

Boring beetles are not necessarily dull: New notocupedins (Insecta: Coleoptera) from the Mesozoic of Eurasia and East Gondwana



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ABSTRACT

Beetles belonging to the extinct tribe Notocupedini (Coleoptera: Cupedidae: Ommatinae) are widespread in Mesozoic deposits of eastern Pangaea. Four new species are proposed in the genus/collective group *Zygadenia*: *Z. liui* sp. nov. (Aptian: Yixian Formation, China), *Z. martiniae* sp. nov. (Sinemurian–Toarcian: Cattamarra Coal Measures, Australia), *Z. floodpagei* sp. nov. and *Z. simpsoni* sp. nov. (Hauterivian–Barremian: Weald Clay Group, UK). The Purbeck species *Z. tuberculata* and *Z. angliae* are figured from the Weald Clay Group for the first time. It is also proposed that *Notocupes*, the largest genus in this presumably xylophagous, warm climate tribe, be divided into two subgenera: *Notocupes* subgen. n. and *Amblomma* stat. nov. In addition, the palaeoecological significance of colour markings in these Mesozoic beetles is also discussed for the first time. These discoveries extend the geographic distribution/stratigraphic range of *Zygadenia* and shed new light on the palaeoecology and diversity of so-called 'primitive' beetles in pre-angiospermous woodlands.

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1. Introduction

With some 350,000 described species, beetles (Coleoptera L., 1758) are easily the largest order of insects: the Cupedina Laporte, 1836, however, is the smallest and most basal suborder totaling only about 100 living species and often split into two smaller suborders, the archostematans and myxophagans (Beutel et al., 2007; Hörschemeyer, 2011). Several hundred nominal species of fossil Cupedina have been described from the Permian onwards (e.g., Ponomarenko, 1969, 2002; Kirejtshuk et al., 2010; Tan et al., 2012; Jarzembowski et al., 2013a,b; Yan et al., in press). This paper is concerned with early Jurassic and Cretaceous archostematans belonging to the extinct tribe Notocupedini Ponomarenko, 1966, commonly placed in the extant subfamily Ommatinae Sharp and Muir, 1912 (Ponomarenko, 1969). Opinion is divided as to whether the latter are a subfamily of the extant family Cupedidae (Ponomarenko, 2002), or a separate family with the tetraphalerins (Beutel and Friedrich, 2008). For consistency with Jarzembowski

et al. (2013a,b), we have maintained the former, especially as some cupedine-like features are emerging (Section 5). The notocupedins are the typical reticulated beetles of the Mesozoic with over 60 named species in at least four genera (Kirejtshuk and Ponomarenko, 2013). A recent phylogenetic analysis suggests that they are a monophyletic group if limited to including only *Rhabdocupes* Ponomarenko, 1966, *Notocupes* Ponomarenko, 1964, *Zygadenia* Handlirsch, 1906, and *Amblomma* Tan, Ren and Liu, 2005 (Tan et al., 2012). Kirejtshuk et al. (2010) considered *Amblomma* to be a synonym of *Notocupes* whilst resurrecting *Zygadenia* from synonymy with the latter. If the Triassic *Rhabdocupes* is excluded, that still leaves over 44 Mesozoic species of *Notocupes* sensu lato and *Zygadenia* is considered herein. The taxonomic differences between the notocupedin genera are subtle: proportions of basal antennal segments plus shape of pronotum and structure of underside of head (*Rhabdocupes*); former plus relative length of middle leg in *Amblomma* and *Notocupes* (Kirejtshuk et al., 2010; Tan et al., 2012). To restore taxonomic stability, we propose that *Amblomma* is treated as a subgenus of *Notocupes* and *Zygadenia* becomes a collective group (Section 4). In this paper we also erect four new species of *Zygadenia*, one each in E. Gondwana (Western Australia) and S. E. Asia (N. E. China), and two in W. Eurasia (S. E. England), as well as figure two more from the latter. These discoveries not only extend the palaeogeographic and stratigraphic

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range of this notocupedin, but also shed new light on the palaeoecology and diversity of these 'primitive' beetles of early coniferous woodlands (Wang et al., 2013).

2. Geological setting

The Chinese material is from the lower Aptian of northeastern China from a valley near Xisanjia Village, Shifo Township, Ningcheng County, Chifeng City, Inner Mongolia (41° 19' 57" N., 119° 07' 40" E.; Figs. S4–6). It is from the lacustrine Yixian Formation (Jehol Biota) deposited in a shallow volcanic lake/s (Zhang and Sha, 2012). The fossils are preserved as impressions in a fine-grained, laminated, hard tuffaceous siltstone with distinctive small spherules, evidently pyrite pseudomorphs (Wang et al., 2012; Hethke et al., 2013); the matrix is off-white/grey, speckled yellow/brown. The impressions show some original relief so that elytra are convex on the part and concave on the counterpart. They show some deformation like other Yixian ommatines (Jarzembowski et al., 2013a).

