



New archidermapteran earwigs (Dermaptera) from the Middle Jurassic of Inner Mongolia, China

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Abstract

Two new species of Archidermaptera are described and figured from the Middle Jurassic Jiulonghsan Formation of Daohugou, Inner Mongolia, China. *Aneuroderma oiodes* **gen. & sp. nov.** is described in the family Protodiplatyidae and *Sinopalaeodermata concavum* **sp. nov.** is established in the family Dermapteridae. Both new species share the typical characters of the extinct suborder Archidermaptera (e.g., pentamerous metatarsi, filiform and multimerous cerci, externalized ovipositor). *Aneuroderma* **gen. nov.** is compared with other genera of the Protodiplatyidae, while *S. concavum* **sp. nov.** allows us to emend the diagnosis of the genus *Sinopalaeodermata*. We briefly discuss the diversity of Archidermaptera and challenges to understanding relationships among this mid-Mesozoic diversity.

Keywords

Dermapteridae, earwigs, new genus, new species, Protodiplatyidae, systematic palaeontology

Introduction

The Dermaptera (earwigs) are, like all organisms, an interesting mosaic of primitive and derived traits – on the one hand they have a typical 'orthopteroid' habitus with chewing mouthparts, while on the other extant species have specialized cerci

modified as forceps; a vestigial ovipositor; reduced tarsal count; a shortened and tegminized forewing; a unique hind wing composed of a greatly enlarged anal fan, reduced remigium, and distinctive folding pattern; and have lost ocelli (Haas 1995; Grimaldi and Engel 2005). Dermaptera also have specialized maternal care widespread through the order, and date to at least the Early Cretaceous, and perhaps the latest Jurassic (Engel 2009). While the order is of unexceptional diversity in terms of species numbers, with only about 2000 extant species, there is considerable morphological variety, particularly in the form of the thoraces, tegmina, abdomens, and cerci (Haas 1995; Sakai 1996; Grimaldi and Engel 2005). The order is of modest age, with crown-group representatives extending to the Early Cretaceous, and the clade as a whole extending to the Triassic when considering stem groups (Bey-Bienko 1936; Vishniakova 1980; Carpenter 1992). It is possible that the extinct order Protelytroptera are further stem-Dermaptera, extending the combined lineage into the Early Permian (Haas and Kukalová-Peck 2001; Grimaldi and Engel 2005).

Excluding the Protelytroptera, the earliest definitive earwigs are classified in the suborder Archidermaptera, distinguished from other suborders by the pentamerous metatarsi, frequent presence of venation in the forewing tegmina, which are often longer, and a prominent externalized ovipositor (Engel 2003). In addition, species plesiomorphically retain ocelli and usually long, multiarticulated cerci that are, of course, not forcipate. In addition, the pro- and mesotarsi are more developed than their counterparts of the Eodermaptera and Neodermaptera, with 4 or 5 tarsomeres rather than the trimerous condition of more derived clades. Presently, there are three families recognized within the family: Protodiplatyidae, Turanoviidae, and Dermapteridae (Engel 2003; Engel and Haas 2007). Hitherto, there have been 31 species classified in 19 genera, with specimens being comparatively rare (Xing et al. 2016a; Xing et al. 2016b; Tihelka 2019). Current records are from the Late Triassic of England, Australia, and Kyrgyzstan; the Middle Jurassic of China; the Late Jurassic of Kazakhstan; and the Early Cretaceous of China (Martynov 1925; Bey-Bienko 1936; Vishniakova 1980; Zhang 1994, 2002; Jarzembowski 1999; Wappler et al. 2005; Shcherbakov 2008; Zhao et al. 2011) (Table 1).

Herein we describe a new genus and species of Protodiplatyidae and a new species of Dermapteridae, both preserved in the Middle Jurassic Jiulongshan Formation of Inner Mongolia Province, China. This discovery increases the diversity of Archidermaptera and complements our limited understanding of this suborder.

Materials and methods

Three specimens were collected from the Middle Jurassic Jiulongshan Formation at Daohugou Village, Ningcheng County, Inner Mongolia, northeastern China. The age of the fossil deposit is approximately 164–165 Ma (Chen et al. 2004; Ren et al. 2010; Gao et al. 2021; Yang et al. 2021), within the Callovian stage of the later Middle Jurassic. The material is housed in the Key Lab of Insect Evolution and Environmental Changes, the College of Life Sciences, Capital Normal University, Beijing

Table 1. Hierarchical classification of Archidermaptera and summary of tarsal formulae, where known. Interrogative marks (?) indicate missing data.

