

# On the behavioural biology of a morpho-variant of *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869) (Araneae: Salticidae) with taxonomic notes

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## Abstract

We hereby report an isolated population of a rare morpho-variant of the ant-mimicking jumping spider *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869) from Hazaribagh Wildlife Sanctuary, Hazaribagh, Jharkhand, India, which is also the first record of this species from the state of Jharkhand, India. Descriptions of both male and female spiders, the female's exuviae, its eggs and habitat are presented. We have studied its moulting, feeding and sexual behaviour in detail, and have recorded various behavioural aspects that were never documented before, such as debris-rolling behaviour, photokinetic response, starvation response and oxygen deprivation response. We here report the occurrence of this spider near the colonies of the ground-nesting ant *Camponotus compressus* (Fabricius, 1787). This spider is known to mimic the Asian weaver ant *Oecophylla smaragdina* (Fabricius, 1775), which are greenish orange to red in colour. Specimens collected by us are dark brown to black in coloration whereas the commonly reported specimens are often greenish orange to red. We propose that the darker coloration would have been naturally selected in this isolated population of *M. plataleoides* as an adaptation to coexist with *C. compressus*, which is also black in coloration and abundant around the spiders. Study of the moulting behaviour of the morpho-variant further reveals the display of a novel mechanism of ant mimicry among these spiders which we have named as temporal myrmecomorphy. Temporal myrmecomorphy has been proposed to be a protective mechanism used by a harmless mimic against the attacks of the aggressive models so that it can co-exist with the models. Present study establishes the usefulness of a morpho-variant as an important model in understanding the evolution and behaviour of a species holistically.

## Keywords

Behaviour; *Camponotus compressus*; evolution; Jharkhand; myrmecomorphy; temporal mimicry

## Abbreviations

ALE anterior lateral eye

AME anterior median eye

PLE posterior lateral eye

PME posterior median eye

## Introduction

*Myrmaplata* Prószyński, 2016 is a small genus comprising only five described species, out of which only one is known to occur in India, i.e., *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869) (Caleb, 2016, 2020; Prószyński, 2016; Caleb & Shankaran, 2022; World Spider Catalog, 2022). Earlier this species was part of the genus *Myrmarachne* MacLeay, 1839 but recently it has been placed in a new genus *Myrmaplata* that was established on the basis of morphological differences in the structure of the copulatory organs of its member species with respect to the genus *Myrmarachne* (Prószyński, 2016; Yamasaki et al., 2018). Like all species of the genus *Myrmarachne*, members of the genus *Myrmaplata* also exhibit Batesian mimicry, displaying striking morphological as well as behavioural resemblances towards ants. *M. plataleoides* is the type species of the genus *Myrmaplata* (Prószyński, 2016). This species was originally described from Sri Lanka (earlier Ceylon) as *Salticus plataleoides* O. Pickard-Cambridge, 1869. Conventionally *M. plataleoides* is known to mimic the red ant *Oecophylla smaragdina* (Fabricius, 1775) (Hymenoptera: Formicidae: Formicinae) (Edmunds & Prószyński, 2003; Edmunds, 2006; Ramachandra & Hill, 2018), but in some studies, *M. plataleoides* is also reported to exhibit polymorphism (Borges et al., 2007; Caleb, 2016). Different colour morphs of *M. plataleoides* have been reported to mimic different models in the habitat besides *O. smaragdina* (Borges et al., 2007). This is termed polymorphic mimicry (Cushing, 2012). Even after the more than 153 years since it was first described, the taxonomy and behavioural biology of this spider is still an unsolved mystery.

In the present study, an isolated population of an unusual dark brown to black-coloured morpho-variant of *M. plataleoides* was discovered from Hazaribagh Wildlife Sanctuary, Hazaribagh, Jharkhand, India. This is the first record of this species from the state of Jharkhand. Apart from morphological investigations to ascertain its taxonomy, we have also studied its behavioural biology both *in situ* and *ex situ*. As many as 21 specimens were collected alive from near the colonies of the ground-nesting black ant *Camponotus compressus* (Fabricius, 1787). Moulting behaviour, courtship behaviour, egg laying, feeding behaviour, mimicry, response to various stimuli and other important behavioural aspects have been studied in detail. Possible causes for the evolution of this morpho-variant are also discussed.

The present study summarizes many aspects of the natural history of this morpho-variant.

## Materials and methods

### *Study area*

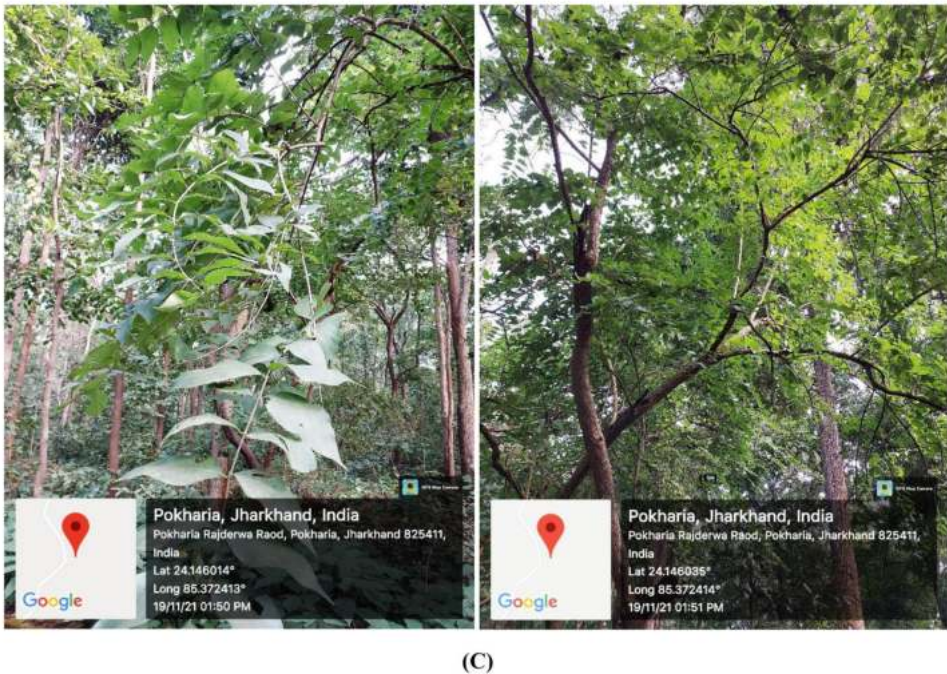
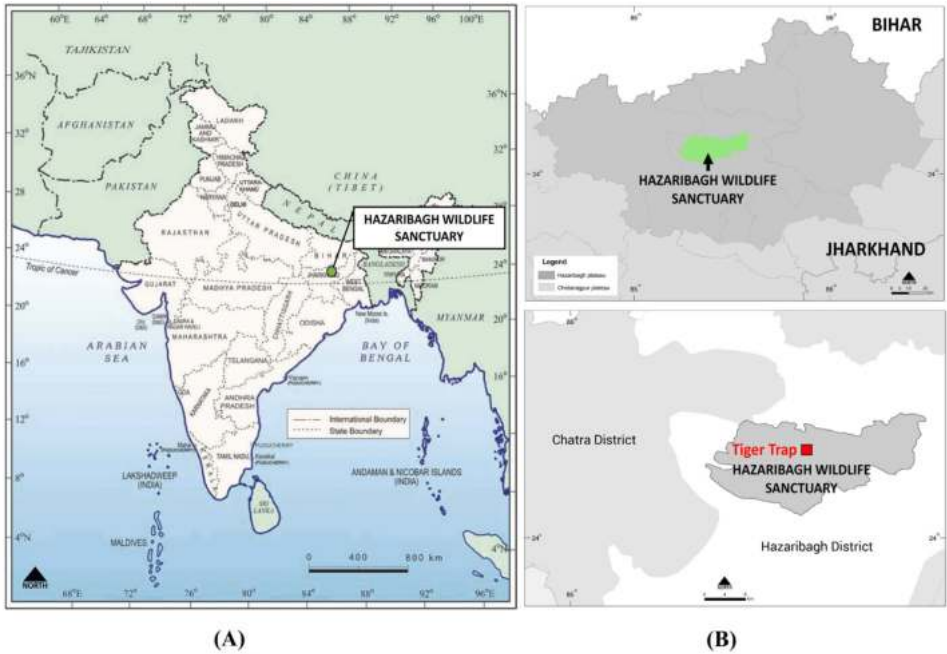
Hazaribagh Wildlife Sanctuary, Hazaribagh, Jharkhand, India was selected as the area of study. It mainly consists of forest areas dominated by sal (*Shorea robusta* C.F.Gaertn.) with small patches of bamboo, khair (*Senegalia catechu* (L.f.) P.J.H.Hurter & Mabb.) and eucalyptus trees. The easternmost forested area of Hazaribagh Wildlife Sanctuary, where the present study was conducted, is called Saptarni due to the abundant presence of sal trees. It forms the largest forested area of Hazaribagh Plateau which in turn is an important part of Chotanagpur Plateau. Chotanagpur Plateau consists of the oldest known landmass on earth with geological signatures of ancient river channels, tidal plains and beaches over 3.2 billion years old, representing the earliest crust exposed to air (Chowdhury et al., 2021). The area of Chotanagpur Plateau coincides with the state of Jharkhand with a small part extending to the neighbouring states of West Bengal, Odisha and Chhattisgarh. Being ancient in origin and densely forested, Chotanagpur Plateau has a rich biodiversity. The majority of the invertebrate faunal diversity is still undocumented. Hazaribagh Plateau occupies most of the areas of the Northern Chotanagpur Plateau. The area of Hazaribagh Plateau consists of the present districts of Hazaribagh, Chatra, Koderma and Giridih with some parts of Bokaro and Ramgarh (fig. 1).

