The fluvial sandstone of the Pliocene Lower Tipam Formation cropping out at the Amarpur locality, ~65 km SE from Agartala (along the Amarpur-Udaipur road), in Tripura, northeast India, contains an abundance of well-preserved, interconnected chambered trace fossils. These trace fossils resemble nests of social insects such as termites, but previous workers considered them sandstone concretions. These new ichnofossils are described, compared with fossilized and extant termite nests, and named in the present work. The discovery is noteworthy as far as the geology of Tripura state is concerned, as such chambered traces have not previously been reported from the Indian sub-continent. Morphology of the studied specimens point toward a new ichnospecies, *Vondrichnus amarpurensis* isp. nov. of the ichnofamily Krausichnidae.

**Key words**: Chambers, termite nest, boxwork, burrows, fluvial sandstone, Pliocene.

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**INTRODUCTION**

The fluvial sandstone of the Pliocene Lower Tipam Formation cropping out at the Amarpur locality, ~65 km SE from Agartala (along the Amarpur-Udaipur road), in Tripura, northeast India, contains an abundance of well-preserved, interconnected chambered trace fossils. These trace fossils resemble nests of social insects such as termites, but previous workers considered them sandstone concretions. These new ichnofossils are described, compared with fossilized and extant termite nests, and named in the present work. Herein, the documented morphological architecture and distribution patterns of this new occurrence of fossilized nests represents the first trace fossil record related to social insects from the Neogene successions of the Indian sub-continent. The objectives of the present contribution are: (1) to report a new ichnospecies of social insect (termite) trace fossil, and (2) to illustrate the presence of continental ichnofossils from the stratigraphic successions for which no such report was so far available.

**GEOLOGIC SETTING**

The Tripura state lies in the eastern part of India bounded by latitudes 22°56′N–24°32′N, and longitudes 91°10′E–92°21′E within the western flank of the Assam-Arakan Basin. The area is geologically complex and was influenced by two major orogenic episodes: the east-west trending Himalayan orogenic belt situated in the north and the north-south trending Indo-Burmese orogenic belt in the east. The rock successions are folded into a series of sub-parallel, elongated, doubly plunging anticlines trending mainly in a N-S direction that are separated by wide and flat synclines (Nandy, 1972; Nandy et al., 1983). The rock formations in Tripura comprise Palaeogene and Neogene successions subdivided, from oldest to youngest, into the Surma Group, the Tipam Group and the Dupitila Formation (Fig. 1). The continuity of sedimentary successions from Assam (Evans, 1932) has allowed the adoption of the Assam Cenozoic lithostratigraphic scheme for
the Tripura state with minor modifications (Tab. 1). Uplift and exposure of the Surma-Tipam pile of sedimentary rocks constituted the major tectonic episode of this region. After deposition of the Tipam strata, partial submergence of the basin took place when the Dupitila Formation was deposited (Ganguly, 1975; Sarkar and Nandy, 1977).

The Tipam Group is considered to be of fluvial origin based on previous studies (Johnson and Alam, 1991; Nanjundaswamy and Kandwal, 1993; Borgohain, 2012; Jena et al., 2012). Some of the important supporting sedimentological characters are the: 1) development of medium to small-sized incised channels, 15–25 m across as

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**Fig. 1.** Geological map of Tripura (modified from Kesari, 2011). Trace fossil locality is marked with a star. The locality is about 65 km southeast of Agartala, capital of Tripura.
Generalized stratigraphic succession of Tripura, modified from Karunakaran, 1974; Ganju, 1975; Tiwari and Kachhara, 2003; Kesari, 2011).

<table>
<thead>
<tr>
<th>Age Group Formation</th>
<th>Thickness (in m)</th>
<th>Lithology</th>
<th>Depositional environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Pliocene to Lower Pleistocene</td>
<td>Dupitila</td>
<td>?</td>
<td>Sand pockets, fossil wood, thin sand pebble conglomerate common.</td>
</tr>
<tr>
<td>~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~ Unconformity ~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pliocene Upper Tipam</td>
<td>+900</td>
<td>Thick, massive, cross-bedded, medium to coarse grained sandstone; calcareous concretion, coal streaks and silicified wood.</td>
<td>Fluvial</td>
</tr>
<tr>
<td>Lower Tipam</td>
<td></td>
<td>Thick, planar cross-beded, fine to medium grained subarkosic sandstone; siltstone and sandy mudstone.</td>
<td></td>
</tr>
<tr>
<td>Miocene to Upper Oligocene Surma Bokabil</td>
<td>+950</td>
<td>Shales, siltstones, sandstones; conglomerate horizon above.</td>
<td>Shallow marine</td>
</tr>
<tr>
<td>Bhuban</td>
<td>+5000</td>
<td>Sandstones, siltstones, shales. Calcareous sandstone and shell limestone.</td>
<td>Deltaic, shallow marine</td>
</tr>
<tr>
<td>Basement not exposed</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

