The early amber caught the worm.

A 100 million-year-old onychophoran reveals past migrations

The split of the supercontinent Pangaea into southern Gondwana and northern Laurasia divided the fauna of these two regions. Therefore, the present-day occurrence of supposedly Gondwanan organisms in Laurasian-derived regions remains a puzzle of palaeobiogeographical history. We studied the oldest amber-embedded species of velvet worms (Onychophora) in order to illuminate the colonisation of Southeast Asia by Gondwanan lineages of these animals. Our results indicate that an early Eurogondwanan migration is the most likely scenario for Onychophora, while an 'Out-of-India' colonisation of Southeast Asia would instead be incompatible with the age of the amber fossil studied. This suggests a recent colonisation of India by onychophorans and refutes their Gondwanan relict status in this region.

Burmese amber from Myanmar is known not only for its physical beauty but also for preserving one of the richest palaeobiota in the world, being arguably the most relevant fossil resin for studying terrestrial diversity during the mid-Cretaceous period, approximately 100 million years ago [1]. Among the most consequential organisms found in Burmese amber is the oldest amber-embedded representative of Onychophora — a small group of soft-bodied, terrestrial invertebrates pivotal for understanding animal evolution and biogeography. Onychophorans are extremely rare in fossiliferous amber, with the Burmese †*Cretoperipatus burmiticus* being only the third species ever discovered [2]. Indeed, this species is crucial for clarifying the question of how onychophorans colonised Southeast Asia, one of the most enigmatic and controversially discussed biogeographical issues relating to this group.

Representatives of Peripatidae, an onychophoran subgroup to which †*C. burmiticus* was suggested to belong, show a disjointed distribution pattern across three distinct geographical regions — the Neotropic zone, Tropical Africa, and Southeast Asia — each home to a monophyletic group. Molecular data suggest that these clades diverged during the time of the supercontinent Pangaea, approximately 286–244 million years ago [3]. Hence, it is commonly assumed that their current discontinuous distribution resulted from past tectonic shifts and/or climatic events. While continental drift could explain the split between the Neotropical and Tropical African Peripatidae, the major question is how peripatids reached Southeast Asia, as this area has never been in direct contact with the other two landmasses.

It has previously been suggested that peripatids from Gondwana arrived in Southeast Asia prior to the split of continents (= continental drift) via a land bridge formed by Europe, a hypothesis recently named the Eurogondwana model [4]. Alternatively, since onychophorans are poor dispersers, it was proposed that the Indian subcontinent acted as a raft during its northward drift and brought Gondwanan species of Peripatidae to Southeast Asia after the so-called 'India–Asia collision', a biogeographical model commonly called 'Out–of–India' [5]. Accordingly, the only onychophoran species reported from India, *Typhloperipatus williamsoni* [6], is putatively described as being a Gondwanan relict that survived

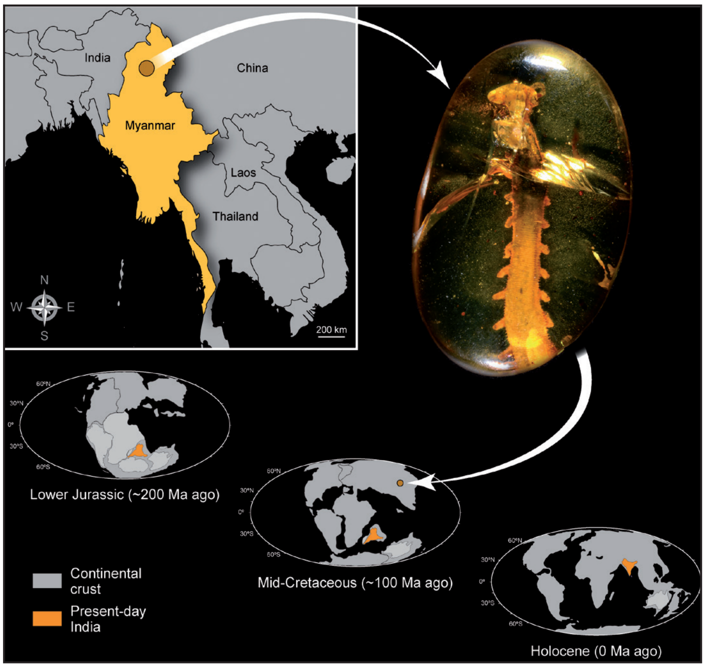

Figure 1

The geographic position of the Hukawng Valley amber deposit in Myanmar (brown circle), where the exceptionally well-preserved material of †*Cretoperipatus burmiticus* (photograph) was found. Bottom row shows the drift of India through time. Notice that the fossil species inhabited Southeast Asia during a period when India was still an island.

the ~100-million-year isolation of the Indian subcontinent as it moved towards Southeast Asia. Depending on which scenario is considered, extinction has been invoked for explaining the current lack of present-day peripatids in Europe (Eurogondwana model), or in the great part of India ('Out–of–India' hypothesis). It is important to note, however, that these two hypotheses are not mutually exclusive, as onychophorans may have found their way to Southeast Asia via both routes simultaneously. In any case, hypotheses on vicariance, dispersion and extinction require fossil data to be tested empirically.

