

# Ignotingidae fam. nov. (Insecta: Heteroptera: Tingioidea), the earliest lace bugs from the upper Mesozoic of eastern China

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## Abstract

An extinct new family of lace bugs, Ignotingidae, with one new genus and species, *Ignotingis mirifica*, is described from the Laiyang Formation (terminal Jurassic or basal Cretaceous) in Laiyang, Shandong, China. The homology of hemelytral veins in Tingioidea and the position of the superfamily within Cimicomorpha are discussed.

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## 1. Introduction

The lace bug family Tingidae Laporte, 1833 comprises about 250 extant genera and 2600 species of small phytophagous bugs living on angiosperms (mainly on woody dicots, some feeding on tree roots or making flower galls) and mosses and distributed worldwide (Schuh and Slater, 1995). A closely related Neotropical group with two described extant genera and five species of eyeless, coleopteroid, flightless myrmecophilous inquilines was established as the family Vianaididae Kormilev, 1955, but later often treated as a subfamily of Tingidae s.l.; flying macropterous vianaidids are known but not yet formally described (Schuh and Slater, 1995). Two subfamilies, Cantacaderinae Stål, 1873 (with tribes Cantacaderini and Phatnomatini) and Tinginae (with three tribes), are usually recognized within the Tingidae s.s. (Froeschner, 1996). Recently it was proposed to split the former subfamily because

it is paraphyletic, and to raise Cantacaderini to full family status and Phatnomatini to a subfamily of the Tingidae (Lis, 1999), but this classification is not widely accepted and not referred to further herein.

Some 20 genera (ten of them extinct) and more than 30 species of Tingidae s.s. have been recorded from the Cenozoic, about ten of these species from Baltic amber (Golub and Popov, 1999, 2002; Wappler, 2003). Two extinct genera of macropterous Vianaididae are known from Late Cretaceous New Jersey amber (Golub and Popov, 2000, 2003). The oldest tingoids, found in Early Cretaceous deposits of Mongolia (Bon-Tsagaan Group, Aptian?) and Transbaikalia (Baissa locality, Zaza Formation, dated as Berriasian–Hauterivian), were assigned to the genera *Golmonia* Popov, 1989 (Golmoniini, possibly deserving subfamily rank) and *Sinaldocader* Popov, 1989 (Phatnomatini; Popov, 1989).

A rich entomofauna from the Laiyang Formation, Shandong, eastern China is dated as latest Jurassic (late Tithonian) or earliest Cretaceous (Berriasian) (Zhang, 1992, 1999, 2000; Zhang and Zhang, 2003; Zhang and Rasnitsyn, 2004) and is similar to the faunas known from the Yixian and Zaza formations (Zhang and Rasnitsyn, 2004). Thousands of insect fossils

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represent 14 orders, and owing to the excellent preservation even tiny specimens may be studied in considerable detail (Hong and Wang, 1990), although the systematic positions of many taxa need to be reassessed. The most abundant species are those living in or near water at least when immature, such as the beetle *Coptoclava longipoda* Ping, 1928 and the midge *Chironomaptera gregaria* Grabau, 1923.

True bugs are very common in the Laiyang assemblage. Extremely numerous is the shore bug *Mesolygaeus laiyangensis* Ping, 1928 belonging to an extinct subfamily Enicocorinae Popov, 1980 (= Mesolygaeidae Zhang, 1989, 1991; Hong and Wang, 1990) of the family Saldidae (Shcherbakov and Popov, 2002); its very long tarsi indicate that it inhabited swamps near the ancient Laiyang lake, or floating plants, like primitive groups of extant Gerromorpha. Other waterside inhabitants are velvety shore bugs (Ochteridae). Water bugs are represented by the backswimmer *Clypostemma xyphiale* Popov, 1964 (Notonectidae) and several corixid species. Terrestrial bugs are quite diverse, including various coreoids in the broadest sense, pentatomoids, mirid- and anthocorid-like forms. One of the most important finds is a series of bizarre long-legged lace bugs that can be placed in neither the Tingidae nor the Vianaididae. They are described below in a family of their own. This is the earliest fossil record of the superfamily Tingoidea.

## 2. Systematic palaeontology

Order: Heteroptera Latreille, 1810

Infraorder: Cimicomorpha Leston, Pendergrast and Southwood, 1954

Superfamily: Tingoidea Laporte, 1833

Family: Ignotingidae fam. nov.

*Diagnosis.* Body not dorsoventrally depressed; head and thorax coarsely punctate. Antennae very long, four-segmented, third segment longest, second much longer than first. Head rather large, vertical, hypognathous (rostrum inserted on ventral surface of head), shorter than wide, without protruding mandibular plates or prominent bucculae. Rostrum thick and moderately long, directed caudally but not appressed to body venter, movable at base. Pronotum with areolate dorsal projection and paranota, expanded onto mesonotum leaving scutellum free. Thoracic sternal laminae absent. Hemelytron: corium and clavus areolate between strong veins; corium continued up to hemelytral apex, with several cells; no costal fracture; R+M strongest vein; clavus large, triangular, commissura clavi long; posterior claval vein submarginal; membrane (zone of hemelytral overlap) not areolate, long and narrow. Rotatory hind coxae more widely separated than mid and fore ones. Legs very long; all tibiae with small apical fossula spongiosa; tarsi short, three-segmented. Second–third abdominal sternites fused. Pygophore symmetrical, parameres directed dorsocaudad. Lacinate ovipositor not concealed by paratergites. (For comparison see “Discussion” below).

*Ignotingis* gen. nov.