		Genus	Species	Data
		Genus Brevicula Whalley, 1985	B. gradus Whalley, 1985	4/5-4/5-5
	08		B. maculata Kelly et al., 2018	?-?-?
		Genus Dacryoderma Engel, 2021	D. teres (Tihelka, 2019)	?-?-?
	61	Genus Dermapteron Martynov, 1925	D. incerta Martynov, 1925	?-?-?
	Family Dermapteridae Vishniakova, 1980	Genus Dimapteron Kelly et al., 2018	D. corami Kelly et al., 2018	3-3-3
		Genus Jurassimedeola Zhang, 2002	J. orientalis Zhang, 2002	?-?-?
		Genus Palaeodermapteron Zhao et al., 2011	P. dicranum Zhao et al., 2011	5-5-5
		Genus <i>Phanerogramma</i> Cockerell, 1915	P. australis Kelly et al., 2018	3-3-3
			P. dunstani Kelly et al., 2018	3-3-3
			P. gouldsbroughi Kelly et al., 2018	?-?-?
			P. heeri (Giebel, 1856)	?-?-?
			P. kellyi Tihelka, 2019	3-3-3
52		Genus Sinopalaeodermata Zhang, 2002	S. concavum sp. nov.	5-5-5
192	Fan		S. neimonggolense Zhang, 2002, nom. emend.	5-5-5
101,		Genus Trivenapteron Kelly et al., 2018	T. moorei Kelly et al., 2018	3-3-3
Superfamily Protodiplatyoidea Martynov, 1925		Genus Valdopteron Kelly et al., 2018	V. woodi Kelly et al., 2018	?-?-?
Ma	Family Protodiplatyidae Martynov, 1925	Genus Abrderma Xing et al., 2016b	A. gracilentum Xing et al., 2016b	?-?-5
lea		Genus Aneuroderma gen. nov.	A. oiodes sp. nov.	5-5-5
yoi		Genus Archidermapteron Vishniakova, 1980	A. martynovi Vishniakova, 1980	4-4-5
plat		Genus Asiodiplatys Vishniakova, 1980	A. speciosus Vishniakova, 1980	4-4-5
ibo		Genus Barbderma Xing et al., 2016a	B. oblonguatum Xing et al., 2016a	?-?-?
Prot		Genus Longicerciata Zhang, 1994	L. mesozoica Zhang, 1994	5-5-5
ily.]			L. rumpens Zhang, 1994	5-5-5
fam		Genus Microdiplatys Vishniakova, 1980	M. campodeiformis Vishniakova, 1980	4-4-5
per			M. oculatus Vishniakova, 1980	4-4-5
Su			M. perfectus Vishniakova, 1985	4-4-5
	0010	Genus Perissoderma Xing et al., 2016b	P. triangulum Xing et al., 2016b	5-5-5
	, Pro	Genus <i>Protodiplatys</i> Martynov, 1925	P. fortis Martynov, 1925	4-4-5
	uli		P. gracilis Vishniakova, 1980	4-4-5
	Гат		P. mongoliensis Vishniakova, 1986	4-4-5
		Genus Sinoprotodiplatys Nel et al., 2012	S. ellipsoideuata Xing et al., 2016a	5-5-5
			S. zhangi Nel et al., 2012	5-5-5
	Family Turanoviidae Engel, 2003 (Turanodermaptera Engel, 2019)	Genus <i>Turanovia</i> Vishniakova, 1980	T. incompleta Vishniakova, 1980	?-?-?

^{*}Note that Whalley (1985) indicated that he could not determine the number of tarsomeres, stating that, "It is not possible to count the exact number of tarsal segments, of which there are certainly four and may well be five." Thus, we can only state that there are at least four tarsomeres, but it could be fully pentamerous.

(CNU; Dong Ren, Curator). Specimens were examined using a Leica M205C dissecting microscope, with ethanol added to help improve clarity and contrast with the surrounding matrix, thereby aiding the identification of fine details and the preparation of photographs. The detailed and enlarged photos were taken using a Nikon SMZ 25 microscope with a Nikon DS-Ri 2 digital camera. Line drawings were prepared using Adobe Illustrator CC and Adobe Photoshop CS5 graphics software. The higher classification followed herein is that of Engel and Haas (2007), and the morphological terminology employed in this paper is based on that of Giles (1963), Günther and Herter (1974).

Systematic palaeontology

Order Dermaptera de Geer, 1773 Suborder Archidermaptera Bey-Bienko, 1936 Family Protodiplatyidae Martynov, 1925

Genus *Aneuroderma* Xiong, Engel & Ren, gen. nov. http://zoobank.org/1A4122EC-F912-4D76-9D89-A581796CF071

Diagnosis. Moderate-sized earwigs, with numerous setose and distinctively sculptured (densely punctate-granulose throughout, particularly on head and thorax). Head broad, nearly as wide as anterior border of pronotum, posterior margin nearly straight. Antenna with 20 antennomeres; scape robust and slightly broader than remaining antennomeres; pedicel slightly longer than wide; all flagellomeres longer than wide. Compound eyes large and situated at posterior temples; ocelli absent. Dorsal surface without Y-shaped ecdysial cleavage scar. Pronotum approximately oval, anterior and posterior margins subequal in width, lateral margin convex and rounded. Tegmina without longitudinal veins; tegmina and squamata covering abdominal segment II. Legs with abundant short setae; femora carinulate; all tarsi pentamerous (i.e., tarsal formula 5-5-5 rather than the 4-4-5 of some genera); pretarsal claws simple. Female with exposed ovipositor. Pygidium small. Cerci filiform and long, with about 30 cercomeres.

