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FIRST RECORD OF AN AQUATIC BEETLE LARVA (INSECTA: COLEOPTERA) FROM THE PARSORA FORMATION (PERMO-TRIASSIC), INDIA

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Abstract: The fossilized larva of an aquatic beetle, *Protodytiscus johillaensis* gen. et sp. nov., is described from a ferruginous micaceous siltstone bed of the Permo-Triassic Parsora Formation of the South Rewa Gondwana Basin, Madhya Pradesh, India, and its systematic position and ordinal relationships within the coleopterous suborder Adephaga are discussed. Hitherto, the oldest known fossils of the hydradephagan superfamily Dytiscoidea have been Jurassic. The discovery of *P. johillaensis* extends the range of the Dytiscoidea back to the Permo-Triassic period.

Key words: Coleoptera, Dytiscoidea, estheriids, Gondwana rocks, Permo-Triassic, relationships.

THE discovery of a fossil aquatic beetle larva is a relatively rare occurrence. Fossil beetles are of great significance because they provide vital clues to the evolutionary history of the Coleoptera. However, their study is generally neglected by modern coleopterists (Ponomarenko 1995). This paper describes an aquatic larva of the dytiscoid beetle group of late Permian–early Triassic age from the Gondwana Supergroup of peninsular India. The fossil horizon occurs on the eastern slope of Dhaurai Hill in a thin, brick-red micaceous siltstone within the Parsora Formation of the Johilla coalfield in Madhya Pradesh. The importance of the fossil to the evolutionary history and phyletic lines of the Hydradephaga is discussed. We have elected not to undertake familial placement, but the character-states displayed by the larva are elucidated as far as possible. They differ from those of other families of the superfamily Dytiscoidea and in due course this beetle might well become the 'type' of an as yet undescribed family. A new family is not erected here because we have insufficient knowledge of the adult characters of the species.

GEOLOGICAL BACKGROUND

The sediment from which the fossil was derived is exposed at the base of Dhaurai Hill (23°23′00″N, 81°02′30″E), *c.* 2 km north of the Birsinghpur-Pali railway station. It is a red ferruginous micaceous siltstone band rich in estheriids with some plant remains. The study area (Text-fig. 1), constituting the western part of the Johilla Coalfield in Son Valley, is bounded to the east by Umaria-Korar and to the south by the Sohagpur Coalfields. The sedimentary strata in the southern sector of the area overlie Precambrian metamorphic rocks unconformably. The Gondwanan Talchir, Barakar and Supra-Barakar formations are progressively exposed northward. The Upper Cretaceous Lameta Formation, exposed in the western part of the basin, onlaps the post Barakar formations (Shah 2000).

The general stratigraphic succession of the Johilla Basin is given in Table 1. Besides a rich assemblage of *Palaeolimnadiopsis,* the estheriid fauna is characterized by the coexistence of *Leaia* (*Leaia*) and *Estheriella*. The former is a typical Palaeozoic fossil and has not previously been reported from Triassic strata, whereas *Estheriella* is an early Triassic index fossil (Weiss 1875; Ghosh and Shah 1977). Some 6 km to the east, on the slope of Karkati Hill (23°22′55″N, 81°6′25″E) in a similar red micaceous siltstone band, the coexistence of *Glossopteris* and *Dicroidium* has been reported from the Parsora Formation (Shah 2000). Thus, the fauna including the insect fossil of Dhaurai Hill is unique in character. The stratigraphy of the section and the occurrence of fossils is presented in Table 2.

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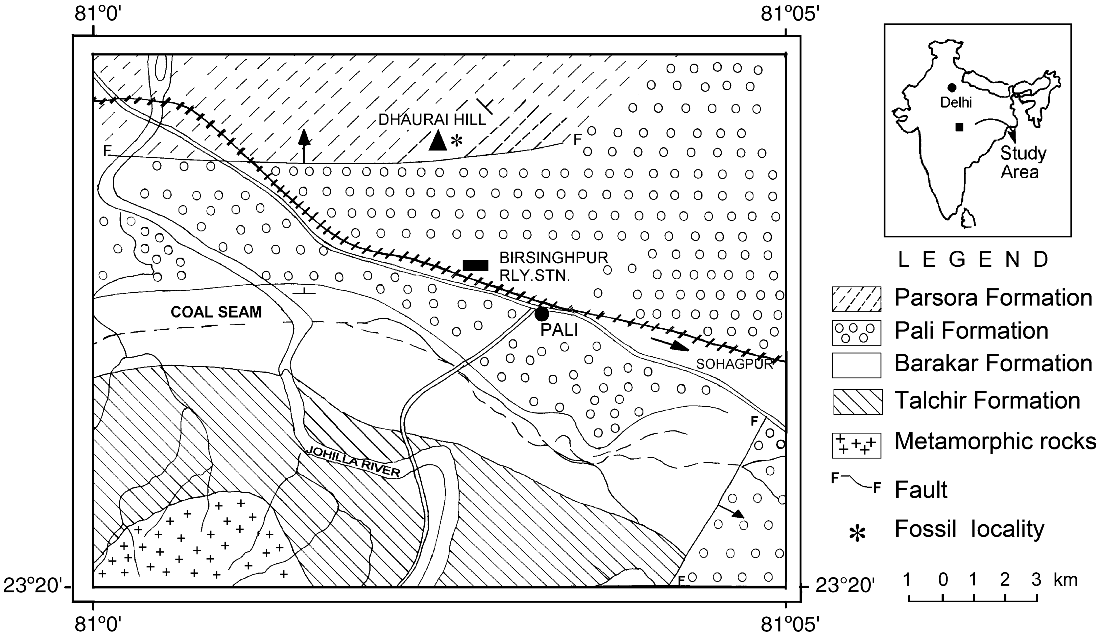