*Derivation of name.* Latin, *ignotus*, unknown, and the extant genus *Tingis* (gender feminine).

*Species included.* The type species only.

*Diagnosis.* Small bugs with very long, slender antennae and legs (not unlike Berytidae). Body not dorsoventrally depressed (thorax excluding pronotal projection as high as long). Head and thorax heavily punctate, dorsum areolate. Antennae originate near lower eye margin, first segment stoutest and shortest, second nearly twice as long as the first, slightly thickened apically, third most slender and longer than three remaining combined, fourth slender, slightly fusiform, longer than second. Head much shorter than high, weakly arcuately produced in front of eyes, without antennal tubercles or other projections, its upper surface declivous; ocelli not traceable; eyes rather small, ovoid, protruding, not far from posterior head margin; head narrowed behind eyes. Rostrum reaching base of abdomen, four-segmented: first–second segments quite wide, third–fourth much narrower, short and more sclerotized, first elongate, second longest, longer than third and fourth combined. Pronotum with moderately narrow collar, rounded lateral margins and nearly straight posterior margin, covering mesonotum (except for small triangular scutellum), with a high, crest-like dorsomedial projection (semi-circular in profile) and rather narrow paranota (maybe deflected dorsad or swollen). Hemelytra macropterous, with raised main veins, narrow precostal area (“costal area” of authors; for the vein homology and nomenclature see below), no stenocostal area, three large costal cells along anterior margin from base up to apex of hemelytron (in so-called “subcostal area”), three discal cells (inner smallest) in addition to oblong basal cell (four latter cells together correspond to “discoidal area”) and two narrow cubital cells, which together correspond to proximal extension of “sutural area” [anterior cubital cell between CuA and CuP (= claval furrow) and posterior cubital cell between CuP and Pcu (= 1A of authors)]; C (“hypocostal vein”) terminating just beyond apex of distal costal cell; “discoidal area” beyond claval apex wider than “subcostal” one; clavus one-third length of hemelytron; areolation irregular, extended up to base of distal costal cell and three-quarters of distal discal cell. Fore and mid coxae rounded triangular, narrowly separated, hind coxae rotatory, set apart for more than their diameter. Femora slightly clavate distally. All tibiae long, with apices almost twice as wide as bases, apices (ventral to insertion of tarsus) truncate, slightly oblique and concave, and marked with golden tinge, representing a pad of modified setae (fossula spongiosa); tarsi almost invariably preserved nearly at right angles or even at an acute angle to the tibia; tibial modification is more obvious in males; first tarsal segment shortest, third longest. Abdomen not reaching hemelytral apices (in some male specimens extended post-mortem), its sternites short, more sclerotized in their anterior zone, second–eighth (males) or second–seventh (females) nearly equally developed, fifth widest; second and third not separated by dark intersegmental line. Pygophore broad and short, barrel-shaped, parameres

inserted at its sides, proctiger rounded triangular. Ovipositor one-third as long as abdomen, slightly projecting beyond last paratergites; posterior margins of fifth–seventh sternites weakly V-shaped in female.

*Ignotingis mirifica* sp. nov.

Figs. 1–4

*Derivation of name.* Latin *mirificus*, wonderful, strange.