Etymology. The generic name is a combination of the Greek prefix a– ($\check{\alpha}$ –, alpha privativum designating negation), $ne\hat{u}ron$ ($ve\tilde{v}\rho ov$, meaning, "nerve"), and $d\acute{e}rma$ ($\delta\acute{e}\rho\mu\check{\alpha}$, genitive $d\acute{e}rmatos$, meaning, "skin" – an allusion to the leathery tegmina and from which the ordinal name is derived, Dermaptera literally meaning, "skin wings"), referencing the absence of tegminal venation, a rare feature among Archidermaptera. The gender of the name is neuter.

Aneuroderma oiodes Xiong, Engel & Ren, gen. et sp. nov. http://zoobank.org/3AE3DBE5-7926-461C-866C-EE41EBDB272A Figs 1–3

Diagnosis. As for the genus (vide supra).

Type material. Holotype, a completely preserved female, CNU-DER-NN2021003C/P; **paratype**, CNU-DER-NN2021004C/P. All type material deposited in the College of Life Sciences, Capital Normal University, Beijing, China.

Locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China.

Description. Adult female, preserved in both dorsal and ventral aspects. Body with numerous setae and distinctively sculptured (densely punctate-granulose throughout, particularly on head and thorax). Total length as preserved (excluding antennae, ovipositor, and cerci) about 10.75 mm. Head medial length from clypeal apex to pos-

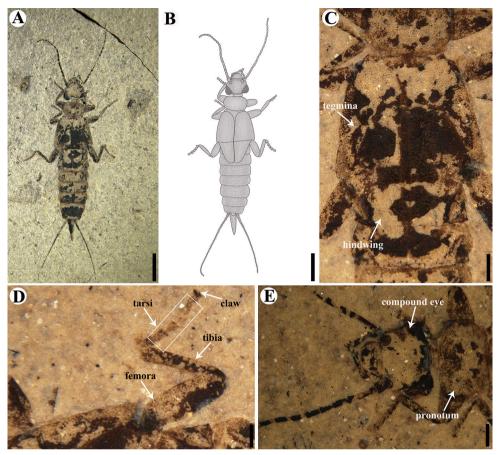


Figure 1. Holotype of *Aneuroderma oiodes* gen. et sp. nov. CNU-DER-NN2021003C. **A** Photograph of dorsal aspect **B** line drawing of dorsal aspect **C** dorsal view of tegmina and squamata of hind wings **D** anterior lateral (prolateral) view of right midleg **E** dorsal aspect of head. Scale bars: 2.0 mm (**A, B**); 0.5 mm (**C, D, E**). The tegmina and squamata of the hind wings in **C**, the right midleg in **D**, and the head in **C** are photographed under ethanol.

terior border 1.57 mm, maximum width (across level of compound eyes) 1.56 mm, prognathous; maxillary palpus pentamerous, ca 1.33 mm long (Fig. 1E). Antennal length 5.2 mm, with 20 elongate antennomeres; scape thick, broader than remaining antennomeres, longer than wide, length 0.31 mm, apical width 0.22 mm; pedicel shortest, length 0.17 mm; flagellomeres longer than wide and distally becoming tapered. Compound eyes large and prominent, located near posterior margin of head, compound eye length 0.72 mm; distance between compound eyes distinctly longer than compound eye length (Fig. 1E). Ocelli absent. Pronotum approximately oval and almost as broad as posterior margin of head, medial length 1.12 mm, maximum width 1.71 mm; anterior margin 1.56 mm wide, posterior margin 1.53 mm wide, anterior margin nearly straight, posterior margin slightly convex and lateral margins convex-

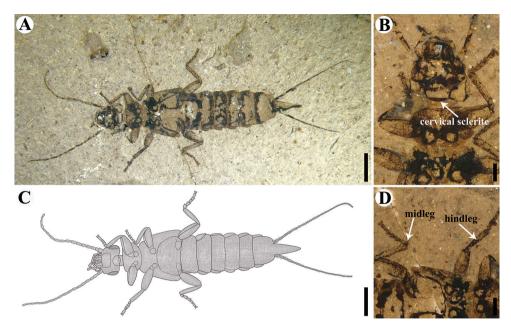


Figure 2. Holotype of *Aneuroderma oiodes* gen. et sp. nov. CNU-DER-NN2021003P. **A** Photograph of ventral aspect **B** ventral view of head **C** line drawing of ventral aspect **D** ventral view of midleg and hindleg. Scale bars: 2.0 mm (**A, C**); 0.5 mm (**B, D**). The head in **C** and the right midleg and hindleg in **D** are photographed under ethanol.

