# Cheliferoid pseudoscorpions (Arachnida, Chelonethi) from the Lower Cretaceous of France

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**ABSTRACT**

Three pseudoscorpion fossils are reported from the Lower Cretaceous (uppermost Albian) amber of Archingeay (Charente-Maritime, France). These are the oldest described members of the Cheliferoidea Risso, 1826 and the first fossil pseudoscorpions to be described from France. *Heurtaultia rossiorum* n. gen., n. sp. is described from two incomplete adults. The new genus is characterized by having gaping chelal fingers, elongate tarsal setae on leg I (probably sexually dimorphic characters limited to male) and the basal position of the tactile seta on the tarsus of legs III and IV. The systematic position of *Heurtaultia* n. gen is uncertain, but it is provisionally assigned to the extant family Cheliferidae Risso, 1826. The third fossil is complete and probably represents a tritonymph of a different species of Cheliferidae, but it is not named. This specimen is partly enclosed in a layer of silk, which is interpreted as a moulting nest.

**KEY WORDS**
Arachnida,
Pseudoscorpion,
Cheliferoidea,
fossil,
amber,
Cretaceous,
Albian,
France,
new genus,
new species.

**RÉSUMÉ**

*Pseudoscorpions Cheliferoidea (Arachnida, Chelonethi) du Crétacé inférieur de France.*

Trois fossiles de pseudoscorpions sont signalés de l'ambre du Crétacé inférieur (Albien terminal) provenant d'Archingeay (Charente-Maritime, France). Ce sont les plus anciens représentants décrits de la superfamille des Cheliferoidea Risso, 1826 et les premiers pseudoscorpions fossiles décrits de France. *Heurtaultia rossiorum* n. gen., n. sp. est décrit à partir de deux adultes incomplets. Le nouveau genre se distingue par les doigts béants des pinces, des soies allongées sur le tarse I (probablement des dimorphismes sexuels restreints au mâle) et la position basale de la soie tactile du tarse des pattes III et IV. La position systématique de *Heurtaultia* n. gen. est incertaine, mais il est attribué provisoirement à la famille actuelle des Cheliferidae Risso, 1826. Le troisième fossile est complet et semble être une tritonymphe d'une autre espèce des Cheliferidae, mais elle n'est pas nommée. Ce spécimen est partiellement entouré de soie, considérée comme un nid de mue.

**MOTS CLÉS**
Arachnida,
Pseudoscorpion,
Cheliferoidea,
fossile,
ambre,
Crétacé,
Albien,
France,
genre nouveau,
espèce nouvelle.

## INTRODUCTION

Pseudoscorpions are one of the oldest groups of extant terrestrial arthropods, being represented by fossils from the middle Devonian (Shear *et al.* 1989; Schawaller *et al.* 1991). However, they are extremely rare in sedimentary rocks and only reappear in the fossil record some 260 Ma later, as Lower Cretaceous amber inclusions (Schawaller 1991). Until recently, very little was known about Mesozoic pseudoscorpions. A nymphal Cheliferoidea Risso, 1826 was described by Schawaller (1991) from Upper Cretaceous (Campanian) Canadian amber, but the immaturity of the specimen prevented it from being named and its assignment to the Recent family Chernetidae Menge, 1855 is tentative. Undescribed pseudoscorpions have been reported in Upper Cretaceous (Turonian) New Jersey amber (Grimaldi *et al.* 2002), Lower Cretaceous (Aptian/Neocomian) Lebanese amber (Whalley 1980; Grimaldi 1996) and Lower Cretaceous (Albian) amber from Álava, Spain (Delclòs *et al.* 2007). The only named Mesozoic pseudoscorpions are *Amblyolpium burmiticum* (Cockerell, 1920) and *Electrobisium acutum* Cockerell, 1917 (Cockerell 1917, 1920; Judson 1997, 2000), both from Burmese amber, which is now dated as Lower Cretaceous (probably Upper Albian) (Cruickshank & Ko 2003). Judson (2000) referred to unidentified fragments of Cheliferoidea in Burmese amber and Grimaldi *et al.* (2002) published a photograph of a probable member of this superfamily in Burmese amber.

The presence of pseudoscorpions in Lower Cretaceous (Upper Albian) amber from Archingeay (Charente-Maritime), France has recently been reported by Néraudeau *et al.* (2002), Perrichot (2004, 2005) and Perrichot *et al.* (2007). The material represents two species of the superfamily Cheliferoidea, which are described here. The only other records of fossil pseudoscorpions from France are from the Tertiary. Nel *et al.* (1999) mentioned a pseudoscorpion from lower Eocene (Ypresian) Parisian amber, which belongs to the family Garypinidae (pers. obs.). Hope (1847) recorded a "Chelifer" (then a general term for any pseudoscorpion) from Oligocene sedimentary rocks of Aix-en-Provence, but no description or figures were given and the fossil appears to be lost: it is not present in either the Oxford University Museum of Natural History (G. C. McGavin *in litt.*) or The Natural History Museum, London (A. J. Ross *in litt.*).