TEXT-FIG. 1. Geological map of Johilla Coalfield area, Madhya Pradesh, India, showing the fossil locality.

TABLE 1. Lithostratigraphic succession of rocks in the Johilla Coalfield, Madhya Pradesh.

Group	Formation	Geological age
	Alluvium	Recent
Post Gondwana	Deccan Trap	Late Cretaceous–Palaeocene
	Lameta	Late Cretaceous
	Bansa beds	Early Cretaceous
Upper Gondwana	Hartala	Jurassic
	Tihiki	
	Parsora	Triassic
	Pali	Late Permian
Lower Gondwana	Barakar	Early Permian
	Talchir	
	Unconformity	
	Granite, gneiss and schists	Precambrian

SYSTEMATIC PALAEONTOLOGY

Class INSECTA Linnaeus, 1758
Order COLEOPTERA Linnaeus, 1758
Suborder ADEPHAGA Schellenberg, 1806
Superfamily DYTISCOIDEA Bell, 1966

Genus PROTODYTISCUS gen. nov.

Derivation of name. Greek *protos*, first, combined with *Dytiscus*, the genotype of Dytiscidae.

Type species. Protodytiscus johillaensis gen. et sp. nov., by monotypy and present designation.

Diagnosis. Elongate, subcylindrical body, antennae and legs well developed. Head well developed, sclerotized,

TABLE 2. Stratigraphy of the section at Dhaurai Hill within which the insect fossil was found.

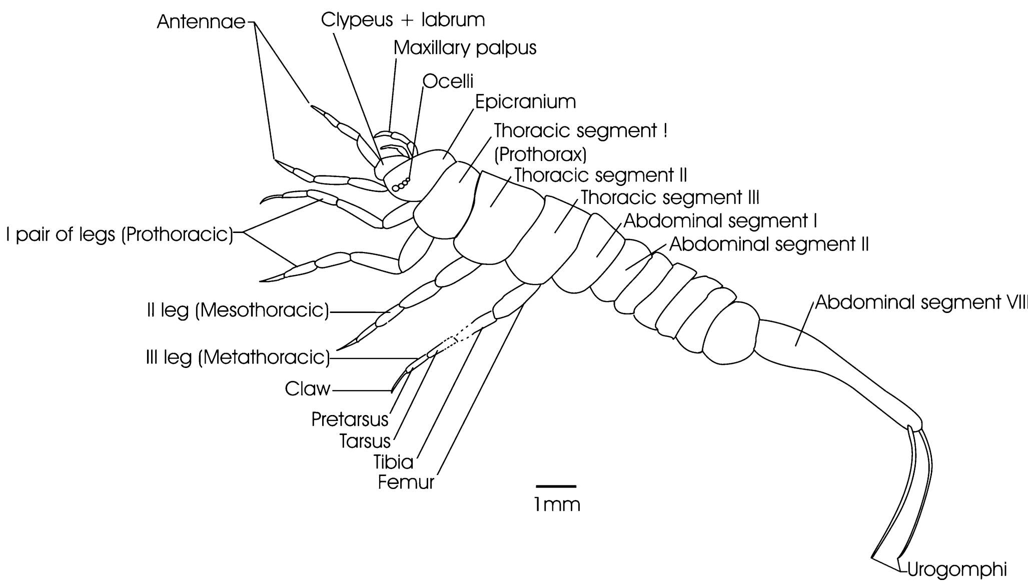
Formation	Bed descriptions	Thickness (m)	Remarks
	Top not seen		
Parsora	5. Coarse-grained cross-bedded variegated sandstone	5	Estheriids
	4. Brick red, micaceous siltstone	0·25	Root burrows
	3. Brown laminated shale	1	Insect fossil
	2. Hard, silicified white sandstone, fault affected	10	
Unconformity			Faulted contact
Pali	1. Red, coarse–medium grained sandstone	2+	
	Base not seen		