The Australian material is from the Sinemurian–Toarcian of Western Australia from a gully outcrop in the Minaja Hills, Perth Basin (coordinates withheld for site security; Figs. S1–3). It is from the Cattamarra Coal Measures and considered to have been deposited in a well-oxygenated, shallow pool in an upper delta plain environment (Martin, 2010b). The fossils are preserved as impressions in a fine brown siltstone and show original relief as well as some sedimentary fracturing (Martin, 2008).

The Wealden specimens are from the Weald Clay Group (Hauterivian–Barremian) in the county of Surrey in southern England (Jarzembowski, 1991; Batten and Austen, 2011; Figs. S7–9). They are preserved in sideritic ironstone concretions (lower Barremian at Smokejacks; National Grid Reference TQ 115372), phosphatic concretions (upper Barremian at Beare Green; TQ 185423), or siltstone scour fills (upper Hauterivian at Clockhouse; TQ 175385). The English material is relatively undeformed and unoxidised; it originated, however, in a more energetic palaeoenvironment with associated disarticulation and transportation under a fluvial rather than lacustrine regime as in China (Jarzembowski, 1995; Chang, 2003). The material described from Xisanjia, however, is unusual in that it is also disarticulated, a mode of preservation rarely reported in contrast to the exceptionally preserved insects in these deposits (Wang et al., 2008; C. Cai, pers. comm.: May, 2012). It is consistent, however, with periodic influxes of fluvial siliciclastics into the palaeolake (as after rainfall; Hethke et al., 2013). The elytra and occasional body parts of Cupedina form a small but distinctive element of the English insect assemblages (less than 5%, personal tally, EAJ), whereas in China, Cupedina can form 15% of the entomofauna (Zhang et al., 2010), where perhaps the climate was slightly cooler. They are just under 5% of the Australian assemblage (Martin, 2010a).

3. Material and method

The Chinese study material is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, specimen numbers prefixed NIGP ex Haichun Zhang collection (HZ). The Australian material is in the Western Australian Museum, Perth, specimen nos prefixed WAM (ex Arthur Mory and Sarah Martin collections (AM/SM)). The English material is in the Natural History Museum, London (NHM), specimen nos prefixed II (ex Ed and Bidy Jarzembowski or Andrew Ross collections (EBJ and AR respectively)); original field numbers are given in parentheses for continuity.

Specimens were examined dry and wetted with ethanol under a Nikon SMZ1000 binocular microscope with fibreoptics and uncoated in a LEO1530VP SEM. Photographs other than archive (EAJ; Wealden) were taken with a Dxm1200 digital camera connected to the same binocular microscope; all material figured herein is

photographed dry. Preparation was undertaken with Paleo-Tools Micro-Jack3 and Burgess Engraver vibrotool. Drawings were prepared from photographs and specimens by hand (EAJ) and drawing conventions are solid line, distinct margin; dashed line, indistinct; dotted line, extrapolation; dashed-and-dotted, fold.

Standard beetle terminology is used with other terminology (as in cited literature) given in parenthesis; venation follows Jarzembowski et al. (2013b) and abbreviations are A2/3, second and third anal veins; C, costa; Cu, cubitus; M, median; R, radius; Sc, subcosta.

4. Systematic palaeontology

Class: INSECTA Linnaeus, 1758
 Order: COLEOPTERA Linnaeus, 1758
 Suborder: CUPEDINA Laporte, 1836
 Family: CUPEDIDAE Laporte, 1836
 Subfamily: OMMATINAE Sharp and Muir, 1912
 Tribe: NOTOCUPEDINI Ponomarenko, 1966
 Genus *Zygadenia* Handlirsch, 1906

Type species. *Curculionites tuberculatus* Giebel, 1856 (by monotypy), Purbeck Limestone Group, Berriasian; Durlston Bay, Dorset, UK.

Diagnosis. Elytron comparatively broad, convex; four main veins present usually well differentiated from intercalaries (intermediate veins); A2 (second) and Cu (third vein) fused before elytral apex, A2 + Cu (common vein) ending on sutural margin; two longitudinal rows of window cells present between main veins, 20–30 cells per row; epipleural rim moderately wide with or without a row of cells; elytral apex may have a tail-like process (sensu Ponomarenko, 2006).

Remarks. Plesiomorphies: venation/reticulation distinct (indistinct in *Cionocoleus* Ren (Ommatini); Jarzembowski et al., 2013a); epipleural rim with no more than single row of cells and moderately wide (widened in *Brochocoleus* Hong (Brochocoleini); Jarzembowski et al., 2013b); A2 and Cu fused before apex (R and M also fused and joined in *Brochocoleus*: loc. cit.). Apomorphy: reticulation accentuated and window cells enlarged (absent in Lithocupedini and *Rhabdocupes* Ponomarenko; Tan et al., 2012) but pentagonal cells absent along sutural margin (present in 'Pronotocupedini': loc. cit., but name needs correcting; Dubois et al., 2013).