## MATERIAL AND METHODS

The fossils were collected from a quarry between the villages of Archingeay and Les Nouillers, near Saint-Savinien (Charente-Maritime), in midwest France (Néraudeau *et al.* 2002; Perrichot 2004, 2005). The amber is dated as uppermost Albian (lithological subunit A1 *sensu* Néraudeau & Moreau 1989), giving an age of about 100 Ma, and is thought to have been deposited near a coastal delta (Néraudeau *et al.* 2002; Perrichot 2004, 2005; Dejax & Masure 2005). Most of the amber is derived from resin of the conifer genus *Agathoxylon* Hartig, 1848 (Araucariaceae) (Perrichot 2004), but Perrichot (2005) suggests that some pieces might be derived from resin of Cheirolepidaceae.

Two of the specimens (AR 92.1 and 92.2) had been mounted on slides in Canada balsam, while the third (ARC 186.1 R) had been mounted in balsam between two coverslips enclosed by epoxy resin. The mountant of slide AR 92.1 was still fluid when received, hence the slide was replaced by a second coverslip to facilitate examination. Details of the preparation and cataloguing of specimens are given by Perrichot (2004). All three specimens are deposited in the Palaeoentomology collections of the Muséum national d'Histoire naturelle, Paris (MNHN).

Specimen AR 92.1 (holotype of *H. rossiorum* n. gen., n. sp.) is very incomplete because the body was cut through, and largely lost, during the initial preparation of the opaque amber; only the left palp, trochanter of left palp, right legs III and IV, part of the prosoma and part of right side of the opisthosoma remain, with the latter largely obscured by leg IV. Specimen AR 92.2 (paratype of *H. rossiorum* n. gen., n. sp.) has suffered a very similar fate and only some lateral parts of the carapace, right palp (minus distal ends of fingers) and ends of two legs (right III and IV) are present; the amber is fractured and very cloudy, making the fossil difficult to examine in detail. Specimen ARC 186.1 R is a complete and well orientated nymph, but observation is hampered by a dense layer of fibrous material that is interpreted as silk (see Discussion below). The ventral surfaces, along with the ends of most of the legs, are obscured by a layer of crazed and darkened amber.

Observations were made with Leitz Laborlux S compound microscope equipped with a drawing tube and medium-power Leitz objectives of long working distance, using both transmitted and reflected light. Measurements were taken with an ocular micrometer, using the reference points proposed by Chamberlin (1931). Lengths of inclined parts were calculated by triangulation, using the fine focus of the microscope to obtain values in the z-axis. Measurements are expressed in millimetres, followed by standard ratios in parentheses; inclusion of the pedicel in measurements of the chela is indicated by a plus sign (e.g., palm$^+$) and its exclusion by a minus sign (e.g., palm$^-$) (Judson 2007a). Photographs were taken using a Nikon Coolpix 995 digital camera mounted on a Wild stereomicroscope using reflected light. Terminology largely follows Chamberlin (1931), with modifications by Shultz (1989) for appendicular segmentation; notations for the chelal sensilla follow Judson (2007b).

## SYSTEMATICS

### Superfamily CHELIFEROIDEA Risso, 1826
### Family CHELIFERIDAE? Risso, 1826

### Genus *Heurtaultia* n. gen.

TYPE SPECIES. — *Heurtaultia rossiorum* n. sp.

ETYMOLOGY. — The genus is dedicated to the late Jacqueline Heurtault, a dear friend and colleague who made many important contributions to our knowledge of extant French pseudoscorpions; gender feminine.

DIAGNOSIS. — Mesozoic Cheliferoidea with elongate body. Setae generally small and dentate, not on raised tubercles. Granulation dense, even and low. Carapace much longer than broad; median furrow weakly marked, posterior furrow either weak or absent; one pair of large eyes with moderate lenses. Palp trochanter large, without lobes. Chelal fingers strongly gaping in male when closed. Trichobothrium *it* near middle of finger. Teeth of chela long, upright and cusped; accessory teeth absent. Joint between femur and patella of anterior legs moderately oblique, femur only slightly broader than patella. Coxa IV of male without lateral spur and posterior margin not excavated; probably without coxal sac. Leg I with elongate setae on tarsus of male (presumed sexual dimorphism). Leg tarsi III and IV with a long tactile seta near base. Subterminal setae simple. Leg claws simple. Arolia broad and slightly shorter than claws.