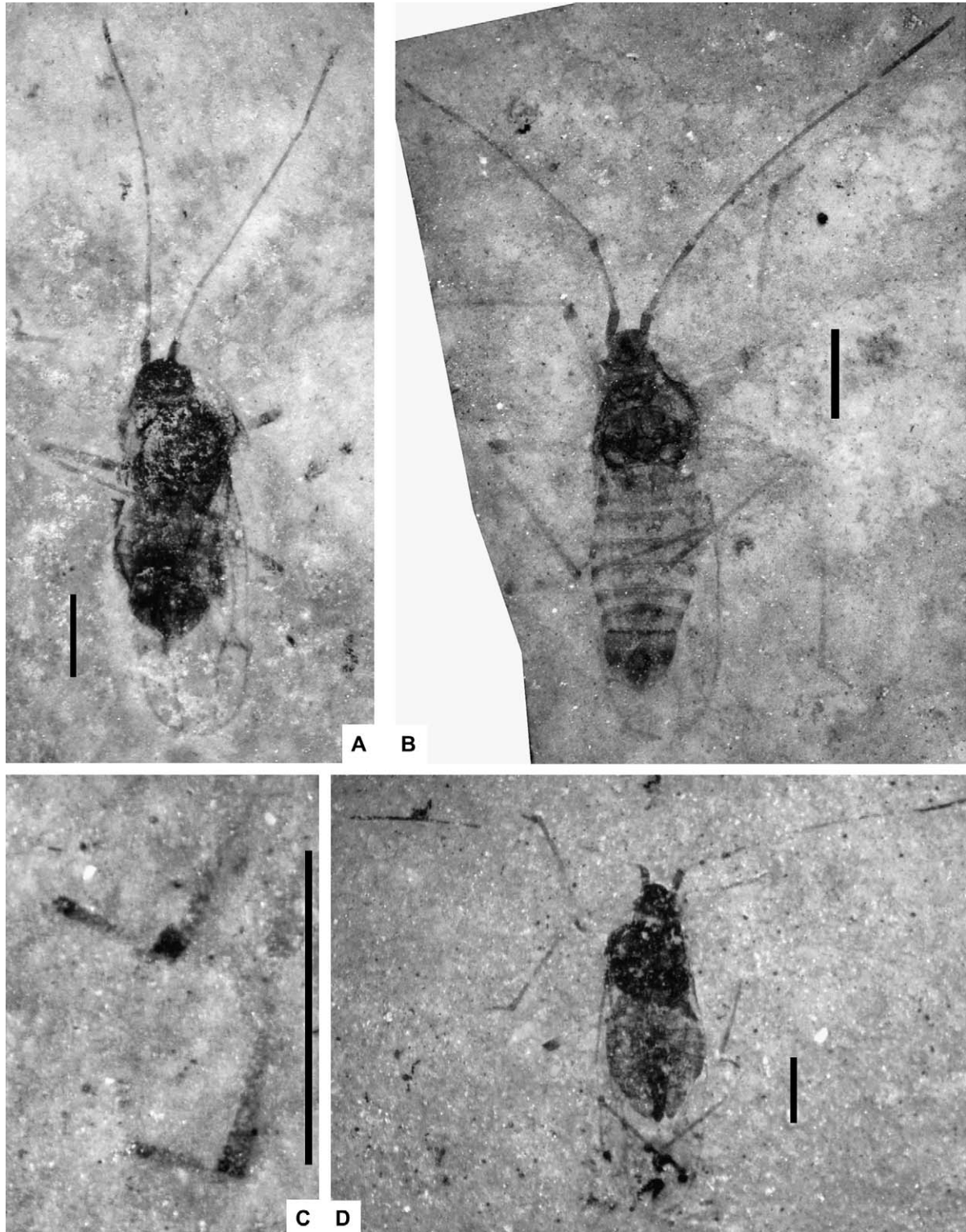


Fig. 1. *Ignotingis mirifica* sp. nov. A, paratype, female, L86817. B, holotype, male, L86812. C, tibiae and tarsi of fore leg, L86814. D, paratype, female, L86818. Scale bars represent 1 mm.

**Material.** Holotype L86812, male; paratypes: L86811, L86813–L86815, males; L86816–L86818, females (L86814–L86816 are preserved in profile, the other five more or less dorsoventrally) from the uppermost Jurassic (upper Tithonian) or lowermost Cretaceous (Berriasian) Laiyang Formation in the vicinity of Nanligeshuang, Laiyang, Shandong; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

**Description.** Body quite narrow, about three times (males) or 2.5 times (females) longer than wide. Antennae slightly longer (males) or slightly shorter (females) than body including hemelytra. Head 0.7 as wide as pronotum. Hemelytron more than three times longer than wide; anterior margin of precostal carina not thickened, vein-like but much less conspicuous than veins. Hind tibiae as long as abdomen, much longer than femora. Abdomen in ventral aspect oblong in males, ovate in females. Head and most of thorax dark brown, abdomen less darkened. Antennae suffused, especially first and fourth

segments and distal part of second segment. Rostrum with third–fourth segments brown; second pale, and first suffused. Pronotum with dark collar and longitudinal streaks anteriorly at the bases of medial crest and paranota. Hemelytra pale, suffused near base, with fuscous veins and irregular dark spots (in proximal costal and basal cells, in proximal discal cell, and an oblique one from the base of distal costal cell to distal discal cell). Femora suffused at bases and apices; tibiae more or less extensively suffused distally; tarsi fuscous. Parameres much paler than pygophore, which is darkest near their bases. Ovipositor dark brown.

In the male holotype, L86812, body length 5.0 mm including, and 4.4 mm excluding hemelytra; length of extended abdomen 2.6 mm, width 1.3 mm; hemelytron length 3.6 mm, width of combined hemelytra in repose ca. 1.6 mm; head width 0.9 mm; pronotum length 1.0 mm, pronotum width 1.3 mm, length of antenna 5.4 mm, length of antennal segments I:II:III:IV = 0.4:0.9:2.8:1.15 mm; length of fore leg segments: femur 1.2 mm, tibia 2.1 mm, tarsus 0.4 mm; mid