observed, on the top of the Bokabil Formation, 2) highly variable thickness of the Tipam fluvial wedge, and 3) presence of erosive bases, which are typical of deposition in an actively migrating braided and meandering fluvial system. Johnson and Alam (1991) observed the characteristics of the Tipam strata, such as the coarse-grained units, the large-scale sedimentary structures, including trough and planar cross-bedding with sets as thick as 150 cm, and the vertical sedimentary sequence and suggested deposition in a bedload-dominated (probably braided) fluvial system. Further, they perceived the presence of fine-grained intraformational clasts, which indicated that these rivers were at times flanked by flood plains on which fine-grained sediments were deposited and subsequently eroded. The basal part of the Lower Tipam Formation is characterized by the presence of planar-cross bedded, medium-grained sandstones, carbonate debris and clay and mud lenses.

Figure 2 includes field photographs showing the nature of rock type of Lower Tipam Formation in the fossil locality and occurrence of chambered trace fossils. Figure 3 illustrates the generalized lithostratigraphy of the Tipam Group showing the position of occurrence of the trace fossils described herein. The Upper Tipam Formation consists of coarse-grained, poorly sorted and massive arkosic sandstone with occasional laminated layers of sandy shale, calcareous concretions and fragments of silicified fossil wood. Roy et al. (2006) inferred a semi-humid to humid climatic condition for the deposition of the Tipam Formation.

**SYSTEMATIC ICHNOLOGY**

Ichnofamily KRAUSICHNIDAE Genise, 2004
Ichnogenus *Vondrichnus* Genise and Bown, 1994b

**Type ichnospecies:** *Vondrichnus obovatus* Genise and Bown, 1994b.

**Diagnosis:** Diffuse, polychambered, excavated subterranean systems. Obovate chambers occur in dense swarms of near 300 in cross-section. Burrows simple, branched or unbranched, exiting from one or more points on periphery of chamber and comprising a dense mass of anastomosing burrow that may connect chambers. Sediment in the centre of the chambers is alveolar and commonly arranged in concentric bands. Chambers expanded by apposition of 1–3 chambers against one another (Genise and Bown, 1994b).

*Vondrichnus amarpurensis* isp. nov.
Figs 2, 4–6

**Etymology:** After Ampur in Tripura, India, the locality of its occurrence.

**Holotype and paratype:** One specimen consisting of a chamber and an attached inclined shaft (MIM/IC-001) is deposited in the Mantrimayum Ichnological Museum (MIM) (Manipur, India) as the holotype. Another specimen of a chamber with a near horizontal tunnel (MIM/IC-002) is deposited in the MIM collection as paratype.

**Horizon and locality:** The type locality (N23°30.059′, E091°36.331′; 120 m above mean sea level) represents a fluvial channel succession consisting of medium-grained sandstones with planar cross-bedding. Each of the bed sets in the planar cross-bedded sandstone is about 30 cm thick.

**Diagnosis:** *Vondrichnus amarpurensis* is a diffuse, polychambered subterranean system composed of oblate chambers with an average diameter of 3–4 cm, interconnected by a boxwork of simple, unbranched straight to curving burrows in different horizontal and inclined planes, exiting from one or more points on the periphery of chamber.
Occurrence of between 25–30 chambers in one square metre in a vertical exposure; with 1–3 chambers in apposition. Chambers are internally structureless. Half-filled chambers less common. The ichnospecies is different from *V. obovatus* by: 1) absence of alveolar sediment within the chambers, and 2) presence of 25–30 chambers in a single exposure with respect to 277 chambers of the later; and from *V. planoglobus* by: 1) absence of flat floor chambers, and 2) arrangement in different horizontal planes in contrast to the single horizontal plane arrangement of *V. planoglobus*.

**Description**: In the field, specimens of *Vondrichnus amarpurensis* are found preserved in full-relief in a vertical roadside hill-cut in sandstone (Fig. 4). The average size of a chamber is around 4 cm in diameter and 3 cm in height. The smallest observed chamber has a diameter of 2 cm and a height of 1.5 cm; the largest identified is 16 cm in diameter and 5.5 cm in height. Almost all chambers studied are slightly flattened. Of the 20 chambers with a diameter of 2 cm and more (as illustrated in Figure 4A–E), only four chambers are found partially filled. There is similarity in the shape of the filled and unfilled chambers. The filling materials are relatively finer and darker in tone in comparison with the medium-grained host sandstone. This characteristic may be clearly observed in Figure 6B. The chamber fills have a lesser degree of compactness than the host sandstone. The above mentioned features of the chamber fills suggest the passively filled nature of the burrows and the interconnected tunnels.