REMARKS

Although *Heurtaultia* n. gen. clearly belongs in the Cheliferoidea, its exact position is uncertain because of lack of information about some important characters, notably those of the male genitalia, in the fossils. The absence of accessory teeth and the large *venedens* (implying presence of venom duct) of the fixed finger of the chela would seem to exclude *Heurtaultia* n. gen. from the crown-group (*sensu* Hennig 1969, 1981; Jefferies 1979) of Chernetidae as usually defined. However, some modern Chernetidae lack accessory teeth (Beier 1948; Hoff 1949; Judson 1985) and a vestigial venom duct is present in the fixed finger of some taxa (Chamberlin 1931; Beier 1948). An additional character that might exclude *Heurtaultia* n. gen. from Chernetidae is the presence of eye lenses. With (1906, 1908) emphasized the distinction between “true” eyes (i.e. those with a lens) and eyes that were reduced to spots or absent, when diagnosing his species-groups of *Chelifer* (s.l.), which have since been recognized as families within Cheliferoidea (Chamberlin 1931; Weygoldt 1970). Later authors have paid relatively little attention to this character, but Schawaller (1991) noted its usefulness for assigning fossil cheliferoids to families. The only chernetid genus known to have lenses is *Gigantochernes* Beier, 1932, but in this case they have an unusual form (With 1908; pers. obs. of *G. rudis* (Balzan, 1887)) which might have arisen secondarily.

The well-developed *venedens* of the movable finger excludes *Heurtaultia* n. gen. from the crown-group of Atemnidae Chamberlin, 1931 and the slightly oblique nature of the articulation between the

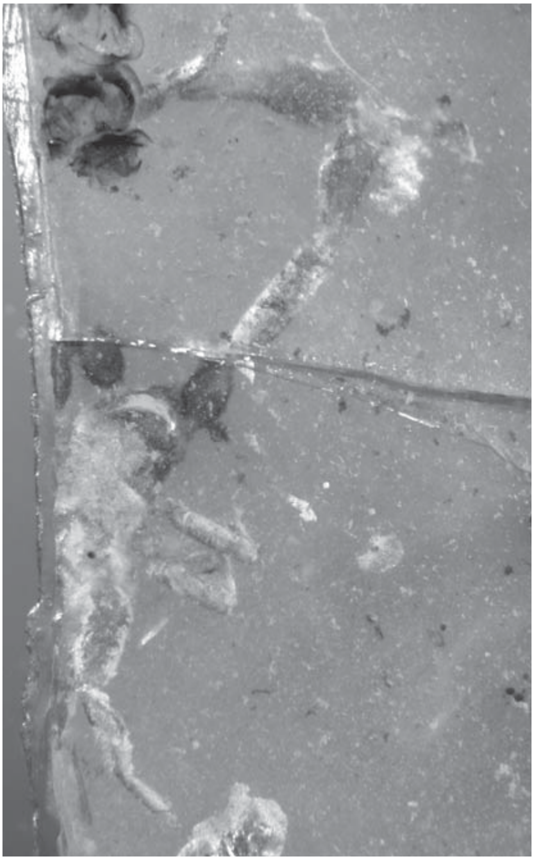

FIG. 1. — *Heurtaultia rossiorum* n. gen., n. sp., holotype, dorsal view of fossil. Magnification × 25.

femur and patella on the anterior legs, and the basal position of the tactile seta on leg IV exclude it from the crown-group of Withiidae Chamberlin, 1931.

This leaves the Cheliferidae as the only extant family to which *Heurtaultia* n. gen. might be assigned. Partial support for such a placement is provided by the elongation of the seta on the tarsus of leg I, which is here interpreted as a secondary sexual character of the genus. Modifications of the tarsus and claws of leg I are found in males of most Cheliferidae, in which they play a role during mating (Kew 1912; Weygoldt 1966, 1969). These can also entail modifications in the setation of the tarsus, although comparisons with the tarsi of the other legs and with the tarsus of leg I of the female are rarely made in the literature. Sexual dimorphism of leg I, including modified setation in the male, is present in a small number of genera of the Chernetidae (Muchmore 1997a, b), but in these cases the tibia is always involved (the setation of the tarsus may also be modified in these chernetids, but never on its own).

The proximal position of the tactile seta of the tarsi of legs III and IV distinguishes *Heurtaultia* n. gen. from all modern genera of Cheliferidae, in which (when present) it is situated near the middle of the segment or in a distal position. This is probably a plesiomorphic character, based on comparisons with non-cheliferoid pseudoscorpions.

