**Zeitschrift:** Entomologica Basiliensia et Collectionis Frey

Herausgeber: Naturhistorisches Museum Basel, Entomologische Sammlungen

**Band:** 30 (2008)

**Artikel:** Taxonomic status of the Mesozoic genera Anhuistoma Lin, 1985,

Eotenebroides Ren, 1995, Lithostoma Martynov, 1926,

Palaeoendomychus Zhang, 1992, and Sinosoronia Zhang, 1992

(Coleoptera)

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**DOI:** https://doi.org/10.5169/seals-981055

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# Taxonomic status of the Mesozoic genera Anhuistoma Lin, 1985, Eotenebroides Ren, 1995, Lithostoma Martynov, 1926, Palaeoendomychus Zhang, 1992, and Sinosoronia Zhang, 1992 (Coleoptera)

by Jiří Kolibáč & Huang Di-Ying

Abstract. Five Mesozoic genera described from China and Kazakhstan, formerly classified within Trogossitidae (Cleroidea), were studied and re-classified. The specimen of *Anhuistoma hyla* Lin, 1985 is poorly preserved and the morphological information it yields is inadequate. The species is therefore removed from Trogossitidae and classified as Coleoptera *incertae sedis*. Detailed photographs of the species and an ink-drawn reconstruction are presented here. The systematic position of *Eotenebroides tumoculus* Ren, 1995 is confirmed in Trogossitinae and its classification within the tribe Trogossitini is suggested. *Lithostoma expansum* Martynov, 1926 was described in Trogossitidae (Peltinae). The species is removed to the subfamily Trogossitinae and the new tribe Lithostomini trib.nov. is established for it. *Palaeoendomychus gymnus* Zhang, 1992, originally described in Endomychidae, is shifted back to Cucujoidea. *Sinosoronia longiantennata* Zhang, 1992 is confirmed as a member of Trogossitidae and classified within the tribe Ancyronini (the subfamily Peltinae). Illustrations of the all species are provided.

**Keywords.** Coleoptera – Cucujoidea – Cleroidea – Trogossitidae – *Anhuistoma hyla – Eotenebroides tumoculus – Lithostoma expansum – Palaeoendomychus gymnus – Sinosoronia longiantennata* – Lithostomini trib.nov. – Mesozoic – China – Kazakhstan

#### Introduction

Systematic positions for the Mesozoic trogossitid genera *Cretocateres* Ponomarenko, 1986, *Thoracotes* Handlirsch, 1906, *Juralithinus* Kireichuk et Ponomarenko, 1990, *Meligethiella* Medvedev, 1969, *Ostomalynus* Kireichuk et Ponomarenko, 1990, and *Peltocoleops* Ponomarenko, 1990 were suggested by Kolibáč (2006). Three other Mesozoic fossils found in China have recently been classified within Trogossitidae (Ponomarenko & Kireichuk 2005–2008): *Anhuistoma hyla* Lin, 1985, *Palaeoendomychus gymnus* Zhang, 1992, and *Sinosoronia longiantennata* Zhang, 1992. These species were listed as *incertae sedis* by Kolibáč (2006). An attempt to classify the species named is presented here.

The first of the species, *Anhuistoma hyla*, was described from the Middle Jurassic (Hanshan Formation) in Anhui Province (LIN 1985). It was classified within "Ostomatidae Reitter, 1882" <sup>1)</sup>, i.e. modern Trogossitidae. The specimen is poorly preserved; moreover, the original description and illustrations are not clear enough. The species has therefore been newly studied and figures of it are presented here.

<sup>&</sup>lt;sup>1)</sup>REITTER (1882) did not establish the family "Ostomatidae" but the group "Ostomini" in the sense of a subfamily of Trogossitidae. He renamed only "Peltini", which had been used earlier for the same group (REITTER 1876).

Palaeoendomychus gymnus from the Lower Cretaceous Laiyang Formation <sup>2)</sup>, Shandong Province, was described in the family Endomychidae (ZHANG 1992). PONOMARENKO & KIREICHUK (2005–2008) removed the species from Endomychidae to Trogossitidae (Peltinae). The taxonomic position of the species is discussed here.

Sinosoronia longiantennata was found at the same site as the previous species and described in Nitidulidae. Ponomarenko & Kireichuk (2005–2008) shifted the species to Trogossitidae (Peltinae). Their classification is confirmed and specified here.