### *Site mapping and geo-tagging*

The geographical extent of the Hazaribagh Plateau was plotted on a map by geo-referencing available geographical information retrieved via extensive data mining (fig. 1B). Note that precise maps of Hazaribagh Plateau are not publicly available. The outline map of Hazaribagh Wildlife Sanctuary was drawn using the maps already published (Gupta & Pandey, 2021) (fig. 1B). ArcGIS Desktop 10.8.1 software (Environmental Systems Research Institute, Redlands, CA, USA) was used for geo-referencing and mapping purposes. Geo-tagged photographs of the sampling sites were taken using the GPS Map Camera 1.4.4 software installed in a Samsung Galaxy M42 mobile device (Samsung, Suwon-si, South Korea). The same mobile device was used for photography and video-recording whenever required during the study.

### *Sampling*

Multiple trees were screened at random. Spiders for the present study were spotted on the leaves and trunks of an unusually large tree of *Nyctanthes arbor-tristis* L. present in the vicinity of the Tiger Trap, an old structure believed to be constructed about 500 years ago inside Saptarni by some local king to trap tigers which once



**Figure 1.** Area of study. (A) Location of Hazaribagh Wildlife Sanctuary in India. (B) Location of Hazaribagh Wildlife Sanctuary in Hazaribagh Plateau (upper image). Collection site is shown on the outline map of Hazaribagh Wildlife Sanctuary in the lower image. (C) *Nyctanthes* tree on which spiders were spotted. The longitudes and latitudes are indicated in the geo-tagged photographs.

**Table 1.**

Details of collection of the studied morpho-variant of *Myrmaplata platalaeoides* (O. Pickard-Cambridge, 1869) specimens from Hazaribagh Wildlife Sanctuary.

Month	Number of visits	Number of spiders spotted	Number of spiders collected
January 2021	2	0	0
February 2021	3	3	1
March 2021	3	4	1
April 2021	3	8	2 + silk nest containing exuviae
May 2021	3	4	1
June 2021	3	7	2
July 2021	3	5	3 + silk nest containing exuviae
August 2021	3	8	3
September 2021	4	14	6 + silk nest containing eggs
October 2021	3	7	2
November 2021	3	1	0
December 2021	3	0	0

roamed this area (fig. 1C). The height of the tree suggests that this tree has been growing here for a considerable period of time. Surprisingly, a large area around the bole beneath this tree was inhabited by colonies of a ground-nesting black ant, *C. compressus*. On careful examination, we encountered many spiders on the ground as well. It should be noted that we encountered a higher number of female spiders than of male spiders *in situ*. For the present study, this area was visited regularly for almost a year from January to December 2021 for at least two visits per month with the maximum number of visits in the month of September (table 1). In total, 36 visits were conducted in this period. These visits were conducted during daytime, between 11:00 am and 04:00 pm. All *in-situ* observations were recorded in the same time interval. The maximum number of spiders per day was spotted in the month of September. Regular visits were conducted in order to study the behaviour of the spiders *in situ*. In this manner, the whole population of this spider residing in the sampling area was covered.

### *Specimen collection and preservation*

Twenty-one live spiders (five males, six females and ten juveniles) were collected and reared for *ex-situ* behavioural studies. Two females among these were gravid. After behavioural studies were conducted, the dead spiders were preserved in 70% ethanol for further study. One gravid female successfully laid her egg sac in the lab. The female spider's silk nest containing eggs and its exuviae were also collected and preserved for microscopic examination. All studied ethanol-preserved specimens were deposited in the museum collections of the University Department of Zoology, Vinoba Bhave University, Hazaribagh, India.

### *Morphological investigations*

The live spiders were photographed *in situ* using a cellphone camera (Samsung Galaxy M42). One ethanol-preserved female spider was dissected using a fine surgical scalpel to illustrate its epigyne. The epigyne was cleared by boiling it in 10% potassium hydroxide (KOH) solution for a minute. After boiling, the epigyne was rinsed thoroughly in water to remove excess KOH and was temporarily mounted in a drop of glycerol using a coverslip on a glass slide for microscopic observations. The ethanol-preserved female and male habitus (before dissection), undamaged whole-body exuviae of an undifferentiated male, exuviae of the cephalothorax of an adult female, the silk nest of a female containing eggs, the dissected epigyne of a female, palp of amale, and head with chelicerae and fangs of both a male and a female were photographed using a Leica (Wetzlar, Germany) DFC 425C digital camera mounted over a Leica M205FA stereozoom automontage microscope. The dissected epigyne was further stained using safranin staining solution (Labpro, Hyderabad, India). The stained epigyne was washed twice in distilled water and mounted on a glass side using glycerol and a coverslip placed over it. Light pressure was applied uniformly over the mounted stained epigyne using a needle to prepare a squash of the epigyne to reveal its internal anatomical details under the compound microscope. Measurements were taken in millimetres (mm) using the inbuilt settings of the automontage. The format of the description follows Yamasaki et al. (2018) and Caleb (2016). A gravid female was also dissected for its eggs. The number of eggs wa counted and temporarily mounted in a drop of glycerol using a coverslip on a glass slide for microscopic observations using dissecting and compound microscopes. Measurements of the eggs were taken in millimetres (mm) using an ocular micrometer placed within the eyepiece of a compound microscope.

### *Behavioural studies*

Behavioural studies were performed both *in situ* and *ex situ*. *In-situ* behavioural studies included regular visits to the site of study and observing activities of spiders in natural conditions. A total of 36 visits were conducted between January and December 2021. The interaction of spiders with *C. compressus* was also recorded. Ants and their nests were photographed. For the *ex-situ* behavioural studies, spiders were reared in transparent Borosil glass bottles (Borosil Limited, Mumbai, India) with a proper setup for entry and exit of air for breathing (fig. 10A). Differently sized glass bottles were used depending upon the experiment to be performed. Transparent glass bottles of 50 ml capacity were used when only one spider was under observation, e.g., for studying feeding behaviour, moulting behaviour and response to various stimuli. Transparent glass bottles of 100 ml capacity were used when more study required multiple spiders to stay together for studying courtship behaviour, sexual aggression and mate selection. For studying moulting behaviour, a complete leaf of *Nyctanthes* tree containing a gravid female in its silk nest was

labelled and constantly monitored on a daily basis. Ten juvenile spiders were collected just after emerging from the silk nest in which they had stayed for almost a week after hatching. These spiders were reared and allowed to moult in captivity. A total of six spiders were allowed to moult for a limited time and sacrificed for microscopy whereas four spiders were allowed to moult until becoming adult. These spiders were sacrificed and preserved in 70% ethanol after the 3rd, sixth, seventh and eighth moults. Images of these samples were taken using the Leica DFC 425C digital camera mounted over the Leica M205FA stereozoom automontage microscope. Images of a live spider in the process of moulting were taken using a cellphone camera (Samsung Galaxy M42).

