



Fossil evidence in Australia for oldest known freshwater crayfish of Gondwana

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Abstract

Early Cretaceous body and trace fossils in Victoria, Australia, establish the oldest known presence of parastacid crayfish (Decapoda: Astacoidea, Parastacoidea) in freshwater environments of Australia, and the oldest known crayfish in Gondwana. Parastacid body fossils, comprised of a partial abdomen (*Palaeoechinastacus australianus*, gen. et sp. nov.) and two chelae, are from a fluvial deposit in the Otway Group (Albian). Trace fossils in fluvial deposits of the Otway Group and Strzelecki Group (Aptian) also closely resemble modern parastacid burrow systems, supplying independent verification of crayfish presence and their burrowing habits in Australia at this time. Paleoenvironments in this region were high-latitude and periglacial, indicating that these crayfish were adapted to cold-water ecosystems. The combined fossil evidence provides a starting point for the previously unknown paleoecology and evolutionary history of Mesozoic parastacids in Australia, while supporting phylogenies that suggest parastacid radiation from southeastern Australia before the complete breakup of Gondwana.

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1. Introduction

Freshwater crayfish likely diverged from marine lobsters (Nephropoidea) during the Permian or Triassic, resulting in their radiation and dispersal before the breakup of Pangaea (Crandall et al., 2000; Ah Yong and O'Meally, 2004; Schram and Dixon, 2004; Porter et al., 2005). Their subsequent spread in Mesozoic freshwater ecosystems, coupled with the separation of Laurasia and Gondwana, probably contributed to the divergence of the two superfamilies, Parastacoidea in the Southern Hemisphere, from Astacoidea, its Northern Hemisphere sister clade, during the Jurassic (Crandall et al., 2000; Rode and Babcock, 2003; Ah Yong and O'Meally, 2004). The evolutionary history of Southern

Hemisphere freshwater crayfish (Parastacidae) has vexed researchers since the 19th century, primarily because of their poor fossil record (Huxley, 1879; Sokol, 1987; Hasiotis, 2002; Rode and Babcock, 2003), but it is agreed that they radiated during the Early Cretaceous (Porter et al., 2005). This hypothesis, however, is only supported in the geologic record by Mesozoic astacoidean body fossils and trace fossils ascribed to astacoideans in former Laurasian continents (Kowalewski et al., 1998; Taylor et al., 1999; Shen et al., 2001; Rode and Babcock, 2003) and most recently, parastacoidean trace fossils interpreted from the Late Jurassic–Late Cretaceous of Argentina (Bedatou et al., 2008). In contrast, all previous reports of parastacid body fossils are of post-Mesozoic forms (Sokol, 1987; Aguirre-Urreta, 1992; Feldmann and Pole, 1994), and no parastacid trace fossils have been interpreted from Gondwanan continents other than South America (Hasiotis, 2002; Rode and Babcock, 2003; Bedatou et al., 2008).

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Here we describe the oldest known body fossils of parastacid crayfish of Gondwana and parastacid trace fossils in Early Cretaceous freshwater (fluvial) facies of Victoria, Australia. The body fossils, consisting of a partial abdomen (holotype for *Palaeoechinastacus australianus*, gen. et sp. nov.) and two chelae, are from the Otway Group (Albian), whereas the trace fossils are complex burrow systems in the Otway Group and Strzelecki Group (Aptian). The age range (about 106–116 Ma) and locations of these fossils indicate the first known links between Mesozoic lineages of parastacids and their descendants in southeastern Australia, while also more than doubling the previously documented geologic range for their body fossil record (Sokol, 1987; Hasiotis, 2002; Rode and Babcock, 2003). Additionally, the high-latitude, periglacial setting of this region of Australia during the Early Cretaceous (Gregory et al., 1989; Veevers et al., 1991; Constantine et al., 1998) indicates that these crayfish, like some modern parastacids, were adapted to and burrowing in cold-water ecosystems. These discoveries thus give novel perspectives on the early evolutionary history and paleoecology of Southern Hemisphere crayfish, particularly in Australia, where they are most abundant and diverse today (Riek, 1972; Hobbs, 1988; Crandall et al., 2000).