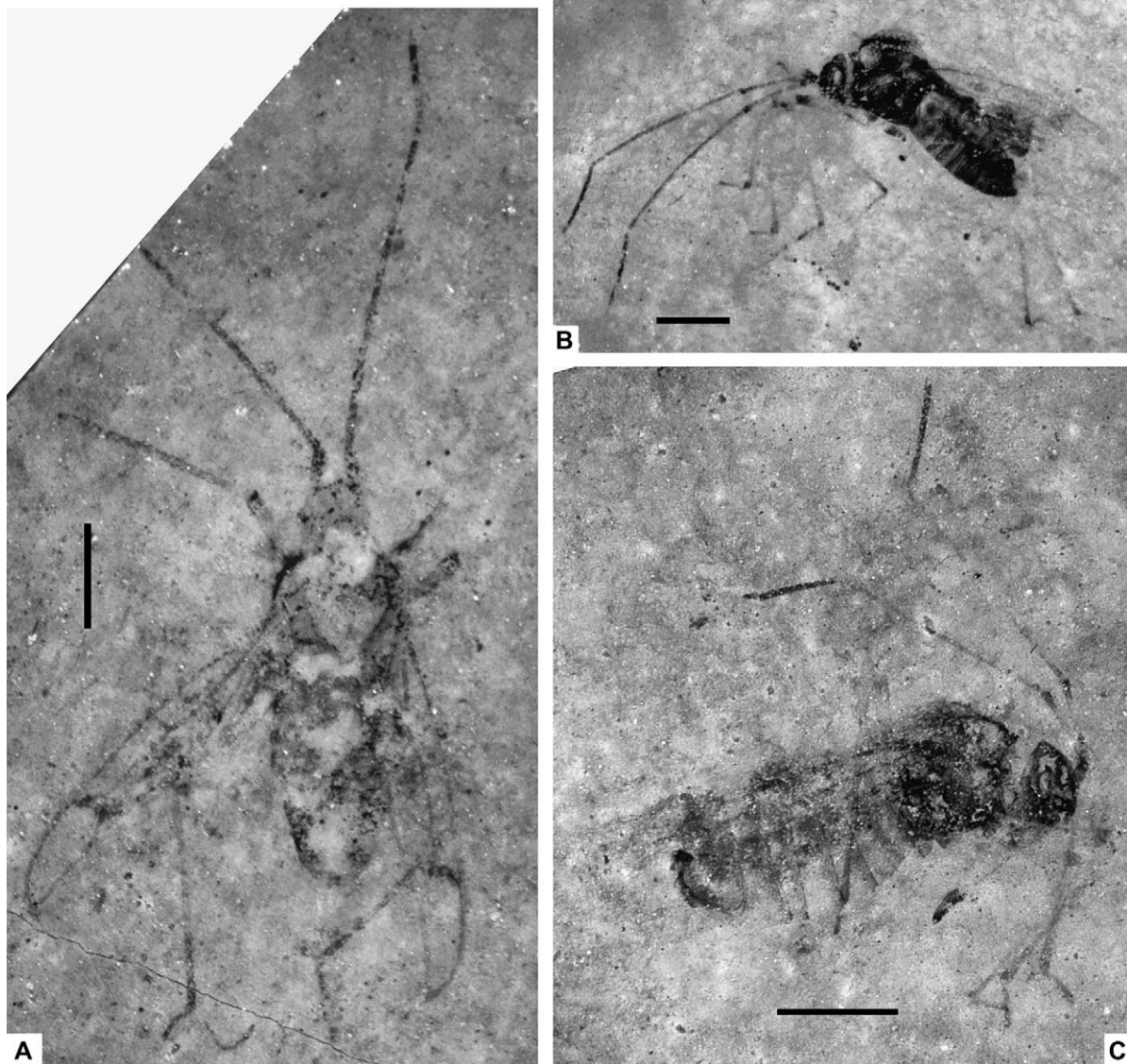


Fig. 2. *Ignotingis mirifica* sp. nov. A, paratype, male, L86813. B, paratype, male, L86814. C, paratype, female, L86816. Scale bars represent 1 mm.

leg: femur 1.5 mm, tibia 1.9 mm, tarsus 0.35 mm; hind leg: femur 1.9 mm, tibia 2.5 mm, tarsus 0.45 mm. In the male paratype L86813, hemelytron length 3.3 mm, width ca. 1.0 mm. In the female paratype L86818, body length 4.9 mm including and 3.5 mm excluding hemelytra; length of unextended abdomen 1.9 mm, width 1.5 mm; hemelytron length 3.6 mm, width of combined hemelytra in repose ca. 1.8 mm; head width 0.85 mm; pronotum length 1.0 mm, pronotum width 1.3 mm, length of antenna 4.6 mm, length of antennal segments I:II:III:IV = 0.4:0.7:2.6:0.9 mm; length of fore leg segments: femur 1.1 mm, tibia 1.6 mm, tarsus 0.3 mm; mid leg: femur 1.3 mm, tibia 1.6 mm, tarsus 0.35 mm; hind leg: femur 1.6 mm, tibia 2.3 mm. In the female paratype L86816, body length 3.3 mm excluding hemelytra; rostrum length ca. 1.2 mm.

### 3. Homology of veins and areas in hemelytra of Tingioidea

Comparison of *Ignotingis* (Fig. 3C) with other lace bugs (Fig. 5) confirmed that the vein and area nomenclature used for tingid hemelytra (e.g. in Drake and Davis, 1960) does not conform to the forewing vein homology across Hemiptera and all Pterygota. The so-called “discoidal area” in its basal portion corresponds to the basal cell between R+M and Cu–CuA, and in its distal portion at least partly to the radial and medial areas of the corium (morphologically an area or cell should be named after the vein bounding it anteriorly). The

“subcostal area” at least proximally is homologous to the costal area of other insects because, so far as is known in all extant hemipteran groups, Sc (except for apex and sometimes base) is invariably fused to (R+M)–R (Shcherbakov, 1996), and the “hypocosta”, a vein occupying a lower position in the wing membrane and basally fixed on pterothoracic pleura in repose, is merely concave C (often bearing a hypocostal carina or lamina directed ventrally). The “costal area” is another extension of C directed anteriorly and should be termed the precostal area (or precostal carina). The stenocostal area found only in Cantacaderini has no homologues in other Hemiptera and is a synapomorphy of the tribe (Froeschner, 1996). This structure represents a trough on the ventral hemelytral surface (it may not involve modification of the dorsal surface), basally crossing the precostal area and serving to conduct the scent-gland fluid from the metapleural peritreme to the precostal area for evaporation; the ostiolar-stenocostal system shows steps of increasing complexity within Cantacaderini (Froeschner, 1996) and, therefore, is not a groundplan character for Tingioidea. The narrow proximal extension of the “sutural area” is equivalent to the space between CuA and Pcu (= 1A of authors), in that the claval furrow (= CuP) is usually reduced, i.e. to the combined anterior and posterior cubital areas (between CuA and CuP, and CuP and Pcu, respectively). The posterior claval vein 1A (= 2A of authors) runs along the hind margin of the clavus (commisura clavi); it forms this margin in the Tingidae, but is still