Two other Mesozoic genera and species remain unrevised – *Lithostoma expansum* Martynov, 1926 and *Eotenebroides tumoculus* Ren, 1995. Both species were omitted by Ponomarenko and Kireichuk from their list of fossils in 2005 (but *Lithostoma* is included in the updated 2008 list) as well as by Kolibáč (2006).

Lithostoma expansum was described from Upper Jurassic paper-shales in the Karatau region (southern Kazakhstan) and classified within Trogossitidae (Peltinae). We found important structures in the original photograph and the original Russian description that allow us to remove the species to the subfamily Trogossitinae.

*Eotenebroides tumoculus* (Lower Cretaceous, Lushangfen Formation) was described from the vicinity of Beijing and classified within Tenebroidinae, i.e. modern Trogossitinae. The classification is confirmed and some morphological characters are specified.

#### **COLEOPTERA** incertae sedis

#### Anhuistoma Lin, 1985

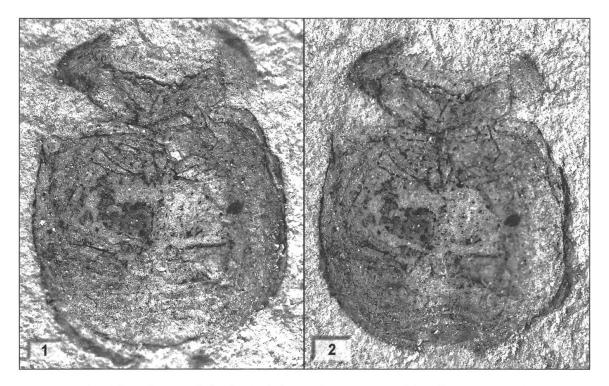
Lin (1985): 305 [in Chinese], 309 [in English] (sub "Ostomatidae", = Trogossitidae: Peltinae).

Type species: Anhuistoma hyla Lin, 1985 (designated by author).

**Original description.** "A broadly elliptic beetle of small size; pronotum broadly hemiorbicular (hemispherical?); elytra short and broad, ornamented with many longitudinal striae; legs short, three pairs of coxae clearly separated, fore-coxa transverse, mid-coxa rounded, both posterior coxae transverse and connected with each other; abdomen with 5 visible sternites." (LIN 1985: 309)

Remarks. The author (LIN 1985) considered the new genus related to *Lithostoma* Martynov, 1926 (see below). However, there are no common character states shared by *Anhuistoma* and *Lithostoma* except for a general Trogossitidae body shape. The body shape and size, as well as the forms of the pronotum, front coxal cavities and front coxae are appropriate to the former classification in Trogossitidae but the presence of coxal plates (or roofs) in the hind coxae and the structure of the abdomen exclude such a taxonomic position. The fossil is poorly preserved (Figs 1, 2) and so, although we present new figures of the specimen, it must be considered Coleoptera 'incertae sedis'.

<sup>&</sup>lt;sup>2)</sup>ZHANG (1992) considered that the Laiyang Formation probably dates to the Upper Jurassic.



Figs 1–2. Anhuistoma hyla Lin: 1 – holotype; 2 – counterpart (photo by Huang D.-Y.).

## Anhuistoma hyla Lin, 1985

LIN (1985): 305 [in Chinese], 309 [in English].

**Material examined.** Coll. No. 2p43-H26-243; Cat. No. 81286. Middle Jurassic, Hanshan Formation, Pengzhuang village, Anhui Province, China.

Original description. "The body of a small beetle with head and legs missing, 3.5 mm long and 2.3 mm wide. Body broadly elliptic. Pronotum in hemiorbicular (hemispherical?) form, slightly broader than long; anterior margin of pronotum concave, posterior margin of pronotum as wide as the anterior. Anterior coxa transverse and disjointed. Mid-thorax slightly smaller than metathorax. Both mid-coxae rounded and disjointed from one another. Posterior coxae transversely connected. Elytra much broader at base, gradually narrowing toward apex, rounded at apical angle; surface covered with several longitudinal striae. Abdomen with 5 visible sternites." (LIN 1985: 309)

**Remarks.** This small beetle displays strong three-dimensional preservation. It split between the dorsal and ventral skeletons (the holotype is the ventral specimen), so the ventral structures are rather well preserved and the moulage of the elytra is still just

visible. It has 5 visible abdominal sternites, the first of them (sternite III) rather long; 2nd—4th visible sternites short, of similar length; fifth sternite as long as total of 2nd—4th together. Elytra bear a few longitudinal carinae but, contrary to the original drawing, exhibit somewhat oblique and dense ridges. Both front and middle coxae transverse; front coxae narrowly separated, middle coxae apart, hind coxal plates developed, meeting one another, but hind coxae widely separated.