2. Geologic setting

The Otway and Strzelecki Groups crop out west and east of Melbourne, respectively, in extensive cliff-face and marine-platform exposures along the southern coast of Victoria (Fig. 1). The Otway and Strzelecki Groups are well known for their fossil vertebrates, e.g., labyrinthodonts, turtles, dinosaurs, and mammals; also common are terrestrial plants, such as bryophytes, pteridophytes, and conifers (Vickers-Rich et al., 1988; Wagstaff and McEwen-Mason, 1989; Rich et al., 1997, 2002, 2005). Most previously reported invertebrate body fossils consist of insects, but include branchiopods and other non-decapod crustaceans (Vickers-Rich et al., 1988, Rich et al., 2002). Rock types of the Otway and Strzelecki Groups are similar, consisting of mudstones, cross-bedded sandstones, clay-intraclast conglomerates, and thin coal beds, with considerable volcanoclastic content within most lithofacies (Constantine et al., 1998; Tosolini et al., 1999; Miller et al., 2002).

Sediments of the Otway and Strzelecki Groups were deposited in the Otway and Gippsland basins, respectively. Both formed as rift basins during extensional tectonics associated with initial separation of Australia from Antarctica during the Early Cretaceous (Tosolini et al., 1999; Miller et al., 2002; Veevers, 2006). Depositional environments included freshwater lakes and braided streams, the latter preserved as channel-fill and overbank deposits and composed of reworked mud and sand derived from nearby volcanic highlands (Vickers-Rich et al., 1988; Constantine et al., 1998). Depositional regimes were mostly high-energy and episodic, caused by flooding associated with seasonal thaws and volcanoclastic input (Vickers-Rich et al., 1988; Constantine et al., 1998; Tosolini et al., 1999). Periglacial conditions, with seasonal freezing and formation of permafrosts, are inferred for both groups. Paleolatitudes are estimated to have been $78 \pm 5^\circ$ S (Veevers et al., 1991), and mean annual air temperatures were

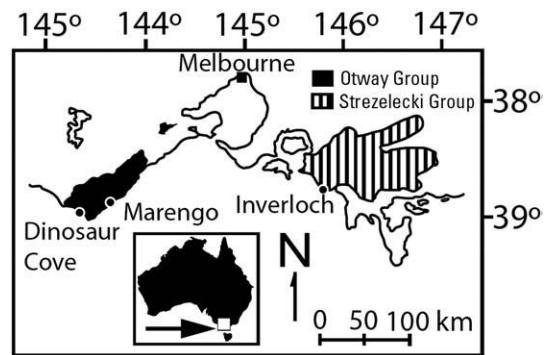


Fig. 1. Outcrop areas of Strzelecki and Otway Groups in Victoria, Australia, and localities of parastacid trace fossils (Flat Rocks site, Inverloch; Marengo) and body fossils (Dinosaur Cove). Field locations of the trace and body fossils, using latitude–longitude, are as follows: Flat Rocks (Bunurong Marine Park), $38^\circ 39' 42''$ S, $145^\circ 40' 49''$ E; Marengo (Marengo Beach), $38^\circ 46' 58''$ S, $143^\circ 39' 43''$ E; Dinosaur Cove (Slippery Rocks site), $38^\circ 46' 54''$ S, $143^\circ 24' 15''$ E.

likely within the range of -6° to $+5^\circ$ C, based on cryoturbation structures, oxygen isotopes, and paleogeography (Gregory et al., 1989; Wagstaff and McEwen-Mason, 1989; Constantine et al., 1998).

