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New Early Cambrian bivalved arthropods from southern France

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Abstract – The Lower Cambrian Pardailhan Formation of the Montagne Noire (Southern France) has yielded a diverse fossil assemblage including bivalved arthropods (the bradoriids *Monceretia erisylvia* gen. et sp. nov., *Cambria danvizcainia* sp. nov. and *Matthoria*? sp., together with *Isoxys* sp.) associated with trilobites, hyolithids, inarticulate brachiopods, sponge spicules, ichnofossils and chancelloriid sclerites. This assemblage provides new evidence about the biodiversity of Early Cambrian marine communities in palaeocontinental Gondwana. The bradoriids are Cambriidae, a family with widespread distribution in offshore shelf marine environments during Early Cambrian times. The present study confirms the presence of cambriids within a subtropical latitudinal belt that encompasses Laurentia, Siberia and the Gondwanan margins from Southern France to South China. Although knowledge of the distribution of fossil cambriids is patchy, at the generic level they appear to be provincial, with *Petrianna* from Laurentia, *Shangsiella* and *Auriculatella* from South China, *Cambria* from Siberia and Gondwana (Armorica), and *Monceretia* gen nov. from Gondwana (Armorica). The presence of *Isoxys* in the Montagne-Noire confirms the cosmopolitan distribution of this genus in the Early and Middle Cambrian tropics. Cambriid bradoriids occupy a biostratigraphically narrow time interval, probably equating to part of the Atdabanian and Botomian stages of Russian terminology. Their presence in the Pardailhan Formation supports the notion of a Botomian age, determined from archaeocyathan evidence. The North American bradoriid genus *Matthoria*, also possibly present in the Pardailhan Formation, is reassigned to the Cambriidae.

Keywords: Cambrian, arthropods, stratigraphy, biogeography, taxonomy.

1. Introduction

Much of the Lower Cambrian rock sequence of the Montagne Noire, southern France, is fossil poor (Alvaro, Debrenne & Vizcaïno, 2001), but at certain horizons within the sequence, particularly within the Pardailhan Formation, there are relatively rich assemblages of bivalved arthropods including bradoriids and *Isoxys*, trilobites (ellipsocephalids, redlichiids, abadiellids), inarticulate brachiopods, hyolithids, sponge spicules, chancelloriid sclerites, ichnofossils and possible arthropod appendages (see Vizcaïno, Alvaro & Monceret, 2004 for faunal inventory). These provide evidence about the biodiversity of Cambrian assemblages living on the margins of the Gondwana palaeocontinent (Alvaro, Debrenne & Vizcaïno, 2001). The new bradoriid material is composed entirely of cambriids, a family that is particularly well represented in the Lower Cambrian of China (Hou *et al.* 2001), Greenland (Siveter *et al.* 1996) and Siberia (Melnikova, Siveter & Williams, 1997). *Monceretia erisylvia* gen. et sp. nov. and *Cambria danvizcainia* sp. nov. are described. A third species, *Matthoria*? sp., is described in open nomenclature. These bradoriids provide additional biostratigraphical data bearing on the age of the Pardailhan Formation, and the biogeographical distribution of cambriids during the Early Cambrian.

2. Origin of the material, preservation and terminology

2.a. Material

The bivalved arthropods (bradoriids and *Isoxys*) are sourced from several adjacent outcrops in the Forêt des Soulanes de Nore, along the road to Pujol du Bosc, 850 m southeast of the forest house of Marcelly (longitude 2°53′ E, latitude 43°32′ N) to the north of the small town of Villeneuve-Minervois, Aude, southern France (Fig. 1). Although more than 50 bradoriid specimens have been recovered (Université Claude Bernard Lyon-1, collection numbers FSL877001–877033, and additional unnumbered specimens), specimens of *Isoxys* are rare (FSL877034 and FSL877035). The

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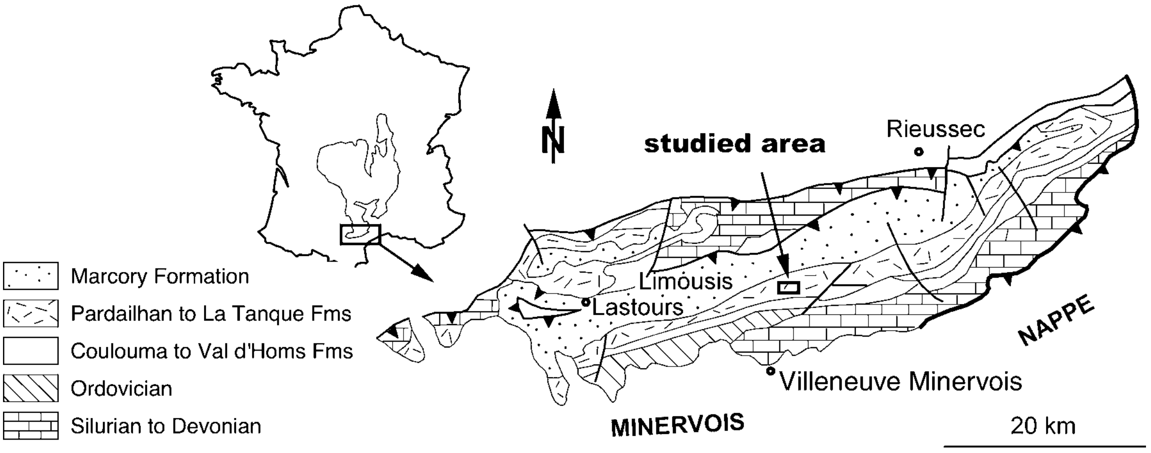

Figure 1. Geological setting of the bivalved arthropods (bradoriids and *Isoxys*) from the Montagne Noire, southern France (map after Vizcaïno, Alvaro & Monceret, 2004).