Further, a live spider after the sixth moult was placed with live minor, medium and major ants in the same glass bottle. The same was done with sixth and seventh moults, respectively. In another setup, all three of these moults were placed with minor, medium and major ants in the same bottle. Lastly, different moults were placed with different workers in pairs in different glass bottles. The sixth moult of the spider and a minor worker were placed together, the seventh moult of the spider was placed with a medium worker, and the eighth moult of the spider and a major worker were kept together. This ant–spider combination was further shuffled to get six further combinations. All these experiments were first carried out in glass bottles of 50 ml capacity followed by glass bottles of 100 ml capacity to assess if the distance between spiders and ants had any effect on their behaviour. The behaviour of the spiders and the ants was recorded in all these conditions. These experiments were conducted to understand if these seemingly redundant sixth, seventh and eighth moulting stages have any special purpose with respect to ant mimicry. All these experiments were repeated twice.

For studying feeding behaviour, spiders were provided with various kind of food including common insects of different sizes and belonging to different orders, both dead and alive. Some small pieces of green leaves of *Nyctanthes* were also added. One other set containing four spiders was subjected to different intensities of light incident from a specific direction. A 35-Watt sodium vapour lamp was used for higher-intensity light and 9-Watt LED bulbs were used for low-intensity light. Here, intensity, refers to the brightness of the incident light. Four spiders were subjected to continuous starvation with *C. compressus* taken as control. The purpose of starvation was to identify fixed action patterns which are not affected even during nutrient deprivation conditions. Similarly, one set containing four spiders was subjected to prolonged oxygen deprivation by closing off the airways of the bottle, with *C. compressus* taken as control. The purpose of subjecting spiders to low-oxygen conditions was also to identify fixed action patterns which are not affected even during oxygen deprivation conditions. Ants were used as control to ascertain the lack of oxygen in the bottle as these are unable to survive longer under low-oxygen conditions. Both starvation and oxygen deprivation are stressors which would permit us to identify behaviours that are not altered during stress conditions.

For studying sexual aggression, courtship behaviour and mate selection, four experimental groups were created and constantly observed. In the first set, two mature males and one mature female were kept together. In the second group, two mature females and one mature male were kept together. Both of these experiments were conducted to study sexual conflict among two spiders of the same sex for a single potential mate. After studying sexual aggression, two more sets of spiders were taken for studying courtship behaviour and mate selection. In a third group, one mature male and one immature female were kept together for studying mate preference. The immature female was one with less developed genital structures and a smaller body size. In a fourth group, one mature male and one mature female was kept together to study courtship and mating. All these groups were kept under constant observation and experiments were repeated thrice by reshuffling different males and females. Images and videos were taken using a cellphone camera (Samsung Galaxy M42).

## Results

### *Taxonomic notes*

*Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869) Figures 2A–F, 3A–E, 7A  
*Myrmaplata plataleoides* Prószyński, 2018: 165, fig. 22F; Prószyński, 2016: 9, figs. 1E–F, 2G, 3H; Caleb, 2020: 15737, fig. 28M.  
*Myrmarachne plataleoides* Caleb, 2016: 411, figs. 31–54; Roy et al., 2016: 25, figs. 21A–G, 26A, 28A–C; Peng, 2020: 250, figs. 174A–J.  
 Taxonomic references older than 2016 may be found in World Spider Catalog (2022).

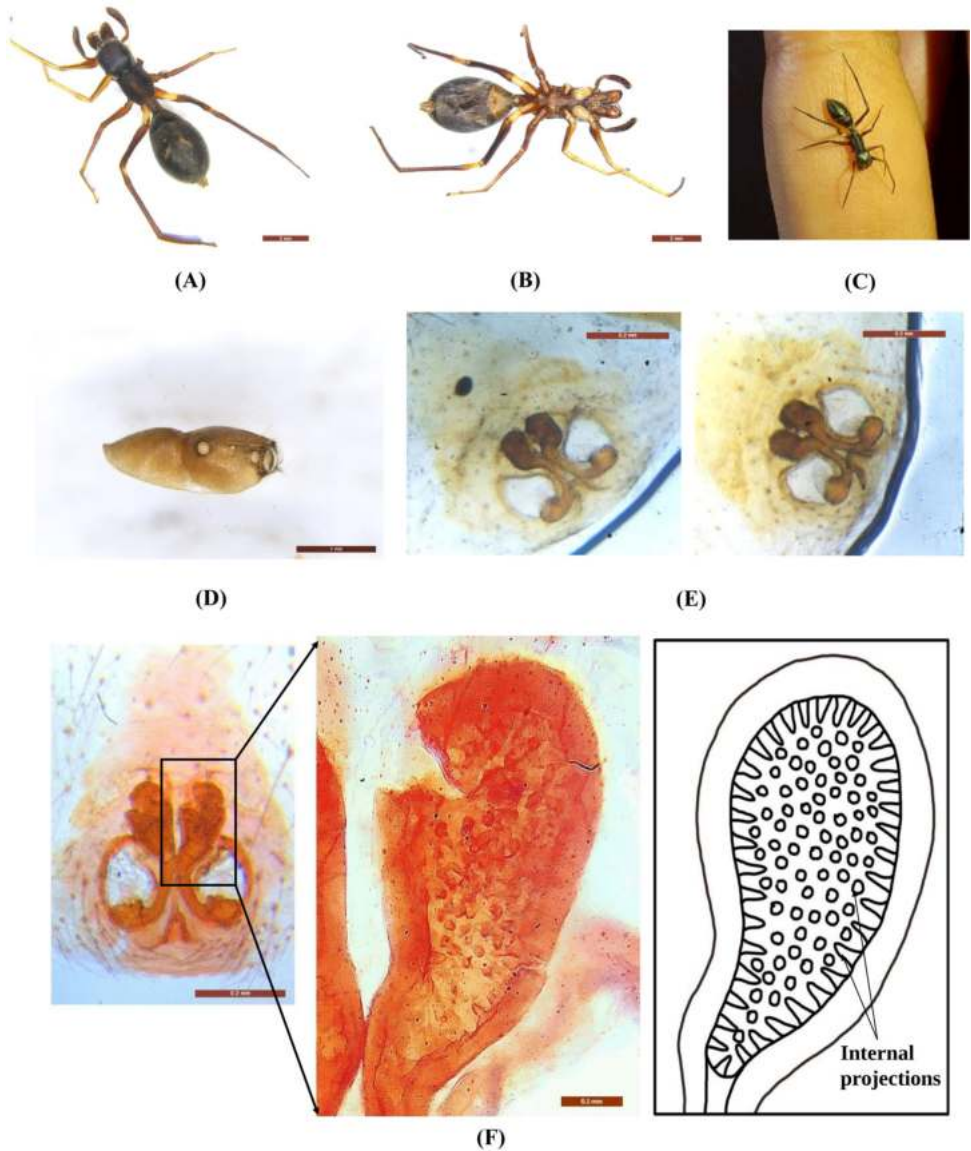
### *Materials examined for taxonomic studies (n = 13)*

Six adult females, five adult males, one preserved whole-body exuvia of an undifferentiated male collected after the third moulting event, and one preserved exuvia of the cephalothorax of an adult female collected after the sixth moulting event. Tiger Trap, Hazaribagh Wildlife Sanctuary (24°8′45.6504″N, 85°22′20.6868″E), Hazaribagh, Jharkhand, India, 20.09.2021, R. Kumar.