3. Fossil evidence of parastacid crayfish

3.1. Parastacid body fossils

3.1.1. Systematic paleontology

Decapoda Latreille, 1802
 Astacidea Latreille, 1802
 Parastacoidea Huxley, 1879
 Parastacidae Huxley, 1879

Palaeoechinastacus australianus gen. et sp. nov.

Etymology: The generic name comes from the Greek *palaeo* (*palaaios*), *echinos*, and *astacus*, meaning “ancient spiny crayfish”. The species name is “from Australia”.

Description of Holotype: NMV-P186041 (Fig. 2A–C) is a partial abdomen and is preserved in three dimensions, but with the abdomen crushed laterally. The specimen was damaged by a rock saw at the time of its discovery and later during preparation, but nonetheless retains important diagnostic features. Most of the right side of the specimen is exposed (Fig. 2A), and it consists of, distally to proximally: a telson and both right uropodal rami (mesial endopod and lateral exopod); six abdominal somites; four partially preserved pereopods (2–5); and a small posterior portion of the branchiostegite. Anatomical details observable on the specimen include: (1) overlapping of the posterior margin of each abdominal somite over the anterior margin of the succeeding somite; (2) a quadrate telson (Fig. 2B); and (3) small (less than 1 mm diameter), blunt, dorsolateral (D–L) spines, two on somite 2 and one on each of somites 3 and 4, evident on the left side (Fig. 2C) but not visible on the right. An irregularity akin to a transverse suture is discernable on the exopodal uropod, but no such feature can be seen on the endopod or telson. Likewise, longitudinal median carinae are evident on the uropodal endopod and exopod, but also may be artifacts of preservation. The pereopods are

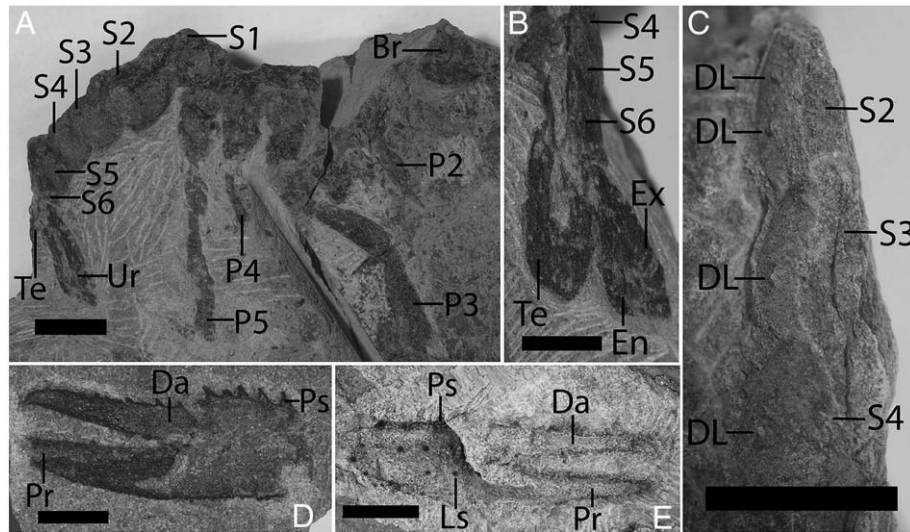


Fig. 2. Body fossils interpreted as parastacid crayfish from the Early Cretaceous Otway Group, Dinosaur Cove, Victoria, Australia. (A) NMV-P186041, dextral view of abdomen, showing abdominal somites (S1–6), partial tail-fan (right uropods, Ur, and telson, Te), branchiostegite (Br), and pereopods 2–5 (P2–P5). (B) Quadrate telson (Te), right uropodal endopod and exopods (En and Ex, respectively), and abdominal somites (S4–6). (C) Left-side abdominal somites (S2–4) showing positions of blunt dorsolateral (DL) spines on each. (D) NMV-P186042, left chela with propodus (Pr), dactylus (Da), and basal propodal spines (Ps); also note dactylar spines. (E) NMV-P186009, right chela, with propodus, dactylus, basal propodal spines, and depressions indicating former positions of lateral propodal spines (Ls) aligned in longitudinal rows. Scale bars = 10 mm.

insufficiently preserved to determine whether they are chelated. Detailed measurements of the specimen are provided in Appendix A.

