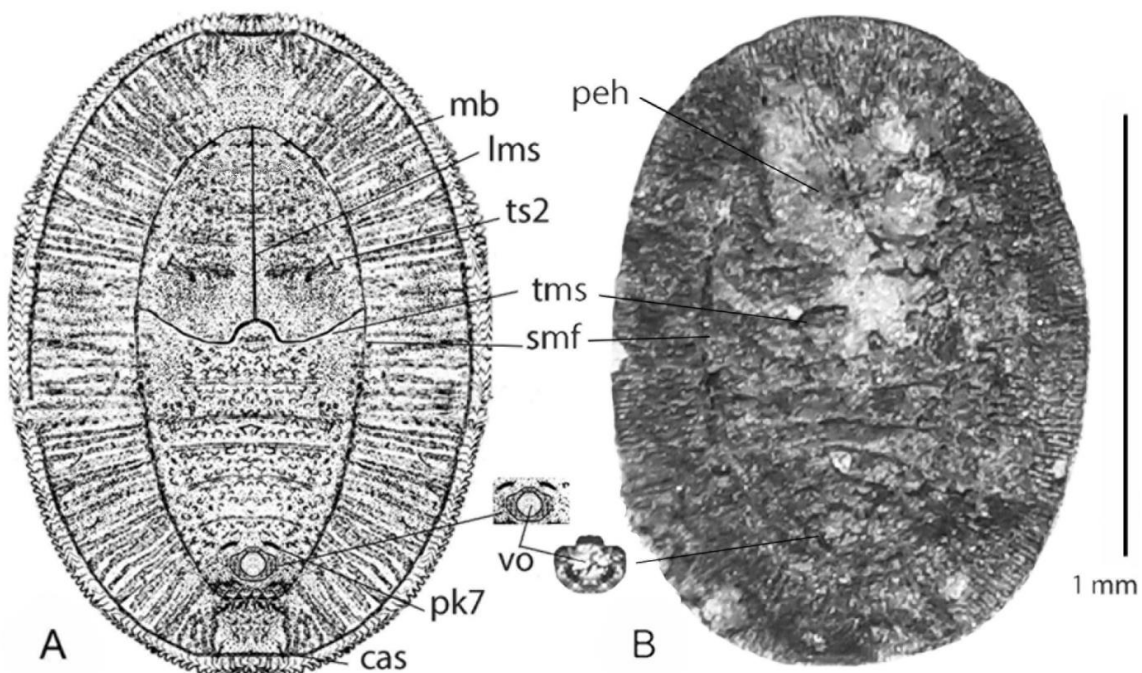


Figure 4. Puparia of *Praealeurolobus indicus*. (A) Line drawing. (B) Scanned image. Abbreviations used: cas (caudal setae), lms (longitudinal molting suture), mb (marginal band), peh (parasitoid emergence hole), pk7 (pockets on 7th abdominal segment), smf (submarginal furrow), tms (transverse molting suture), ts2 (mesothoracic setae), vo (vasiform orifice). Scale bar = 1 mm.