The preserved specimen of *Anhuistoma hyla* has no characters remarkable enough to serve for classification. Thus, its systematic position at family level remains uncertain.

New photographs of the fossil are shown as in Figs 1, 2 a new drawing in Fig. 3.

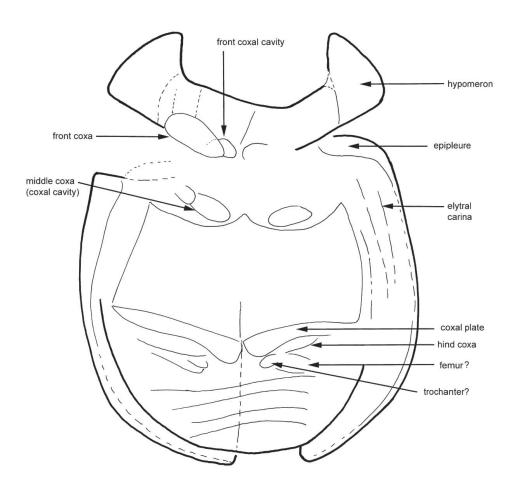


Fig. 3. Anhuistoma hyla Lin: ventral side.

### **CUCUJOIDEA** incertae sedis

## Palaeoendomychus Zhang, 1992

ZHANG (1992): 334 [in Chinese], 337 [in English] (*sub* Endomychidae).

PONOMARENKO & KIREICHUK (2005–2008): http://zin.ru/animalia/Coleoptera/rus/paleosy2.htm (*sub* Peltidae, = Trogossitidae: Peltinae).

Type species: Palaeoendomychus gymnus Zhang, 1992 (designated by author).

Original description. <sup>3)</sup> "Body minute and compact, oval, hairless. Head deeply sunk into pronotum. Eyes rather large, widely separated, slightly prominent. Antennae short, flagellum cylindrical. Pronotum transverse, short (Chin.: raised at centre), without membrane (sic) in front, but with lateral sides (Chin.: edges) broadly flattened, posterior angles prominent. Scutellum small, narrowly triangular, distinctly longer than broad. Elytra wide, dehiscent, as wide at base as pronotum, and both closely connected to one another, humeral angles rounded, terminal angles prominent, surface with striae. Legs normal, with tarsi short and narrow (Chin.: 3 tarsomeres visible), first and second tarsal segments triangular, each about as long as wide, third cylindrical, noticeably longer than wide." (Zhang 1992: 334, 337)

**Remarks.** The author (ZHANG 1992: 337) compares the genus with pantropical *Stenotarsus* Perty, 1832 with about 250 recent species which are very variable in shape.

Antennae are clubbed, clypeus protracted, all pairs of coxae widely distant, elytra with carinae, and hind tarsomeres widened or lobate in *Palaeoendomychus*. The nature of the morphological structure of the line marked with the question mark in Fig. 4 is unclear. In consideration of the characters mentioned, *Palaeoendomychus* is moved out of Cleroidea. A combination of characters similar to those in *Palaeoendomychus* may be found, for example, in Endomychidae and Nitidulidae; however, the opinion of a Cucujoidea specialist would contribute greatly to a decision in the matter.

# Palaeoendomychus gymnus Zhang, 1992

ZHANG (1992): 334 [in Chinese], 337 [in English]. PONOMARENKO & KIREICHUK (2005–2008): http://zin.ru/animalia/Coleoptera/rus/paleosy2.htm.

Locality. Lower Cretaceous, Laiyang Formation, Nanligezhuang village, Laiyang City, Shandong Province, China.