prognathous, mouthparts not distinguishable in preserved material, epicranial suture not visible, front-clypeal suture well marked; clypeus and labrum fused, shorter than rest of head; antenna comprises four segments, elongate, slender; segment I greatest in length but slightly shorter than combined lengths of other three, segments II–IV progressively shorter in length; ocelli on lateral side of head (number not distinguishable). Thorax wider than head, comprising three segments: prothorax, mesothorax and metathorax; mesothoracic segment longer than pro- and metathoracic segments; thoracic segments longer than abdominal segments I–VI; one pair of legs ventrally on each of the three thoracic segments; legs long, slender, comprising coxa and trochanter (not visible), femur, tibia, tarsus, pretarsus and claw. Abdomen narrower than thorax, with eight visible segments; segments I–VII much broader than long, segment VIII distinctly elongate and narrower than other abdominal segments; paired urogomphi slender and elongate.

Protodytiscus johillaensis gen. et sp. nov.
Text-figures 2–3

Derivation of name. After the Johilla Basin in which the fossil was found.

TEXT-FIG. 2. Photograph of *Protodytiscus johillaensis* gen. et sp. nov.; fragment of fossil conchostracan within white circle. Scale bar represents 1 mm.



TEXT-FIG. 3. Interpretative drawing of *Protodytiscus johillaensis.*

Material. Holotype, Geological Survey of India, Kolkata, Type no. 21307.

Type locality. Johilla Coalfield, south-east slope of Dhaurai Hill: 23°23′00″N, 81°02′30″E.

Description. Subcylindrical body widest near meso- and metathoracic regions; head (excluding labrum) about 0·82 times as long as prothorax; lengths of pro-, meso- and metathorax 1·00 : 1·38 : 0·77 mm; abdominal segments I–VII together about 1·05 times as long as segment VIII, segment VIII about 7·25 times as long as wide; urogomphi about 0·75 times as long as abdominal segment VIII.

Measurements of holotype (in mm). Total length, 14·11; length of head including labrum, 0·76; width of head, 1·19; length of prothorax, 0·85; width of prothorax, 1·44; length of abdominal segment VIII, 4·50; width of abdominal segment VIII, 0·62.

DISCUSSION

The Parsora Formation is underlain by the Pali Formation, the uppermost formation of the Lower Gondwana succession in the South Rewa Basin. It is considered to be equivalent to the Barren Measures and Raniganj Formation of the Damodar Valley basins. At Dhaurai Hill the contact between the two formations is faulted. A Triassic age for the Parsora Formation was suggested by Fox (1931), Sahni (1931), Cotter (1938), Srivastava *et al.* (1990) and Mitra (1993). The boundary relationship between it and the Pali Formation is an angular discordance in the Johilla River section (Dutta and Ghosh 1993), and has suggested a younger age. The age of the Pali Formation is late Permian (Tiwari and Ram Awatar 1986; Ram Awatar 1987).

The plant megafossils from the Parsora Formation consist of *Glossopteris* and *Dicroidium* and these occur on the same bedding plane, implying (according to Shah 2000) a late Early Triassic age for the red beds around Karkati Hill, in contrast to the apparently mixed Permo-Triassic assemblage of conchostracans (see above) on the south-eastern slope of Dhaurai Hill. The age of the formation was extended into the Middle Jurassic by Cotter (1938).

Hence, the exact stratigraphic position of the insect-bearing red bed is difficult to ascertain owing to the lack of a biostratigraphic marker in surface exposures and of borehole data in the vicinity. It is further confused by the prevalence of the red colour of both the distal and the proximal facies of the rocks. As a result, although the red bed in question appears to belong to the Parsora Formation (as noted on the published geological map of the area) it could, in fact, belong to the underlying late Permian Pali Formation (A. Mukhopadhyay, pers. comm. 2005). The geological age of the fossil insect is therefore only loosely constrained as late Permian–late early Triassic.