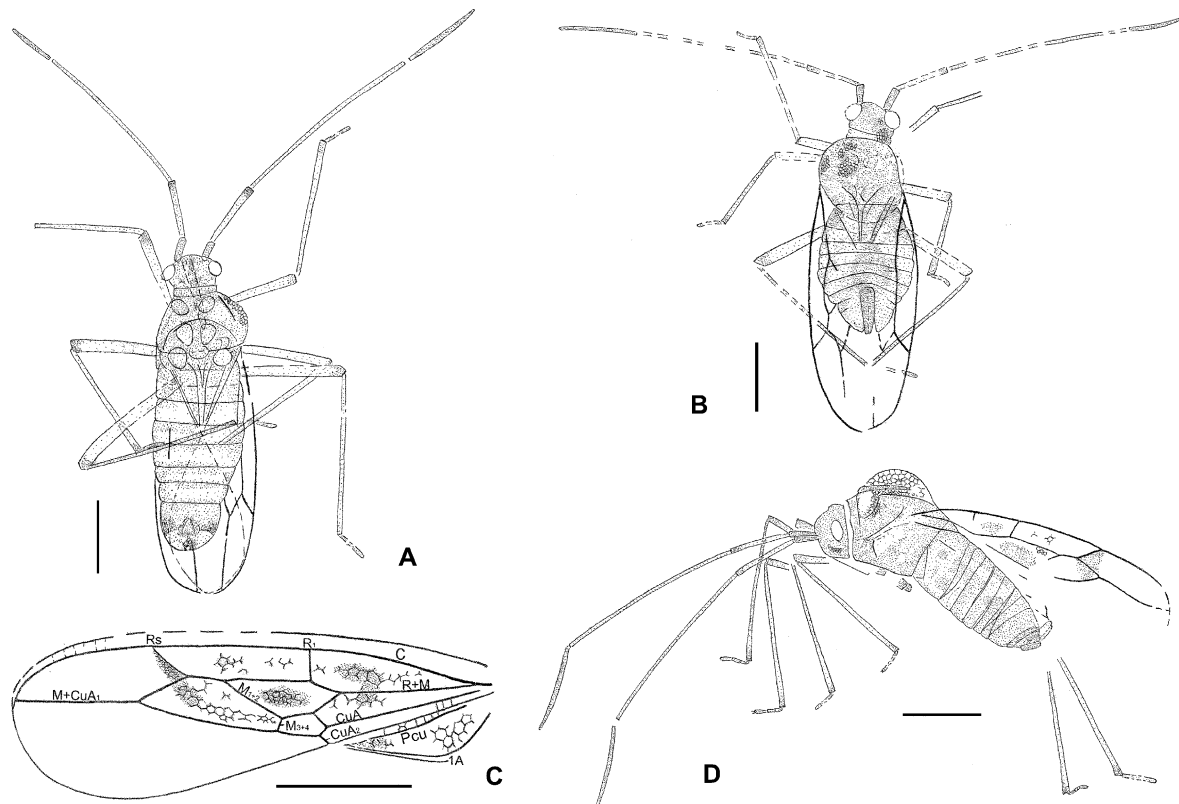


Fig. 3. *Ignotingis mirifica* sp. nov. A, male, dorsal aspect, camera lucida drawing of specimen L86812. B, female, dorsal aspect, camera lucida drawing of specimen L86818. C, left hemelytron, camera lucida drawing of specimen L86813; precostal area added from specimen L86817. D, male, lateral aspect, camera lucida drawing of specimen L86814. Scale bars represent 1 mm.

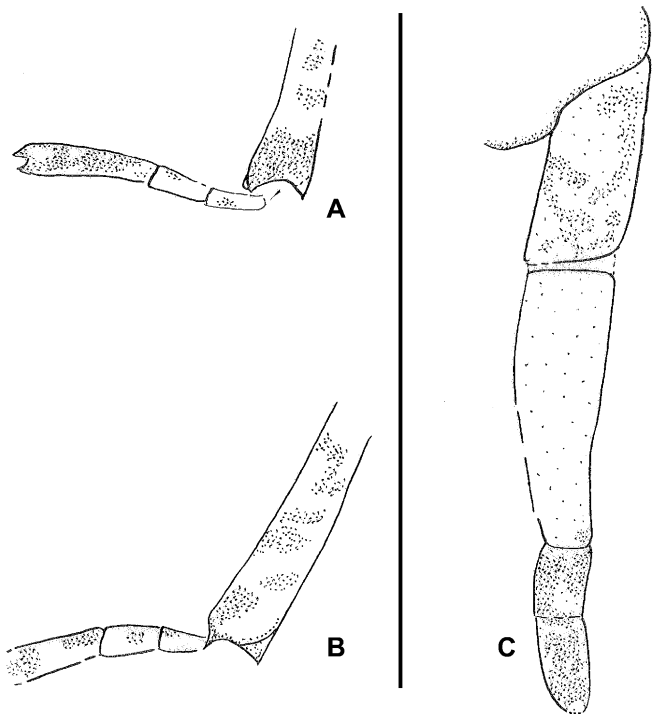


Fig. 4. *Ignotingis mirifica* sp. nov. A, tibia and tarsus of fore leg, camera lucida drawing of specimen L86814. B, tibia and tarsus of mid leg, camera lucida drawing of specimen L86818. C, rostrum, lateral aspect, camera lucida drawing of specimen L86816. Scale bars represent 1 mm.

submarginal in the Ignotingidae. The “sutural area” itself (zone of hemelytral overlap) seems to be homologous only to the posterodistal part of the membrane in other Cimicomorpha, owing to cells 1–4 at the membrane base (see Schuh and

Štys, 1991) being incorporated into the corium (sensu lato). The free posterior vein of the membrane developed in some Tinginae and several families of the Cimicomorpha (e.g. Miridae, Microphysidae; see Schuh and Štys, 1991) is not a postcubitus; its nature remains uncertain. Proposed homologies are summarized in Table 1.