Occasionally mis-spelt *Zigadenia*, this genus was synonymised with *Notocupes* by Ponomarenko (2000), but resurrected by Kirejtshuk et al. (2010) as a 'form' (morpho-) genus for species based on disarticulated remains (elytra). This is because not all species of *Zygadenia* could be reassigned to natural notocupedine genera defined on body characters (Section 1), although they provide valuable additional palaeodiversity data (both stratigraphic and geographic). Unfortunately, form genera are not recognised by ICZN (1999) but we comply with the code by treating *Zygadenia* as a collective group as adopted elsewhere in fossil Coleoptera (Jarzembowski, 2003). This will help to maintain taxonomic stability (by not having a type species that can enter into generic synonymy) as will recognising *Amblomma* stat. nov. as a subgenus of *Notocupes*, other species being simply referable to the subgenus *Notocupes* nov. sensu Ponomarenko (1964). This also reduces the risk of paraphyly in this tribe (see Tan et al., 2012, who also noted comparatively large and well differentiated elytral cells as present in both *Amblomma* and *Notocupes*).

The elytra of Triassic *Rhabdocupes* are readily distinguished from *Zygadenia* by their finer cells and pronounced elongation (4.5–4.75 times as long as broad; Ponomarenko, 1966, 1969).

Included species. One species from the Lower Cretaceous of N. E. China: *Z. liui* sp. nov., (Yixian Formation, Aptian). Four species from

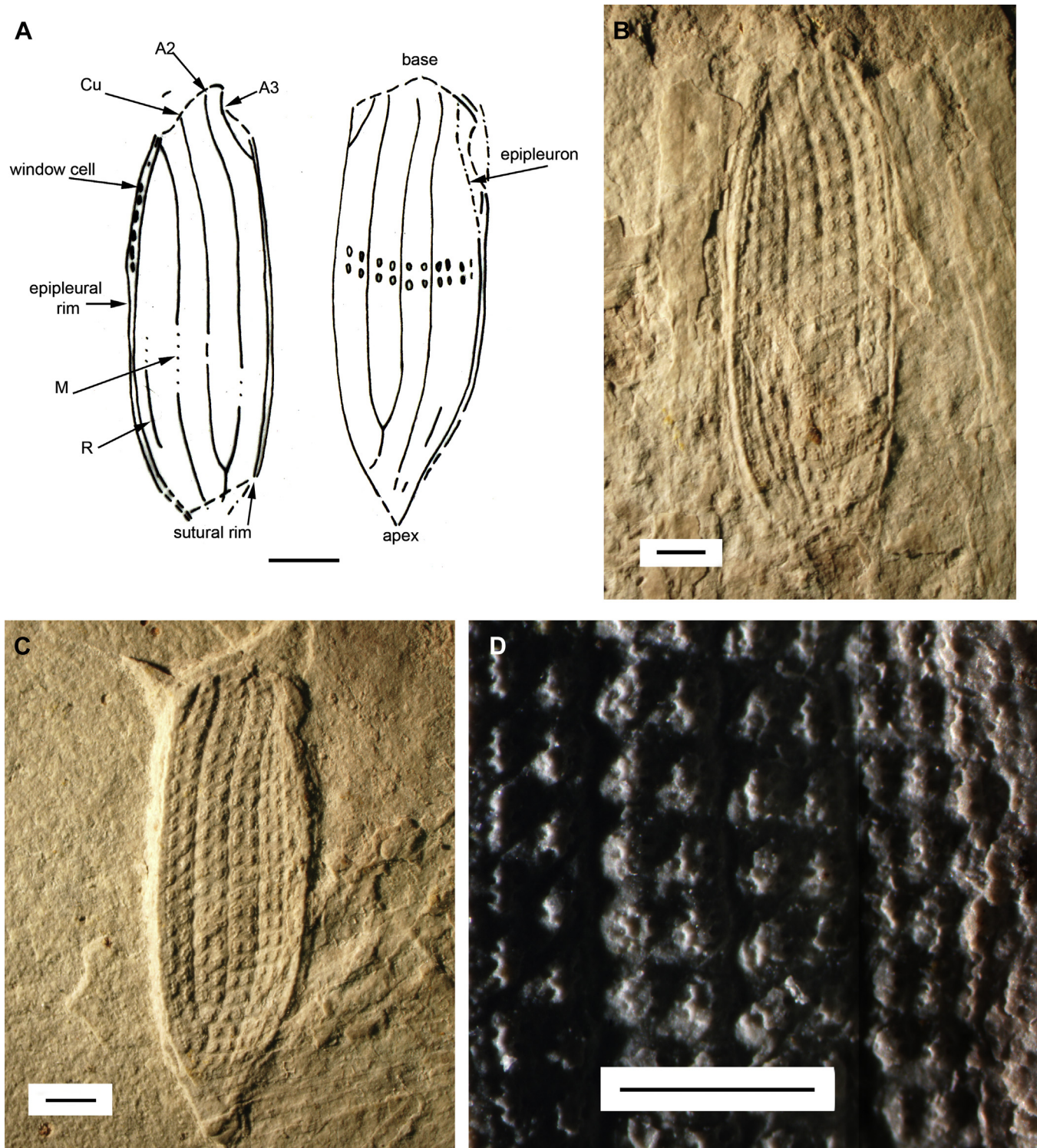


Fig. 1. *Zygadenia liui* sp. n., types; Xisanjia, lower Aptian. A, habitus drawings (paratype, left; holotype, right, with representative cells); photographs B, paratype $\times 10$, C, holotype $\times 10$, D, external moulds of window cells on holotype $\times 40$. Scale bar = 1 mm.