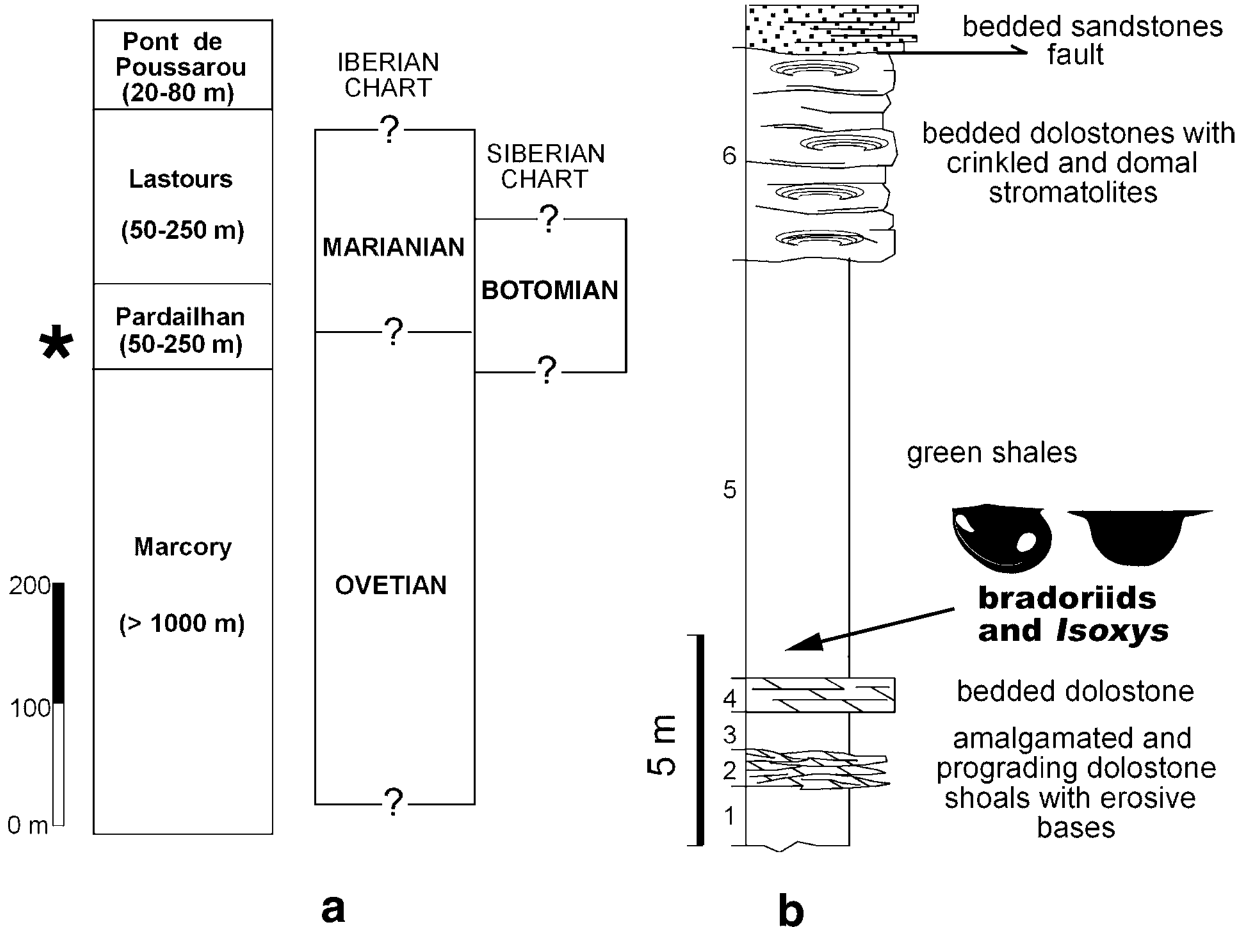

Figure 2. Stratigraphical setting of the bivalved arthropod material from the Montagne Noire, France (after Vizcaïno, Alvaro & Monceret, 2004). (a) Approximate chronostratigraphical position of the Pardailhan Formation in terms of the Iberian and Russian stages. The asterix indicates the level of the Pardailhan Formation within the Forêt des Soulanes de Nore sequence. (b) Position of the bivalved arthropod material within the Pardailhan Formation as it is exposed in the Forêt des Soulanes de Nore.

material comes from the Pardailhan Formation, a unit of between 50 and 250 m thickness, within the Lower Cambrian sequence (Alvaro, Debrenne & Vizcaïno, 2001; Vizcaïno, Alvaro & Monceret, 2004). In the area of Villeneuve-Minervois, the Pardailhan Formation occurs as a mixed succession of stromatolitic and massive dolostones, grey sandstones and greenish to brownish shales (Fig. 2). The sandstone and dolostone beds were deposited in relatively high-energy shallow water, whereas the mudstone intercalations, from which bradoriids were recovered, may indicate a deeper depositional setting under quiet-water conditions (Vizcaïno, Alvaro & Monceret, 2004). The carbonate units are often rich in archaeocyathans, enabling correlation, in part, with the Siberian-based Botomian Stage of the Lower Cambrian (Debrenne, Rozanov & Zhuravlev, 1990; Alvaro, Debrenne & Vizcaïno, 2001). The sandstones yield trilobites such as the redlichiid *Eoredlichia noiri* (Jago), and hyolithids (Alvaro, Debrenne & Vizcaïno, 2001).

2.b. Preservation

Bradoriid specimens are preserved mostly as disarticulated valves, though a few are still fully articulated carapaces, occasionally preserved in 'butterfly' orientation, with the two valves splayed open on the sediment surface (Figs 3–5). Many specimens are incomplete, and this, together with their co-occurrence with fragmentary trilobites, spicules of sponges, sclerites of chancelloriids and other shelly organisms, suggests transportation. As the bradoriids appear to be present at only one horizon in the Forêt des Soulanes de Nore, in a formation up to 250 m thick, they may originally have been living in a more shallow marine setting and transported here post-mortem.

The valves of the bradoriids are phosphatic, a feature which is now regarded to be of secondary, diagenetic origin (Briggs *et al.* 1993; Briggs & Wilby, 1996; Hof & Briggs, 1997; Wilby & Briggs, 1997). Indeed, the range of shape variation in the two species described here suggests that the carapace may have been quite flexible and largely unmineralized during life. The valves of the bradoriids from the Montagne Noire preserve fine detail of the ornament, including small pustules on the lateral surface and lobes (Figs 3, 4).

2.c. Terminology

The morphological terminology of the bradoriid carapace follows Williams & Siveter (1998) and Hou *et al.* (2001).

3. Bradoriids

3.a. Distribution of bradoriids

Bradoriids are small (generally less than 1 cm long) dorsoventrally flattened arthropods capped by a folded dorsal shield, and known from the Cambrian and Lower Ordovician. They are recorded worldwide, from China (Hou *et al.* 2001), North America (Siveter & Williams, 1997), Australia (Jones & McKenzie, 1980; Hinz-Schallreuter, 1993*a*), Russia and central Asia (Melnikova, Siveter & Williams, 1997), Britain (Siveter & Williams, 1995; Williams & Siveter, 1998), Scandinavia (Hinz-Schallreuter, 1993*b*,*c*), Spain (Gozalo & Hinz-Schallreuter, 2002; Gozalo, Dies & Chirivella, 2004), Greenland (Siveter *et al.* 1996) and Antarctica (Rode, Lieberman & Rowell, 2003). Bradoriids are known to have both local and regional biostratigraphical value. For example, *Indiana lentiformis* (Cobbold) has been used to correlate the Lower Cambrian sequences of England and Wales (Siveter & Williams, 1995), whilst *Anabarochilina primordialis* (Linnarsson) is a widespread index fossil for the level of the *Lejopyge laevigata* trilobite Biozone in Britain, Scandinavia and Russia (Siveter *et al.* 1993; Melnikova, Siveter & Williams, 1997). Bradoriids can also be used to reconstruct Cambrian palaeobiogeography (e.g. Siveter *et al.* 1996; Hou *et al.* 2001; Rode, Lieberman & Rowell, 2003). Here we report the first bradoriids from the Lower Cambrian of the Montagne Noire, France.