### ***Heurtaultia rossiorum*** n. sp.
(Figs 1-3)

Pseudoscorpionida indet. – Perrichot 2004: 14; 2005: 47, table 2.

Cheliferidae indet. – Perrichot *et al.* 2007: 217, table 2.

TYPE MATERIAL. — Holotype adult (probably ♂) (MNHN, AR 92.1) and paratype adult (MNHN, AR 92.2) originally in single piece of turbid amber from Archingeay-Les Nouillers, Charente-Maritime, France: Lower Cretaceous, uppermost Albian, lithological subunit A1 *sensu* Néraudeau & Moreau (1989).

ETYMOLOGY. — The species is named after Marie-Noëlle and Jean-Marc Rossi.

#### DESCRIPTION OF HOLOTYPE

Carapace (Fig. 2A) with small, regular and dense granules, eyes large (maximum diameter 0.061 mm). Chelicera (Fig. 2C) with five setae on palm, *b* and *sb* shorter than others, but without obvious denticulation, *es* long; seta of movable finger subapical, extending past tip of spinneret; spinneret with about three or four, non-terminal, rudimentary rami; palm and movable finger reticulate. Coxae (Fig. 2B) normal; setae small and sparse. Palps (Fig. 3A-C, E) moderately granulate; fixed finger with small, sparse granules extending for about half length of finger on paraxial side. Setae short, apart from a patch of longer setae ventrally just after pedicel (Fig. 3C). Femur

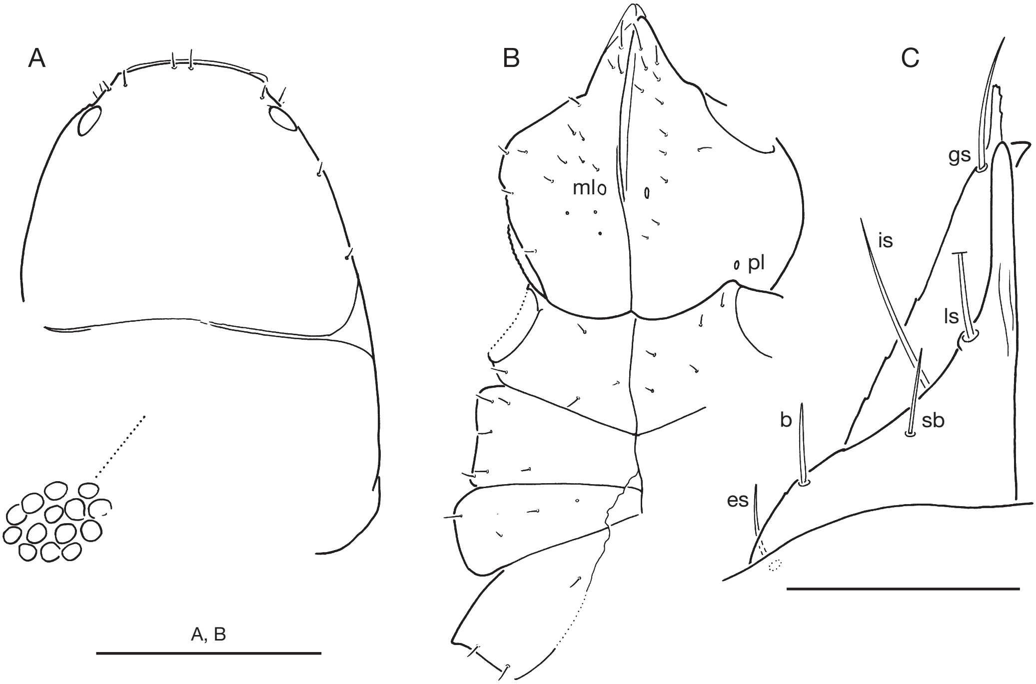

FIG. 2. — *Heurtaultia rossiorum* n. gen., n. sp., holotype male: **A**, carapace (incomplete), foreshortened posterodorsal view, with detail (× 4) of granulation on mesozone; **B**, coxae of palp and legs (incomplete), anteroventral view; **C**, left chelicera, dorso-antiaxial view. Abbreviations: **b**, **es**, **is**, **gs**, **ls**, **sb**, setae of chelicera; **ml**, median maxillary lyrifissure; **pl**, posterior maxillary lyrifissure. Scale bars: A, B, 0.3 mm; C, 0.1 mm.