The idea that the tingoid corium includes cells of the former membrane, is confirmed by the fact that in *Ignotingis* most of the apical costal cell and part of apical discal cell are non-areolate (the distal boundary of areolation is marked by an oblique dark spot). If so, then the apical discal cell of *Ignotingis* (or its distal part only) corresponds to the membrane cell 2(+3+4) of the Miridae, and the vein M+CuA<sub>1</sub> delimiting the apical costal cell to the vein emanating from the membrane cell 2 in some Cimicomorpha. When this vein is quite long and extended to near the hemelytral apex (in Pachynomidae: Schuh and Štys, 1991, fig. 6B) or to near C (in Velocipedidae: van Doesburg, 2004, fig. 26), it is “dead” (fold-like, devoid of sensilla) distally, but sometimes represents a continuation of the sensillae-bearing basal “stub” (processus corial). This distally “dead” vein M + CuA<sub>1</sub> is not extended up to the wing margin in Cimicomorpha other than in Tingoidea. The condition found in *Ignotingis* allows us to suppose that this “stub vein” vein is live and reaches C near the hemelytral apex in all Tingoidea. This character is either plesiomorphic within the infraorder or a reversal from an early stage of the stub vein reduction.

*Ignotingis* retains a primitive pattern of corium venation (as, e.g. in the Saldidae or Nabidae), with three veins (R, M and CuA) emanating separately from the apex of a large basal cell. This pattern is not preserved in other tingoids, except in the Early Cretaceous *Golmonia*, which is similar to some

Table 1

Nomenclature and homology of the veins and areas in hemelytra of the Tingoidea, as elucidated by *Ignotingis*

Drake and Davis, 1960, Péricart, 1983	Lis, 1999	This paper
stenocostal area (Cantacaderini only) – unique structure, no homologues in other Hemiptera		
Sc (submarginal) in Cantacaderini		thickened posterior margin of stenocostal area, not homologous to any vein
Sc (marginal) in other Tingidae		anterior hemelytral margin
costal area	expansion of (C+)Sc	precostal area (or carina)
Hc (hypocosta)	(C+)Sc	C (costa) bearing hypocostal carina (or lamina)
subcostal area, consisting of 3(–5) cells in some Cantacaderinae		costal area (basal costal cell) + interradial area between R <sub>1</sub> and R <sub>s</sub> (middle costal cell) + membrane cell 1 (apical costal cell)
RM (fused R and M)	R+M	(Sc+)R+M
discoidal area, consisting of 3 cells in some Cantacaderinae		basal cell (basal discal cell) + medial area of corium (middle discal cell) + radial area and membrane cells 2–4 (apical discal cell)
Cu		CuA (straight proximal portion) + distal boundary of membrane cells 2–4 (curved distal portion)
– (proximal extension of sutural area)		anterior cubital area (between CuA and CuP=claval furrow) + posterior cubital area (between claval furrow and Pcu)
sutural area itself		hemelytral membrane excluding membrane cells
Pc (postcubitus)		free posterior vein of membrane (homology uncertain)
Cl (clavus)		clavus containing Pcu (postcubitus) and 1A (in other notation, 1A and 2A)

Thaumastocoridae: Xylastodorinae (in particular to extant *Discocoris* Kormilev, 1955 and *Proxylastodoris* Heiss and Popov, 2002 from Baltic amber) and Thaicorinae (extant *Thaicoris* Kormilev, 1969; Heiss and Popov, 2002) rather than to *Ignotingis* in the structure of hemelytron. Among Cenozoic tingoids, the least modified hemelytral venation nearest to that of *Ignotingis* is found in several genera of Cantacaderinae retaining (1) a costal (“subcostal”) area divided into three cells, (2) a discoidal area divided into three cells, and (3) CuP as claval furrow or its vestige (faint ridge between two puncture rows). Some of these genera are included in Phatnomatini (mainly from Africa), e.g. *Sinalda* Distant, 1904 (Baltic amber, recent in southern Africa), *Astolophos* Distant, 1904 (South Africa), *Etesinalda* Froeschner, 1996 (Island of São Tome). Some other genera belonging to Cantacaderini are even more primitive in retaining the basal cell joining the base of the hemelytron (not stalked owing to basal fusion of R+M with CuA, as in *Cyperobia* Bergroth, 1927 from New Zealand and Phatnomatini), but more derived in the separated stenocostal area; these are *Paleocader* Froeschner, 1996 and *Weitschatiella* Heiss, 2002 from Baltic amber, and Recent genera of a Gondwanan distribution, namely *Ceratocader* Drake, 1950 from Tasmania and Australia, *Nectocader* Drake, 1928 from Brazil, *Pseudophatnoma* Blöte, 1945 from Indonesia, *Stenocader* Drake and Hambleton, 1944 from Chile, *Pseudophatnoma* Blöte, 1945 from Indonesia, and *Teratocader* Drake,

1950 from Malaya (Fig. 5). The venation of all known Cantacaderinae differs from that of ignotingids in that (1) M leaves R beyond the basal cell (usually transverse and far beyond the basal cell, but sometimes still oblique and close to it, e.g. in *Etesinalda*, *Stenocader* and especially in *Exulmus* Froeschner, 1996 (Phatnomatini, Congo), and (2) there is one less discal cell (presumably due to fusion of the anterior and distal discal cells of *Ignotingis*).