3.b. Bradoriids in the marine ecosystem

Bradoriid arthropods encompass a huge variety of carapace design that probably reflects a range of ecological niches and lifestyles, including possible pelagic forms. In life attitude, the dorsal shield of many bradoriids may have been held widely open in so-called 'butterfly position' (Shu *et al.* 1999). The preserved ventral anatomy (e.g. *Kunmingella*: Hou *et al.* 1996; Shu *et al.* 1999) supports the view that some bradoriids were motile epibenthic dwellers of the sediment–water interface, and had a lifestyle and ecological niche probably similar to Recent ostracod crustaceans. Bradoriids may have been detritus feeders or, similarly to some Recent crustaceans (Vannier, Abe & Ikuta, 1998), micro-scavengers or micro-predators of unknown non-mineralized animals (e.g. meiofaunal organisms). Along with hyolithids, bradoriids were amongst the most abundant animals of the Early Cambrian epibenthos (e.g. Yu'anshan Member, Heilinpu Formation (formerly Qiongzhusi Formation) southern China: Vannier & Chen, 2005). Their frequent high abundance suggests that bradoriids, along with other invertebrates, may have been important recyclers on the Early Cambrian seabed (Shu *et al.* 1999). Bradoriids may have been an important food source for larger animals as is suggested by coprolite evidence (Vannier & Chen, 2005).

3.c. Affinities of bradoriids

The Order Bradoriida of Raymond (1935) embraced what are now known to be two distinct groups of Cambrian bivalved arthropods, namely the Bradoriida *s.s.* and the Phosphatocopida Müller, 1964. Differences between the carapace morphology of Bradoriida and Phosphatocopida are documented by Williams & Siveter (1998). Because of their bivalved form, general morphology and overall size, both groups were assigned traditionally to the ostracod crustaceans (Müller, 1964, 1979; Jones & McKenzie, 1980). However, soft-part evidence from the Chinese bradoriid *Kunmingella*

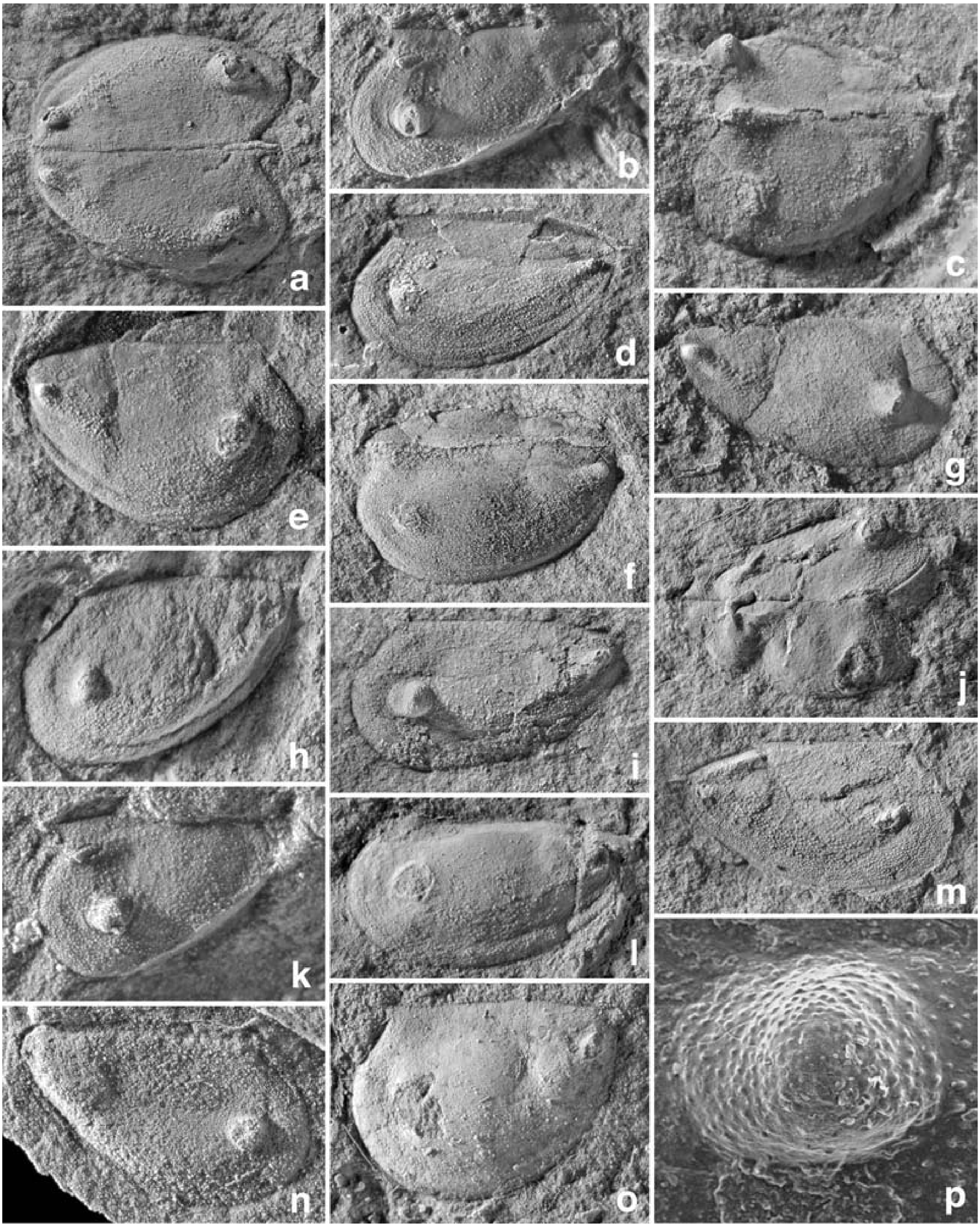

Figure 3. *Monceretia erisylvia* sp. nov., from the Pardailhan Formation (Lower Cambrian) of the Montagne Noire, southern France. All specimens are from the Forêt des Soulanes de Nore. The range of images is designed to indicate the variation in the carapace shape and morphology of this species. (a–o) are digital photographs taken with the specimens lightly coated by ammonium chloride. (p) is a scanning electron micrograph. Magnifications are: (a, c, d) × 9; (b, e, g, k), × 9.5; (f, o), × 7.5; (h, m), × 6.7; (i, j, n), × 10; (l), × 11; (p), × 60. (a) FSL877001a, holotype, open carapace (left valve below). Well-developed pustulose ornament demarcates the position of the weakly developed connecting lobe. (b) FSL877002a, ventrally damaged right valve. (c) FSL877001b, open carapace, with very well-developed posterior lobe on the left valve (top). (d) FSL877003, flattened right valve with pustulose ornament concentrated in the ventral part of the valve, and marginal area demarcated by a narrow concave rim. (e) FSL877010, left valve with well-developed