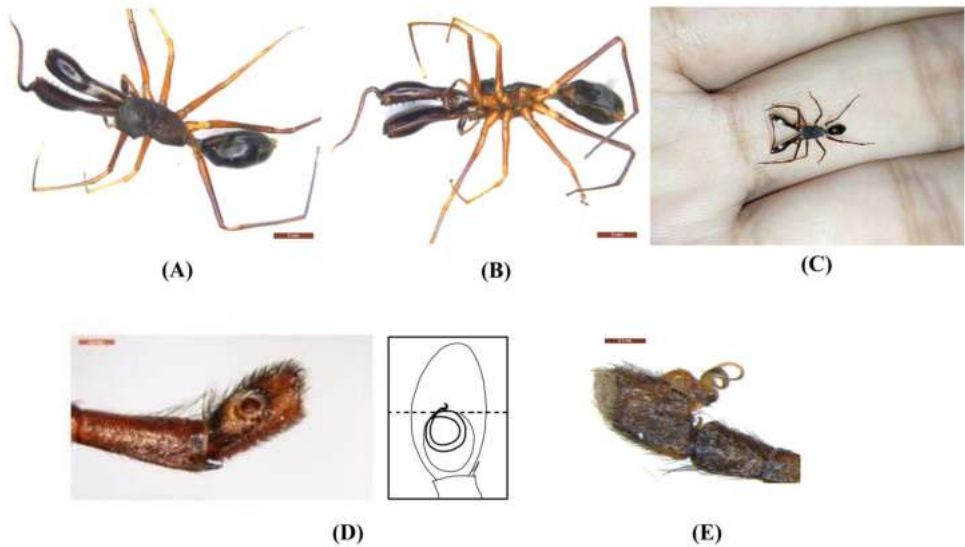
### *Diagnosis (following Prószyński, 2016)*

Epigyne with long narrow spermathecal tract with large round copulatory atria in the lateral sides; copulatory ducts terminate parallel to the anterior end of the copulatory atria, directly opening into oval spermatheca. Base of the spermathecal tract swollen, bulb-like, present exactly at the posterior end of the copulatory atria. These tracts terminate at the anterior end with conspicuous oval chambers. Anterior oval chambers have been found to have spine-like internal projections (Prószyński, 2016). Such internal projections are not visible in an unstained slide but are clearly visible in the stained squash preparation (fig. 2F). Posterior terminal ends are also





**Figure 2.** The studied morpho-variant of *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869) (female). (A) Habitus in dorsal view (scale bar 2 mm). (B) Habitus in ventral view (scale bar 2 mm). (C) Live spider. (D) Exuviae of cephalothorax region indicating position of eyes in lateral view (scale bar 1 mm). (E) Epigyne in dorsal (left image) and ventral (right image) view (scale bar 0.2 mm). (F) Stained squash preparation of epigyne showing internal details of the anterior oval chamber (left image scale bar 0.2 mm, middle image scale bar 0.1 mm). Digital illustration on the right side shows the organization of internal spine-like projections of the anterior oval chamber as revealed in the stained squash preparation.



**Figure 3.** The studied morpho-variant of *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869) (male). (A) Habitus in dorsal view (scale bar 2 mm). (B) Habitus in ventral view (scale bar 2 mm). (C) Live spider. (D) Palp in ventral view (scale bar 0.2 mm). Precise position of the loop of embolus is marked by a discontinuous line passing through the middle of the bulbus in the digital illustration shown on the right. (E) Palp in dorsal view (scale bar 0.2 mm). Loop of embolus has been stretched out to reveal the coiling.

swollen bulb-like structures. The key character that distinguishes it from the genus *Myrmarachne* is the absence of a transverse detour in the spermathecal tract (fig. 2E). *M. plataleoides* differs from other species of the genus *Myrmaplata* by the presence of a shorter loop of the male embolus, which occupies only the anterior half of the bulbus, and in the tip of the embolus, which is darkly pigmented, recurved backward and truncate (fig. 3D). It should be noted that the structure of the epigyne is very similar in all species of the genus *Myrmaplata*, and this is the characteristic feature of this genus. All five known species of the genus *Myrmaplata* can be distinguished from one another through differences in the morphology of their male palp. For more diagnostic features refer to Edwards & Benjamin (2009, pp. 16–17) and Prószyński (2016, p. 10).

### Female

Measurements are based on one of the six adult females (fig. 2). Body length 7.9 mm; carapace length 3.4 mm, width 1.6 mm; abdomen length 3.9 mm, width 2.2 mm. Width of eye row I 1.4 mm; II 1. mm; III 1.6 mm. Eye sizes and interdistances: AME 0.5 mm, ALE 0.28 mm, PME 0.1 mm, PLE 0.3 mm; AME–AME 0.4 mm, ALE–AME 0.34 mm, ALE–ALE 0.91 mm, PME–PME 1 mm, PLE–PME 0.5 mm, PLE–PLE 1.1 mm, ALE–PLE 0.73 mm, AME–PME 0.52 mm. Pedicel 0.6 mm

long. Cephalic region rugulose, dorsally black, ventrally dark brown, dorsally covered with white hairs; thoracic region dorsally black, ventrally dark brown, sparsely covered with fine white hairs. Cephalic plate roughly prism-like, slightly higher than thoracic region which is convex, dome-like. Lateral margin of the carapace slightly constricted between legs II and III. Sternum dark brown with a yellowish brown band continuous up to legs III towards posterior. Geniculate chelicerae, dorsally black, with dark brown gradient towards the tip, dark brown ventrally, with six promarginal and 10 retromarginal teeth. Fangs dark brown with black base. Legs I and II lighter in colour than legs III and IV. Coxa I white, coxae II, III and IV brown, femurs I and II light brown, femurs III and IV dark brown, trochanter IV white, patella IV white. Leg IV longest. Paddle-shaped and truncate palp fringed with preening setae. Abdomen black, without constriction, inflated in appearance, covered with fine white hairs, almost oval, with light brown laterodorsal markings and ventral dark brown area towards anterior abruptly terminating at less than one fourth of the abdomen with continuous black coloration throughout. Spinneret light brown. Epigyne with long narrow spermathecal tract with large round copulatory atria in the lateral sides; copulatory ducts terminate parallel to the anterior end of the copulatory atria, directly opening into oval spermatheca. Base of the spermathecal tract swollen, bulb-like, present exactly at the posterior end of copulatory atria (fig. 2A–E).

### *Exuviae*

Morphological features of the undamaged whole-body exuvia exhibit external characteristics of an undifferentiated male spider during third moulting stage: exuvia dark brown in colour, measuring 5.8 mm from tip of fangs to the posterior end of the abdomen. All limbs, undamaged limb segments, chelicerae with the hairy processes, curved fangs and paddle-shaped pedipalps are clearly visible in the exuvia (fig. 7A below). An undifferentiated male shares many external morphological features with an adult female. Another exuvia was incomplete. It belongs to cephalothorax of a female spider. It nicely reflects the placement of the eyes and the eye pattern (fig. 2D).

### *Male*

Measurements are based on one of the five adult males (fig. 3). Body length 8.5 mm; carapace length 3.9 mm, width 2.1 mm; abdomen length 4 mm, width 2 mm; chelicerae 3.5 mm; fang 3.1 mm. Pedicel 0.6 mm long. Eye sizes and interdistances: AME 0.45 mm, ALE 0.2 mm, PME 0.1 mm, PLE 0.25 mm; AME–AME 0.38 mm, ALE–AME 0.3 mm, ALE–ALE 0.87 mm, PME–PME 1 mm, PLE–PME 0.48 mm, PLEPLE 1.1 mm, ALE–PLE 0.8 mm, AME–PME 0.5 mm. Legs I and II dark brown becoming lighter towards the tips, legs III and IV dark brown. Trochanters of leg IV white. Leg IV longest. Cephalic region rugulose and black, roughly cuboidal; thoracic region black, dome-like. Cephalic region slightly higher than thoracic region.

