

THE IDENTITY OF *PHRYSSONOTUS* *BURMITICUS* (COCKERELL, 1917) (DIPLOPODA, POLYXENIDA, SYNXENIDAE) IN CRETACEOUS AMBER FROM MYANMAR

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SYNOPSIS Based on a study of the holotype and of five presumably topotypic and conspecific juveniles, the millipede *Phryssonotus burmiticus* (Cockerell, 1917) from Lower Cretaceous (Albian) Myanmar amber (Burmite) is revised and redescribed. All relevant millipede material from Burmite can now be unequivocally assigned to *Phryssonotus* and represents the geologically oldest member of the order Polyxenida known to date.

KEY WORDS Burmese amber, Myanmar, Cretaceous, taxonomy, zoogeography, relics

INTRODUCTION

The millipede genus *Phryssonotus* Scudder, 1885 as currently accepted (Hoffman 1980; Condé & Nguyen Duy-Jacquemin 1984) comprises six or seven species, of which at least one is a fossil, *P. hystrix* (Menge 1854), from the Eocene Baltic amber (Bachofen von Echt 1942; Kraus & Brauckmann 2003). The remaining five or six living species are disparately scattered over South America: *P. orientalis* (Silvestri, 1900: Uruguay), *P. chilensis* (Silvestri, 1948: Chile); Central America: *P. cubanus* (Silvestri, 1948; Cuba); southern Africa and New Guinea: *P. capensis* (Silvestri, 1923: Republic of South Africa, Mozambique, Madagascar, Papua New Guinea); Australia: *P. novae-hollandiae* (Silvestri 1923) and the Mediterranean region: *P. platycephalus* (Lucas, 1846: North Africa, Spain and Italy; Silvestri 1948; Condé 1954a).

Polyxenus burmiticus (Cockerell, 1917), from the Cretaceous amber of Burma, or Myanmar (also called Burmite), has long been referred to as a member of the Synxenoidea (Condé & Jacquemin 1963: 69) or even the Synxenidae (Eskov 1987; Ross & York 2000; Rasnitsyn & Ross 2000). Recently Nguyen Duy-Jacquemin & Geoffroy (2003) mentioned *burmiticus* under *Phryssonotus*. This species still remains the only diplopod to be reported from Burmite.

Taxonomically, *Phryssonotus* is thus the sole accepted genus in the family Synxenidae, a taxon characterised by its 12, not 10–11, body segments (= 17 leg pairs) in adults, two rows of striated scales per tergite, extremely elongate female vulvae and the exceedingly long and dense tergal

trichome. Since the modern systematics of the Polyxenida is largely based on the location, number and shape of the highly delicate sensilla on the antennae, species determination often appears to be very difficult to impossible for juvenile and/or fossil material. No wonder that the only available key to *Phryssonotus* species (Silvestri 1923) solely concerns four Recent forms. The main distinguishing characters used in the key were the number of ocelli and the number of trichomes (2–6) arranged in a row near the anterior trichobothrium with a short funicle.

Synxenidae have often been viewed as an example of the so-called austral distribution pattern, with the disjunct occurrences in the Southern Hemisphere believed to reflect Gondwanaland fragmentation. However, as there are records of some Recent members in the Northern Hemisphere, let alone of the Eocene *P. hystrix* in the Baltic region, any such speculation is bound to remain groundless. Instead, the pattern is far more explicable in terms of extinction (Eskov 1992, 2002). However, based on a number of plesiomorphies as well as the highly patchy/sporadic distribution both of fossil and Recent species, both *Phryssonotus* and Synxenidae have rightly been recognised as truly relict elements in the world's millipede fauna (e.g. Hoffman *et al.* 2002).