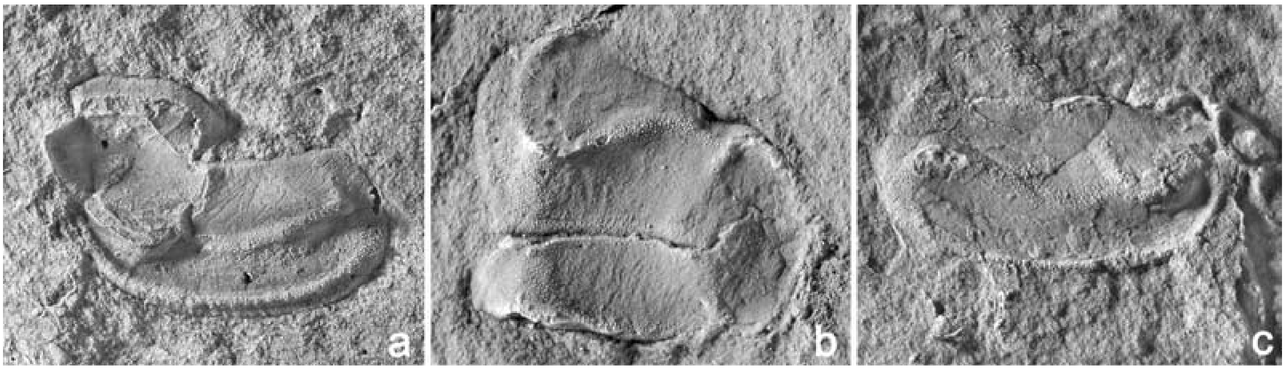

Figure 4. *Cambria danvizcainia* sp. nov., from the Pardailhan Formation (Lower Cambrian) of the Montagne Noire, southern France. All specimens are from the Forêt des Soulanes de Nore and are latex casts of external moulds. (a–c) are digital photographs of specimens coated with ammonium chloride. (a) FSL877014a, holotype left valve, partially obscured anterodorsally by a second specimen, × 5.5. (b) FSL877015, articulated carapace, partly obscured by sediment, indicating the concentration of pustulose ornament adjacent the dorsal hinge and on the lobes, × 7.5. (c) FSL877016a, incomplete right valve, × 6.5.

Figure 5. *Matthoria*? sp. from the Pardailhan Formation (Lower Cambrian), Montagne Noire, Forêt des Soulanes de Nore. Magnification × 15. FSL877018b, left valve.

(Hou *et al*. 1996; Shu *et al*. 1999) indicates that typical representatives of the group lie outside the Ostracoda, and indeed outside the crown-group of the Crustacea *s.s.* Nevertheless, it is probable that the Bradoriida represents a polyphyletic taxon of perhaps several groups of arthropods that have convergently acquired a bivalved carapace. Thus, the group might include ancestral ostracods (Jones & McKenzie, 1980), a notion that can only be confirmed from preserved soft anatomy. Ostracods are known from the lowermost Ordovician of Baltoscandia (Tinn & Meidla, 2004) and Argentina (M. J. Salas & J. Vannier, unpub. data) but so far have no confirmed ancestors in the Cambrian. Evidence from the soft anatomy of Phosphatocopida (see Siveter, Williams & Waloszek, 2001; Siveter, Waloszek & Williams, 2003; Maas, Waloszek & Müller, 2003) confirms that typical bradoriids (like *Kunmingella*) and phosphatocopids do not belong to the same group.

4. *Isoxys*

Part of the assemblage in the Pardailhan Formation includes *Isoxys* (Fig. 6), a widespread arthropod with a bivalved dorsal shield, typical of the Lower and Middle Cambrian (Williams, Siveter & Peel, 1996; Vannier & Chen, 2000). *Isoxys* is generally found in deposits of offshore shelf marine origin, such as the dark grey mudstones of the Buen Formation in Northern Greenland (Siveter *et al*. 1996; Williams, Siveter & Peel, 1996) or Yu'anshan Member of the Heilinpu Formation of southern China (formerly known as the Maotianshan Shale; Vannier & Chen, 2000), in accordance with its probable pelagic mode of life.

Representatives of *Isoxys* with preserved soft anatomy (Vannier & Chen, 2000; Hou *et al*. 2004) indicate a body plan different from that of *Kunmingella*, the only bradoriid that preserves soft anatomy, with a uniform series of leaf-like appendages and no protruding abdomen. *Isoxys* possesses a very distinctive spinose

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dorsal cusp and marginal area demarcated by a narrow concave rim. (f) FSL877009, partially exposed carapace (right valve below). (g) FSL877004, markedly postplete left valve, with connecting lobe only partially developed posteroventral of the anterodorsal lobe. (h) FSL877008, right valve with well-developed marginal rim. (i) FSL877005, right valve with well-developed posterior lobe. (j) FSL877013b, incompletely exposed carapace showing probable early (post-mortem) deformation of the anterodorsal area (left valve below). (k) FSL877002b, right valve with well-developed posterior lobe, but valve markedly damaged ventrally. (l) FSL877011, elongated right valve. (m) FSL877006, flattened left valve preserving pustulose ornament particularly in the ventral part of the valve. (n) FSL877007, left valve with well-developed posterior lobe. (o) FSL877012, right valve with phosphatized carapace peeling away at the point of the posterior lobe. (p) FSL877005, close-up of pustulose ornament on the posteroventral lobe.

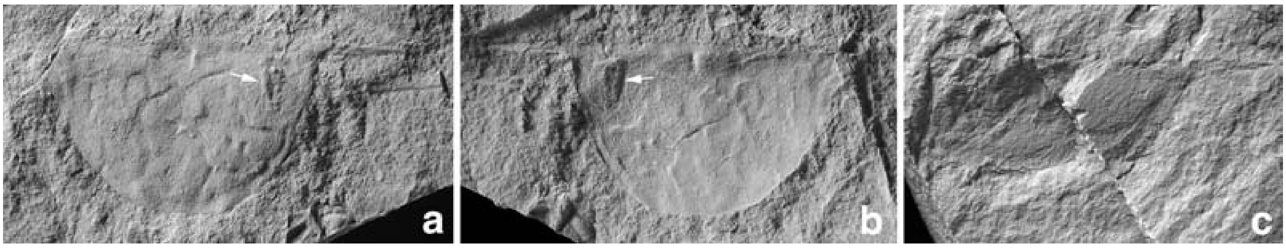

Figure 6. *Isoxys* sp. from the Pardailhan Formation (Lower Cambrian), Montagne Noire, Forêt des Soulanes de Nore. (a, b) FSL877034, part and counterpart of a right valve (posterior cardinal spine broken), × 1.5; white arrows indicate possible pit-like structure. (c) FSL877035, damaged, probable right valve, × 1.65.

carapace and was interpreted recently as a member of the mid-water-marine community along with other swimmers and drifters (Vannier & Chen, 2000).