ly rounded. Tegmina well developed, without venation, length 2.41 mm, maximum width 1.39 mm, lateral margins arc-shaped, posterior margins truncate, squamata extending well beyond tegminal apex, tegmina and squamata covering abdominal terga I and II (Fig. 1C). Femora compressed and ventrally carinulate; tibiae elongate, slender, almost as long as femora; all tarsi pentamerous (Fig. 2D). Pretarsal claws present and simple; arolium absent (Fig. 1D). Abdomen cylindrical, with dense, soft, short setae, lateral margins relatively convex, almost all segments wider than long with apical margins straight, abdominal length as preserved (excluding cerci) 5.38 mm, maximum width 2.41 mm. Abdomen distally with external ovipositor, length 1.64 mm. Pygidium small. Cerci 5.33 mm long, longer than one-half abdominal length, with ca 30 elongate cercomeres, margins with abundant short setae.

Etymology. The specific epithet is the Greek neuter adjective $\delta i\delta des$ ($\phi \tilde{\omega} \delta \epsilon \varsigma$, meaning, "oval" or "egg-like"), as a reference to the ovoid pronotum.

Remarks. The new genus is placed within Protodiplatyidae on the basis of the characteristic filiform antenna with 17–23 antennomeres; pedicel and flagellomere I subequal in size; pentamerous metatarsus; cerci elongate, slender, and multimerous; and externalized ovipositor in females.

Key diagnostic characters of *Aneuroderma* gen. nov. are summarized in Table 2 and compared with those of nine genera of Protodiplatyidae. *Aneuroderma* gen. nov. can be distinguished from *Archidermapteron* Vishniakova, 1980 by the posterior margin of head as wide as anterior border of pronotum, 20 antennomeres, tegmina without lon-

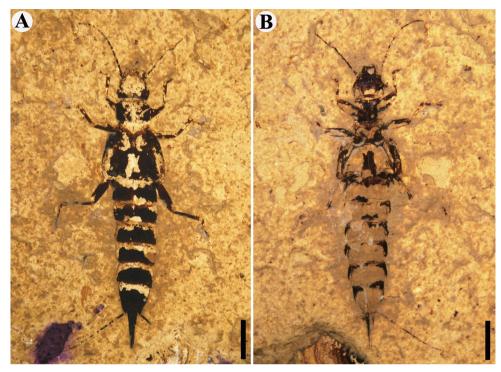


Figure 3. Paratype of *Aneuroderma oiodes* gen. et sp. nov. CNU-DER-NN2021004C/P. **A** Photograph of dorsal aspect **B** photograph of ventral aspect. Scale bars, 2.0 mm (**A, B**). The body in **A** and **B** are photographed under ethanol.

gitudinal veins, and hind wings extending to apex of abdominal segment II, pygidium small, 30 cercomeres, and a cercus/body ratio of 0.5. By contrast, Archidermapteron has the head narrower than the pronotum, the tegmina with longitudinal veins, hind wings extending beyond abdominal segment IV, pygidium transverse and trapeziform, and 40 cercomeres that together are slightly shorter than the body. Aneuroderma gen. nov. differs from Longicerciata Zhang, 1994 by the latter with the head broader than the pronotum, 26 antennomeres, at least 36 cercomeres, and a cercus/body ratio of 1. Aneuroderma gen. nov. differs from Barbderma Xing et al., 2016a in the number of antennomeres (20 instead of 19), and the hind wings extending to the apex of abdominal segment II, instead of segment I. Aneuroderma gen. nov. is similar to Asiodiplatys Vishniakova, 1980 in that the tegmina lack longitudinal veins and the hind wings extend to the apex of abdominal segment II, but the former differs from the latter in only 20 antennomeres (vs. 22 antennomeres), the posterior margin of the pronotum straight (vs. pronotum with shallow, broad notch anteriorly), and 30 cercomeres (vs. 40 cercomeres). Aneuroderma gen. nov. can be separated from Abrderma Xing et al., 2016b, Microdiplatys Vishniakova, 1980, Perissoderma Xing et al., 2016b, and Protodiplatys Martynov, 1925, by the following traits: (1) absence of longitudinal veins in tegmina (present in the aforementioned genera), and (2) 20 antennomeres (vs. 17 to 19 in the other genera). The new genus is readily differentiated from Sinoprotodiplatys Nel et al.,

Table 2. Summary and comparisons of key characters for several described genera of Protodiplatyidae.								
Interrogative marks (?) indicate data unavailable.								
Genus	Head	Number of	Pronotum	Teomina	Pvoidium	Cerci (ratio		