gradually pedicellate; palm ovate, but not as robust as Figure 3A suggests (foreshortened due to oblique view). Trichobothriotaxy as illustrated (Fig. 3E); *ib* situated in a shallow furrow; *it* near middle of finger, slightly distad of *est*; *st* slightly nearer to *t* than to *sb*. Spot sensilla not clearly visible, but a lighter spot between trichobothria *st* and *t* might represent coupled sensilla *pc* (i.e. $p_1 + p_2$) (Fig. 3E). Teeth large, contiguous, cusped (not triangular) and upright. Trochanters of legs with one ventral seta longer than others. Leg I with tarsus of normal shape (Fig. 3F), but distal setae longer (longest 0.15 mm) and more numerous than on other tarsi. Claws of leg I largely obscured, but anterior (paraxial) claw seems to be simple; claws of other legs simple. Legs III and IV (Fig. 3G) with a long (*c.* 0.30 mm on IV) tactile seta near base (TS IV index 0.19); subterminal setae simple, curved. Arolia shorter than claws and fan-shaped.

### *Measurements of holotype*

Carapace *c.* 0.82 × ?0.53 (*c.* 1.6). Palp trochanter 0.37 × 0.2 (1.7), femur *c.* 0.82 × 0.20 (4.0), patella ? × 0.24, chela$^+$ 0.92 × < 0.33 (> 2.8), chela$^-$ 0.89 (> 2.7), palm$^+$ 0.49 (> 1.5), palm$^-$ 0.46 (> 1.4), movable finger 0.49 (1.0 × palm$^+$). Leg I tarsus 0.33 × 0.07 (4.7). Leg III tibia 0.49 × 0.14, tarsus 0.38 × 0.079.

### DESCRIPTION OF PARATYPE

The few parts of the palp and posterior legs that can be observed clearly are very similar to those of the holotype. The only additional information provided by this specimen concerns the form of the palp patella (Fig. 3D), which is better preserved than that of the holotype.

### *Measurements of paratype*

Palp femur 0.78 × 0.20 (4.0), patella *c.* 0.69 × 0.25 (*c.* 2.8), palm$^+$ *c.* 0.54 × 0.30 (*c.* 1.8), palm$^-$ *c.* 0.49 (*c.* 1.7).