**Original description.** "Head transverse, 1.5 times as broad as long. Eyes oval, about two-thirds the width of head. Basal segments and club of antennae ill-preserved, only six segments of flagellum visible, each about twice as long as wide. Pronotum excluding lateral borders triangular, yellowish-brown in colour, posterior margin sinuate. Scutellum 1.5 times as long as wide, with apex acute. Elytra widest near median part, each elytron 2.2 times as long as wide, with six shallow striae. Legs ill-preserved,

<sup>&</sup>lt;sup>3)</sup> The Chinese and English texts are somewhat different from one another. Important items from the Chinese are translated in parentheses.

anterior and middle coxal cavities seemingly circular, widely separated, posterior femora about as long and wide as tibiae, tarsi less than half the length of tibiae, third tarsal segment as long as the first and second together. Total length 4.2 mm, width 2.8 mm." (Zhang 1992: 337)

**Remarks.** The original picture of the specimen is redrawn and fundamental morphological structures are marked in Fig. 4.

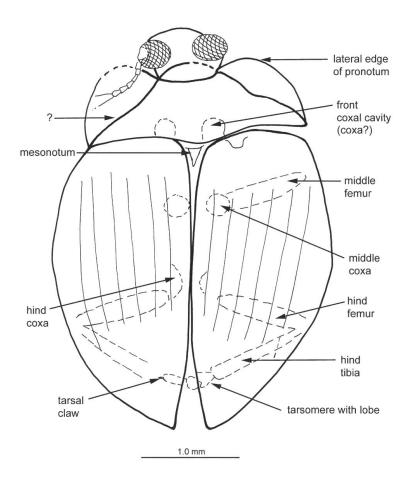


Fig. 4. Palaeoendomychus gymnus Zhang (ex ZHANG 1992, modified; labelling by authors).

#### CLEROIDEA: TROGOSSITIDAE: TROGOSSITINAE

## Trogossitini Latreille, 1802

## Eotenebroides Ren, 1995

REN (1995): 88 [in Chinese], 189 [in English] (sub "Tenebroidinae", = Trogossitidae: Trogossitinae).

**Original description.** "Head triangular, longer than wide. Eyes distinct, larger, situated laterally at median. Last 3 segments of antennae not thickened. Basal part of lateral margin of pronotum not narrowed. Scutellum larger. Coxa of middle and hind legs very close. Elytra not longer than abdomen, surface with 5 visible longitudinal streaks. Length 6.1 mm, width 2.4 mm." (Ren 1995: 189)

**Remarks.** One morphological feature resembles the genus *Parandrexis* Martynov, 1926 (Cucujiformia: Parandrexidae), of similar body shape and size — the elytra of *Eotenebroides* are shorter than the abdomen. However, the character may have been an artificial result of pressure on the fossil (elytra and abdomen are in different axes in the specimen). Tenebrionidae is another similar family. We excluded such classification on the basis of the shape of the front coxae. The head is distinctly narrower than the pronotum, femora non-clavate, front coxae transverse, elytra with conspicuous carinae, pronotum trapezoidal or weakly cordate: this combination of features indicates a classification of *Eotenebroides* within Trogossitinae.

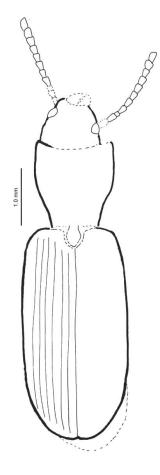
The following characters allow us to classify *Eotenebroides* within the tribe Trogossitini. (1) Antennae are not clubbed but segments probably successively widening from about segment 5 to 10; moreover, these segments are perhaps weakly asymmetrical. (2) Elytra with 6 to 8 carinae but imperceptible sculpture. (3) Pronotum trapezoidal or possibly weakly cordate, without distinctly projecting anterior corners. (4) Body elongate.

# Eotenebroides tumoculus Ren, 1995

REN (1995): 89 [in Chinese], (species description in Chinese only).

Locality. Lower Cretaceous, Lushangfen Formation; Chongqing reservoir, SW Beijing, China.