Genus	Head	Number of antennomeres	Pronotum	Tegmina	Pygidium	Cerci (ratio lengths cercus/ body, cercomeres)
Abrderma	Broader than	17–19	Elliptical, anterior	With venation,	Small	0.2, ?
	pronotum		and posterior margins	reaching second		
			subequal in width	abdominal segment		
Archidermapteron	Narrower	17–19	Reniform, broad	With venation,	Transverse,	1.0, at least 40
	than		notch anteriorly	reaching fourth	trapeziform	
	pronotum			abdominal segment		
Asiodiplatys	Narrower	22	With shallow, broad	Without venation,	?	0.5, 40
	than		notch anteriorly	not reaching second		
	pronotum			abdominal segment		
Barbderma	?	19	Oblong or	With venation,	Small	0.42, ?
			trapezoidal, anterior	reaching first		
			and posterior margins	abdominal segment		
			subequal in width			
Longicerciata	Broader than	26	Transverse, anterior	Without venation,	?	1.0, at least 36
	pronotum		margin wider than	reaching fourth		
			posterior margin	abdominal segment		
Microdiplatys	Broader than	19	Transverse	With venation,	Not	1.0, at least 36
	pronotum			reaching fourth	protruding	
				abdominal segment		
Perissoderma	Narrower	17	Elliptical, anterior	With venation,	Small	0.5, ?
	than		margin wider than	reaching third		
	pronotum		posterior margin	abdominal segment		
Protodiplatys	Narrower	17–18	Transverse, notch	With venation,	Transverse,	0.5, no more
	than		in front, broadly	reaching fourth	trapeziform	than 40
	pronotum		rounded posteriorly	abdominal segment		
Sinoprotodiplatys	Narrower	18	Anterior and	Without venation,	?	0.8, 20
	than		posterior margins	reaching fourth		
	pronotum		subequal in width	abdominal segment		
<i>Aneurod</i> erma	As wide as	20	Oval, anterior and	Without venation,	Small	0.5, 30
gen. nov.	pronotum		posterior margins	reaching second		
			subequal in width	abdominal segment		

2012 by the posterior margin of the head and anterior border of the pronotum equal in width (head narrower than pronotum in the latter), 20 antennomeres, and 30 cercomeres (18 antennomeres and 20 cercomeres in the latter). Lastly, the distinctive punctate sculpture of the new genus is quite distinctive among several Archidermaptera.

Family Dermapteridae Vishniakova, 1980

Genus Sinopalaeodermata Zhang, 2002

Sinopalaeodermata Zhang, 2002: 351. Type species: Sinopalaeodermata neimonggolensis Zhang, 2002, nomen imperfectum [recte neimonggolense], by original designation.

Emended diagnosis [modified from Zhang (2002)]. Moderate-sized earwigs, with short and fine pubescence; head triangular, length subequal to width, mandibles denticulate; antenna filiform, with at least 19 antennomeres (as noted by Zhang

(2002)), scape stout and enlarged, pedicel rather small, clearly shorter than scape and flagellomere I; ocelli present; neck prominent, divided into anterior and posterior cervical sclerites ('blattoid' neck arrangement). Pronotum transverse, broader than long and about as broad as head. Femora compressed and ventrally carinulate; all tarsi pentamerous, shorter than tibiae; pretarsal claws well developed and bearing broom-shaped arolia. Procoxal cavities positioned close to each other; mesocoxal cavities remote, metacoxal cavities elongate transversely and moderately separated. Tegmina with longitudinal veins strongly developed, main veins of Sc, R, M, and Cu present. Female with a pair of elongate valvulae entirely exposed. Cerci flexible, long, filiform, and multimerous.

Included species. Aside from the type species, the genus currently includes *S. concavum* Xiong, Engel & Ren, sp. nov. (*infra*).

Sinopalaeodermata concavum Xiong, Engel & Ren, sp. nov. http://zoobank.org/9759E27B-8954-48A1-B220-57514C01F07F Figures 4, 5

Diagnosis. The new species can be distinguished from the type species, *Sinopalaeodermata neimonggolense* (note that the name *Sinopalaeodermata* is neuter, not feminine, as *dérmata* is the neuter nominative plural of *dérma*; and given that the specific epithet is adjectival it must still agree in gender with the generic name) by the relatively straight apical margin of the penultimate sternum (in *S. neimonggolense* the penultimate sternum has a concave margin); the roughly reniform pronotum, with the anterior margin concave medially the posterior margin weakly convex, and lateral margins rounded (in *S. neimonggolense* the pronotum is approximately rectangular, with the anterior margin almost as wide as the posterior margin, and the lateral margins relatively straight and parallel to each other); the tegmina with a more pronounced concave arc marginally at the apex of Rs (in *S. neimonggolense* the margin is more sloping rather than deeply concave); and M does not extend to near the apex of CuA, with CuP terminating more proximal to CuA (even before the tangent with M) (in *S. neimonggolense* M terminates more proximally and CuP extends to the apex of CuA).

Holotype. A completely preserved female, CNU-DER-NN2021005C/P, deposited in the College of Life Sciences, Capital Normal University, Beijing, China.

Locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China.