#### 4. Affinities of Ignotingidae and Tingoidea

Ignotingidae are assigned to the Tingoidea on account of their areolate hemelytra with no costal fracture and a corium that continues up to the hemelytral apex, a coarsely punctate head and thorax, a very long third antennal segment, a non-predatory rostrum with an elongate first segment, a pronotum that is expanded onto the mesonotum and bears areolate dorsal and lateral projections, short tarsi, fused second and third abdominal sternites, a symmetrical pygophore and a lacinate ovipositor. The new family is distinct from the Miridae in its expanded pronotum, in the structure of the hemelytra, and in having rotatory hind coxae, a symmetrical pygophore and a fossula spongiosa. Ignotingidae differ from Thaumastocoridae in that the mandibular plates are not enlarged, the first segment of the rostrum is elongate, and the tarsi are

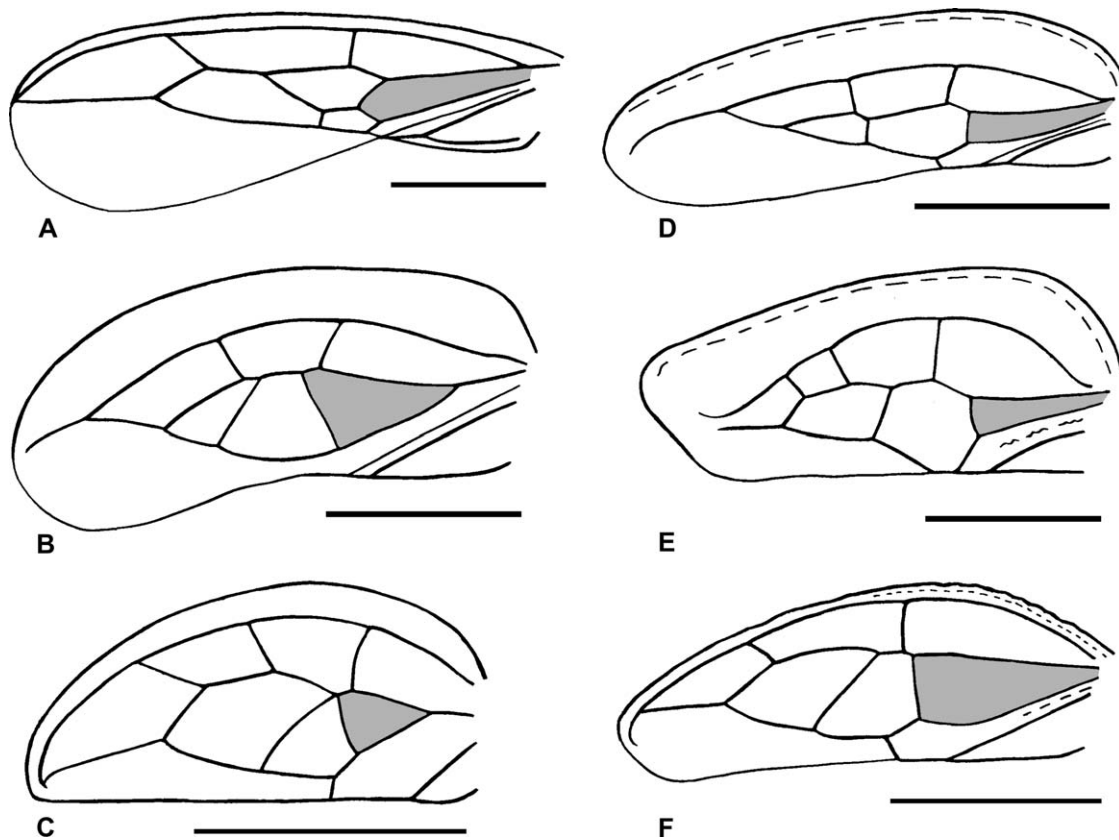


Fig. 5. Hemelytral venation in *Ignotingis* and some genera of Cantacaderinae (Tingidae; based on Froeschner, 1996, figs. 7, 10, 12, 22, 23). A, *Ignotingis mirifica* sp. nov. B, *Etesinalda laticosta* Froeschner, 1996, Recent. C, *Exulmus engaeus* (Drake and Ruhoff, 1961), Recent. D, *Paleocader avitus* Drake, 1950, Baltic amber. E, *Stenocader tingoides* Drake and Hambleton, 1944, Recent. F, *Ceratocader armatus* Hacker, 1928, Recent. Basal cell shaded; posterior margin of stenocostal area and rudimentary claval furrow in broken line. Scale bars represent 1 mm.

three-segmented, and in having a lacinate ovipositor, a symmetrical pygophore and parameres directed caudad. It is distinct from the Thaumastocoridae, Tingidae and Vianaididae in having a body that is not dorsoventrally depressed, a thick rostrum that is not appressed to the venter, and in details of the hemelytral venation. It is also distinct from the Tingidae and Vianaididae in having a vertical head, bucculae that are not prominent, no thoracic sternal laminae, a three-segmented tarsi, an ovipositor that is not concealed by paratergites, and a fossula spongiosa. Ignotingidae are similar to Vianaididae (including macropterous forms; see Schuh and Slater, 1995) and distinct from the Tingidae in that the second antennal segment is much longer than the first and the membrane is not areolate. They are distinct from the Vianaididae and similar to Tingidae in having an areolate dorsum, conspicuous pronotal projections, and a similar basic pattern of hemelytral venation.