Recently, additional material of †*C. burmiticus*, including an exceptionally well-preserved amber-embedded specimen, was discovered at the species type locality in Myanmar (Fig. 1). This fossil dates to the mid-Cretaceous, a period in time after the continental drift but before the 'India–Asia collision', i.e., sometime between the two suggested scenarios accounting for the colonisation of Southeast Asia by peripatids. Thus, its relevance for clarifying these biogeographical and evolutionary issues should not be understated. Using the imaging beamline P05 at PETRA III, we performed a full micro-CT scan of this specimen in amber and used these data to reconstruct hitherto unknown anatomical details of †*C. burmiticus* (Fig. 2). By performing a morphological analysis of this animal and comparing it to extant taxa, we confirmed †*C. burmiticus* to be a member of the Peripatidae and resolved the Indian species *T. williamsoni* as its closest relative.

These findings support an early migration of Peripatidae to Southeast Asia, i.e. the Eurogondwana hypothesis, followed by a posterior colonisation of India by onychophorans from Southeast Asia. In other words, the fact that †*C. burmiticus* roamed Southeast Asia long before there was a terrestrial connection with India excludes this species as originating from India, while its sister-group relationship to *T. williamsoni* refutes the putative Gondwanan relict status of the latter. Furthermore, this suggests that the migration of onychophorans into India happened not earlier than ~25 million years ago, i.e., after the 'India–Asia collision' and much later than what was previously thought.

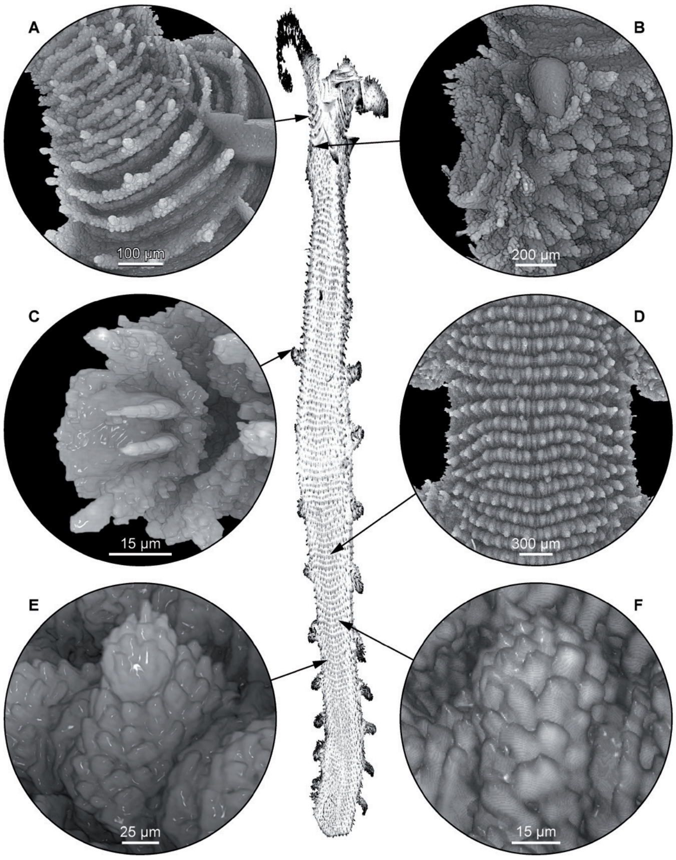

Figure 2

Novel morphological features of †*Cretoperipatus burmiticus* revealed by synchrotron radiation micro-computed tomography (= SRµCT). (a) Detail of the antenna. (b) Eye and slime papilla. (c) Foot. (d) Overview of the dorsal integument. (e) A dorsal primary papilla. (f) A dorsal accessory papilla.

This study demonstrates the utility of X-ray microtomography for accessing morphological characters that were previously unavailable to traditional techniques due to the nature of fossilisation. Thus, it opens the door to generating a wealth of new data from fossil specimens that have been kept for years in museums or private collections and using these data to address long-standing issues.

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