the Lower Cretaceous of southern England: *Z. tuberculata* (Giebel, 1856), *Z. angliae* (Giebel, 1856) (Purbeck Limestone Group, Berriasian, and Weald Clay Group, Hauterivian–Barremian), *Z. floodpagei* sp. nov., *Z. simpsoni* sp. nov. (Weald Clay Group, Hauterivian–Barremian). Two species from the Lower Jurassic of Australia: *Z. westraliensis* (Riek, 1968), *Z. martinae* sp. nov. (Cattamarra Coal Measures, Sinemurian–Toarcian).

Excluded species. Three '*Zygadenia*' species described from the Lower Cretaceous (Neocomian) of Semyon (Semen), Russia (Ponomarenko, 2000) and five from the Lower Cretaceous (Barremian) of Montsech, Spain (Soriano and Delclòs, 2006) which all now belong to *Notocupes* (*Notocupes*); '*Zygadenia*' *reticulata* (Oppenheim, 1888) is reinstated in *Notocupes* (following Ponomarenko, 1971).

Occurrence. Lower Middle Triassic (Anisian)–lower Palaeocene (Danian) of Laurasia and Gondwana (including unnamed records).

Zygadenia liui sp. n.

Fig. 1A–D

Derivation of name. After Qing Liu, palaeontologist; masculine.

Holotype. Left elytron: NIGP 154979 [LBSH05261] concave counterpart only. Xisanjia, Yixian Formation, lower Aptian; collected by HZ.

Paratype. Right elytron: number, horizon, locality and collector as for holotype.

Diagnosis. Elytron moderately large (c. 10 mm long), elongate (three times longer than broad), apex pointed with slight tail-like process; veins well differentiated from intercalaries except R; some 22 window cells in longitudinal rows on disc, and epipleural rim with one row of cells anteriorly.

Description. Elytron 9.8 mm long, 3.3 mm wide, elongate, tuberculate; apex acutely pointed with slight ‘tail’; outer (anterior) margin curved, nearly straight in middle, incurved basally and towards tail; disc transversely convex with well-developed longitudinal, ridged striae and five double rows of slightly offset cells, c. 22 per row; cells elongated with up to 6/7 lateral tubercles, less prominent on outer part of disc; main veins more pronounced than intercalaries: vein A3 short, running obliquely to narrow sutural rim; A2 and Cu joined evenly apically, M flexed but simple, R mainly indistinct; epipleural rim narrow, broadening slightly basally with row of cells; epipleuron long, running obliquely to edge of disc.

Remarks. Both elytra are somewhat compressed with incomplete bases and apices. The same sedimentary parting also contains a possible *Atrematopodites* elytron and orthopteran wing fragment, the different elytra being the same side up. The material was probably washed into the palaeolake but the holotype and paratype could be the left and right elytra of the same individual suggesting limited transport. The epipleuron (elytral outer rim) is indicated by

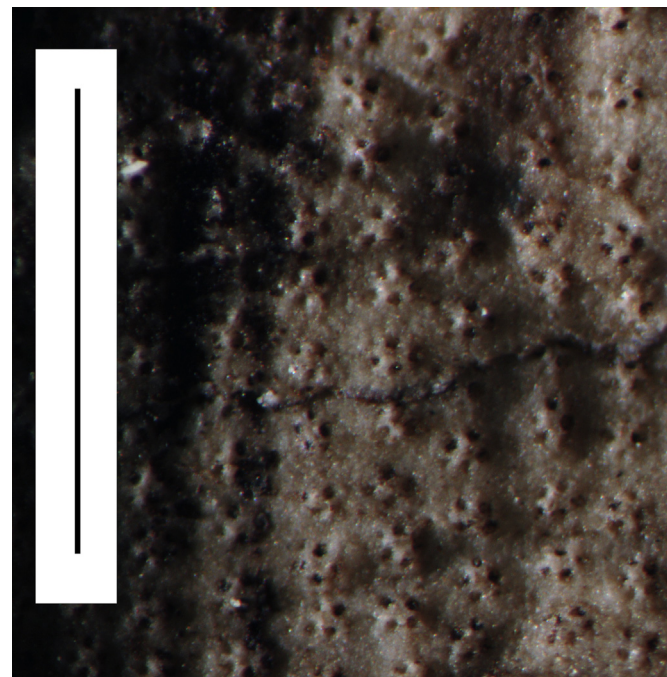


Fig. 2. Archostematan elytron, NIGP154980 [NND08169], Daohugou lagerstätte, Middle Jurassic, showing external moulds of window cells with maculae preserved $\times 80$. Scale bar = 1 mm.

a ridge corresponding to a downfold on the holotype. Being external moulds, the elytral cells are in relief with indented margins (Fig. 1D) corresponding to the position of former maculae sensu Tan and Ren (2009). These are actually the lateral tubercles seen in the elytral window cells of extant cupedids (Lawrence et al., 2011, fig. 43E) and the dark tips may be preserved in compression fossils (Fig. 2).