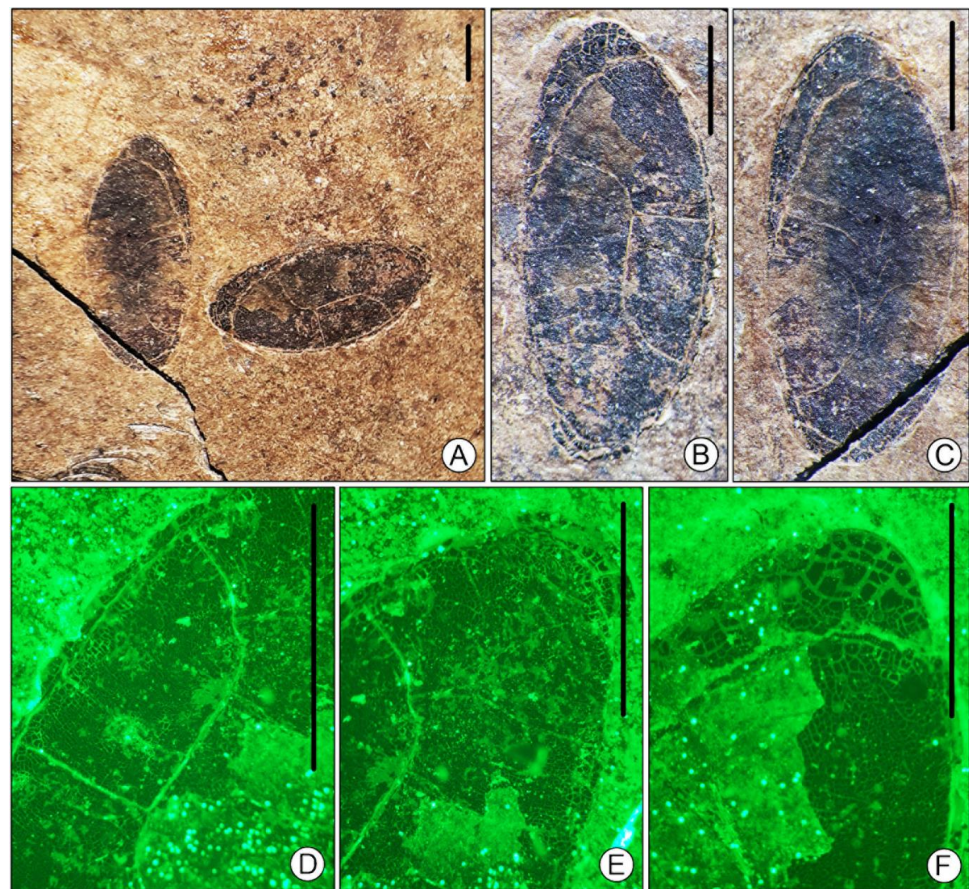


Figure 5. Close-up view of specimen SKBUH/PPL/JH/I3. (A–C) Stereo-zoom microscopic images of dipteran pupal cases. (D–F) Fluorescence microscopy images of the same adpressions. Scale bar = 1 mm.



Figure 6. Hypothetical reconstruction of the whitefly puparia-mediated angiosperm leaf.

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3. Geological Setting

Fossil insect impressions were collected from the latest Neogene sediments (Pliocene) of the Mahuadanr valley within the Chotanagpur Plateau region of Latehar District of Jharkhand, eastern India. Geologically, Chotanagpur Plateau is mainly composed of Archean granites and gneisses, with patches of Gondwana and Dharwar sediments (Figure 1). The sedimentary outcrop from where insect specimens were collected is stratigraphically assigned to the Rajdanda Formation, exposed along the left bank of Birha River, and its tributaries are between Rajdanda and Mahuadanr along a length of approximately 2.6 km and a width of 1.5 km. The surrounding regions have a variety of lithologies, including pyroclastic deposits, conglomerates, sandstones, and shales. The volcanic sandstone contains angular fragments of gneisses, amphibolites, and feldspars [33]. Conglomerate, medium to fine-grained ripple laminated sandstone, and clayey shale make up the sedimentary succession at the base. The lithology in the studied section includes mostly shale (upper 0.5 m of the sedimentary unit) and sandstone. The color of the clayey shale ranges from grey to black, whilst the arenaceous shale has a brownish tint. The clayey shale unit exhibits thin layers that frequently fracture along the plane of deposition into tiny flakes known as “Paper Shale”. Yellowish-brown sandstones are interbedded between the shale layers of the sedimentary unit. This sandstone unit has rounded to elliptical-shaped armored mudballs with covered sand grains. The mudballs are formed from the mudclasts derived from previously deposited clays, which, during transportation, developed a round shape and a sandy coating [33]. The fossil remains are preserved in compact sandstone and dark-colored carbonaceous shale [33]. The stratum yielded many impressed and compressed fossil leaves affiliated with modern thermophilic angiosperm taxa, such as *Albizia* Durazz., *Abroma* Jacq., *Sterculia* L., *Pterygota* Schott & Endl., *Grewia* L., *Thespesia* Sol. ex Corrêa, etc.), carbonized wood fragments similar to *Sindora* Miq. *Terminalia* L., *Lagerstroemia* L., etc.), fruit remains similar to *Engelhardia* Lesch. ex Blume, *Peltophorum* (Vogel) Benth., *Ventilago* Gaertn., etc., and flower impressions similar to *Galactica* P. Browne, *Bombax* L., etc. [33–48]. In addition, fossilized fishes, bird remains, and insects have been also reported from the same formation [33,41,42,46,47]. The excellent preservation of fossil biota suggests a reducing condition during the time of deposition [33]. Clusters of euhedral and anhedral pyrite that occur within the fossiliferous shale layer also indicate the presence of a reducing lacustrine environment with fluvial incursions (possibly during flood events) [49,50]. As of now, no absolute dating is available for this formation, but plant megafossil study and palynological analysis could correlate to being ‘late Tertiary’ (Pliocene) [35–39,51,52]. Occurrences of *Sindora* wood from the same formation typically indicate Pliocene age, as *Sindora* is an index fossil of the Pliocene age [53]. Additionally, the district resource map, as published by the Geological Survey of India of Palamau, Jharkhand, also assigns a Pliocene age to the Rajdanda Formation (https://www.gsi.gov.in/webcenter/portal/OCBIS/pages_pageMAPS/pageMapsSeries; accessed on 7 November 2022).