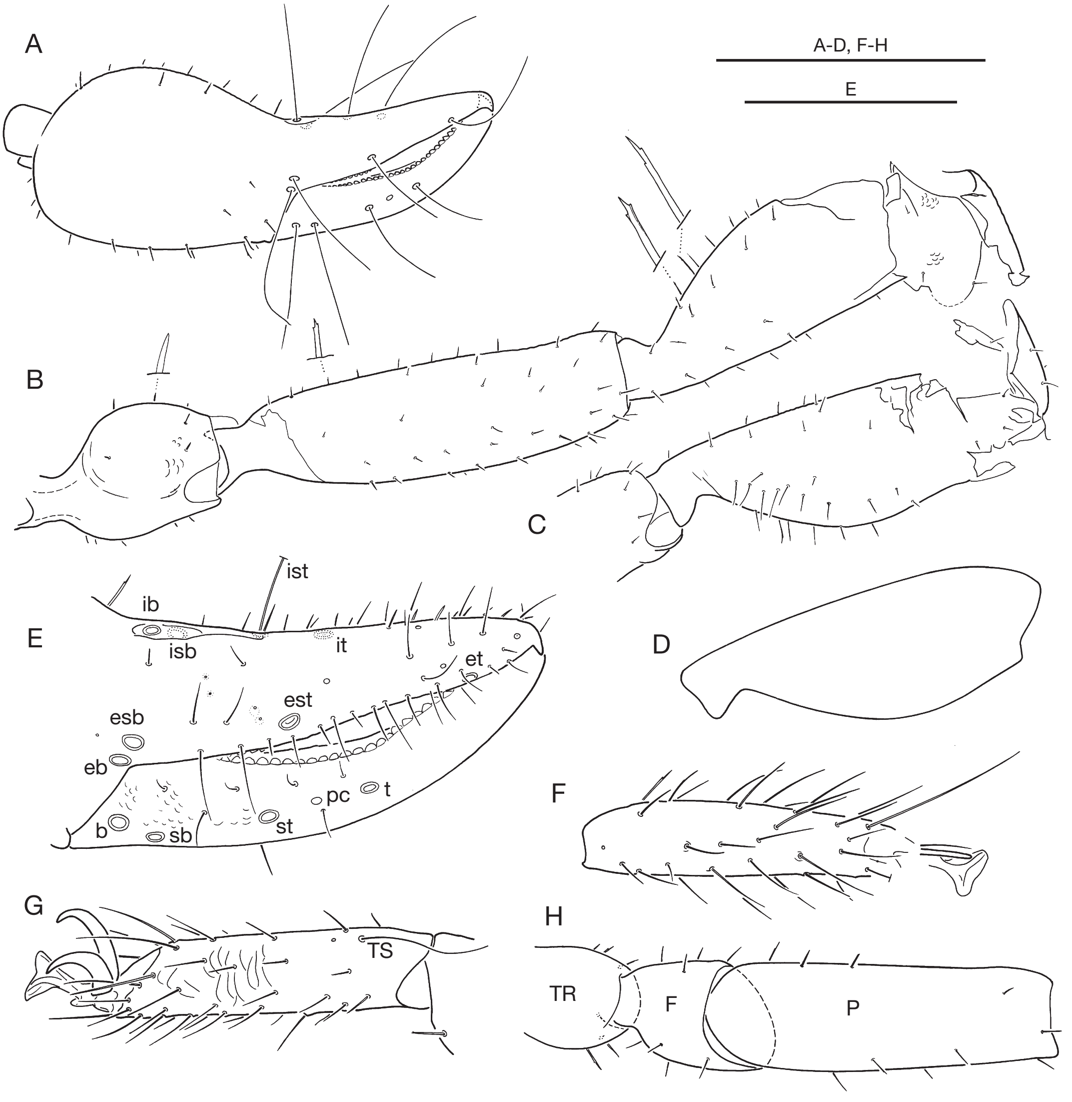

FIG. 3. — *Heurtaultia rossiorum* n. gen., n. sp., holotype male, except for D (paratype): **A**, chela of right palp (moderately foreshortened), dorsolateral view; **B**, trochanter, femur and patella of right palp, near-dorsal (slightly antiaxial) view, femur reconstructed (broken along irregular line shown just after pedicel), distal part of patella shattered, details of setae × 4; **C**, patella of right palp in near-ventral (slightly paraxial) view, showing patch of longer setae; **D**, patella of left palp of paratype, reconstructed, dorsal view; **E**, fingers of right chela, dorsolateral view (moderately foreshortened); **F**, tarsus and apotele of leg I (distal parts obscured by debris), near-dorsal (slightly antiaxial) view; **G**, tarsus and apotele of right leg IV, near-paraxial (slightly dorsal) view; **H**, trochanter, femur and patella of right leg I, dorsal view. Abbreviations: **b**, **eb**, **esb**, **est**, **et**, **ib**, **isb**, **ist**, **it**, **sb**, **st**, **t**, trichobothria of chela; **F**, femur; **P**, patella; **pc**, spot interpreted as possible paired sensilla; **TR**, trochanter; **TS**, tactile seta. Scale bars: A-D, F-H, 0.5 mm; E, 0.2 mm.

### REMARKS

The holotype lies close to an incomplete specimen of a heteropteran, but the association between the two is probably fortuitous.

## Cheliferidae? indet.
(Figs 4; 5)

Pseudoscorpionida indet. – Néraudeau *et al.* 2002: 237. —

Perrichot 2004: 14; 2005: 45, 69, tables 1, 3.

Cheliferidae indet. – Perrichot *et al.* 2007: 217, table 2.

MATERIAL EXAMINED. — One tritonymph (MNHN ARC 186.1 R), amber from Archingeay-Les Nouillers, Charente-Maritime, France: Lower Cretaceous, uppermost Albian, lithological subunit A1 *sensu* Néraudeau & Moreau (1989).

DESCRIPTION

Carapace clearly longer than broad; eyes not seen, their likely position being obscured (left side) or unfavourably inclined (right side); anterior furrow well marked, about 0.42 length of carapace from posterior margin; posterior furrow weak, about 0.10 from posterior margin; prozone with sparse, conicular granulation; mesozone and metazone scaly; setae sparse, six on anterior margin. Tergites probably divided, as suggested by a fold running along the midline of tergites I-X; exact chaetotaxy not determined, but probably four or five setae on each half-tergite of most segments; tergites X and XI with a long tactile seta near middle of each half-tergite. Leg coxae almost smooth; setae long, simple and few in number (about five on coxae III and IV). Coxa IV without coxal sac or spurs. Articulation between femur and patella of anterior legs moderately oblique (about 45° to axis) in dorsal view, femur relatively long in comparison with modern Cheliferoidea; femur not much broader than patella, hence the joint between them allows only a normal degree of flexibility. Chelicera (Fig. 5A) with five setae on palm, *es* long. Spinneret with three, small, terminal rami of equal length. Palps attenuate, with strong, regular, conicular granulation. Vestitural setae moderately long, each with two or three denticulations, not clavate or raised on tubercles. Leg claws simple. Setae of tarsus I of the same length as those of the other leg tarsi. Chelal fingers largely obscured, hence not all trichobothria could be observed, but *isb* present near *ib*, which is only slightly distad of *eb*; *it* near middle of finger (Fig. 5B).