Z. liui is elongate (three times longer than broad) with epipleural cells like *Z. tuberculata* but is smaller with more discal cells in the longitudinal rows and has a tail-like process unlike the latter (Ponomarenko, 2006). It is more similar in size and number of cells to *Notocupes (Amblomma) rudis* Tan, Ren and Liu, 2005 from the Yixian Formation of Chaomidian, Liaoning (elytron 9.5 mm long, 23 cells in a row), but the latter has simpler cells and a broader, rounded elytral apex. The early Cretaceous *Notocupes (Notocupes) ludongensis* Wang and Liu, 1996 from the Laiyang Formation of Huangyadi, Shandong, N. E. China (elytron 10.3 mm long) also has an indistinct R, but 26 cells



Fig. 3. *Zygadenia tuberculata* (Giebel, 1856), II 3063a, right elytron, part; Smokejacks, lower Barremian. Scale bar = 1 mm.

and a more rounded apex. The *Xisanjia* species is therefore placed in *Zygadenia* pending the discovery of embodied material.

Zygadenia martinae sp. nov.

Derivation of name. After Dr Sarah Martin, palaeoentomologist; feminine.

Holotype. Right elytron: WAM 08.173 part. Mintaja, Cattamarra Coal Measures, Sinemurian–Toarcian; collected by AM/SM.

Paratype. Left elytron: WAM 08.47 part. Locality, horizon and collector as for holotype.

Diagnosis. Elytron very small (c. 3 mm long), a little short (2.8 times longer than broad), apex pointed with slight tail-like process; veins well differentiated from intercalaries; window cells small with 20 in longitudinal row on disc, and epipleural rim with one row of a few large cells.

Remarks. Martin (2010a) gave a good, well-illustrated description of this species which is not repeated here. *Z. martinae* differs from *Z. westraliensis*, also from the Cattamarra Coal Measures, in its smaller size (latter is 7 mm long), more convex disc, more distinct cross-ribs, narrower intercalaries, fewer cells per longitudinal row (c. 30 in latter), and cells present only in the basal one-third of the epipleural rim (more extensively in latter). *Z. tuberculata* (below) has a similar number of longitudinal cells per row, but is otherwise different in size and form.

Zygadenia tuberculata (Giebel, 1856)

Fig. 3

Material. Right elytron: II 3063 [S671] a, b part and counterpart. Smokejacks, Upper Weald Clay Formation, lower Barremian; collected by AR.

Diagnosis. Elytron large (10–13 mm long), elongate (3–3 1/4 times longer than broad), no tail-like process at apex; main longitudinal veins much more prominent than intercalaries; window cells large with 20 in row on disc, and epipleural rim moderately wide with row of cells.

Remarks. Ponomarenko (2006) reported that this Purbeck species was also found in the Weald Clay (despite a gap in the Valanginian) but gave no further details of the latter occurrence. A general species diagnosis is given above and an elytron figured from the Upper Weald Clay which is incomplete basally and a little smaller (c. 3 mm wide) than the Purbeck one (4 mm wide). This size difference is proportionately a bit more than the variation in length of *Z. martinae* from the Lower Jurassic of Australia, but the latter is only known from one formation and locality (Martin, 2010a). The Wealden elytron is preserved as a carbonised impression unlike the oxidised Purbeck and above Yixian impressions; it is associated with insect wing fragments including an aeshnidiid dragonfly.

Zygadenia angliae (Giebel, 1856)

Fig. 4

Material. Left elytron: II 3064 [CH9] a, b part and counterpart. Clockhouse, Lower Weald Clay Formation, upper Hauterivian; collected by EBJ.

Diagnosis. Elytron small (4–5 mm long), elongate, no tail-like process at apex; main longitudinal veins little differentiated from