Description. Adult female, preserved in both dorsal and ventral aspects. Total length as preserved (excluding antennae, cerci, and valvulae) about 18.02 mm. Body with sparse pubescence and punctate. Head medial length from clypeal apex to posterior border 2.08 mm, maximum width (across level of compound eyes) 2.27 mm, triangular. Compound eye large, ovate, located near posterior margin of head; compound eye length 0.91 mm; width between compound eyes 2.58 mm. Ocelli comparatively small. Cervix with large anterior and posterior cervical sclerites, anterior sclerite slightly larger than posterior sclerite. Pronotum approximately reniform, medial length 1.46

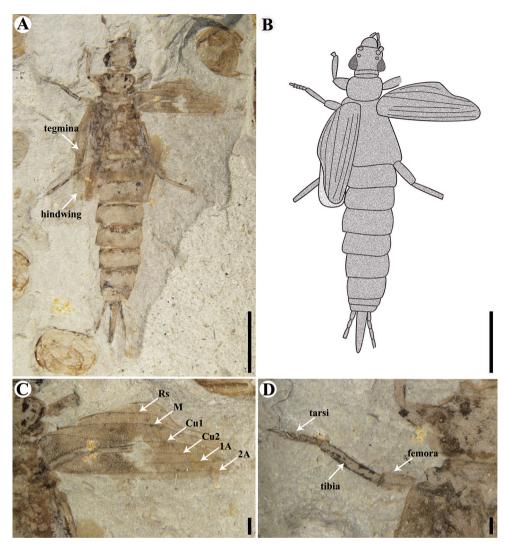


Figure 4. Holotype of *Sinopalaeodermata concavum* sp. nov. CNU-DER-NN2021005C. **A** Photograph of dorsal aspect **B** line drawing of dorsal aspect **C** dorsal view of right tegmen **D** anterior lateral (prolateral) view of left midleg. Scale bars: 4.0 mm (**A**, **B**); 0.5 mm (**C**, **D**).

mm, maximum width 2.58 mm, anterior width 1.64 mm, posterior width 2.07 mm, anterior margin concave and posterior margin arched, lateral margins convexly rounded. Mesoscutellum large, elliptical, entirely exposed. Tegmina present, not truncated, length 6.73 mm, maximum width 2.55 mm, with medially sinuate anterior (lateral) margin and straight posterior (mesal) margin. Veins simple, Rs curved anterior margin, fading out just before margin; M simple, basally and apically straight, gently curved medially; Cu with two branches (CuA and CuP), CuP terminates proximal to CuA; A1 and A2 simple and straight, running parallel to each other and posterior margin,

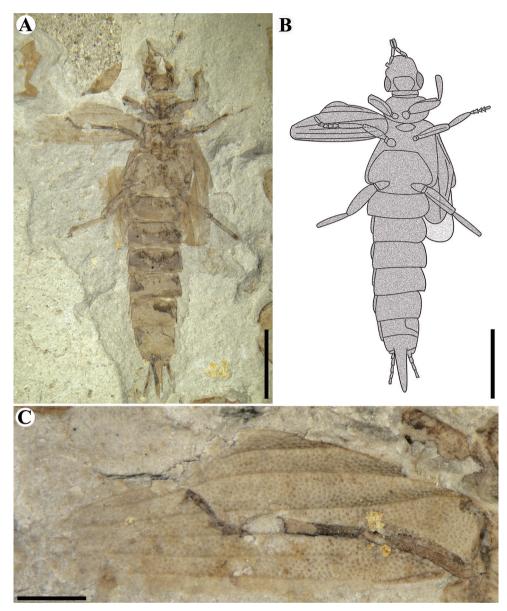


Figure 5. Holotype of *Sinopalaeodermata concavum* sp. nov. CNU-DER-NN2021005P. **A** Photograph of ventral aspect **B** line drawing of ventral aspect **C** ventral view of right midleg and tegmen. Scale bars: 4.0 mm (**A**, **B**); 1 mm (**C**).

terminating apically (Fig. 4C). Femora compressed and ventrally carinulate (Fig. 4D); tibiae elongate, slender, and almost as long as femora; tarsi pentamerous, tarsomere IV slightly extending under base of tarsomere V (Fig. 5C). Pretarsal claws present but not well preserved. Abdominal length as preserved (excluding cerci) 9.75 mm, maximum width 3.52 mm; all segments distinctly wider than long, lateral abdominal margins

gently convex. Pygidium not evident. Ovipositor exposed, 2.84 mm long. Cerci as preserved only 2.9 mm long, with segments but not clearly preserved.

Etymology. The specific epithet is taken from the Latin adjective *concavus* (meaning, "concave"), in reference to the more pronounced concave margin to the tegmina relative to the type species.

Discussion

Both of the new species described herein are easily recognized as archidermapterans owing to the pentamerous metatarsi (and more than three pro- and mesotarsomeres); elongate, flexible, and multimerous cerci; and the externalized ovipositor. Jurassic earwigs are known mostly from four assemblages: the Jiulongshan flora of the Middle Jurassic, the England flora of the Early and Late Jurassic, and the Karatau flora of the Late Jurassic (Vishniakova 1980; Zhang 1994, 2002; Zhao et al. 2011; Kelly et al. 2018; Tihelka 2019). Archidermaptera were seemingly the most abundant form of earwigs during these epochs, with 28 species in 21 genera (Table 1), compared to only seven species in five genera of Eodermaptera. Numerous fossil insects and plants have been described from the Jiulongshan Formation (e.g., Ren et al. 2010; Gao et al. 2021), yet earwigs are comparatively rare, with only eight species reported from the locality.