5. Stratigraphical significance

Cambriid bradoriids are known from a stratigraphically short range in the Lower Cambrian of China (Qiongzhusian Stage: Hou *et al.* 2001), Greenland (*Bonnia–Olenellus* biozones: Siveter *et al.* 1996), New York State (*Protolenus–Callavia* Biozone: Siveter & Williams, 1997 = *Matthoria*) and Siberia (Atdabanian and Botomian: Melnikova, Siveter & Williams, 1997). Although precise correlation between the various stratigraphies of the Lower Cambrian is still in flux (see Lieberman, 2002, p. 700), cambriid bradoriids are useful general markers worldwide for intervals equivalent to parts of the Atdabanian and Botomian stages of Russian usage (Fig. 7). Thus, their occurrence in the Pardailhan Formation supports the notion that the formation is probably Botomian, an age that is consistent with previous data obtained from archaeocyathans

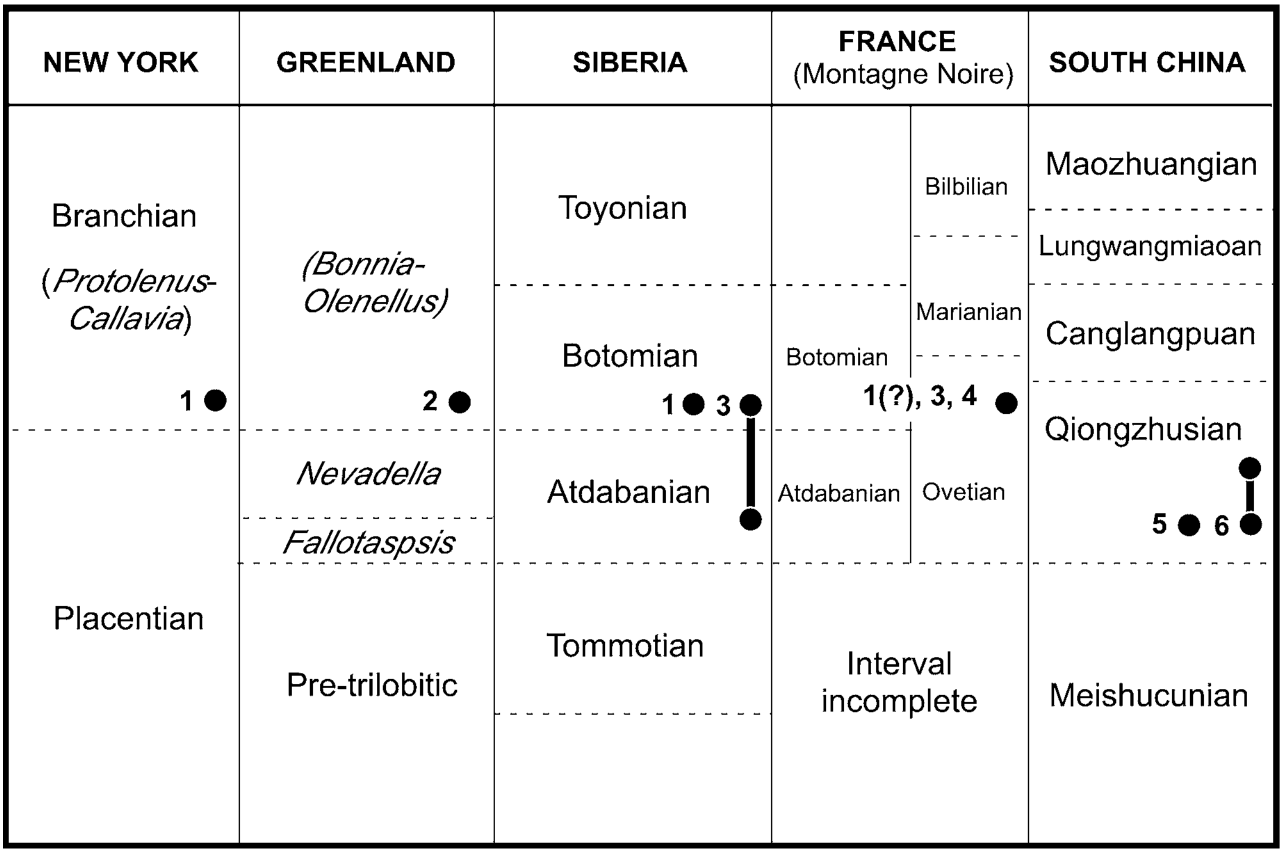

Figure 7. Approximate chronostratigraphical distribution of cambriid bradoriids within the Early Cambrian. The precise correlation of the various Laurentian, Siberian, Chinese and Gondwanan (Armorican) stages/biozones is uncertain, hence the use of dotted lines (e.g. see Lieberman, 2002). Bradoriids are: 1 – *Matthoria* (Siveter & Williams, 1997, and this paper); 2 – *Petrianna* (Siveter *et al.* 1996); 3 – *Cambria* (Melnikova, Siveter & Williams, 1997, and this paper); 4 – *Monceretia* (this paper); 5 – *Auriculatella* (Hou *et al.* 2001); 6 – *Shangsiella* (Hou *et al.* 2001). The relative chronostratigraphical ranges of the cambriid taxa within the individual stages and biozones are approximate.

(Debrenne, 1964; Alvaro, Debrenne & Vizcaïno, 2001). Although none of the cambriid species currently described is widespread, and thus the group is of limited use for international correlation, the presence of a possible *Matthoria* species in the Pardailhan Formation also supports a Botomian age. Elsewhere, *Matthoria* is recorded from the Botomian of Siberia (Melnikova, Siveter & Williams, 1997 = *Bradoria ordinata*), and from the *Protolenus–Callavia* Biozone of New York State (Siveter & Williams, 1997) and possibly southern Britain (Williams & Siveter, 1998).

6. Habitat, mode of life and biogeography of cambriids

6.a. Habitat

The sedimentology of the Pardailhan Formation is still poorly understood (Alvaro, Debrenne & Vizcaïno, 2001; Vizcaïno, Alvaro & Monceret, 2004), but the underlying Lastours Formation appears to have been deposited in shallow marine settings with periodic emergence (Alvaro, Debrenne & Vizcaïno, 2001). The common occurrence of carbonate bioherms in the Pardailhan Formation probably suggests a relatively shallow marine shelf setting, though the bradoriids are sourced from mudstones that may have been deposited in slightly deeper carbonate-poor settings.

In northern Greenland, the cambriid *Petrianna* occurs in deep shelf facies of the Buen Formation during the acme of transgression onto the marine shelf (Siveter *et al.* 1996). In South China, *Shangsiella* and *Auriculatella* occur in shelf marine facies of the Heilinpu Formation in central and northern Sichuan and Shaanxi provinces (Hou *et al.* 2001). In southern Britain, *Matthoria*(?) occurs in more offshore marine shelf deposits of the Purley Shales Formation (Williams & Siveter, 1998). Thus, the environmental range of cambriids appears to have encompassed open marine shelf habitats, though they may have occupied more inshore localities, as suggested by their presence in the Pardailhan Formation.

6.b. Mode of life

The carapace of cambriids provides few clues to their mode of life. Although fossilized carapaces are phosphatic, the original carapace may have been non-mineralized, quite thin and flexible, as witnessed by the wide range of variation in shape within a single species (Fig. 3). The majority of Recent arthropods (e.g. halocyprid ostracods, phyllocarids, daphniids) with a non-mineralized, thin carapace are temporary or permanent inhabitants of the water column. Cambriids may have had comparable habits. Cambriids also appear to be morphologically similar to some species referred to *Isoxys* (e.g. *Isoxys volucris*: see Williams, Siveter & Peel, 1996), a group of widespread Early and Middle Cambrian bivalved arthropods considered to have a mid-water ecology (Vannier & Chen, 2000). The wide global distribution of cambriids in a relatively narrow time interval during Early Cambrian times may have been facilitated largely by capabilities for dispersal in the water column (swimming in the water column, passive drifting or sinking). The cosmopolitan distribution of Recent halocypridid ostracods relies on similar biotic factors (Angel, 1994; Vannier & Chen, 2000). Bradoriids may have occupied a wide range of ecological niches from epibenthic to mid-water. It is possible that a benthic-to-pelagic ecological transition occurred relatively early in the evolution of the group. Early Cambrian bradoriids may belong to these mid-water pioneers. Similar transitions occurred in other Early Palaeozoic bivalved arthropods including Ordovician phyllocarids (Vannier *et al.* 2003) and Silurian ostracods (Siveter, Vannier & Palmer, 1991).