Original description. Translation of Chinese description: "Head: head slightly longer than wide; mandible robust, slightly curved; antenna with 11 segments, scapus a littler longer than others, length of other segments similar to one another, last three segments not thickened; eyes large, around 1/3 as long as head (excluding mandible), not projecting, clearly separated from front edge of pronotum. Thorax: pronotum longer than wide, anterior edge concave, anterio-lateral angles projecting, sharp, posterio-lateral angles rounded, posterior edge straight, as long as anterior edge; connection of pronotum with elytra forming a neck; scutellum large, triangular; metepisternum visible, not making contact with mid-coxa; front coxae transverse, well-separated, femur thick;



**Fig. 5.** *Eotenebroides tumoculus* Ren: simplified body outline.

middle coxae rounded, close to one another, femur thicker than tibia; hind coxae nearly rounded, close to one another, hind femur as wide as middle femur. Elytra: elytra does not reach end of abdomen, its base as wide as pronotum, equipped with 5 longitudinal ridges. Abdomen: 6 sternites visible." (REN 1995: 89)

**Remarks.** The body outline in the original drawing (REN 1995: Fig. 3-47) seems inconsistent with the species photograph (*l.c.*: Pl. 12, Fig. 5). A simplified drawing is therefore presented here (Fig. 5).

#### Lithostomini trib.nov.

Type genus: Lithostoma Martynov, 1926

**Diagnosis.** Classification within Trogossitinae is based on the presence of sensorial fields in enlarged parts of the antennal segments. Small tubercles occurring in pronotum and elytra are known in trogossitine genera *Calitys* Thomson, 1859 and *Phanodesta* Reitter, 1876 only, no peltine representative possesses such structures. The tribe differs from the recent and fossil members of Trogossitinae in broadly oval body (this occurs in some Gymnochilini only), pronotum narrowed anteriad, antennae without conspicuous club and asymmetrical segments in flagellum, head narrowed towards base. The shape of antennal segments 10 and 11 is unknown

because they are missing (only a trace of segment 10 is visible). Antennae may be only 10-segmented, last segment may be enlarged (as in e.g. Egoliini).

The new tribe is probably isolated from other tribes of Trogossitinae and may be considered a sister group to them.

# Lithostoma Martynov, 1926

Martynov (1926): 13 [in Russian], 32 [in English] (*sub* "Ostomatidae", = Trogossitidae: Peltinae). Ponomarenko & Kireichuk (2005–2008): http://zin.ru/animalia/Coleoptera/rus/paleosy2.htm.

**Original descriptions.** "Head free, dilated between the eyes (Russ.: and narrowed backwards); mandibulae strong, sharply bent inwards, with perhaps two teeth at the apices; antennae resembling those in living Ostomatinae (Russ.: in Ostoma and other genera); basal joint large, bulbous anteriorly, second much smaller, third still smaller,

<sup>&</sup>lt;sup>4)</sup> The Russian and English texts vary somewhat from one another; the Russian is more comprehensive. Some important statements deriving from the Russian are translated in parentheses.

short, fourth joint of the same width but elongated, 5–7th joints elongated but becoming gradually thicker towards the tip (Russ.: joints 10 and 11 not preserved), last 8–11 joints only slightly thicker, without distinct apical club (clavus). Pronotum broadening posteriorly, apparently furnished with marginal dilatations (Russ.: as in Ostoma); covered all over with numerous point-like pits. Elytra broad, rounded at postero-lateral margins (Russ.: as in Ostoma), with perhaps 8 longitudinal stripes, each containing two rows of raised black points; intermediate narrow stripes barely elevated; both marginal dilatations also with pits and points (Russ.: Body size about 6 mm.)." (MARTYNOV 1926: 32)

Remarks. This very interesting fossil beetle differs from all other Mesozoic Trogossitidae described to date. If Martynov (1926) interpreted the shapes of the head and antennal segments well (the original photograph is unclear), it is the first known member of Trogossitidae without a distinct antennal club and with the head narrowed towards base. The question is, of course, if our classification of *Lithostoma* is correct. The following features of Trogossitidae appear in the fossil (see also description of the species): (1) general shape and size of body, (2) distinctly flattened sides of pronotum and elytra, (3) double rows of punctures/tubercles among elytral carinae, (4) robust bidentate mandibles, (5) extremely large scapus, and (6) dilated antennal segments with what are perhaps sensorial fields in enlarged parts of each segment. The last-cited character (sensorial fields in antennae), in particular, allows us to classify *Lithostoma* within the subfamily Trogossitinae. With respect to two of the features mentioned above (shapes of head and antenna), we establish a new tribe for the genus.

### Lithostoma expansum Martynov, 1926

MARTYNOV (1926): 13 [in Russian], 32 [in English].