Lateral margin of the carapace slightly constricted between legs II and III. Porrect chelicerae, black, with brownish tinge at the base, spoon-like anteriorly, with five promarginal and 10 retromarginal teeth. Chelicerae as long as the cephalothorax. Fangs without apophysis, as long as chelicerae, slender, curved at the base. Sternum dark brown. Abdomen with slight constriction towards the anterior, elongated, oval, covered with fine white hairs, black, with a ventral dark brown area towards the anterior abruptly terminating at less than one fourth of the abdomen with continuous black coloration throughout. Spinneret light brown. Palp dark brown, more hairy on dorsal side, with oval cymbium and round tegulum. Embolus with two coils, loop of embolus occupying only the anterior half of the bulbus. Loop long, gradually tapering, with diameter of the loop narrowing at the top and ending in a recurved and truncate embolus tip. Retrolateral tibial apophysis conical, spine-like, with broad base and slightly curved pointed tip (fig. 3).

### Remarks

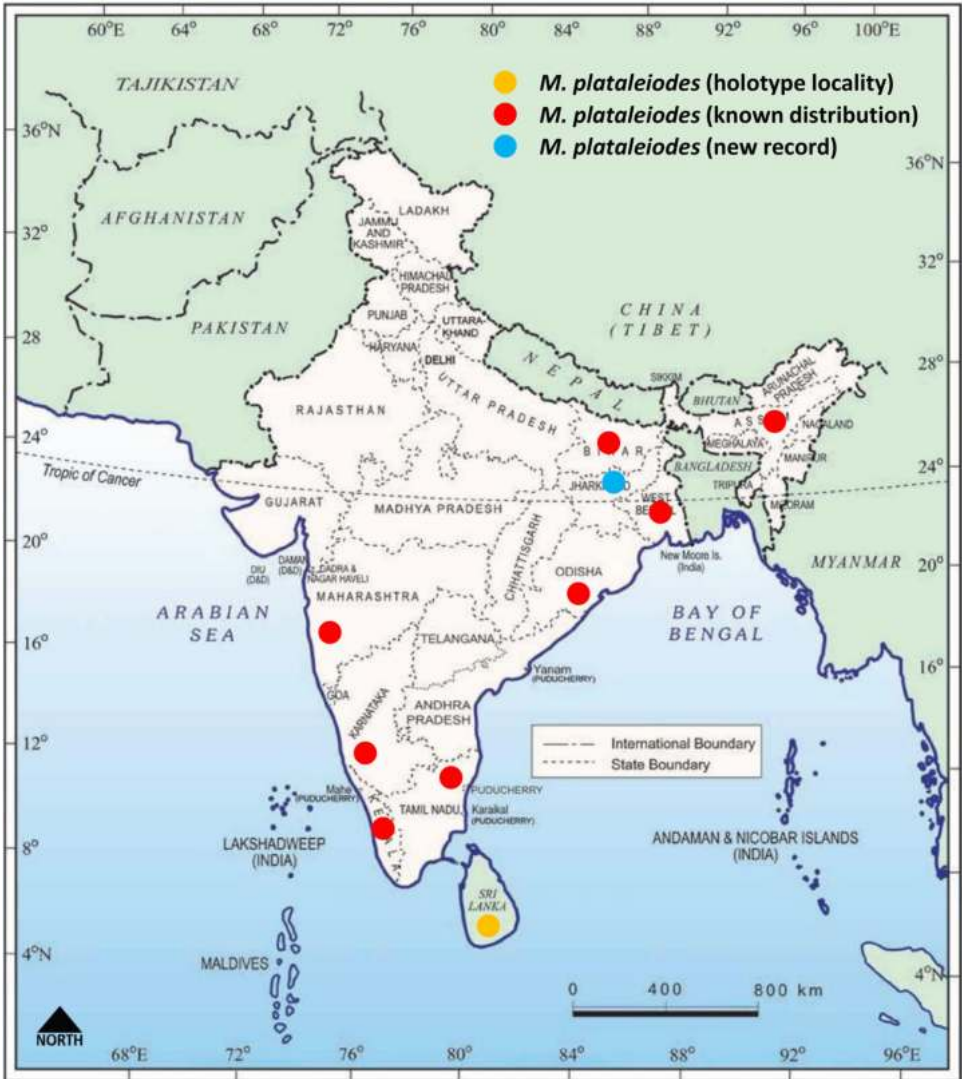
All morphological features including the structure of the genitalia (except the body coloration) are consistent with the characteristics of *M. plataleoides*. Polymorphism with respect to its body coloration has also been reported by other workers, some of whom have also misidentified it and considered it a different species altogether (Ganesh Kumar & Mohanasundaram, 1998; Caleb, 2016, 2020). However, the complete natural history involving both the sexes of any morpho-variant of this species has not been studied so far. In many animals, an unusual colour phenotype may appear spontaneously in an individual by genetic mutation which may or may not necessarily become fixed in the population; here, we have discovered and studied a whole population of morpho-variants with all-black individuals coexisting successfully with colonies of the black ant *C. compressus*. Prima facie, different body colour and mimetic preferences form a ground to consider this spider to be a different species but we refrain from doing so due to reports of polymorphism and polymorphic mimicry in this spider in previous works (Ganesh Kumar & Mohanasundaram, 1998; Borges et al., 2007; Caleb, 2016, 2020).

### Natural history

The spiders were spotted on leaves and branches of an old *Nyctanthes* tree as well as on the forest floor beneath this tree standing aloof in the sal-dominated forest. See the behavioural biology and discussion in subsequent sections for more insights into its natural history.

### Distribution

India, China, Sri Lanka (holotype locality), Malaysia, Thailand, Pakistan (Metzner, 2019); the records from India include the states of Assam, Kerala, Maharashtra, Odisha, Tamil Nadu, Karnataka, West Bengal, Bihar (Roy et al., 2016; Caleb, 2020) and Jharkhand (present study) (fig. 4).

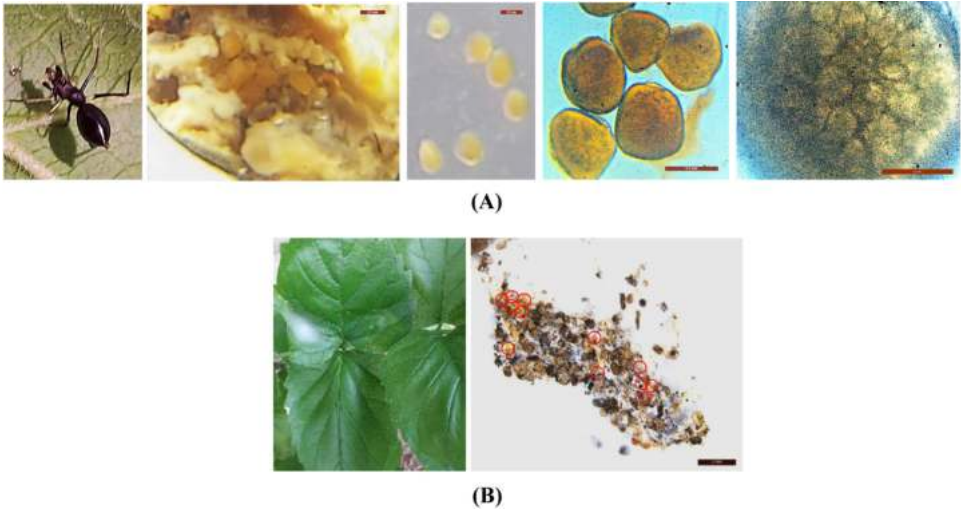


**Figure 4.** State-wise distribution of *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869) in India. The holotype locality, which is outside India, is also indicated.