Host plant: cf. family Malvaceae. The leaves are partially preserved, symmetrical, mesophyllous with incomplete lamina, and have an entire margin; the petiole is not preserved. The primary venation is suprabasal actinodromous, with the primary veins arising from a single point. The secondary venation is brochidodromous, moderately curved near the margin, and irregularly spaced. The angle of divergence is acute. The tertiary venation is percurrent, sometimes branched, oblique in relation to primary veins, and predominantly alternate and distant; the quaternary veins are very faint.

Remarks. The large size, entire margin, suprabasal actinodromous primary venation, and brochidodromous secondary veins are the important characteristics of the fossil leaf. The abovementioned combination of characters shows a close resemblance to modern leaves of the members of Malvaceae. However, due to the incomplete preservation of the

recovered fossil leaves, details of its morphology, such as the characteristics of its cuticle, are not visible and the host cannot be assigned to a particular genus of Malvaceae; *Thespesia populnea* (L.) Sol. ex Corrêa (Malvaceae), known as the Indian tulip, was found recently in the Pliocene Rajdanda Formation [48] and may represent the same species.

4. Systematic Paleontology

Order Hemiptera Linnaeus, 1758 [54].

Suborder Sternorrhyncha Amyot et Audinet-Serville, 1843 [55].

Family Aleyrodidae Westwood, 1840 [9].

Subfamily Aleyrodinae Westwood, 1840 [9].

Tribe Aleurolobini Takahashi, 1954 [56].

Genus *Praealeurolobus* gen. nov.

LSID urn:lsid:zoobank.org:act:DD207F97-1B12-4E52-8991-D9D548BB269D

Type species. *Praealeurolobus indicus* sp. nov.; by original designation and monotypy.

Diagnosis. *Praealeurolobus* is similar to extant species of *Aleurolobus* Quaintance et Baker, 1914 [57] in that it has an oval-shaped body, the dorsal disk divided by a submarginal furrow/ridge which encompasses the body and is not interrupted below the vasiform orifice and has a small trilobed area surrounding the vasiform orifice. It differs from *Aleurolobus* in that the teeth along the margin do not appear to be differentiated at the tracheal opening, the submarginal furrow is uninterrupted under the vasiform orifice, whereas the latter is interrupted below the vasiform orifice in many species of *Aleurolobus* and the dorsum is reticulate at least medially, which is unusual for most extant whiteflies, including *Aleurolobus* species. The genus *Aleurolobus* is one of the largest genera of whiteflies with 91 described species; of these, 64 species were described from the Indomalayan region, of which 54 species were described from India. *Praealeurolobus* may be an early ancestor of modern-day *Aleurolobus* species.