Tarsal formulae have been used to distinguished significant groups of fossil Dermaptera. All Neodmerpatera and Eodermaptera have three tarsomeres (3-3-3), while the number of tarsomeres is greater, where known, among Archidermaptera (Table 1) (Engel 2003). Unfortunately, tarsi are unknown for many fossil genera, particularly among the Dermapteridae, and so general patterns are difficult to determine. Nonetheless, historically the Dermapteridae have been considered to have a 5-5-5 forumula, while Protodiplatyidae include genera with 5-5-5 and 4-4-5 formulae (Engel 2003; Zhao et al. 2011). What remains to be ascertained from a detailed phylogenetic study is whether the variable tarsal formulae among Protodiplatyidae is reflective of paraphyly on the part of this family, or whether it renders Dermapteridae paraphyletic. Unfortunately, currently available specimens and data do not allow for a robust resolution of this difficulty, thus emphasizing the need for further exploration of Jurassic and Late Triassic deposits throughout the world in the hope of recovering more completely preserved material of these lineages and allowing a comprehensive comparison among living and fossil Dermaptera.

Conclusion

Based on three well-preserved fossil specimens from the Middle Jurassic, we describe a new genus and two new species, *Aneuroderma oiodes* gen. et sp. nov. (Protodiplatyidae) and *Sinopalaeodermata concavum* sp. nov. (Dermapteridae). We make extensive comparisons with other Archidermaptera and discuss challenges in understanding relationships among these Triassic and Jurassic lineages.

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References

- Bey-Bienko GYa (1936) Insectes dermaptères, Faune de l'URSS. Akadem iya Nauk SSSR, Zoologicheskij Institute, Moscow, 239 pp.
- Carpenter FM (1992) Treatise on Invertebrate Paleontology, Part R Arthropoda 4, Vol. 3: Superclass Hexapoda. The Geological Society of America, Inc. & The University of Kansas, Kansas. 655 pp.
- Chen W, Ji Q, Liu DY, Zhang Y, Song B, Liu XY (2004) Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. Geological Bulletin of China 23(12): 1165–1169.
- Cockerell TDA (1915) British fossil insects. Proceedings of the United States National Museum 49: 469–499. https://doi.org/10.5479/si.00963801.49-2119.469
- Engel MS (2003) The earwigs of Kansas, with a key to genera north of Mexico (Insecta: Dermaptera). Transactions of the Kansas Academy of Science 106: 115–123. https://doi.org/10.1660/0022-8443(2003)106[0115:TEOKWA]2.0.CO;2
- Engel MS (2009) Gregarious behaviour in Cretaceous earwig nymphs (Insecta, Dermaptera) from southwestern France. Geodiversitas 31: 129–135. https://doi.org/10.5252/g2009n1a11
- Engel MS (2019) A new species of spongiphorine earwig in Miocene amber from the Dominican Republic (Dermaptera: Spongiphoridae). Novitates Paleoentomologicae 2(6): 560–565. https://doi.org/10.11646/palaeoentomology.2.6.3
- Engel MS (2021) A new genus of Early Jurassic earwigs from England (Dermaptera). Novitates Paleoentomologicae 22: 1–3. https://doi.org/10.17161/np.22.15759
- $Engel MS, Haas F (2007) Family-group names for earwigs (Dermaptera). American Museum Novitates 3567: 1-20. \ https://doi.org/10.1206/0003-0082(2007)539 [1:FNFED] 2.0. CO; 2007 [1:FNFED] 2.0. CO; 2$
- Gao TP, Shih CK, Ren D (2021) Behaviors and interactions of insects in mid-Mesozoic ecosystems of northeastern China. Annual Review of Entomology 66: 337–354. https://doi.org/10.1146/annurev-ento-072720-095043
- Geer CDE (1773) Mémoires pour servir à l'histoire des insectes (tome troisième). Hesselberg, Stockholm, 696 pp.
- Giebel GC (1856) Die Insecten und Spinnen der Vorwelt mit steter Berücksichtigung der lebenden Insekten und Spinnen. Die Fauna der Vorwelt 2: 1–511.
- Giles ET (1963) The comparative external morphology and affinities of the Dermaptera. Transactions of the Royal Entomological Society of London 115: 95–164. https://doi.org/10.1111/j.1365-2311.1963.tb00816.x