*Behavioural biology*

*Egg laying*

Dissection of a gravid female revealed the presence of as many as 20 globular eggs inside its body at the time of egg laying. Microscopic examination of the female’s silk nest containing eggs also confirmed the number of eggs laid to be 18–20, which is different from the previous report of 8–12 eggs (Bhattacharya, 1938). Eggs were yellowish in colour and roughly spherical in shape. Each egg was about 0.3 mm in diameter. At higher magnification, each egg was found to have a thick outer



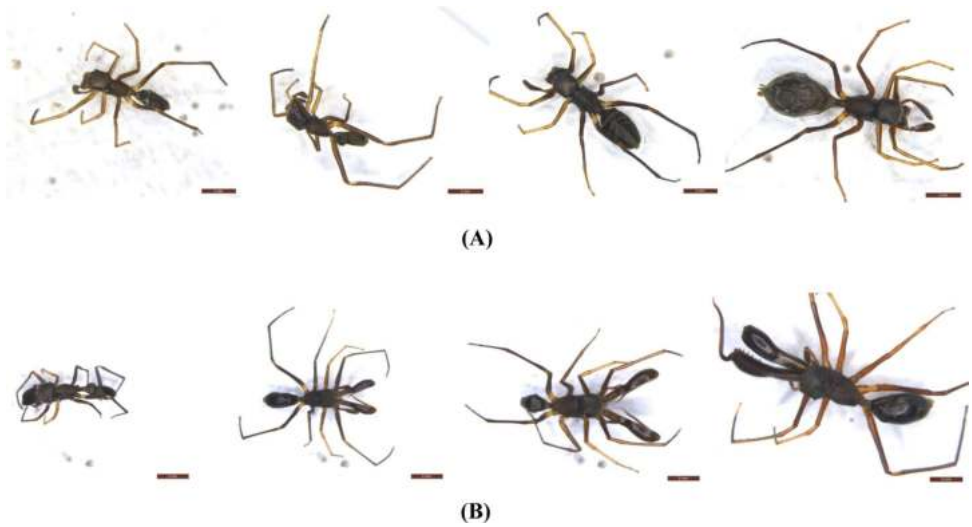
**Figure 5.** Egg laying in the studied morpho-variant of *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869). (A) A gravid female spider (extreme left image, scale bar 0.2 mm) was dissected to reveal eggs (second image from left, scale bar 0.2 mm). Eggs were visualized at different magnifications (third, fourth and fifth images from left, scale bars 0.2 mm for third and fourth images, and 0.1 mm for fifth image). Eggs were yellowish in colour and roughly spherical in shape. Each egg was about 0.3 mm in diameter. At higher magnification, each egg was found to have a thick outer lining and dense yolk present inside it in a compartmentalized manner in small sub-globules (fifth image from left). (B) Silk nest of spider on a leaf containing eggs (left image). Some eggs are indicated by red circles as seen under the microscope (right image, scale bar 2 mm). A large quantity of debris was found to be stuck in the strands of silk.

lining and dense yolk present inside it in a compartmentalized manner in small subglobules (fig. 5).

#### *Moulting behaviour*

*Myrmaplata plataleoides* juveniles emerge from the silk nest of the mother 20 days after egg laying. A previous study reported that each egg takes 12 to 15 days to hatch and juveniles stay inside the mother's silk nest for about five to six days (Bhattacharya, 1938). Spiders appear greenish with a more or less translucent anterior region at this stage, with the posterior abdominal region darker than other parts of the body. The morphology of spiders at this stage appears like a typical salticid. These juveniles measure only 1 mm in length. First moulting outside the mother's silk nest occurs after almost a week, followed by a second moult after two more weeks. With these moults, the spider becomes darker than before with body becoming more or less ant-like. The third moulting brings drastic morphological changes. It occurs within a week after the second moult. The spider acquires its characteristic shape and colour at this stage but no sexual dimorphism (fig. 6). The fourth and fifth moulting stages are quick to arrive with a gap of only two days between them within a week after the third moulting event. The fourth moulting event leads





**Figure 6.** Moulting in the studied morpho-variant of *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869). (A) Female spider at moulting stage 3, 6, 7 and 8 (from left to right, scale bars 2 mm). (B) Male spider at moulting stage 3, 6, 7 and 8 (from left to right, scale bars 2 mm).

to both an increase in body length and the appearance of characteristic body markings. The fifth moulting event appears to be a repetition of the fourth moulting event with the only significant change being an increase in body length from the fourth to the fifth moult. At this stage, the spider acquires the normal size of an adult. Like the third moulting event, the sixth moulting event is a turning point in the moulting process of these spiders. Sexual dimorphism becomes prominent after the sixth moulting stage. Spiders are as long as 10 mm at this stage. Male spiders acquire more striking changes like development of their characteristic mandibular structure at this stage, which appears morphologically similar to a female's up to the third moulting stage and is reproductively underdeveloped up to the fifth moulting stage. Both male and female spiders acquire reproductive maturity after the sixth moulting stage (fig. 6). The duration of the sixth moulting event between inception and culmination is less. It gets completed within 30 minutes. The time duration between the shedding of exuviae and transformation of the newly metamorphosed mandibular structures of the male spider from translucent white to opaque black was recorded to be just 15 minutes (fig. 7B). We also recorded the seventh and eighth moulting events making the spider quite bulkier than before (fig. 6). The purpose of these later moulting events is not very clear. The possible reason may be associated with its myrmevomorphic behaviour which is described in the next paragraph. Note that each moulting event was completed inside a silk nest freshly constructed by the moulting spider (fig. 7B).



**Figure 7.** Exuviae of the studied morpho-variant of *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869). (A) An undamaged whole-body exuvia of an undifferentiated male spider collected after the third moulting event (scale bar 2 mm). (B) Male spider displaying sixth moulting event. The recently casted exuvia is present on the left side of the spider moulting inside its silk nest. The time duration between shedding of exuvia and transformation of the newly metamorphosed mandibular structures of the male spider from translucent white (left image) to opaque black (right image) was recorded to be just 15 minutes.

#### *Temporal myrmecomorphy*

*Myrmaplata plataleoides* achieves sexual dimorphism, both in terms of morphology and appearance of fully developed reproductive structures, just after the sixth moulting stage. Then the seventh and eighth moulting events appear to lead to a manyfold increase in size of the spider. We could observe up to eight moulting events, after which no further moulting was observed. Spiders at the sixth, seventh and eighth moulting stages exhibit striking resemblances with minor, medium and major workers of *C. compressus* respectively (figs 6, 8, 9). Like the bulkiest eighth moult of the spider, major workers are the bulkiest of the workers. We consider this temporal myrmecomorphy, where a spider at a specific moulting stage in its developmental timeline mimics a worker ant of a specific size. Such a strategy may provide a mimic with additional survival benefits.



**Figure 8.** Mimic and model. The studied morpho-variant of *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869) female (left) and male (centre) is shown alongside its model ant *Camponotus compressus* (Fabricius, 1787) to display morphological similarities.





**Figure 9.** Workers of *Camponotus compressus* (Fabricius, 1787). (A) A colony in action. (B) Differently sized workers are found in the colony of *C. compressus*. Minor, medium and major sub-castes of workers are distinguished by their respective sizes, minor being the smallest (shown inside green enclosure), major is the bulkiest (shown inside red enclosure) and medium is of intermediate size between minor and major workers (shown inside yellow enclosure).