Description. See description of the species; the genus is monotypic so far.

Etymology. The generic name is a combination of Latin prefix *prae-*, meaning before, and the generic name *Aleurolobus*. Gender: masculine.

Praealeurolobus indicus sp. nov.

LSID urn:lsid:zoobank.org:act:3DBB0C03-D71D-4043-8D35-21D1B78D8250

(Figure 2A, Figure 3A–H and Figure 4A,B)

Type material. **Holotype**—Imprint of puparium (specimen marked with an asterisk in Figure 2A), on Malvaceae leaf. No. SKBUH/PPL/JH/I2, deposited in the Museum of the Palaeobotany and Palynology Laboratory, Department of Botany, Sidho-Kanho-Birsha University, Purulia. **Paratypes**—three puparia (specimens marked with a dot) on Malvaceae leaf. No. SKBUH/PPL/JH/I2, deposited in the Museum of the Palaeobotany and Palynology Laboratory, Department of Botany, Sidho-Kanho-Birsha University, Purulia.

Description. The puparium body is broadly oval-shaped, 1.4 mm long by 1.0 mm wide, with a lateral margin with closely set teeth, apparently not differentiated at the tracheal opening, a sub-margin broad with striate sculpturing, divided from the dorsal disk by a submarginal furrow that extends around the entire body, not interrupted below the vasiform orifice, located at about $0.5 \times$ the radius of the body, the latter measured from the intersection of the longitudinal and transverse molting sutures across the transverse suture to the lateral margin, just medial to the lateral margin is another thin band that circumscribes the body and is not interrupted under the vasiform orifice, abdomen with reticulate or pebbly sculpturing, sutures marking the abdominal segments more or less straight, extending laterally to the submarginal furrow, and vasiform orifice located medially above the posterior margin of the submarginal furrow and is roundish with a small trilobed area surrounding it. The chaetotaxy of the dorsal surface is unclear, but it appears to have a pair of caudal and mesothoracic setae and possibly a pair on the eighth abdominal segment; however, the latter may be the pockets located on the seventh abdominal segment. The sculpturing on the puparia in Figure 3C,D,G,H appears to be entirely reticulate; however, a similar pattern occurs on the leaf beside each one, so it may be an artifact. The

cephalothorax of some specimens has a large, irregularly shaped hole with jagged edges, typical of the emergence holes of parasitoids of modern-day whiteflies [57–59].

Etymology. Specific epithet derived from country of specimen origin—India.

Age and occurrence. Neogene, Pliocene, India.