*Measurements*

Body *c.* 1.3; carapace length *c.* 0.72. Palp femur *c.* 0.51 × 0.12 (4.4), patella 0.39 × 0.13 (2.9), chela$^+$ 0.89 × 0.20 (4.4), palm$^+$ 0.45 (2.2), palm$^-$ 0.40 (2.0), movable finger 0.49 (1.1 × palm$^+$).

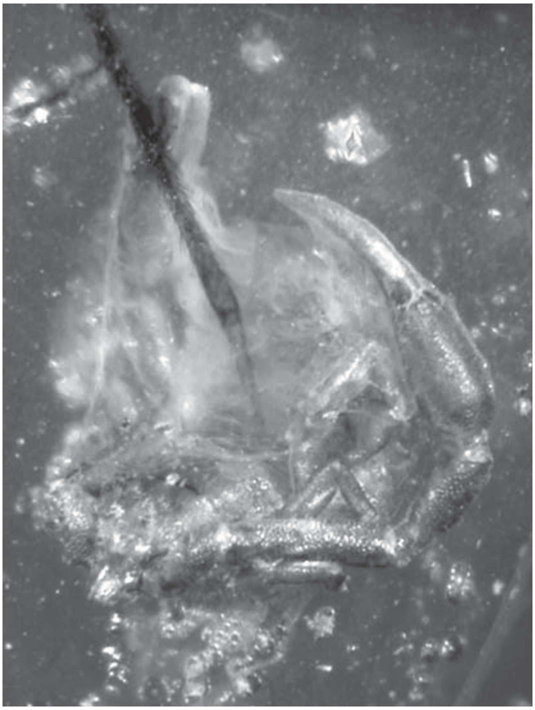

FIG. 4. — Cheliferidae indet., tritonymph (ARC 186.1R), oblique dorsal view of fossil. Magnification × 50.

REMARKS

The differences in the form of the carapace, the granulation of the integument and the proportions of the palp preclude the possibility of this specimen being a nymph of *Heurtaultia rossiorum* n. gen., n. sp. It is attributed to the Cheliferidae on the basis of its general appearance, notably that of the palps, and the presence of a *venedens* on both fingers, but its systematic position will probably remain uncertain unless information about the adults, particularly the male, becomes available.

## DISCUSSION

The Archingeay fossils are approximately contemporary with the Cheliferoidea present in Lower Cretaceous Burmese amber. Burmese amber has been dated as Lower Cenomanian to Upper Albian, with the latter being judged the most likely