**Locality.** Upper Jurassic, Oxfordian(?) paper-shales near Galkino (approximately 42°15′N–70°02′E), "Turkestan" (now southern Kazakhstan), Chimkentskaya oblast district, 1924. "Geologicheskiy komitet" Collection (today in Paleontologicheskiy institut, Moscow?).

**Original descriptions.** <sup>5)</sup> English text: "Head and antennae as in generic description; sides of pronotum convex, points distinct; elytra broad, rounded at the postero-lateral margins; marginal dilatations rather broad; the dividing stripes not elevated. Length of the body 6 mm." (MARTYNOV 1926: 32)

Translation of Russian text: "Head free, strongly projecting anteriorly (partly artificial condition in compressed specimen). Mandibles robust, left mandible bidentate (right inconspicuous). Antennae as described above, each joint weakly dilated at apex; each dilated area with thin (sic), dark, round rim. Final two joints torn off, only a trace of joint 10 present. Pronotum widened backwards, with shallow punctures interspersed with small tubercles. Elytra wide, rounded apically and dorsally (sic); flattened sides well-developed and probably lighter than dark brown convex portion of elytra. Elytra,

<sup>&</sup>lt;sup>5)</sup> The English and Russian texts are different from one another; the Russian description is therefore translated here.

including flattened sides, with rows of well-developed small, black tubercles (orig.: "convex punctures"); carinae among them not higher than tubercles. Length of body from anterior margin of labrum to apex of elytra – 6 mm." (MARTYNOV 1926: 13)

**Remarks.** An original picture of the specimen is redrawn with modifications to the antenna and pronotum (Fig. 6). The antenna of the fossil is 9-segmented, with only a trace of segment 10. The depiction of the pronotum is somewhat confusing in the original drawing; the margins of the pronotum are drawn in fine dotted lines and the inner borders of the flattened portion of the pronotum appear as full lines. However, the outline of pronotum is visible in the photograph (MARTYNOV 1926: Tab. 1, Fig. 3).

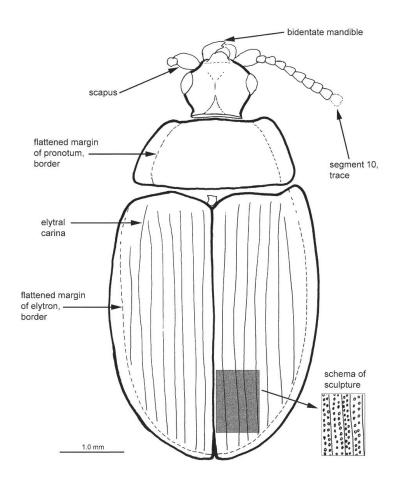


Fig. 6. Lithostoma expansum Martynov (ex MARTYNOV 1926, modified; labelling by authors).

# **CLEROIDEA: TROGOSSITIDAE: PELTINAE**

# Ancyronini Kolibáč, 2006

# Sinosoronia Zhang, 1992

ZHANG (1992): 333 [in Chinese], 336 [in English] (sub Nitidulidae).

PONOMARENKO & KIREICHUK (2005–2008): http://zin.ru/animalia/Coleoptera/rus/paleosy2.htm (*sub* Peltidae, = Trogossitidae: Peltinae).

Type species: Sinosoronia longiantennata Zhang, 1992 (designated by author).

**Original description.** "Body minute, oval. Head of medium size, triangular, deeply sunk into pronotum. Eyes large. Antennae elongate, with loose club. Pronotum short, wide, anterior angles acute, clearly expanded forwards, posterior angles prominent, posterior margin as wide as base of elytra. Scutellum small, semicircular. Elytra long, dehiscent, covering apex of abdomen, shoulder prominent, terminal angles acute." (Zhang 1992: 336)