Hypotypes, location, and horizon: The holotype and two other parastacid body fossils consist of two separate chelae (NMV-P186042 and NMV-P186009), neither of which are named, and are herein considered as hypotypes. All three body fossils were collected from a fine-grained lithic sandstone in the Otway Group at Dinosaur Cove, interpreted as a fluvial channel-lag deposit (Vickers-Rich et al., 1988; Rich and Vickers-Rich, 1989), and are stored at the National Museum of Victoria in Melbourne (Appendix A). Information recorded at the time of their cataloging does not allow us to assume that any of these three parts came from the same animal. Moreover, the chelae differ sufficiently to suggest they may have come from two species, but sexual dimorphism, dimorphic chelae within a species, or ontogenetic changes could also account for their dissimilarity. Regardless, because we cannot verify whether any of the three body fossils come from the same species, we only designate NMV-P186041 as the holotype for *P. australianus*. The chelae will not be regarded as paratypes and will remain unnamed until more body fossil material is found that can clarify any relations these may have to the holotype.

3.1.2. Additional parastacid body fossils (hypotypes)

A part and counterpart comprise NMV-P186042 (Fig. 2D), a left chela. The following description, unless indicated otherwise, deals with the part. The specimen is evident as a longitudinal section outlined by the preserved material, and comprises a dactylus and propodus. Cutting edges of the dactylus and propodus are irregular but nearly straight and separated, with the dactylus tip curving inward distally. Two denticles are on the proximal end of the cutting edge of the dactylus and one is

medial on the cutting edge of the propodal finger. Five large, mesial propodal spines and at least five small, mesial dactylar spines are present. The counterpart, derived from near the exterior of the chela, has two small (<1 mm diameter) elliptical depressions on the propodus and one on the dactylus that probably correspond to the positions of external spines. These depressions, however, do not match the number or arrangement of similar depressions on the other chela specimen.

NMV-P186009 (Fig. 2E) is a right chela (dorsal view), elongate, and comprised of a dactylus and propodus. The proximal part of the chela is preserved as the inside surface of the exoskeleton, whereas the distal part is preserved as a longitudinal section. The dactylus is preserved in an open position, forming a gap with the propodal finger distally. Three denticles are on the cutting edges, one distally on the propodal finger and two proximally on the dactylus. The lateral surface of the propodal palm shows three length-wise rows of three or four equidistant circular depressions (0.1–0.5 mm diameter) that likely correspond to the positions of external spines. Five large mesial propodal spines define the proximal margin of the specimen.

3.2. Parastacid trace fossils

The parastacid trace fossils were discovered as sandstone-filled tubular structures in cliffs and marine-platforms of the Strzelecki Group at the Flat Rocks site, then were observed later in marine-platform exposures of the Otway Group at Marengo. The best-defined structures are mostly horizontal, branching, and interconnecting tunnels, vertical shafts, and large chambers (Fig. 3). Sediments filling the structures are slightly coarser (medium-coarse sand), differently colored, and better cemented than their surrounding lithology. Lenticular sandstones overlie