The connecting galleries are horizontal as well as inclined. The horizontal ones are 0.8–0.9 cm in diameter and are slightly curved, with the curvature either facing upward or downward with a deviation of 5°–10° from the horizontal plane; the moderately inclined tunnels are oriented at angles of about 30°–40°, and the more inclined ones are straight with angles of about 50°–70° (Fig. 4F) with respect to the bedding plane. The inclined burrows are circular in outline, but the horizontal ones are somewhat flattened.

In *Vondrichnus amarpurensis*, 3–4 tunnels of similar diameter radiate from each chamber. The tunnels and shafts from one chamber may connect with other chambers randomly, that is, not at specific positions. However, sideway connection is more common (Fig. 5A, B). As observed from the exposure in the field, there is no specific distribution pattern of the chambers as well. Chambers are situated on all sides of the gallery system. Lengths of tunnels and shafts are also varied; the longest shaft observed is about 21 cm [indicated by black arrow in Fig. 4E], and the shortest one observed is about 3.5 cm long.

**Remarks**: The characteristic features that can be considered for the Amarpur specimen to belong to the ichnogenus *Vondrichnus* are the diffuse polychambered subterranean nature composed of obovate chambers connected by galleries. The nest system of *Vondrichnus amarpurensis* occurs in different horizontal planes, as evidenced from the vertical cut section exposure. The morphological features of
Interconnected chambered trace fossils may be compared with the type ichnospecies *Vondrichnus obovatus* (Genise and Bown, 1994) and the second known ichnospecies *Vondrichnus planoglobus* (Duringer et al., 2007). The present ichnospecies has a close affinity with *V. obovatus* with respect to the oblate shape of the chambers and the way the galleries connect with various chambers. However, primary differences from *V. obovatus* are: (1) lack of alveolar sediment in the centre of the chambers; (2) occurrence of about 25–30 chambers in a single exposure of 1 m² in vertical section unlike the dense swarms of 277 chambers as in *V. obovatus*; (3) the connecting burrows are relatively larger in diameter than those of *V. obovatus*.

Furthermore, *Vondrichnus amarpurensis* is entirely different from the second known ichnospecies *Vondrichnus planoglobus*. The main differences are: (1) *Vondrichnus amarpurensis* does not have chambers with flattened floors as in *V. planoglobus*; (2) gallery system where secondary tunnels are joined with a main rectilinear tunnel as in *V. planoglobus* is not observed in *V. amarpurensis*; (3) chambers of *V. amarpurensis* are arranged in different horizontal planes in contrast to that of *V. planoglobus*, which are arranged in a single horizontal plane; (4) galleries are shorter in *V. amarpurensis*, measuring about 20–30 cm, whereas galleries in *V. planoglobus* are longer and frequently measure up to 10 m.
Moreover comparison of *Vondrichnus amarpurensis* and the ichnogenus *Fleaglellius* Genise and Bown, 1994 showed that in *Fleaglellius* there is successive stacking of chambers, where the top of the lower one completely overlapped the base of the upper chamber; such a feature is not observed in *V. amarpurensis*. It also differs from *Termitichnus* Bown, 1982 in the absence of isolated chambers as expanded globular clusters of chambers, or in associated constellate aggregations of tens to hundreds of chambers. Galleries in *Termitichnus* are ornamented, and the numbers of galleries between chambers are large (cf. Genise, 2004); these characteristics are absent in *V. amarpurensis*. From the above consideration the Amarpur specimen is given a new ichnospecies name as *Vondrichnus amarpurensis*.

So far no concrete indication is observed in support of the possible maker of *Vondrichnus amarpurensis*. However, taking reference to the works of: (1) Grasse (1984), who ascribed nests made up of medium- to small-sized chambers interconnected by larger nets of galleries to activities of Macrotermiteinae, and (2) Genise and Bown (1994), who interpreted *Vondrichnus obovatus* as the work of Macrotermitinae for the same reasons as *Termitichnus simplicidens*; the presently described *Vondrichnus amarpurensis* is also considered to be related to the activities of Macrotermiteinae.