Remarks. The author (ZHANG 1992: 336) compares the genus with Meligethiella Medvedev, 1969, originally described in Nitidulidae (MEDVEDEV 1969). However, Meligethiella had previously been shifted to Trogossitidae (Peltinae) by KIREICHUK & PONOMARENKO (1990) who also described two new species in the genus. Later, Kolibáč (2006) classified Meligethiella within the tribe Thymalini. Another Mesozoic genus, Peltocoleops Ponomarenko, 1990, is probably more closely related to Sinosoronia. The genus was described as "Cleroidea incertae sedis" (PONOMARENKO 1990) and classified within Lophocaterini (Trogossitidae: Peltinae) by Kolibáč (2006). The two genera differ distinctly in the shape of antennal club. It is compact, 3-segmented, with segments weakly asymmetrical in Peltocoleops (PONOMARENKO 1990) but loose, 2- or 3segmented, with segments distinctly asymmetrical in Sinosoronia (Fig. 7). It is therefore suggested that the latter genus be classified within the tribe Ancyronini, which has corresponding features in recent representatives. The large, elevated eyes observed in Sinosoronia also support such a classification. There exists an concurrently described fossil species of the recent genus Ancyrona Reitter, 1876 (SCHMIED et al., in press) from the late middle Eocene of Germany. Thus, although Ancyronini are considered the most advanced tribe in the cluster Decamerini-Lophocaterini-Ancyronini and Peltinae as a whole (Kolibáč 2006, 2007), the splitting of the cluster may be dated to the Lower Cretaceous or earlier.

# Sinosoronia longiantennata Zhang, 1992

ZHANG (1992): 333 [in Chinese], 336 [in English]

PONOMARENKO & KIREICHUK (2005–2008): http://zin.ru/animalia/Coleoptera/rus/paleosy2.htm

Locality. Lower Cretaceous, Laiyang Formation, Nanligezhuang village, Laiyang City, Shandong Province, China.

Original description. "Brown in colour. Head about as long as wide. Mandibles large but dentes indistinguishable. Eyes circular, expanded laterally but exterior margin ill-preserved. Antennae 1.2 times as long as head and prontoum together, several basal segments ill-preserved except for the thickened scape, each flagellum cylindrical, about twice as long as wide, club elongate, nearly one-third the length of antenna, slightly thickened apically. Pronotum 2.1 times as broad as long; anterior margin arched, its median part straight, curved forwards laterally, lateral margins arched, posterior margin sinuate, and closely connected to elytra. Scutellum about as long as wide. Elytra smooth, not striated, exterior and interior margins slightly arched, shoulder rounded, its terminal part distinctly exceeding apex of abdomen, each elytron 2.6 times as long as wide. Middle and posterior femora seemingly clubbed, both tibiae and tarsi absent. Total length 2.3 mm, width 1.3 mm." (ZHANG 1992: 336)

Remarks. The original picture of the specimen is redrawn and fundamental morphological structures are marked in Fig. 7. "Posterior femur" in the original

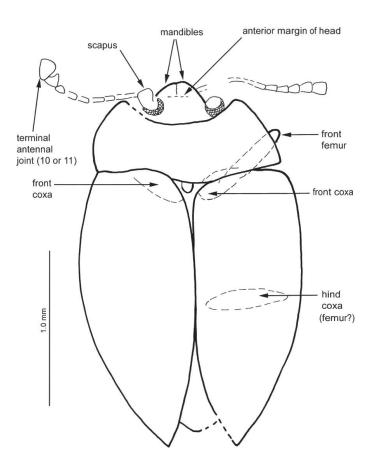


Fig. 7. Sinosoronia longiantennata Zhang (ex ZHANG 1992, modified; labelling by authors).

description is probably hind coxa. The long antenna with a loose club resembles that of species of the *Ancyrona gabonica* species-group, while a similar shape of the pronotum may be found in the *colobicoides* species-group. Such an extremely small size of body is not known in recent Ancyronini but occurs in an concurrently described species from the late middle Eocene (SCHMIED *et al.*, *in press*; see above). Apart from body size, the two species share large, elevated eyes and similar shape of pronotum. The body is not as rounded in the Eocene species (and the antennae are unfortunately missing). The time difference between these two very similar species is about 100 million years, much more than between the Eocene and the present time. Round body and body size might appear indicative of a group of genera related to *Rentonium* Crowson, 1966 (the former Rentoniinae, now Thymalini). However, the body is much smaller (about 1 mm) and the antennae shorter with a symmetrical club in *Rentonium* and allied genera (Kolibáč 2005). If the asymmetrical club is considered an apomorphy, *Sinosoronia* may well be an ancestor of Ancyronini rather than Thymalini.

# Acknowledgements

The participation of J. Kolibáč in this project was supported by the grant ref. MK00009486201 from the Ministry of Culture of the Czech Republic. Huang D.-Y. is grateful to NSFC (grant no. 40672013) and the Major Basic Research Projects of MST of China (2006CB806400) for supporting this project.

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