Scudder (1885) erected his new genus *Phryssonotus* to replace *Lophonotus* Menge, 1854, a preoccupied name, with *Lophonotus hystrix* Menge, 1854 automatically becoming the type-species of *Phryssonotus*. Silvestri (1900), apparently unaware of *Phryssonotus*, described a new genus, *Synxenus*, to accommodate a new South American species, *orientalis*. A few more congeners had been added, largely

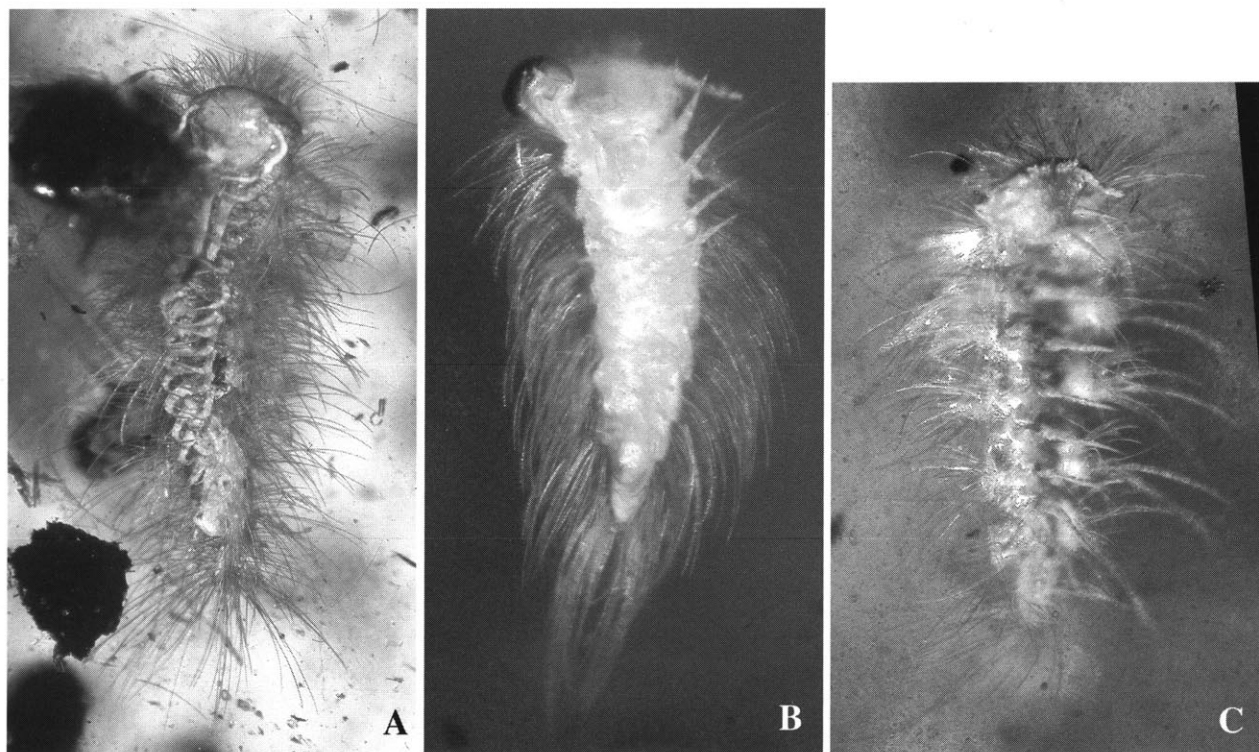


Figure 1 *Phryssonotus burmiticus* (Cockerell, 1917). **A**, holotype BMNH In. 19122. Ventral view. Length (excluding hairs) 2.1 mm. **B**, non-type juvenile BMNH In. 19123(2). Ventral view. Length (excluding hairs) 1.28 mm. **C**, non-type juvenile BMNH In. 19123(6). Moulted cast. Length (excluding hairs) 1.35 mm.

in *Synxenus*, before Silvestri established (1923) and then reviewed (1948) the family Synxenidae. Jones (1937) provided the first synonymies among Recent synxenids. Condé (1954a), in the latest but only partial review of *Phryssonotus* and Synxenidae, was the first to formally synonymise the Recent *Synxenus* under the fossil *Phryssonotus*, but the status of *Polyxenus burmiticus* was still misinterpreted. Since then, *Phryssonotus* and/or Synxenidae have only occasionally been addressed (e.g. Condé 1954b, 1959, 1971; Condé & Jacquemin 1963; Hoffman 1980; Condé & Nguyen Duy-Jacquemin 1984; Hoffman *et al.* 1996, 2002; Hamer 1998; Rasnitsyn & Ross 2000; Ross & York 2000), largely in connection with new and/or reiterated records.