6.c. Biogeography

In addition to southern France, cambriids are reported from Siberia (Williams *et al.* 1994; Siveter *et al.* 1994*a*; Melnikova, Siveter & Williams, 1997), Greenland (Siveter *et al.* 1996), South China (Hou *et al.* 2001), North America (Siveter & Williams, 1997) and possibly Britain (Williams & Siveter, 1998 = *Matthoria*) and Kazakhstan (Melnikova, Siveter & Williams, 1997). They possess a largely tropical to subtropical distribution in the Early Cambrian (Fig. 8), with only *Matthoria* occurring in mid-latitudes. Cambriids are rare or absent in the Cambrian faunas of the Avalonia microcontinent (e.g. southern Britain, parts of eastern North America: see Siveter & Williams, 1997; Williams & Siveter, 1998) or Baltica (e.g. Wiman, 1905). Nevertheless, other bradoriid groups (e.g. Bradoriidae, Hipponicharionidae, Indianidae) are diverse and numerically abundant in these regions (Williams & Siveter, 1998). This indicates that environmental factors, rather than preservation, are probably responsible for the distribution of cambriids. Indeed, their latitudinal preference for the tropics strongly suggests that sea surface temperature may have been the limiting factor for this group of bradoriid arthropods.

Cambriids were particularly widespread longitudinally. This widespread distribution, their occurrence in offshore shelf marine environments and their similarity to other widespread Early Cambrian bivalved arthropods such as *Isoxys* (Williams, Siveter & Peel, 1996; Vannier & Chen, 2000) suggests a highly mobile mode of life (pelagic?) that allowed for wide dispersal. Together with some svealutid bradoriids, such as *Anabarochilina* (e.g. see Siveter *et al.* 1993; Siveter & Williams, 1997; Melnikova, Siveter & Williams, 1997; Williams & Siveter, 1998), cambriids are amongst the most widely distributed bradoriids.

In terms of the distribution of individual genera, *Petrianna* appears to be restricted to palaeocontinental

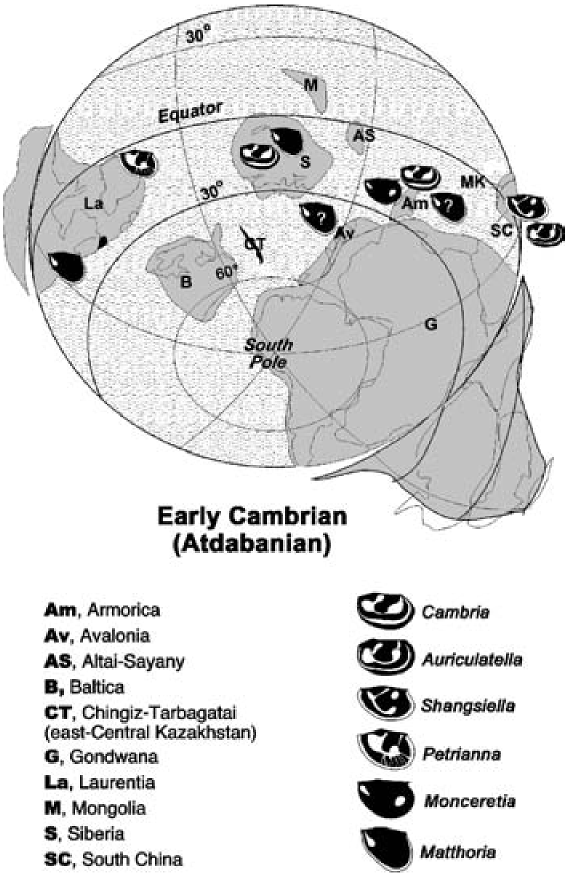

Figure 8. Biogeographical distribution of cambriid bradoriids projected onto an Early Cambrian reconstruction of palaeogeography devised by Drs M. Bassett and L. Popov of the National Museum of Wales, Cardiff. For key to different cambriid genera see Figure 9. Abbreviations: Am – Armorica; AS – Altai-Sayany; Av – Avalonia; B – Baltica; CT – Chingiz-Tarbagatai Island arcs; G – Gondwana; M – Mongolia terrains; MK – Makyi Karatau; La – Laurentia; S – Siberia; SC – South China.

Laurentia, though it is known only from two species in Greenland (Siveter *et al.* 1996). *Auriculatella* and *Shangsiella* are Chinese (Hou *et al.* 2001), and appear to have been limited to the South China plate. *Monceretia* gen. nov. is known only from the Montagne Noire of France, though it bears greatest similarity to the Chinese *Shangsiella*. *Cambria* was more widespread, occurring in Siberia and, based on its occurrence in the Montagne Noire, in peri-Gondwanan sequences (Armorica). *Matthoria* also appears more widespread, occurring in North America, Siberia and possibly France. The global distribution of cambriid genera maps out the same provinces as those of the trilobites with, for example, *Petrianna* in the Olenellid Province (Laurentia) and *Shangsiella, Auriculatella* and *Monceretia* gen. nov. within the Redlichiid Province (South China). However, Lieberman (1999, 2002 and references therein) has shown by detailed phylogenetic analysis of Cambrian trilobites that the Fallotaspidoidea, included within the Olenellid Province, are phylogenetically linked to the Redlichiina. Thus, parts of the Olenellid Province, particularly Laurentia and Siberia (see Lieberman, 1999, p. 177) may have faunas that are more closely related to the Redlichiid Province than to other parts of the Olenellid Province (e.g. Baltica), a pattern that may also explain the presence of cambriids in Greenland, but their absence from Scandinavia. Siveter & Williams (1997) and Hou *et al.* (2001) have also noted similarities between North American (Laurentian) and South Chinese bradoriid faunas.

7. Systematic palaeontology (by Jean Vannier & Mark Williams)

Phylum ARTHROPODA Siebold & Stannius, 1845
Order BRADORIIDA Raymond, 1935
(=Archaeocopida Sylvester-Bradley, 1961)
Family CAMBRIIDAE Lee, 1975

Remarks. The Cambriidae were reviewed by Siveter *et al.* (1996) and Hou *et al.* (2001), who discussed the differences between *Cambria* and the other members of the family, *Shangsiella* Lee, 1975*, Auriculatella* Tan, 1980 and *Petrianna* Siveter *et al.* 1996. Following Hou *et al.* (2001), the Chinese genera *Paracambria* and *Chuanbeiella* are regarded as junior synonyms of *Shangsiella*. Differences in the morphology of cambriid genera are summarized in Figure 9.

In their description of the genus *Matthoria* from New York State, Siveter & Williams (1997, pl. 8, fig. 1) noted its similarity to some cambriids, though at that time they chose to place the genus within the Svealutidae. Given its possession of a well-developed dorsal cusp, prominent anterodorsal lobe, thin ridge between the anterodorsal lobe and the dorsal cusp, marginal rim, cardinal corners with short spines, and in its overall morphology, *Matthoria* is better placed within the Cambriidae (Fig. 9). In its shape and the morphology of its anterodorsal lobe, it bears close similarity to *Monceretia* gen. nov., but differs by lacking a posterior lobe.