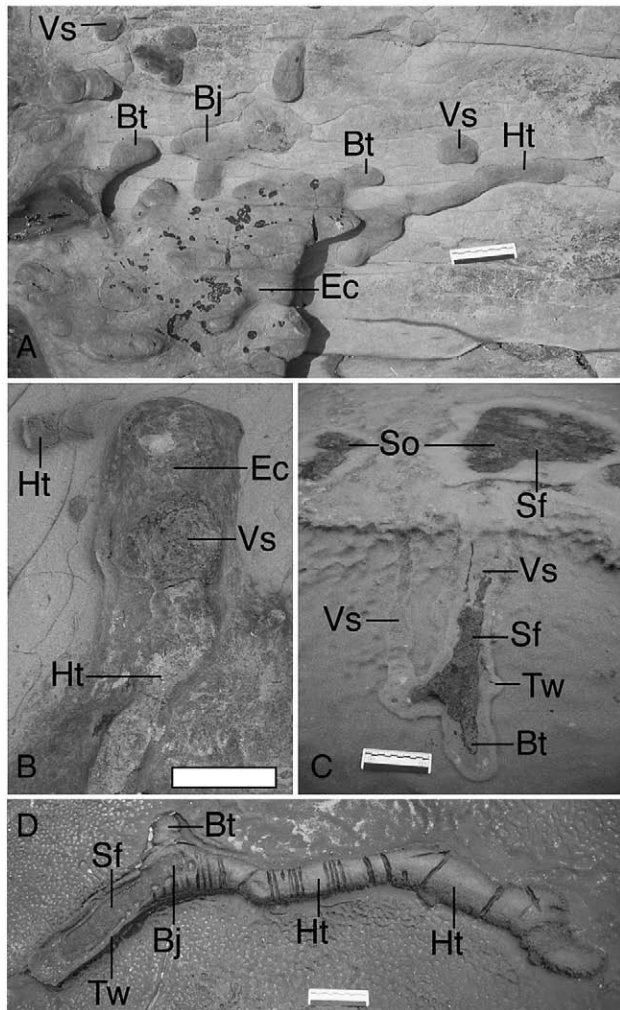


Fig. 3. Trace fossils interpreted as parastacid crayfish burrow systems in Early Cretaceous strata of Victoria, Australia. Key: Bj=burrow junctions, Bt=blind terminations, Ec=expansive chamber, Ht=horizontal tunnel, So=shaft opening, Tw=thickened wall, Vs=vertical shaft. (A) Burrow system showing expansive chamber, blind terminations, burrow junctions, horizontal tunnels, and openings to vertical shafts; bedding plane view, Strzelecki Group, Flat Rocks. (B) Expansive chamber showing interconnections with lower and upper horizontal tunnels and cross-section of vertical shaft; bedding plane view, Strzelecki Group, Flat Rocks. (C) U-shaped burrow with sediment fill differing from host lithology, shaft openings, thickened walls, and blind termination; vertical view in foreground, bedding plane in background; Otway Group, Marengo. (D) Segmented and branching horizontal tunnel with thickened walls, differing sediment fill, blind termination, segmentation, and burrow junction; transverse fractures are interpreted as secondary features of weathering; Otway Group, Marengo. Field scale or scale bars = 10 cm.

and link directly with the structures in places. Some specimens from the Otway Group have thickened, sandy walls distinctive from sediment fills. Lengths of horizontal tunnels were variable and some show segmentation. Some horizontal branches end abruptly in blind terminations, and most form enlarged bulbs or otherwise widen distally. Similar terminations are also observable in vertical sections.

Structure diameters were measured as widths of horizontal tunnels and cross-sections of vertical shafts to test for consistency in size and shape; both types of measurements were taken normal to their linear trends (Tables 1–2). A sample

Table 1
Measurements of burrow structures at Flat Rocks site (Inverloch), Strzelecki Group