Phryssonotus and Synxenidae were encountered and described as fossils before any living member was known, which was also the case for the spider genus *Archaea* C.L. Koch in Koch & Berend, 1854 and the family Archaeidae as a whole (cf. Eskov 1992). Indeed, both Archaeidae and Synxenidae are clearly basal and highly relict families in their respective orders and, likewise, superficially, both have 'Gondwanan' origins. Whereas Archaeidae currently comprises a few recognised genera, Synxenidae remains monogeneric, with as many as five junior synonyms listed for *Phryssonotus*: *Lophonotus* Menge, 1854, *Synxenus* Silvestri, 1900, *Schindalomonotus* Attems, 1926, *Kubanus* Attems, 1926 and *Koubanus* Attems, 1928 (cf. Hoffman 1980). Interestingly, a new archaeid spider has recently been found in Burmite as well (Penney 2003).

Based on J. G. Sheals' restudy of the holotype (adult female) of *Polyxenus burmiticus* Cockerell, 1917, Condé

& Jacquemin (1963: 69) reallocated this species to the Synxenoidea. Yet these authors abstained from any closer identification noting that too few crucial, taxonomically important structures were visible on the fossil. Even the recent colour picture of the holotype published by Ross & York (2000) hardly improves the situation. Since *Phryssonotus* is the only genus currently accepted as valid in Synxenidae, *burmiticus* was incorporated into *Phryssonotus* for the first time by Nguyen Duy-Jacquemin & Geoffroy (2003).

Courtesy of Dr Andrew J. Ross (The Natural History Museum, London, UK), A.P.R. has been privileged not only to revise the holotype of *Polyxenus burmiticus* (In. 19122), take some colour pictures and prepare a number of sketches at high magnification (see Fig. 2A) but also to examine the whole Burmite collection. This contains 60 juvenile inclusions of *Phryssonotus*, of which five (out of 24 enclosed in the single amber block In.19123) were selected for a closer study and photography (Figs 1B–C, 2B–D). A side-by-side comparison of this material reveals that all of them belong to *Phryssonotus* and that they are probably the juveniles of *P. burmiticus* (M. Nguyen Duy-Jacquemin, pers. comm.). Regrettably, no closer identification of the new samples appears to be possible because they are juveniles that are too poorly preserved to show all the necessary details of antennal structure. In addition, in juvenile instars the number and shape of antennal sensilla may be somewhat underdeveloped compared to the adults, in some extant Polyxenida (e.g. Nguyen Duy-Jacquemin & Condé 1982).

The higher classification accepted here is that of Shelley (2003), the relevant nomenclature follows Jeekel (1970).