Genus *Cambria* Neckaja & Ivanova, 1956

Type-species. *Cambria sibirica* Neckaja & Ivanova, 1956, from the Lower Cambrian of Siberia.

Diagnosis. (Modified from Williams *et al.* 1994) Cambriidae with carapace (dorsal shield), approaching 1 cm long as adults, with prominent anterior lobe situated either in the mid-anterior or anterior cardinal area of the valve, elongate or sometimes node-like. This lobe is confluent via a well-developed arcuate connecting ridge to a posterior lobe, which may be ridge-like, and may or may not join up, via a ridge, with the posterior cardinal corner. Posterodorsally of the anterior lobe the valve is elevated to form a dorsal cusp. A narrow ridge passes between this cusp and the anterodorsal lobe. Latero-admarginal ridge is well

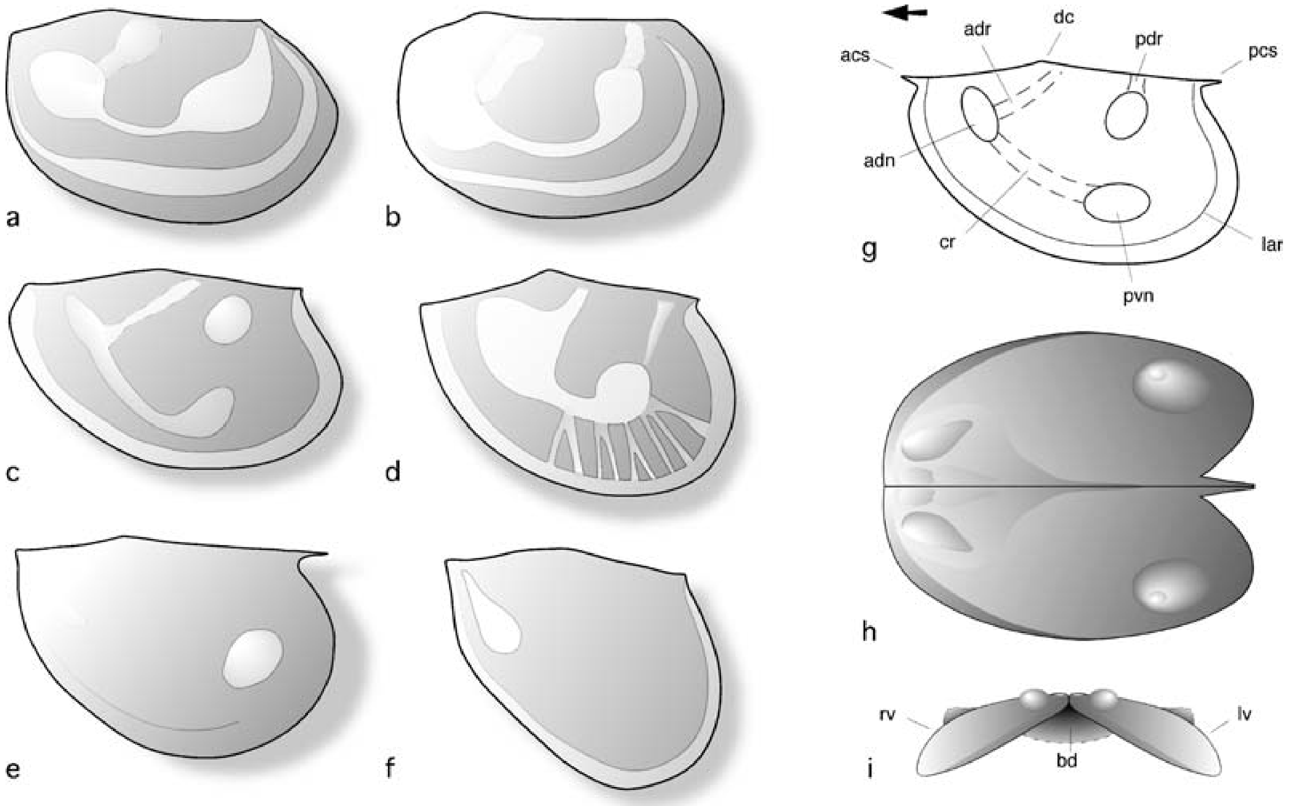

Figure 9. Cambriid external morphology. All valves depicted are left. a – *Cambria*; b – *Auriculatella*; c – *Shangsiella*; d – *Petrianna*; e – *Monceretia*; f – *Matthoria*; g – morphological terms used for the description of cambriids; h, i – recontruction of *Monceretia* in assumed life attitude (in dorsal and frontal views). Key to symbols: acs – anterior cardinal spine; adn – anterodorsal node; adr – anterodorsal ridge; bd – assumed body; cr – connecting ridge; dc – dorsal cusp; lar – latero-admarginal ridge; lv – left valve; rv – right valve; pcs – posterior cardinal spine; pdr – posterodorsal ridge; pvn – posteroventral node.

developed, and may or may not be continuous between cardinal corners. Sometimes a series of anastomosing ridges is developed above the ventral ridge, probably reflecting an internal circulatory system (see Vannier, Williams & Siveter, 1997). Cardinal corners have short spines. Ornament typically pustulose.

Remarks. For a description of *C. sibirica* see Williams *et al*. (1994). The new material of *Cambria* from the Montagne Noire extends the geographical range of this taxon from Siberian to peri-Gondwanan palaeocontinental settings during the Early Cambrian.

Cambria danvizcainia sp. nov.
Figure 4a–c

Derivation of name. For Daniel Vizcaïno of Carcassonne, Aude, southern France, who, with Eric and Sylvie Monceret, first discovered this species.

Holotype. Adult left valve (Fig. 4a), FSL877014a, b, from the Pardailhan Formation, Forêt des Soulanes de Nore, Montagne Noire, Aude, southern France.

Material. Five specimens (FSL877014–877017, FSL877031), including an articulated carapace (FSL877015).

Diagnosis. Species of *Cambria* having, in lateral view, a U-shaped anterior lobe situated in the mid-anterior part of the carapace. Latero-admarginal ridge does not extend to the cardinal corners, but sometimes joins up with the posterior lobe ventrally.

Description. Valves elongate and amplete, adults typically about 8 mm long. Anterior lobe U-shaped, situated in the mid-anterior part of the valve and not extending to the cardinal corner. Posterior lobe as a ridge, does not join up with the posterior cardinal corner, but is connected to the dorsal margin by a weak ridge, terminating in front of the posterior cardinal corner (Fig. 4a). Anterior and posterior lobes joined via a connecting lobe. Latero-admarginal ridge well developed, but does not extend to the cardinal corners, though sometimes joins up with the posterior lobe ventrally (Fig. 4a). Pustulose ornament tends to be best developed in the area of the connecting lobe between the anterior and posterior lobes and on the dorsal lateral surface of the valves adjacent to the hinge-line (Fig. 4a–c). Hinge-line developed as an articulating invagination between the two valves (Fig. 4b).