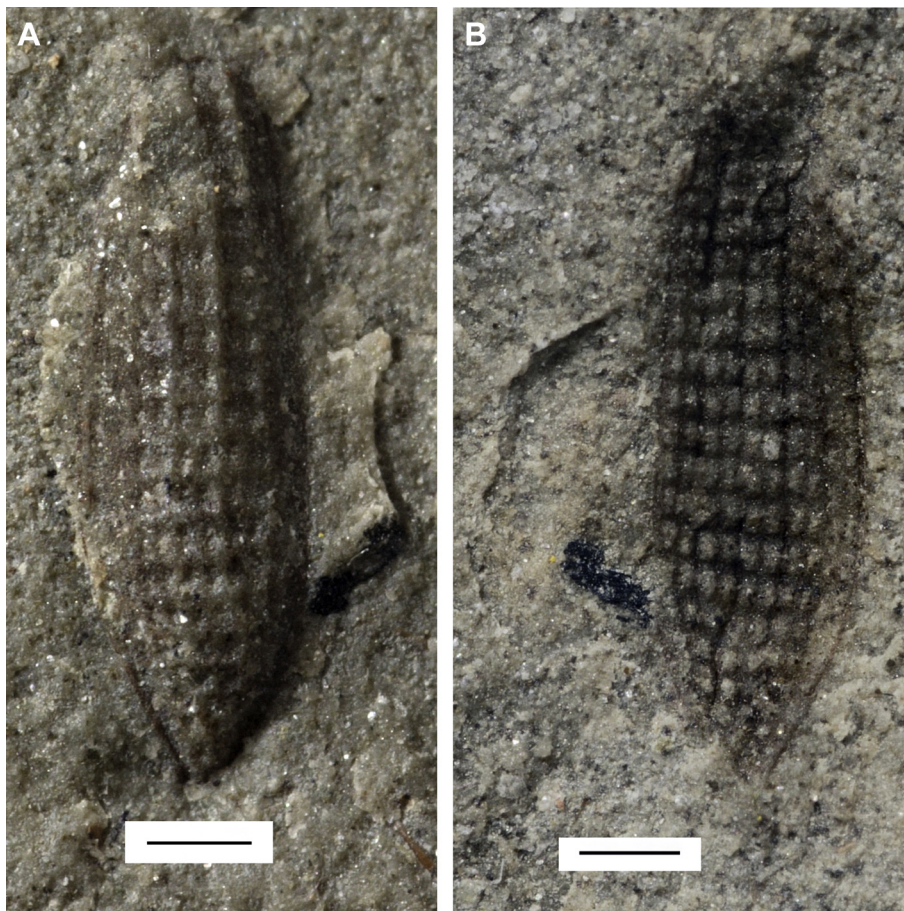


Fig. 4. *Zygadenia angliae* (Giebel, 1856), II 3064a, b, left elytron; Clockhouse, upper Hauterivian. A, part; B, counterpart. Scale bar = 1 mm.

intercalaries which are weakly zigzagged; window cells not large, some 25 in row on disc, and epipleural rim narrow with no cells.

Remarks. Ponomarenko (2006) reported that this Purbeck species was also found in the Weald Clay (despite a gap in the Valanginian) at Clockhouse and Smokejacks brickworks. A general species diagnosis is given above and a nearly complete elytron figured from Clockhouse which is marginally larger (c. 5.1 mm long) than the Purbeck one and preserved also as a carbonised impression but in a coarser (siltstone) matrix.

Zygadenia floodpagei sp. nov.

Fig. 5

Derivation of name. After the late Mr C. M. Flood Page, fossil collector; masculine.

Holotype. Left elytron: II 3065a, b [CH56j+y, xvii] part and counterpart. Clockhouse, Lower Weald Clay, upper Hauterivian; collected by EBJ.

Paratype. Left elytron: II 3066 [B63] a, b part and counterpart. Beare Green, Upper Weald Clay, upper Barremian; collected by EBJ.

Diagnosis. Elytron large (11 mm long), short (2.6 times longer than broad), apical 'tail' absent; veins well differentiated from intercalaries (except R) and zigzagged; 25 window cells in longitudinal rows on disc; epipleural rim moderately broad with long row of cells; colour pattern of distinct dark stripes and spots.

Description. Elytron 11 mm long, 4.2 wide, tuberculate, apex rounded; outer (anterior) margin curved, especially towards base and apex; disc transversely convex with well developed, ridged

striae plus cross-ribs and 10 rows of cells, 25 per row, inner three clearly double rows; cells elongated and less prominent in outer part of disc; main veins more pronounced than intercalaries; Cu flexed outwards basally; R indistinct; epipleural rim moderately broad with cells extending into apical half of elytron; sutural rim moderately wide; colour pattern includes three dark brown transverse stripes and two spots on outer and inner parts of elytral disc respectively.

Remarks. The holotype is a complete elytron except that some of the inner basal part is missing due to a rock fracture. The specimen has been previously figured by Jarzembowski (2011 and refs therein) but is rephotographed here in polarised light to highlight the dark brown colour markings; the photograph has also been reversed (as a right elytron) in order to better appreciate the overall colour pattern. The latter includes three broad, oblique stripes commencing about a 1/3rd of the elytral length from base, with rounded inner ends terminating before the suture; the apical one is thinned laterally. The spots alternate with the stripes, starting more basally, and the middle one is almost lozenge shaped. Several species of *Notocupes* sensu stricto from the late Mesozoic of Asia are patterned (vide figures in Ponomarenko, 1964, 1994). They are unlike *Z. floodpagei*, however: *N. picturatus* Ponomarenko, 1964 from the late Jurassic of Central Asia (Karatau) has five central spots and a broad subapical bar, whereas *N. mongolicus* Ponomarenko, 1994 and *N. elegans* Ponomarenko, 1994, both from the early Cretaceous of Mongolia, have light mottles and irregular stripes respectively. The late Jurassic *N. lentus* Ren, 1995 from N. E. China (previously thought to be a tetrphalerin: Kirejtshuk et al., 2010) appears to have four oblique stripes against a dark background.