From the available evidence, fossil and modern, we suggest that the larvae of *Protodytiscus* were adapted to living in shallow fresh water or near the water's edge, and were general predators on immature stages of other insects or tiny invertebrates. They found their prey by either hunting actively or waiting in ambush. The jaws (mandibles) were sharp and channelled. When the prey was caught the jaw tips pierced through the body wall and a fluid was injected through the channels. This served both to kill the prey and to begin pre-oral digestion of the body content. They sucked the soluble parts leaving only the insoluble behind. A partially crushed shell of a conchostracan, seen below tip of the abdomen (encircled in Text-fig. 2), was perhaps predated by this larva. At the time of pupation the larvae would have left their aquatic habitat and pupated on land near water in an earthen cell in friable soil where the larvae could burrow beneath the surface. The presence of root burrows in bed 4 and estheriids with trail marks on the bedding plane of bed 3 (see Table 2) are of special interest because the estheriids would have thrived in freshwater ephemeral pools. These features identify the beds as palaeosols.

Based on recent diversity coupled with the timing of diversification of the main groups, it is thought that the number of species of beetles may run into the tens of millions over the 250 million years of their evolution. Mesozoic beetles are mostly closely related to Recent taxa, but there are exceptions. According to Ponomarenko (1995), there were two main stages in beetle evolution during the Mesozoic. The first occurred during the Triassic and the early–middle Jurassic (involving the families Triaplidae, Trachypachidae, Coptoclavidae and others), the second during the middle–late Jurassic and early Cretaceous (involving Gyrinidae followed by Dytiscoidea and Caraboidea).

There are about 50 known localities for Triassic beetles and these involve all continental landmasses apart from South America and Antarctica. Although occurring in all stages of the Triassic, the most diverse material comes from the upper half of the system. Among the known forms, the largest Triassic assemblage has been reported from the Madygen Formation in South Fergana, Central Asia. About 65 species referable to nine families have been described. Both terrestrial and aquatic forms have been noted in them. Adults and larvae of the dytiscoids (suborder Adephaga), namely *Necronectulus* and *Colymbothetis*, appeared for the first time during this period (Ponomarenko 1993).

According to Beutel (1995) the earliest Adephaga lived along the edges of rivers or ponds. Three independent invasions of the aquatic habitat were achieved by the adephagan Gyrinidae, Haliplidae and Dytiscoidea. The adephagan larva has a predacious habit, prognathous head with labrum and clypeus firmly fused to head capsule. Larvae of Dytiscoidea are characterized by the large terminal spiracles on abdominal segment VIII. An independent invasion of the aquatic habitat by the common ancestor of a clade comprising Noteridae, Amphizoidae, Hygrobidae and Dytiscidae was suggested by Bell (1966). The monophyly of Dytiscoidea (= dytiscoid families *sensu* Bell 1966) was supported by Beutel (1995) on the basis of apomorphic features of both larvae and adults. Important apomorphic features of larvae of Dytiscoidea include: abdominal segments IX and X reduced, terminal spiracle of VIII enlarged, and urogomphi shifted to ventral side of segment VIII (Beutel 1993).

Beutel (1995) stated that there is sufficient reason to assume that the Gyrinidae were the first group of Adephaga to make use of the aquatic environment. This is supported by the occurrence of such fossils as the Late Permian *Permosilas* (Sharov 1953; Beutel and Roughley 1988) and the Triassic *Triadogyrus* (Ponomarenko 1977). This change of habitat took place very early in adephagan evolutionary history. The most important characteristic of the Dytiscoidea is the loss of abdominal segments IX and X with the acquisition of novel breathing techniques, as noted earlier. This doubtless apomorphic condition indicates that the latest common ancestor of Dytiscoidea was aquatic, at least in the larval stage. Such a character has also been noted in the larvae of the fossil genera *Parahygrobia* (Jurassic), *Stygeonectes* (Jurassic) and *Coptoclava* (Jurassic). The Late Cretaceous *Cretodytes latipes* Ponomarenko is the earliest known fossil of the Dytiscidae. Beutel (1995) doubted that the precise systematic positioning of many of the fossils described by Ponomarenko (1977) was practicable. However, the loss of two terminal segments of the abdomen indicates that the above genera belong to a panmonophylum that also includes extant representatives of the dytiscoid families.

The Triassic beetle faunas of Central Asia are rich and include representatives of all four suborders of Coleoptera, including Adephaga (Lawrence and Britton 1994). According to Lawrence (in Lawrence and Britton 1994), Gyrinidae, Dytiscidae and Carabidae among the Adephaga originated during the Jurassic. *Protodytiscus johillaensis* conforms to a dytiscoid larva in all available characteristics and may well be a primal form of the dytiscoid group. It is placed in the suborder Adephaga and superfamily Dytiscoidea as *incertae sedis*, its family status being uncertain at present. Our results indicate the existence of a predacious dytiscoid larva in the Permo-Triassic rocks of Madhya Pradesh. They also provide new data that may help in defining phyletic lines within the Hydradephaga (aquatic Adephaga), especially the Dytiscoidea, and the time of their divergence.

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