- Grimaldi D, Engel MS (2005) Evolution of the Insects. Cambridge University Press, New York, 755 pp.
- Günther K, Herter K (1974) Dermaptera (Ohrwürmer). Handbuch der Zoologie: Eine Naturgeschichte der Stämme des Tierreiches. IV Band: Arthropoda 2 Hälfte: Insecta, Zweite Auflage, 2 Teil: Spezielles 11: 1–158.
- Haas F (1995) The phylogeny of the Forficulina, a suborder of the Dermaptera. Systematic Entomology 20(2): 85–98. https://doi.org/10.1111/j.1365-3113.1995.tb00085.x
- Haas F, Kukalová-Peck J (2001) Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). European Journal of Entomology 98: 445–509. https://doi.org/10.14411/eje.2001.065
- Jarzembowski EA (1999) Arthropods–2: Insects. In Swift A, Martill DM. (eds) Fossil of the Rhaetian Penarth Group. Palaeontological Association Field Guides to Fossils 9: 149–60. London: The Palaeontological Association, 312 pp.
- Kelly RS, Ross AJ, Jarzembowski EA (2018) Earwigs (Dermaptera) from the Mesozoic of England and Australia, described from isolated tegmina, including the first species to be named from the Triassic. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 107: 129–143. https://doi.org/10.1017/S1755691017000329
- Martynov AV (1925) To the knowledge of fossil insects from Jurassic beds in Turkestan. 2. Raphidioptera (continued), Orthoptera (s.l.), Odonata, Neuroptera. Bulletin de l'Academie des sciences de Russie. VI serie 19: 569–598.
- Nel A, Garrouste C, Waller A, (2012) Evolution and palaeosynecology of the Mesozoic earwigs (Insecta: Dermaptera). Cretaceous Research 33(1): 189–195. https://doi.org/10.1016/j.cretres.2011.10.002
- Ren D, Shih CK, Gao TP, Yao YZ, Zhao YY (2010) Silent Stories Insect Fossil Treasures from Dinosaur Era of the Northeastern China. Science Press, Beijing, 322 pp.
- Sakai S (1996) Notes on the contemporary classification of Dermaptera and recent references on Dermaptera. In: Sakai S (Ed.) Taxonomy of the Dermaptera: Proceedings of 20th International Congress of Entomology. Firenze, Italy, 25–31 August 1996, 1–10.
- Shcherbakov DE (2008) Madygen, Triassic Lagerstätte number one, before and after Sharov. Alavesia 2: 113–124.
- Tihelka E (2019) New Mesozoic earwigs from England, with a catalogue of fossil Dermaptera. Proceedings of the Geologists' Association 130(5): 609–611. https://doi.org/10.1016/j.pgeola.2019.06.003
- Vishniakova VN (1980) Earwig (Insecta: Forficulida) from the Upper Jurassic of the Karatau range. Paleontological Journal 14: 63–79.
- Vishniakova VN (1985) Novaya ukhovertka iz Yury Sibiri. Yurskie Nasekomye Sibiri i Mongolii 146–147.
- Vishniakova VN (1986) Earwigs. Forficulida (=Dermaptera), in Nasekomye v rannemelovykh ekosistemakh zapadnoy Mongolii. The Joint Soviet-Mongolian Palaeontological Expedition 28:171.
- Wappler T, Engel MS, Haas F (2005) The earwigs (Dermaptera: Forficulidae) from the middle Eocene Eckfeld Maar, Germany. Polskie Pismo Entomologiczne 74: 227–250.

- Whalley PES (1985) The Systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. Bulletin of the British Museum (Natural History), Geology Series 39(3): 107–189.
- Xing CY, Shih CK, Zhao YY, Ren D (2016a) New protodiplatyids (Insecta: Dermaptera) from the Lower Cretaceous Yixian Formation of northeastern China. Cretaceous Research 64: 59–66. https://doi.org/10.1016/j.cretres.2016.03.016
- Xing CY, Shih CK, Zhao YY, Ren D (2016b) New earwigs in Protodiplatyidae (Insecta: Dermaptera) from the Middle Jurassic Jiulongshan Formation of northeastern China. Zootaxa 4205(2): 180–188. https://doi.org/10.11646/zootaxa.4205.2.7
- Yang HR, Shi CF, Engel MS, Zhao ZP, Ren D, Gao TP (2021) Early specializations for mimicry and defense in a Jurassic stick insect. National Science Review 8: nwaa056. https://doi.org/10.1093/nsr/nwaa056
- Zhang JF (1994) Discovery of primitive fossil earwigs (Insecta) from Late Jurassic of Laiyang, Shangdong and its significance. Acta Palaeontologica Sinica 33(2): 229–245.
- Zhang JF (2002) The most primitive earwigs (Archidermaptera, Dermaptera insect) from the Upper Jurassic of Nei Monggol Autonomous Region, northeastern China. Acta Micropalaeontologica Sinica 17: 459–464.
- Zhao JX, Shih CK, Ren D, Zhao YY (2011) New primitive fossil earwig from Daohugou, Inner Mongolia, China (Insecta: Dermaptera: Archidermaptera). Acta Geologica Sinica (English Edition) 85(1): 75–80. https://doi.org/10.1111/j.1755-6724.2011.00380.x