Tingidae were classified as Cimicomorpha and placed near the Reduviidae by Leston et al. (1954). Drake and Davis (1960) united the Tingidae s.l. (including Vianaidinae) and Miridae into Miroidea. Schuh and Štys (1991) supported such a grouping and added the Thaumastocoridae to this superfamily as the sister clade of Miridae + Tingidae. Péricart (1983) hypothesized that Tingidae s.l. originated from “pre-Miridae”. By contrast, Kerzhner (1981) considered the Thaumastocoridae to be the nearest relatives of Tingoidea (Tingidae s.s. + Vianaididae) and the Miridae as much more distantly related.

The presence of fossula spongiosa in *Ignotingis*, if true, is totally unexpected. Kerzhner (1981) interpreted this structure as a synapomorphy of Cimicoidea s.l., p.p. (excluding Velocipedidae, but including other Naboidae) plus Reduvidae. By contrast, Schuh and Štys (1991) argued that the Reduvidae represent the most basal lineage within the Cimicomorpha, and that the fossula spongiosa evolved independently in the Reduvidae and Naboidae + Cimicoidea s.s. The tibial appendix of the Thaumastocorinae, formerly also regarded as a fossula spongiosa, is currently considered non-homologous (Kerzhner, 1981, and others), although its setae are modified (Schuh and Slater, 1995, fig. 52.3D) and not simple as stated by Kerzhner (1981). The fossula spongiosa is small and apical in Anthocoridae and other cimicoids, so can be overlooked in fossils and possibly even in some living bugs. If the fossula spongiosa is also developed in primitive mirid-like Tingoidea, it probably belongs to the groundplan of the Cimicomorpha, and the tibial appendix of the Thaumastocorinae possibly represents a modification of this structure.

Thaumastocorid affinities of the Tingoidea seem to be confirmed by the hemelytral venation of Early Cretaceous Golmoniini, but these fossils show no reliable synapomorphies with the Tingoidea in the body structure (Golub and Popov, 2004). By contrast, the Ignotingidae show the same unique set of apomorphic traits as the Tingidae s.s. (areolation, hypertrophied pronotum with median crest, basic structure and venation pattern of hemelytron, very long antennae and

Table 2  
Some phylogenetically important characters of the Tingoidea (incl. Ignotingidae) compared to the Miridae and Thaumastocoridae (mainly after Schuh and Štys, 1991); more apomorphic states shaded

	Thaumastocoridae	Miridae	Ignotingidae	Vianaididae	Tingidae
male pygophore	asymmetrical: thaumastocorid type	asymmetrical: mirid type	symmetrical		
abdominal dorsal laterotergites	fused with mediotergites	not fused	?	not fused	
mandibular plates	greatly enlarged	of normal size			
rostrum segment I	short dilated	long and slender			
parameres directed	cephalad	caudad			
ovipositor	platelike or reduced	lacinate			
hind coxae	rotatory	cardinate	rotatory		
costal fracture	absent	long	absent		
venation of hemelytral membrane	no	1–2 cells + vein	no (1cell?)	no	
buccular bridge	absent	present	present?	present	absent
spermatheca	absent	vermiform gland	?	absent	non-functional
fossula spongiosa	transformed(?) into tibial appendix	absent	present?	absent	
valvifer I and valvula I	connected	disconnected	?	disconnected	
valvifer I and ventral laterotergite 8	not fully fused	fully fused	?	fully fused	
abdominal spiracle I	present	absent	?	absent	
forewing R+M	not raised		raised?	carinate	
ocelli	present	absent?		present	absent
apical seta on 4th antennal segment	absent	absent?		present	absent
pedicel	long				short



legs, shortened tarsi, rotatory hind coxae), combined with several important plesiomorphies not found in other tingoids (vertical head without prominent bucculae or other projections, thick rostrum not appressed to venter, no thoracic sternal laminae, three-segmented tarsi, exposed ovipositor) or even in the Miroidea and other Tingoidea (complete stub vein, fossula spongiosa). In the ventral origin, caudal direction and elongate first segment of the rostrum the Ignotingidae are similar only to the Miridae and other Tingoidea; the rostrum is thick in some mirids; proportions of the rostrum segments approaching those of *Ignotingis* (second segment longer than third plus fourth) are found in some Thaumastocoridae (*Discocoris*; Schuh and Slater, 1995, fig. 52.3B) and Tingidae (e.g. *Stephanitis* Stål, 1873; Péricart, 1983, fig. 1b). Some phylogenetically important characters of the Tingoidea (including Ignotingidae), Miridae and Thaumastocoridae are compared in Table 2 (data mainly after Schuh and Štys, 1991).

*Ignotingis* seems to be a much more plausible member of an ancestral tingoid lineage than *Golmonia*, and in contrast to the latter shows no thaumastocorid characters. The discovery of *Ignotingis* near the Jurassic/Cretaceous boundary as early as, or earlier than known records of the Golmoniini (Berriasian?–Aptian?), agrees with the hypothesis of the origin of the Tingoidea from primitive mirid-like ancestors (which still retained symmetrical genitalia, complete stub vein, and a fossula spongiosa), rather than from thaumastocorid-like forms.

There are fewer extinct families in the Heteroptera than in the Homoptera (Shcherbakov and Popov, 2002), but the Ignotingidae are sufficiently distinct from other cimicomorphan groups to keep the family status even in those classifications that include the Vianaididae in the Tingidae s.l.

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