Remarks. *C. danvizcainia* differs from the type-species *C. sibirica* and the other Siberian species *C. melnikovi* V. Ivanova and *C. egorovae* Melnikova by having the latero-admarginal ridge terminate in the mid-anterior and mid-posterior areas of the valve and by the characteristic lateral shape of its anterior lobe. From the former species, *C. danvizcainia* also differs by having the anterior and posterior lobes not extend towards the cardinal corners.

The hinge of *C. danvizcainia* represents an articulating structure, with an invagination between the two valves probably formed by more flexible tissue. This kind of hinge structure is documented in a number of different bradoriids, including kunmingellids and hipponicharionids (e.g. Siveter *et al.* 1994*b*; Hou *et al.* 2001). However, it does not represent an articulating surface between two discrete valves connected by a ligament, as for example in podocope ostracods (Hinz-Schallreuter & Schallreuter, 1999).

Monceretia gen. nov.

Type-species. *Monceretia erisylvia* sp. nov., from the Lower Cambrian of the Montagne Noire, France.

Derivation of name. After the Monceret family of Cazilhac, Aude, southern France.

Diagnosis. Cambriid with markedly postplete valves, adult carapace (dorsal shield) *c.* 6–7 mm long. Narrow, oblique elongate anterodorsal lobe, terminating just before the anterior cardinal corner. Posterior lobe boss-like, often very elevated and terminating in a narrow spine. Lobes connected by a weak connecting lobe that is sometimes obsolete and only demarcated by pustulose ornament. No latero-admarginal ridge. Posterior cardinal corner with relatively strong spines.

Remarks. *Monceretia* differs from *Shangsiella, Auriculatella* and *Cambria* by having a poorly developed connecting lobe between the anterior and posterior lobes, and by the absence of a latero-admarginal ridge. In its overall shape, it appears close to the Chinese *Shangsiella* (see Hou *et al.* 2001), though it lacks a third lobe dorsal of the posterior lobe. It is similar in the morphology of its anterior lobe to *Matthoria* (see Siveter & Williams, 1997), but differs from that genus by possessing a posterior lobe.

Lobation is absent or poorly developed for small juvenile valves, but the full complement of lobes is already well developed in juvenile specimens 4 mm long, though the connecting lobe between the anterior and posterior lobes is better preserved in those specimens longer than 5 mm.

Monceretia erisylvia sp. nov.
Figure 3a–p

Derivation of name. After Eric and Sylvie Monceret of Cazilhac, Aude, southern France, who with Daniel Vizcaïno, first discovered this species.

Holotype. An articulated carapace (Fig. 3a), FSL877001a, b, from the Pardailhan Formation, Forêt des Soulanes de Nore, Montagne Noire, Aude, southern France.

Material. Over 50 valves and carapaces, including FSL877001–13, FSL877019–30, FSL877032, FSL877033 and unnumbered specimens in the Lyon collection.

Diagnosis. As for the genus; the taxon is monospecific.

Description. Valves markedly postplete, maximum height lies in a line from the dorsal margin through the posterior lobe to the ventral margin. Carapace typically about 6–7 mm long as adults. Narrow, oblique anterodorsal lobe with maximum elevation near the anterior cardinal corner. Posterior lobe boss-like (see Fig. 3b, i, k, p), often very elevated and terminating in a narrow spine. Lobes connected by a very weak lobe, sometimes obsolete and demarcated only by pustulose ornament (Fig. 3a). Valve posterodorsally of the anterior lobe is elevated to form a dorsal cusp. No latero-admarginal ridge, but possible doublure suggested by a narrow furrow running parallel to the ventral margin and demarcating flattened marginal area. Both cardinal corners with spines, more developed in posterior corner. Pustulose ornament concentrated in the ventral part of the lateral surface and on the posterior lobe.

Remarks. Some elongated specimens of *M. erisylvia* (e.g. Fig. 3l) are clearly long-axis parallel to the deformational fabric of the rock. Nevertheless, it is possible that some of the shape variation in this species represents dimorphism, though this is difficult to quantify because of rock deformation. Some carapaces appear to be very high (up to 5 mm) relative to their length (Fig. 3e). Dimorphism is reported from phosphatocopids (e.g. Zhang, 1987), but not from bradoriids. However, there are specimens of *Kunmingella* (females?) with clusters of eggs preserved ventrally (Shu *et al.* 1999). The range of shape variation in some bradoriid species, such as *Bradoria scrutator* Matthew (see Siveter & Williams, 1997), and *Kunmingella douvillei* (Mansuy) is marked (see Hou *et al.* 2001) and might suggest domiciliar dimorphism, though this can only be confirmed by detailed morphometric analysis of undeformed material.

Genus *Matthoria* Siveter & Williams, 1997

Type-species. *Matthoria troyensis* (Ford, 1873) from the Lower Cambrian of New York State (see Siveter & Williams, 1997 for a description).

Matthoria? sp.
Figure 5

Remarks. A single valve from the Forêt des Soulanes de Nore (Fig. 5), 4 mm long, lacks surface ornament or lobation, but possesses the typical dorsal cusp of cambriids. In having poorly developed lobation, it most closely resembles representatives of *Matthoria* (Fig. 9), but its affinities cannot be assessed further without more material.

Arthropoda, Class, Order and Family uncertain
Genus *Isoxys* Walcott, 1890

Type species. *Isoxys chilhoweanus* Walcott, 1890, by original designation; from the Lower Cambrian (*Bonnia–Olenellus* Zone) Chilhowee Group, Tennessee, USA.

Isoxys sp.
Figure 6a–c

Material. Two specimens (FSL877034, FSL877035), from the Forêt des Soulanes de Nore, to the north of the small town of Villeneuve-Minervois, Montagne Noire, Aude (Fig. 1), Pardailhan Formation, Lower Cambrian.

Remarks. This elongate form (L:H ratio, excluding spines, *c*. 1.60) has two strongly developed, straight cardinal spines, lacks lobation and bears a finely reticulated external ornament. Its lateral outline is comparable to that of *Isoxys chilhoweanus* Walcott, 1890, *Isoxys auritus* Jiang *in* Luo *et al*. 1982 and *Isoxys zhurensis* Ivantsov, 1990 from the Lower Cambrian of Laurentia, China and Siberia, respectively (Williams, Siveter & Peel, 1996, Vannier & Chen, 2000). Its cardinal spines are shorter than those of *Isoxys volucris* from the Lower Cambrian of Greenland (Williams, Siveter & Peel, 1996). *Isoxys* sp. from the Montagne Noire shows an elliptical pit-like feature anterodorsally, a feature that may occur also in *Ixoxys auritus* (assumed 'muscle' spot: see Williams, Siveter & Peel, 1996, fig. 7).

The fossil record of *Isoxys* around the west Gondwanan margins is sparse. In addition to *Isoxys* sp. from the Montagne Noire, *Isoxys* is known to occur in Spain (Pedroche Formation, Ossa Morena: Richter & Richter, 1927), in rocks dated of Lower Ovetian age (= early Atdabanian; J. C. Gutierrez-Marco, pers. comm.). However, the unique specimen figured by Richter & Richter (1927) does not allow accurate comparisons with the French material.

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