#### *Advantages of temporal myrmecomorphy*

When spiders after the sixth, seventh and eighth moulting stages were kept together with major, medium and minor ants in the same bottle, it was found that the major ants attacked the sixth and seventh moult more frequently than the eighth moult. Similarly the medium ants were found to attack the sixth moult of the spider more frequently than the seventh moult. The minor ants were not found to attack any of the three moults. The attacks on the later moults were less frequent. Temporal myrmecomorphy, therefore, provides multiple layers of protection to the spiders. Moulting to mimic a larger model protects the spiders from the smaller ants, maximizing their chances of survival. This behaviour was consistent in case of other experimental setups as well where different combinations of ants and spiders were kept inside the glass bottles. It was observed that although the spiders mimicked the ants, the spiders always maintained a safe distance from the ants and avoided ants approaching towards them by running away and hiding inside the edges of bottle caps. When the size of the glass bottle was decreased from 100 ml to 50 ml, attacks of the respective ants on their spider mimics increased twofold. When spiders were distant from ants, ants were not able to recognize the spiders as different. When the spiders were brought closer to the ants, the ants easily recognized the spiders to be different and attacked the spiders to kill them. Therefore, mimicry is more effective when different moults of the spiders are at a distance from their respective ant models. It was also found that the major ants recognize and attack the spiders sooner than the medium and the minor ants from the same distance. In these experiments, male spiders were found to be more frequently attacked by the ants than female spiders. This may be the reason for the higher number of encounters of female spiders in the population studied by us than of the male spiders. Such a differential reaction of ants towards the spiders in their vicinity may be due to the fact that the

female spiders mimic ants more accurately than the male spiders. Ants recognize male spiders to be different more easily and quickly than the female spiders. Attack of the Asian weaver ant *O. smaragdina* on its mimic, the red-coloured variant of *M. plataleoides*, has been reported previously *in situ* (Ramachandra & Hill, 2018). Here, we report the attack of the ground-nesting ant *C. compressus* on its mimic, the black-coloured variant of *M. plataleoides*, *ex situ*, when it comes closer to the ants.

#### *Feeding behaviour and prey preference*

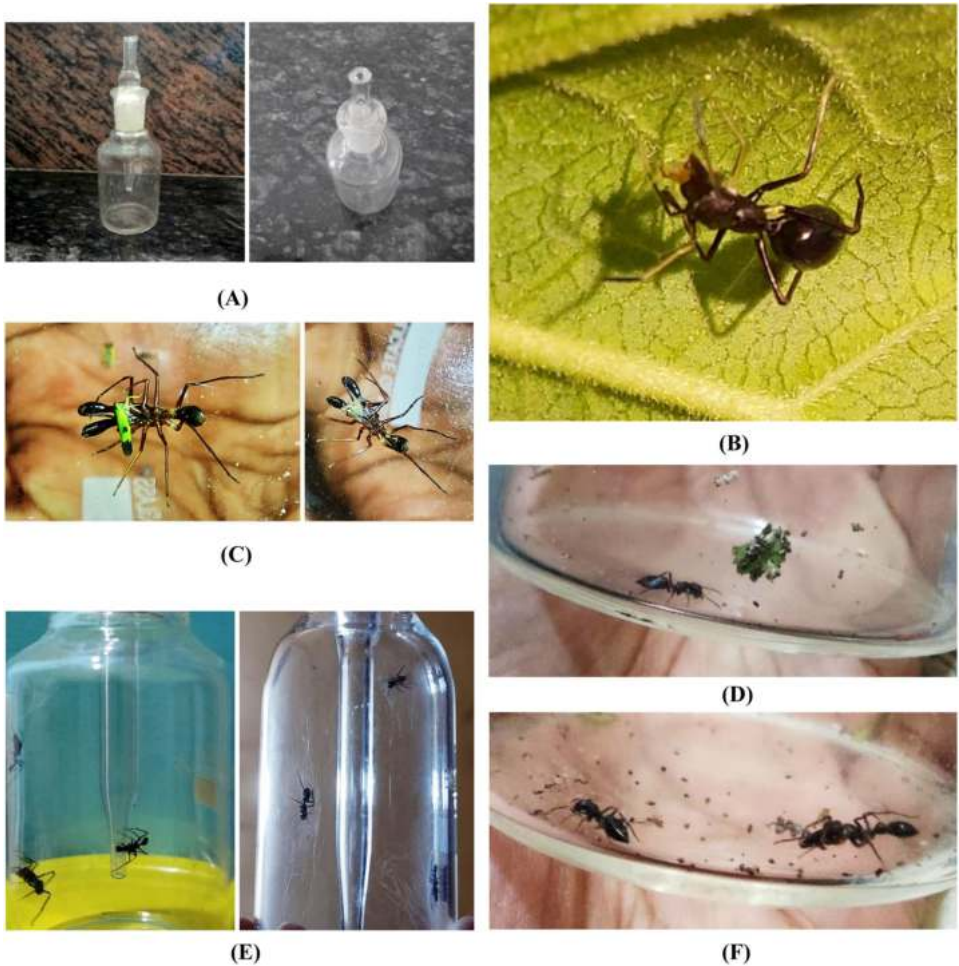
*Myrmaplata plataleoides* feeds irregularly in captivity. Whenever it feeds, it prefers small-sized prey. *Ex-situ* studies show that hemipterans are its preferred prey, followed by dipterans. When both a live fruit fly (*Drosophila* sp.) and a live *Nephotettix* sp. is provided to the spider, it hunts on *Nephotettix* but when a live cockroach and a live fruit fly are provided together, it prefers the fruit fly. Apart from *Nephotettix*, the spider shows similar interest towards other small-sized deltocephaline cicadelids like *Resilia* sp. (fig. 10C). *M. plataleoides* was found not to feed upon dead insects. It feeds only by hunting. Various scientists have observed its feeding preferences *in situ*. They also suggest that hemipterans and dipterans are the preferred prey insect group of this spider (Marson, 1946). Some reports also found this spider feeding on ant larvae in an abandoned nest (Mathew, 1954; Edmunds, 1978). We have further found this spider feeding on a ladybird nymph *in situ* (fig. 10B). At the study area, workers of *C. compressus* were found to regularly visit cow bugs (*Oxyrachis tarandus* Fab.) and its nymphs on branches of a *Nyctanthes* tree. These ants are often found to regularly visit cow bugs for honey dew which is a sugar-rich excretory product of sap-sucking hemipteran insects. Ants are also found to defend cow bugs against predatory attacks. In one instance, we found *M. plataleoides* feeding on cow bug nymphs *in situ* in the absence of ants.

#### *Debris-rolling behaviour*

Adding small-sized foreign materials like pieces of green leaves in the vicinity of *M. plataleoides* in captivity triggers debris-rolling behaviour (fig. 10D). Large-sized materials such as a twig or whole leaf do not elicit such behaviour. Spiders roll debris into spherical structures using their first pair of legs. Debris particles are held together by silk strands. Silk is produced by the spider as a sticky secretion which dries subsequently to form silk strands.

#### *Photokinetic response*

*Myrmaplata plataleoides* was found to move in the direction of low-intensity light projected towards it but avoids light of higher intensity. Prolonged exposure leads to habituation, however. On sunny summer afternoons, the spiders were mostly found foraging on the lower leaf surface. Though it prefers light for hunting as it is mostly dependent upon its visual senses for prey detection, it avoids bright light as this causes disturbances in its field of vision. It is a diurnal hunter. Visual senses are also used to avoid predatory attacks and mate selection.



**Figure 10.** Behavioural studies on the above described morpho-variant of *Myrmaplata plataleoides*. (A) Rearing setup of spiders. For *ex situ* behavioural studies, spiders were reared in transparent Borosil glass bottles with a proper opening for entry and exit of air for breathing. (B) A female spider feeding on a ladybird nymph *in situ*. (C) A male spider feeding on *Nephotettix* (left image) and *Resilia* (right image). (D) A female spider with the rolled pieces of leaves and dirt. (E) Setup to study sexual aggression having one female and two male spiders together (left image), and one male and two female spiders together (right image). (F) A male spider chasing a female spider during courtship.

### *Response to starvation*

*Myrmaplata plataleoides* was found to survive long-term starvation. Where *C. compressus* workers died within 5–7 days, *M. plataleoides* survived for 18–20 days (average of four spiders: 18.5 days). Starvation delayed the moulting process but did not stop it. Spiders were found to moult even during conditions of nutrient deprivation. Similarly, mating behaviour was not affected much by starvation.