**Fig. 4.** Photographs of the field exposure of *Vondrichnus amarpurensis* and the corresponding sketch. A–E. Field photographs. White arrows indicate filled and half-filled chambers. Red arrows in A and D indicate tunnels. Black arrows in C, D, and E indicate shafts. F. Corresponding sketch of the above photographs. Inclinations in degrees of some of the connecting burrows (shafts and tunnels) are also shown.
Fig. 5. Close-up photographs of *Vondrichmus amarpurensis* in the outcrop. **A.** Close-up view of Figure 4A. **B.** Close-up view of Figure 4D. **C.** Close-up view of cast of the largest observed chamber. Notations: C – filled chambers; T – tunnels; S – shafts; B – bed; UC – unfilled chamber.
DISCUSSION

The observed characteristics of Vondrichnus amarpurenensis hint at termites or ants as the potential producers. Two important observations that support that the studied chambers and galleries are trace fossils and not associated with recent termite activity are (1) the lithified nature of the chambers and galleries, and (2) similarity between the degree of compaction of infills and the host rock. The infills might have entered the chambers gravitationally or by forces not related to the behaviour of the trace maker (cf. Bromley, 1996). The difference in colour of the infills and host rock (Fig. 6B) suggests that the fills are no doubt passive in nature. Faecal pellets, other trace fossils and rootlets are also absent between the chamber walls and infills of the chambers. The possibility of active filling of the burrows is also less certain due to the absence of meniscæ in the burrows. The open chambers with smooth interior walls (Fig. 6A), lined with ferruginous clay, have interconnected burrow systems, so they cannot be related to coleopteran pupation chambers, which are discrete structures having an internal cavity with a smooth surface; the outer wall of a coleopteran chamber has a lumpy appearance composed of different layers of soil materials (Genise et al., 2002). However, the presently described features of the chambered trace fossils are common in Macrotermiteinae fungal chambers (cf. Roberts et al., 2016).

As the Amarpur chambered trace fossils are considered to have been produced by social insects such as termites, we may think of a terrestrial environment under which such traces were formed. This could be possible only when the host sediments were exposed to subaerial conditions. This concept has a good support from the work of Mukherjee (2002), who proposed that the Pliocene Lower Tipam sediments have been subjected to periodic exposure in subaerial conditions.

Genise et al. (2004) considered the functions of such trace fossils to be diverse and related to nesting activities or pupation of termites or ants. According to Michener (1974), Grassé (1984), and Hölldobler and Wilson (1990), these types of chambers were used as nests in which social insects

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Fig. 6. Close-up photographs of unfilled and filled chambers. A. An unfilled chamber with ferruginous chamber-wall coating. Three circular dark spots indicated by white arrows are the exit points to horizontal burrows (tunnels). Note the foreset of a cross bed just below the open chamber. B. Close-up of a filled chamber with its connecting shaft. C. Cast of a filled chamber showing a portion of the internal wall of the secondary chamber, white dashed line encircled area indicated by arrow. The dashed line ends up around a chamber-tunnel junction. D. A composite chamber - the area between the white continuous line and the white dashed line is the primary filled chamber, and the portion encircled by a white dashed line is the unfilled secondary chamber.
such as termites, ants, and some bees laid eggs and reared larvae. The observed open chambers in our study area might have been used as storage, or for rearing larvae, or as royal cells; whereas, most of the observed filled chambers may be correlated with the replacement of the fungus combs produced by Macrotermitinae from sand (cf. Grassé, 1984). However, the Amarpur specimens lack visual evidence of any kind of fungus combs, which may be due to passive filling of the empty chambers (cf. Duringer et al., 2006, 2007). The numerous partly hollow chamber trace fossils found in the studied area might be due to partial filling of empty chambers (Fig. 6D). The manner in which fungal gardens were formed may be understood from Roberts et al. (2016).

**CONCLUSION**

A new trace fossil attributed to social insects, possibly termites or ants, is described. In comparison with other previously recognized traces produced by termites, the presently described trace fossil from Tripura can be related to a nest system of the ichnofamily Krausichnidae. This nest system consists of oblate chambers interconnected by a boxwork of simple, unbranched, straight to curvy small burrows in different horizontal and inclined planes, similar to the ichnogenus *Vondrichnus*. The differences between the presented trace fossils and the two previously known *Vondrichnus* ichnospecies, namely *V. obovatus* and *V. planoglobus*, have been studied. The Amarpur chambered trace is found to be clearly dissimilar from *V. obovatus* and *V. planoglobus*. Therefore, it is assigned to a new ichnospecies as *Vondrichnus amarpurensis* isp. nov. These interconnected chambers might possibly be used for storage, rearing larvae, as royal cells, or as fungus gardens.

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