5. Discussion

The recent relative of the genus *Praealeurolobus* gen. nov. described above, viz. *Aleurolobus* Quaintance et Baker, 1914 [60], presents puparia normally black or brown, sometimes pale, oval or rotund in shape, with a lateral margin usually crenulate. The puparium of *Praealeurolobus indica* sp. nov. is oval-shaped; its dorsum has reticulated sculpturing, which is unusual for most extant whiteflies, including *Aleurolobus* species. In *Aleurolobus*, the thoracic and caudal tracheal openings are usually modified with combs of teeth (from two to several) and some ventral stippling is present in the tracheal folds, while in *Praealeurolobus* gen. nov., the teeth along the margin do not appear to be differentiated at the tracheal opening. A concentric dorsal suture-like fold separates the sub-margin from the dorsal disk and is interrupted below the vasiform orifice at the margin of the caudal furrow in most species of *Aleurolobus*, while the submarginal furrow is uninterrupted under the vasiform orifice in *Praealeurolobus* gen. nov. The genus *Aleurolobus* is one of the largest genera of whiteflies with 91 described species; of these, 64 species are described from the Indomalayan region, of which 54 species are described from India. The fossil described herein appears to be closely related to *Aleurolobus*, a member of the tribe Aleurolobini. The Indian taxa of tribe Aleurolobini were reviewed by Regu and David [61] and Dubey and Sundararaj [62]. Manzari and Quicke's [63] cladistical analysis of 430 whitefly species, which included 8 *Aleurolobus* species, revealed that the species in the genus form a clade, but this is not as a monophyletic group. The recent work on whiteflies endosymbionts [64] supported the monophyletic status of the tribe Aleurolobini. Interestingly, the extant *Portiera* endosymbiotic bacteria of the Aleurolobini present a stable gene content, with massive gene loss events occurring only in their common ancestor, and indicate an age of about 70 Mya for the divergence of this tribe. The finding of its fossil representative of the tribe may provide a new impulse for further efforts in studies of these whiteflies to elucidate the phylogeny of the tribe and its members. Several puparia were found in close proximity on the leaf, indicating that *Praealeurolobus indicus* sp. nov. was a gregarious species as opposed to being solitary. The large, irregular-shaped hole in the specimens in Figure 3A,B indicate that the puparia were parasitized and represent the earliest record of a parasitoid associated with whitefly. Among the recent whiteflies, the genus *Aleurolobus* is often parasitized by chalcidoid wasps of the family Aphelinidae, mainly of the genera *Encarsia* Förster, 1878 [65] and *Eretmocerus* Haldeman, 1850 [66], Eulophidae (Entedoninae: Euderomphalini) [67], and sometimes by species of *Amitus* Haldeman, 1850, proctotrupoid wasps of family Platygasteridae (Sceliotrachelinae) [66], and Encyrtidae genus *Metaphycus* Mercet, 1917 in New World [68,69]. As prey, these whiteflies are also attacked by ladybird larvae (Coleoptera, Coccinellidae, Chilocerinae), e.g., of the genus *Brumoides* Chapin, 1965 [70–72]. Aphelinidae and Platygasteridae parasitoids develop within whiteflies nymphs and emerge as imagines from fourth, or sometimes third, instars [57–59]. Parasitoids are estimated to represent up to 20% of the total diversity of extant insects [73], but the origin of this association goes back to the times of the Mid-Mesozoic Parasitoid Revolution [74,75]. This is in congruence with the fossil record of whiteflies, which extends to the Middle Jurassic, as ancient as the first records of parasitoid wasps; therefore, the association of parasitoids and whiteflies seems to be very ancient. Interestingly, Aphelinidae are recorded as fossils since the Eocene Baltic amber, and Platygasteridae since the late Lower Cretaceous of France, and Aleurodinae are recorded from Lower Cretaceous Lebanese amber and Eocene Baltic amber, and the puparium of *Aleurochiton Petri* Rietschel, 1983 is known from Pliocene of Germany [13]. The fossils described above are the first record of whitefly being clearly associated with its host plant. The Malvaceae, the most diverse family within Malvales, was recovered as a monophyletic unit [76,77]. Plants of this family are widely used in agriculture, forestry, and