The paratype is fractured and colour pattern largely obscured by iron-staining. Both types are associated with other coleopteran elytra and some bivalve fragments on the same bedding plane; the paratype is also associated with fish scales and the holotype with other wings and body parts (including cockroaches and bugs) as well as gastropod operculae.

Zygadenia simpsoni sp. nov.

Fig. 6

Derivation of name. After Martin Simpson, geologist; masculine.

Holotype. Right elytron: II 3067 [B64] a, b part and counterpart. Beare Green, Upper Weald Clay, upper Barremian; collected by EBJ.

Paratype. Right elytron: II 3065a [CH56j+y], 3068 [CH56f] part and counterpart. Clockhouse, Lower Weald Clay, upper Hauterivian; collected by EBJ.

Diagnosis. Elytron very large (14 mm long), very elongate (3.7 times longer than broad), apical 'tail' absent; veins well differentiated from intercalaries except R; 31 window cells in longitudinal rows on disc; epipleural rim moderately broad with long row of cells; colour pattern with distinctive central band and apical chevrons.

Description. Elytron 13.9–14.0 mm long, 3.8–3.9 mm wide, long and narrow, tuberculate, apex rounded; outer (anterior) margin straight in middle, curved towards base and apex; disc convex with well developed inner ridged striae, cross ribs and double rows of cells which resemble columns of the Chinese character tian (meaning field); c. 31 prominent, round cells per longitudinal row; main veins more pronounced than intercalaries; short vein A3 present, veins 2A and Cu curved outwards basally, R indistinct; epipleural rim moderately broad with cells extending into apical half of elytron; sutural rim relatively narrow; colour pattern including ring-like, transverse central band and pair of apical chevrons.



Fig. 5. *Zygadenia floodpagei* sp. nov., holotype; Clockhouse, upper Hauterivian. High contrast photograph of part (left) with mirror image adjacent to show hindbody colour pattern. Scale bar = 1 mm.

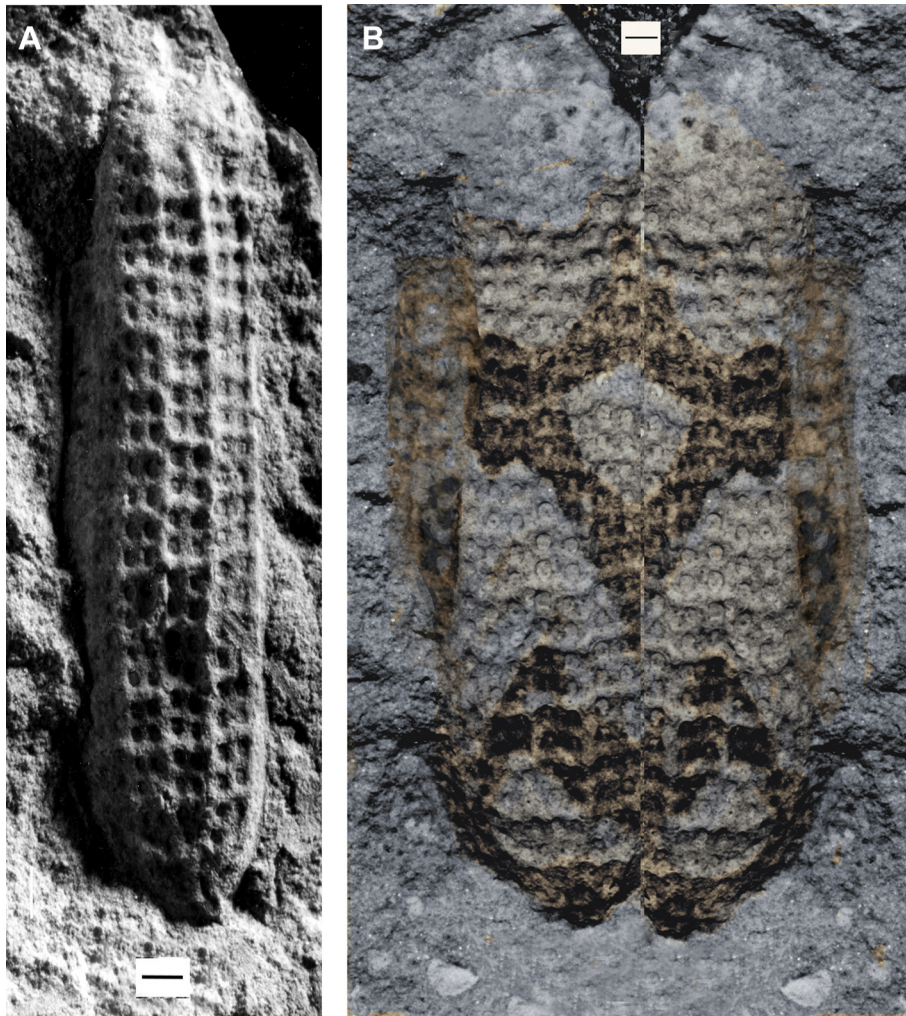


Fig. 6. *Zygadenia simpsoni* sp. nov., holotype; Beare Green, upper Barremian. A, part in normal oblique light to show venation on upper disc; B, high contrast photograph of counterpart (left) with mirror image adjacent to show hindbody colour pattern. Scale bar = 1 mm.