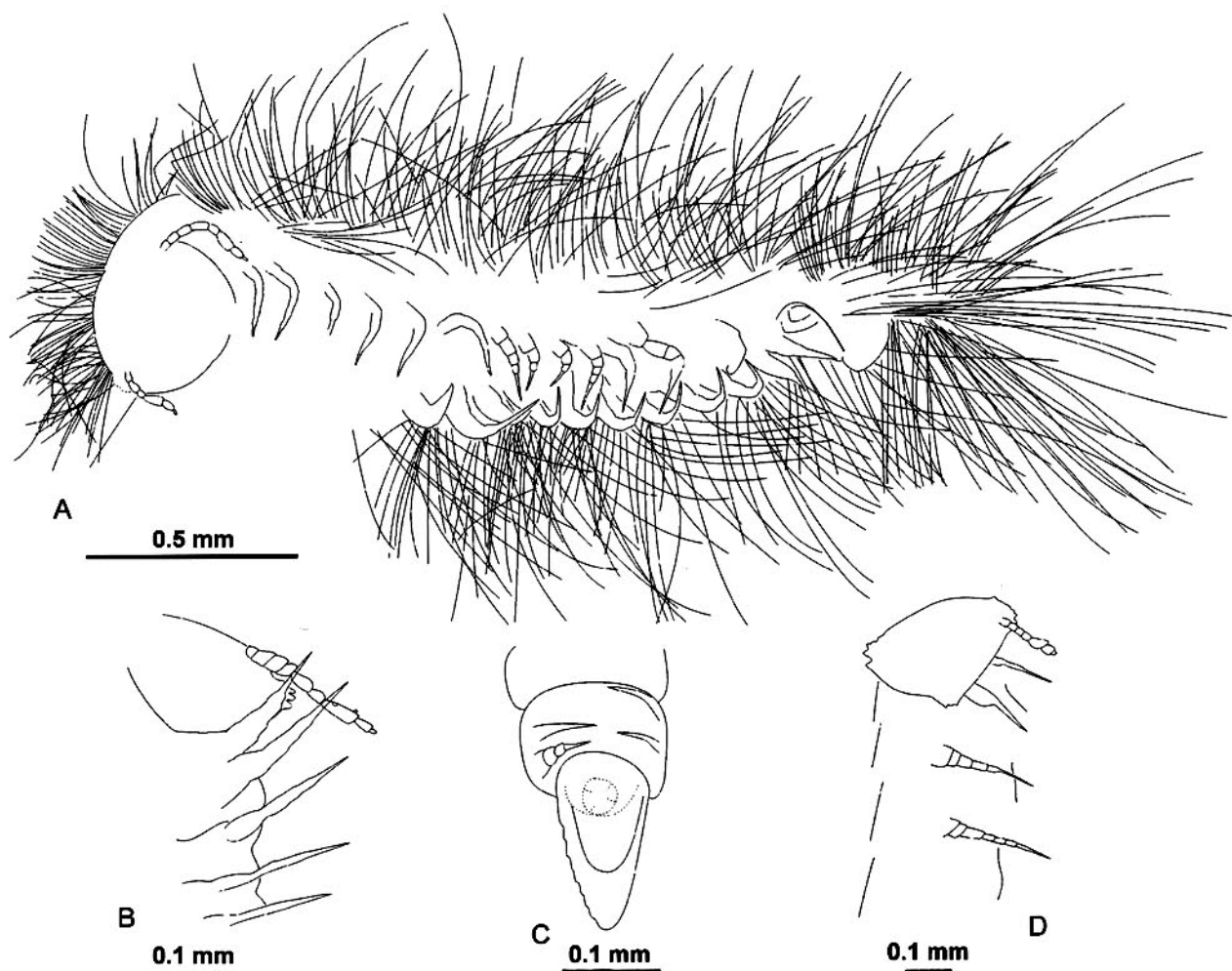


Figure 2 *Phryssonotus burmiticus* (Cockerell, 1917). Line drawings. **A**, holotype BMNH In. 19122, ventral view. **B**, non-type juvenile BMNH In. 19123(2): head with antenna and anterior legs of left side. **C**, non-type juvenile BMNH In. 19123(2): abdominal apex from below. **D**, non-type juvenile BMNH In. 19123(6): head with antenna and anterior legs.

SYSTEMATIC DESCRIPTION

Class **DIPLOPODA** de Blainville in Gervais, 1844

Subclass **PENICILLATA** Latreille, 1825

Order **POLYXENIDA** Verhoeff, 1934

Superfamily **SYNXENOIDEA** Silvestri, 1923

Family **SYNXENIDAE** Silvestri, 1923

Genus **PHYRSSONOTUS** Scudder, 1885

[= *Lophonotus* Menge, 1854 non Stephens, 1829, nec Macquart, 1839, type species: *Lophonotus hystrix* Menge, 1854, fossil from Baltic amber, by monotypy: = *Synxenus* Silvestri, 1900, type species: *Synxenus orientalis* Silvestri, 1900, Uruguay, by original designation: = *Schindalmonotus* Attems, 1926, type species: *Schindalmonotus hystrix* Attems, 1926, South Africa, by monotypy: = *Kubanus* Attems, 1926, type species: *Polyxenus platycephalus* Lucas, 1846, Algeria, by subsequent designation of Jeekel (1970: 2): = *Koubanus* Attems, 1928, type species: *Polyxenus platycephalus* Lucas, 1846, Algeria, by original designation.]