### *Response to hypoxic conditions*

Like in the case of nutrient starvation conditions, *M. plataleoides* was also found to endure long-term oxygen deprivation conditions. Where *C. compressus* workers died within 24 hours, *M. plataleoides* survived for almost a week under hypoxic conditions (average of four spiders: seven days). Like in the case of starvation, oxygen deficit conditions delayed the process of moulting but did not stop it. Spiders were found to moult even during hypoxic conditions. Mating behaviour was also observed under low-oxygen conditions.

### *Courtship behaviour, sexual aggression and mate selection*

Male to male aggression was reported in *M. plataleoides* where one adult male spider was found to deter another adult male spider trying to approach an adult female in the experimental setup consisting of two adult males and one adult female kept together (fig. 10E). Such a phenomenon was not observed in the case of adult females in the experimental setup consisting of two adult females and one adult male kept together (fig. 10E). Further a mature male was found to approach only a mature female. An adult male does not exhibit courtship behaviour towards an immature female. Instead, peaceful side-by-side co-habitation of mature males and immature females in their individual nests was observed inside the glass bottle. Mate selection is therefore precisely regulated in this spider. Courtship behaviour in this spider involves approaching the female from anteriorly followed by the female running away from the male spider. This approach and run is repeated multiple times followed by mounting of the female by the male from the anterior, ending the chase (fig. 10F). An adult male has also been found to court two adult females one after another in the experimental setup consisting of two adult females and one adult male kept together. Mounting was found to be performed mostly under low-light conditions. Male–female mounting was observed *ex situ* mostly during early morning. Mounting is followed by mating which occurs inside the female's nest. These behaviours of the morpho-variant are similar to those of the conventional red ant mimic (Mathew, 1940).

## **Discussion**

### *Myrmecomorphy*

The occurrence of polymorphic mimicry in this species has been observed in previously published work where, due to their different colouration with respect to that in commonly occurring populations, some isolated populations of morpho-variants acquire adaptations in due course to coexist with other species of model ants in place of the conventional model ant species (Borges et al., 2007). *M. plataleoides* is known to mimic the red ant *O. smaragdina* but the spider population studied by us is completely black and is found in the vicinity of ant colonies, predominantly of the black ant *C. compressus*. Careful observations suggest striking similarities between the studied morpho-variant of *M. plataleoides* and *C. compressus* mostly with respect to the coloration (fig. 8). Morphological similarities

in terms of body size and shape are also found. The shape and size of different moults of *M. plataleoides* is also consistent with differently sized workers of *C. compressus* which we have termed temporal myrmecomorphy (figs 6, 8, 9). One study suggests that different moults of *M. plataleoides* mimic different ant species in due course of development in cases where the adult *M. plataleoides* mimics *O. smaragdina* (Bhattacharya, 1938). However, in the case of the black morpho-variant studied by us, temporal mimicry of differently sized workers of the same ant species was more conspicuous than mimicry of the individuals of multiple ant species. The behavioural biology of the morpho-variants of any animal species has not been studied in detail *vis-à-vis* the commonly occurring individuals. By the discovery of a novel kind of ant mimicry using a morpho-variant population as a model, the present study demonstrates the importance of studying morpho-variants in biology.

### *Fixed action patterns*

Behavioural studies reveal many fixed action patterns (FAPs) exhibited by these spiders. Many of these FAPs are shared among the conventional mimic and the morpho-variant. Some FAPs have been observed for the first time in morpho-variants only. Due to the paucity of such studies, comparison with the conventional mimic is difficult, but we assume these FAPs to be consistent as such patterns as mostly specific to a species. Different FAPs observed by us were debris-rolling behaviour, male to male sexual aggression, hunting, mate selection and the courtship pattern. Prey preference is not very consistent as these spiders have occasionally been found to attack species they do not commonly feed upon. In case of prey preference, size matters. We assume prey preference is acquired after birth by trial and error. Hemipterans turn out to be a preferred prey for various reasons. Most hemipterans are sap-sucking insects, which makes them rich in sugar, water and minerals. Being a rich source of energy, preying upon hemipterans is more profitable for the spiders. This information is acquired by spiders after birth by learning as suggested by their occasional random prey choices. Therefore, prey preference is not considered an FAP. Stress conditions like oxygen deprivation and starvation delay but do not stop the execution of FAPs.

### *Evolutionary insights*

Mymecomorphy is widespread among arthropods. Many arthropod species are known to mimic the same ant species at the same time in the same habitat. For instance, *C. compressus* is also known to be mimicked by many other arthropods. A study has also found the existence of nine sympatric ant-mimicking arthropods in a habitat that all mimic the same model ant *C. compressus* (Kumari & Rastogi, 2018). It sounds more intriguing to know that a single arthropod species is mimicking more than one ant species. Many instances of polymorphic mimicry have been documented among spiders. Conventionally a mimic is supposed to coevolve and perfect itself to imitate its model species (Gilbert, 2005; Cushing, 2012). Mimics

certainly coevolve with the model but not necessarily at the same rate. As shown by molecular phylogenetic studies by a group of workers, evolutionary rates of different myrmecomorphs of the genus *Myrmarachne* and their known ant models differ significantly. This study shows that myrmecomorphs radiate considerably from the expected evolutionary trend leading to higher degree of polymorphism which further leads to sympatric association (Ceccarelli & Crozier, 2007; Cushing, 2012). Here 'expected evolutionary trends' refers to the attainment of perfection in mimicking features of a single model in the due course of evolution. We suggest that in the course of adaptive radiation, a number of different morphs appear in the population but the one that mimics a particular obnoxious model species in better ways gets naturally selected unless it acquires other survival strategies against potential predators. In a polymorphic population, it is possible that sympatric speciation causes different populations of the same spider species to mimic different ant species. Here each population represents individuals of a not-so-common morpho-variant of a species which is more common in some other form. For instance, *M. plataleoides* is known to mimic the red ant *O. smaragdina* commonly but its less common morpho-variants are known to mimic other species of ants (Borges et al., 2007). In the present study also, we discuss the natural history of a morpho-variant of the same spider species. It has further been suggested that disruptive selection may be responsible for the existence of polymorphism in populations of *M. plataleoides* (Borges et al., 2007). The tendency to constantly radiate leading to polymorphic mimicry has an advantage against predation as the prey (the mimic) keeps on changing its form over time, leading to enhanced survival of that species in one form or the other. It also becomes difficult for some predators who avoid potentially obnoxious prey to pinpoint a particular morph mimicking the same obnoxious prey, as polymorphism also decreases the number of mimics per model making it difficult to get spotted (Nelson, 2010; Cushing, 2012). An increase in frequency of occurrence may cause a morph to lose its mimetic protection against potential predators. But this loss further leads to the selection of new morphs (Gilbert, 2005; Cushing, 2012). Based on the above discussion, the population of this morpho-variant of *M. plataleoides* may be considered a product of sympatric speciation and disruptive selection owing to a variety of dispersal mechanisms exhibited by spiders. Many spiders exhibit a variety of active and passive dispersal mechanisms (Szymkowiak et al., 2007). Juveniles of spiders could disperse by wind. The presence of a sticky silky nest also enhances the dispersal abilities of both the eggs and the spiders by getting transported on the bodies of bigger animals. Dispersal increases chances of survival by preventing overcrowding and allowing safer grounds to be acquired. In the case of mimics, overcrowding increases the chances of predatory attacks on them (Gilbert, 2005; Cushing, 2012). Therefore, dispersal plays a vital role in the survival and evolutionary success of mimics. Whatever be the dispersal mechanisms, this morpho-variant would have evolved in a population of red-ant mimics only and would have arrived at its present habitat by chance dispersal; its unique morphological features provided it a better chance to coexist with

the prevailing black ants. Alternatively, it is also possible that this morpho-variant appeared in a population of red-ant mimics in the same habitat where red ants would have been in abundance, but with a reduction in the red-ant population and the increased dominance of black ants for some reason, red-ant mimics would have locally perished or migrated to other areas, leaving only the black morpho-variant displaying morphological similarities with the prevailing black ants to be naturally selected to exist here. This relative fitness imposed upon the black morpho-variant may be attributed to polymorphic mimicry existing in *M. plataleoides* populations.

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