Remarks. The holotype is a nearly complete elytron and in a fine-grained, phosphatic nodule, the paratype on the same bedding plane as the holotype of *Z. floodpagei*. The colour pattern differs from the latter, however, the hindbody having a dark-outlined, shield-like central spot flanked by a pair of vertical bars (somewhat resembling the bezel and shoulders of an ornamented finger ring from above). There is also a thick, forward-pointing chevron in the apical part of the elytron (as in extant *Omma rutherfordi* Lawrence, 1999) with some additional darkening of the tip and side of the disc. The basal part of the elytron only has a faint transverse stripe. In extant *Omma*, the colour pattern is contrasted by a lightening of the scale cover on the elytron: SEM examination of Wealden elytra (II 3066a, 3068), however, revealed no scale structure.

The holotype is associated with an insect abdomen and a telost scale and the paratype with a caddis case (*Pelindusia* sp.) and some comminuted plant debris.

5. Conclusion

Extant Ommatinae have larvae which feed on fungus-infested dead wood or tree roots, whereas the adults are thought to subsist on pollen/plant sap; with only six living species they are considered relict, more derived beetle families now also occupying

the wood-feeding niche (Hörnchemeyer, 2005). Extant ommatines are rarely encountered and confined to the southern hemisphere (South America, Australia) whereas notocupedins are also found in the northern hemisphere (Europe as well as Australasia) and may be locally common (Zhang et al., 2010). The pangean distribution of the fossils is in warm/arid regions based on the palaeogeographical maps in Soriano and Delcòs (2006). The living beetles may be active during the day as well as by night when they are more likely to be seen by woodland predators. The brown-coloured *Omma stanleyi* Newman, 1839 goes under bark and feigns death when caught, whereas *Omma mastersi* Macleay, 1871, an active runner on tree trunks, has white markings and is thought to be part of a müllerian mimicry ring (with another beetle and a wasp: Lawrence, 1999; pers. comm.: July, 2013). The highly patterned and dull elytra of *Zygadenia* described above suggest that notocupedins evolved similar behaviour (thanatosis, mimesis below).

The elytra described collectively in *Zygadenia* have added to our knowledge of the palaeodiversity and occurrence of fossil notocupedins, especially *Notocupes* s. l. They have also provided palaeobiological information. By analogy with recent Australian *Omma*, the patterned elytra suggest diurnal activity, or at least visibility, in contrast to concealment on the ground or under bark. The patterns in day-active *Omma* are developed on scales (as in butterflies). No scale structure was observed in *Z. floodpagei* and *Z. simpsoni*: this is

probably due to the relative coarseness of the matrix and future search should target higher fidelity, calcareous micrites (cf. Jarzembowski, 1980). The patterns in *Zygadenia* are of the monotonous type (McNamara, 2013) and the original hue of the lighter, non-melanitic areas is currently unknown. Thus a cryptic interpretation cannot be ruled out (cf. Forbes, 2009, p. 236), as in fossil cupedines (Tan et al., 2010), although the markedly geometric pattern of *Z. simpsoni* points more to procrypsis (dazzle). The possibility of mimetic resemblance to animals rather than to plants in the horizontally banded *Z. floodpagei* is supported by the presence of a striped wasp belonging to *Archisphex* Evans in the Middle Aptian (Laiyang Group) of N. E. China (Hong, 1984); this genus is also found in the English Wealden (Rasnitsyn et al., 1998) and the Yixian Formation (Zhang et al., in prep.).

Although confirmed as an ommatid in the latest phylogenetic analysis (Tan et al., 2012), current research suggests that the family group placing of *Notocupes* is actually less secure because of the cupedine-like abdominal ventrites and a prosternal sprout observed in *Amblomma* (A. G. Ponomarenko, pers. comm.: October, 2013). Recent ommatid ventrites are co-planar (abutting) and not overlapping (and anteriorly depressed) as in cupedids sensu stricto; in addition, the procoxae are contiguous and not separated by the prosternum (Jarzembowski et al., 2013a,b). The overlapping and anteriorly depressed ventrites in *Notocupes* may prove to be a symplesiomorphic trait, but the sprout (a postero-ventrally directed projection anteriorly between the procoxae) is an added complication in family characterisation. Although notocupedines have been studied for over 150 years, their morphology and affinities are not fully resolved. What is certain is that notocupedines were not necessarily dull brown insects like the pestilential modern woodworm, or xylophagous death-watch beetle.

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Appendix A. Supplementary material

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.cretres.2014.03.006>.