horticulture, including well-known examples: cotton (*Gossypium* spp.), cacao (*Theobroma cacao*), okra (*Abelmoschus esculentus*), durian (*Durio zibethinus*), cola (*Cola* spp.), baobab (*Adansonia* spp.), and the highly valued ornamental species of *Hibiscus* and *Alcea* [78]. Among the modern Aleurodicinae, 12 species feeding on 8 host plants of Malvaceae are reported [15], and 21 species of Aleurodinae are reported on 39 host plants. The finding of puparia of the new aleurodid *Praealeurolobus* gen. nov. on a fossil representative of this host plant family is very interesting and is an important contribution to the discussions on the relationships of these insects and their host plants. The oldest record of isolated puparia (three specimens) derives from the Berriasian (Lower Cretaceous) of Durlston Bay, Middle Purbeck Group, United Kingdom [32]. A few isolated specimens (six in total) were recorded in the terminal Eocene deposits of the Isle of Wight, U.K. [26,31]. Another isolated puparium, together with fossilized leaves, was found in Pliocene deposits of Neu-Isenburg (Germany) and described as *Aleurochiton petri* Rietschel, 1983 [17], and believed to have fed on maples *Acer* spp. [17]. Weigelt [30] mentioned a puparium found on the leaf surface from the Middle Eocene Fossil Lagerstätte Geiseltal in Germany, and named it *Aleurochiton eozanenicus* Weigelt, 1940 [30], but he provided no diagnosis or other features which could allow the recognition of the identity of this fossil; therefore, the name was recognized as a *nomen nudum* by Drohojowska et al. [24]. Such scarce fossil records of whitefly puparia raise the question which are taphonomic reasons as to why such findings are uncommon, while fossil leaves and traces of feeding are often found [79,80]. It could be bias resulting from overlooking them, because of their size and delicate nature, and/or that the puparia are easily dislodged from leaves during the fossilization processes [81]. Reducing conditions in the lacustrine environment with fluvial incursions (possibly during flood events) during the time of the deposition of the fossils of Rajdanda Formation was postulated from the presence of sandstone mudballs and flame structures, as well as hedral and anhedral pyrite that occur within the fossiliferous shale layer [33,35,49,50]. These events and conditions, method of preservation, and taphonomic traits could be the reason why the puparia were so well preserved on the surface of the leaf. The importance of the fossil record of nymphal stages and their conservatism was recently discussed by Drohojowska et al. [82]; therefore, the findings of the nymphal stages of the sedentary sternorrhynchs and an understanding of their associations with host plants is an important task. Further efforts in understanding taphonomic traits, including experiments in taphonomy [83,84] of whiteflies puparia, are necessary to answer these questions.

6. Conclusions

The fossil record of whiteflies (Hemiptera, Sternorrhyncha, Aleyrodidae) is still fragmentary on both a chronostratigraphic and geographical scale. The identification and description of a new genus and species of aleyrodidae whitefly in the Pliocene deposits add new, important data to these records. The fossil described above enriches the knowledge of the taxonomic diversity of these insects and enlarges the range and understanding of their disparity. Its morphological features provide a window to the characteristics of the early ancestors and the evolution of whiteflies. The fossils described above are unique as they represent the extremely rare case of the preservation of the puparia of whiteflies on the leaf of their host plant, and this is undoubtedly the first case of such a relationship being preserved in the fossil record of whiteflies. Traces of the emergence holes of hymenopteran parasitoids on some of the puparia represent the earliest record of parasitism of these insects on whiteflies. Putting together all these data and their interpretations generates an invaluable source of information on the palaeoecological and evolutionary traits of the whitefly and the association of the whitefly with its host plant and parasitoids. The finding of whiteflies puparia in connection with allied fossils, the palaeoecological and palaeobiological context of these specimens, not only enriches our knowledge of the fossil record of Aleyrodidae but it also provides new insight into the ecological interactions of the palaeobiota of the Pliocene Rajdanda Formation and the taphonomy of the fossils preserved there.

Author Contributions: Conceptualization, J.D., G.A.E., M.A.K. and J.S.; methodology, G.A.E., M.A.K. and T.H.; validation, J.D. and J.S.; formal analysis, G.A.E. and J.S.; investigation, M.A.K., T.H., G.A.E., J.D. and J.S.; writing—original draft preparation, M.A.K., G.A.E., J.D. and J.S.; writing—review and editing, J.D. and J.S.; visualization, M.A.K. and G.A.E.; supervision, M.A.K., J.D. and J.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: All the data used in this study are presented in the manuscript and figures.

Acknowledgments: T.H. and M.K. gratefully acknowledge the Department of Botany, Sidho-Kanho-Birsha University, West Bengal, India, for providing infrastructural facilities to accomplish this work. We wish to thank Uwe Kaulfuss for the invitation to contribute to this Special Issue “Paleoecology of Insects”.

Conflicts of Interest: The authors declare no conflict of interest.

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