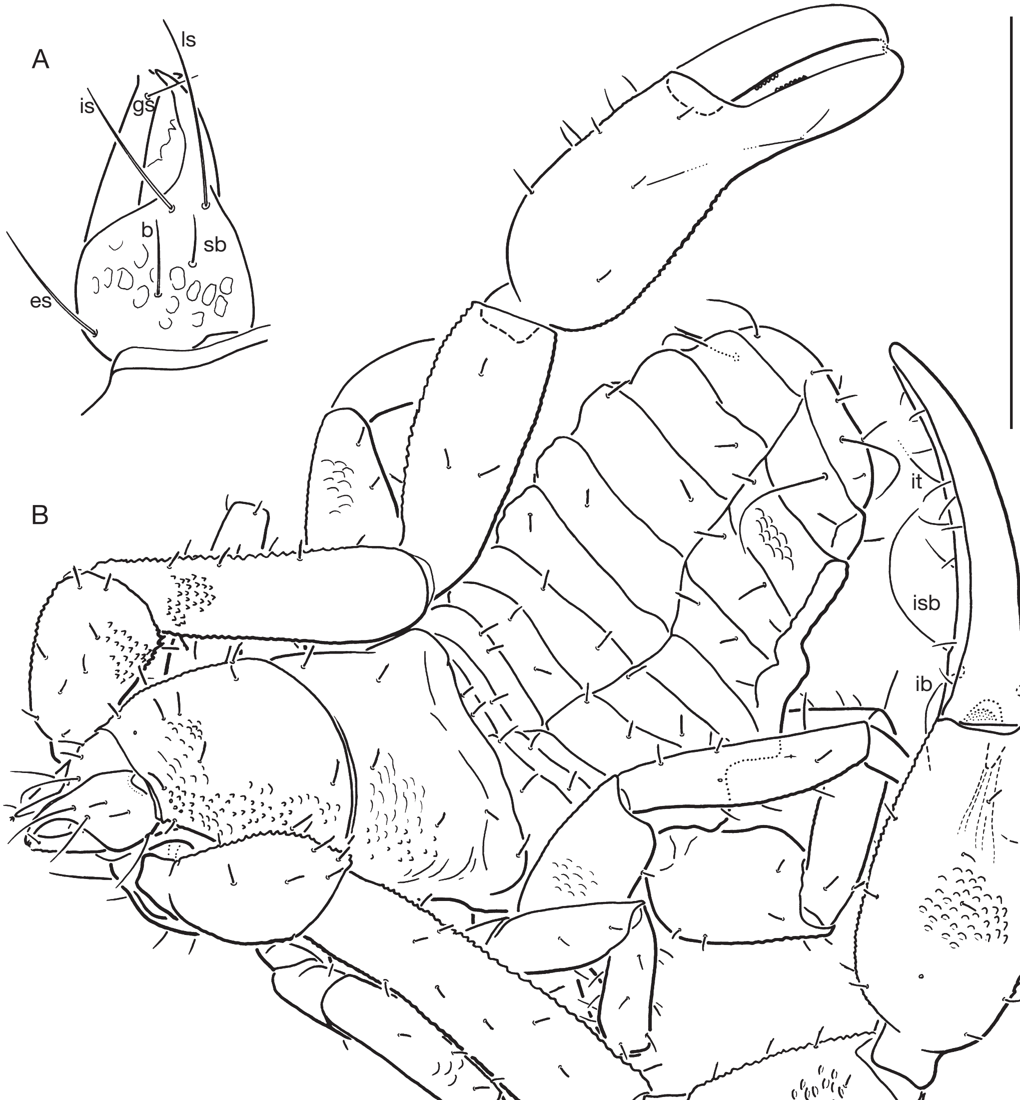

FIG. 5. — Cheliferidae indet., tritonymph (ARC 186.1R): **A**, left chelicera, antiaxial face, spinneret broken; **B**, habitus, oblique dorsal view, some parts obscured, particularly palp and tergites on right side; right chela strongly foreshortened, only a few teeth shown (others not visible), granulation only partly indicated. Abbreviations: **b**, **es**, **is**, **gs**, **ls**, **sb**, setae of chelicera; **eb**, **ib**, **isb**, **it**, trichobothria of chela. Scale bar: A, 0.18 mm; B, 0.5 mm.

age (Cruickshank & Ko 2003). Thus, although the Cheliferoidea are generally considered to be the most derived group of pseudoscorpions in terms of their morphology and behaviour (Chamberlin 1931; Weygoldt 1966, 1969, 1970; Harvey 1992), it is clear that the superfamily was already diverse and widespread by the early Cretaceous, implying a significantly older origin of the group.

Gaping chelal fingers have appeared sporadically in the Cheliferoidea. When present in both sexes or in females alone, they are assumed to be a modification for grasping insects during phoresy (Chamberlin 1949; Heurtault 1994). When limited to males, which are less often phoretic, they presumably represent an adaptation for holding conspecific females during mating (Kew 1912; Chamberlin 1931) or, perhaps, other males during antagonistic interactions. If the holotype of *H. rossiorum* n. gen., n. sp. is a male, this suggests the presence of a mating dance in this species, which concords with the interpretation given above of the elongate setae on the tarsus as a secondary sexual dimorphism. The existence of a mating dance can be also inferred on phylogenetic grounds, since it is synapomorphic for the Cheliferoidea (Weygoldt 1966; Harvey 1992).

The fibrous material surrounding the posterior end of the body of the nymphal cheliferid (ARC 186.1 R) is too fine and homogenous to represent fungal hyphae. It must therefore be silk, spun either by a spider or by the pseudoscorpion itself. The latter interpretation seems more plausible in view of the thinness of the layer, the fact that the pseudoscorpion is intact and the orientation of the palps. During moulting torpor, pseudoscorpions sometimes have the palps directed backwards in a similar way (e.g., Chamberlin 1924). A pseudoscorpion wrapped as prey of a spider would probably be enclosed in a thicker layer of silk, with the palps and legs appressed to the body in a more normal orientation, and might show some signs of damage. If the interpretation of a moulting nest is correct, this represents the earliest direct evidence of silk use in a pseudoscorpion. Schawaller (1978) described silk fibres emanating from the spinneret of the holotype of the Baltic amber pseudoscorpion "*Microcreagris*" *koellnerorum* Schawaller, 1978, but an examination of this specimen suggests that the supposed fibres are just debris: they seem too dense to be silk and are orientated towards a more distal position on the cheliceral finger than that which would normally be occupied by the spinneret (which is obscured in the fossil).

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