TYPE SPECIES. *Lophonotus hystrix* Menge, 1854, Baltic amber.

RANGE: Upper Albian to Recent.

Phryssonotus burmiticus (Cockerell, 1917)
(Figs 1 & 2)

1917 *Polyxenus burmiticus* Cockerell: 40–41, fig. 1.

1954a *Polyxenus burmiticus* Cockerell; Condé: 75.

1963 *Polyxenus burmiticus* Cockerell; Condé & Jacquemin: 69

1978 *Polyxenus burmiticus* Cockerell; Zherikhin: 114.

2000 '*Polyxenus*' *burmiticus* Cockerell; Ross & York: 15.

2000 *Polyxenus burmiticus* Cockerell; Ross & York: fig. 18.

2003. *Phryssonotus burmiticus* (Cockerell); Nguyen Duy-

Jacquemin & Geoffroy: 101.

TYPE MATERIAL. Holotype (adult female), NHM In.19122, Burmese amber of Myanmar (Burmite), Lower Cretaceous (Upper Albian). See Cruickshank & Ko (2003) for dating.

ADDITIONAL MATERIAL: 60 juveniles, NHM In.19123, same provenance.

DIAGNOSIS. Differs from *Phryssonotus hystrix*, from the Upper Eocene Baltic amber, in the extremely long and dense

trichome. No thorough comparison with the extant species is possible because of poor preservation of material.

DESCRIPTION. Adult female holotype apparently with 12 body segments (including collum) and 17 leg pairs (Figs 1A & 2A). Length 2.1 mm, width without trichome 0.3 mm; tergal setae particularly copious, arranged in two transverse rows on all postcollar segments except telson, mostly exceedingly long and uniform (mid-segment setae 0.4–0.5 mm long), these on telson not much longer than those on previous body segments (0.6–0.7 mm long); telson characteristically conical; legs very short. Both photograph (Fig. 1A) and line drawings of the holotype (Fig. 2A) are provided to facilitate recognition. For the juvenile topotypes (Figs 1B, C & 2B–D), the following additional information is available:

In.19123(2) (Figs 1B & 2B, C), 12 leg pairs, body length 1.28 mm, broadest segment 0.3 mm wide; mid-segment side setae 0.4 mm long, setae on telson up to 0.55 mm long.

In.19123(6) (Fig. 2D), moulting cast with 9 leg pairs, moulting cast 1.35 mm long, mid-segment side setae 0.45 mm long, setae on telson up to 0.6 mm long.

In.19123(7), 1.45 mm long, maximum body width 0.4 mm, c. 13 leg pairs (apparently 10 segments, excluding telson), mid-segment side setae 0.5 mm long, setae on telson up to 0.6 mm long.

In.19123(8), apparently 12 leg pairs, 1.65 mm long, widest segment 0.27 mm wide, mid-segment side setae 0.6 mm long, setae on telson up to 0.7 mm long.

In.19123(9), 12 leg pairs, 1.6 mm long, widest segment 0.3 mm wide, mid-segment side setae 0.5 mm long, setae on telson up to 0.65 mm long.

REMARKS. In general, the systematics of Synxenidae is very difficult, since the described species are all very similar and the specific characters in *P. hystrix*, the type-species of *Phryssonotus*, are unknown and are most likely to remain so because the animal is a fossil. Even the Recent species are mostly too poorly studied to attempt a key that would hold. The two South American species, *P. orientalis* and *P. chilensis*, might very well prove to be conspecific (Condé 1971) and the same seems true for the barely distinguishable *P. capensis* and *P. novaehollandiae* (Condé & Nguyen Duy-Jacquemin 1984). Therefore, much revisionary effort is necessary to improve the taxonomy of Synxenidae.

Against this background, progress in our knowledge of *Phryssonotus* in general and of *P. burmiticus* in particular, however modest, allows all relevant material from Burmite to be unequivocally attributed to *Phryssonotus*. Furthermore, there are sound reasons for believing that all the topotypic material likewise represents *P. burmiticus*, the geologically oldest member of the millipede order Polyxenida known to date.

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