(A)				
Specimen #	Width 1	Width 2	Horizontal	Vertical
1	4.7		X	
2	4.9		X	
3	4.6	5.1		X
4	3.9		X	
5	4.4	5.1		X
6	3.9	4.8		X
7	4.2	4.7		X
8	5.1	5.5		X
9	4.8		X	
10	5	5.6		X
11	5.9		X	
12	3.9	4.8		X
13	4.2	4.7		X
14	3.1	3.2		X
15	3.2	3.8		X
16	4.9		X	
17	5.1		X	
18	3.2		X	
19	5.1	5.3		X
20	3.7	4.1		X
21	4.3	4.9		X
22	4.8		X	
23	3.8		X	
24	3.9		X	
25	4.1		X	
26	3.7		X	
27	4.8		X	
28	3.8		X	
29	3.9		X	
30	4.8		X	
31	5.6		X	
32	4.8	5.1		X
33	4.9	5.2		X
34	5.1	5.6		X
35	4.6	5.2		X
36	4.1		X	
37	5.1		X	
38	4.9	5.4		X
39	4.9	5.5		X
40	2.9	3.4		X
41	5.4			X
42	4.5	5.1		X
43	4.5		X	
44	3.9		X	
45	6.1	7.2		X
46	4.8		X	
47	4.1		X	
48	4.1		X	
49	4.1	4.2		X
50	3.1		X	

(B)			
Specimen #	Width 1	Width 2	Ratio
3	4.6	5.1	0.90
5	4.4	5.1	0.86
6	3.9	4.8	0.81
7	4.2	4.7	0.89
8	5.1	5.5	0.93
10	5	5.6	0.89
12	3.9	4.8	0.81

Table 1 (continued)

(B)			
Specimen #	Width 1	Width 2	Ratio
13	4.2	4.7	0.89
14	3.1	3.2	0.97
15	3.2	3.8	0.84
19	5.1	5.3	0.96
20	3.7	4.1	0.90
21	4.3	4.9	0.88
32	4.8	5.1	0.94
33	4.9	5.2	0.94
34	5.1	5.6	0.91
35	4.6	5.2	0.88
38	4.9	5.4	0.91
39	4.9	5.5	0.89
40	2.9	3.4	0.85
42	4.5	5.1	0.88
45	6.1	7.2	0.85
49	4.1	4.2	0.98

(A) Measurements from this locality of horizontal and vertical expressions of burrows. Specimens with a single measurement (Width 1) are of horizontally oriented burrows (tunnels), with Width 1 as the maximum diameter normal to the horizontal length. Specimens with two widths (Width 1, 2) are cross-sections of vertical burrows (shafts), where Width 1 is the least diameter of the cross-section and Width 2 is perpendicular to this width; these measurements were taken normal to the vertical axis of the burrows. All measurements are in centimeters. (B) Measurements of mutually perpendicular cross-sections from vertically oriented burrows (shafts) used for calculations of circularity ratios, where Width 1/Width 2=circularity (with 1.0 as a perfect circle). Specimen numbers correspond to those in (A).

of horizontal structures from the Strzelecki Group had a mean and standard deviation of 4.4 ± 0.7 cm ($n=26$); vertical shaft cross-sections were similarly sized, with short and long dimensions of 4.4 ± 0.7 cm and 4.9 ± 0.8 cm, respectively ($n=23$). Shaft circularity based on these diameters had a mean of 0.9 ± 0.05 ($n=23$), with 1.0 as a perfect circle. A sample of horizontal diameters in the Otway Group (Marengo) indicated widths greater than those at Flat Rocks, 7.8 ± 1.3 cm ($n=20$), but circularity of vertical shaft cross-sections was virtually identical to that of the Strzelecki sample, despite their size differences: 0.9 ± 0.1 ($n=8$).

These structures are interpreted as fossil burrows, rather than physical or chemical sedimentary structures. This interpretation is supported by their regularity in size, forms matching those of documented fossil and modern burrow systems, and facies context. The closest ichnotaxonomic designation for most of the burrows is *Thalassinoides* Ehrenberg, 1944 based on their three-dimensional branching, enlargements at junctions and terminations, and lack of wall ornamentations noted in comparable trace fossils, e.g., *Ophiomorpha* Lundgren, 1891 (Frey et al., 1984; Goldring et al., 2007). A similar ichnogenus is *Camborygma* Hasiotis and Mitchell, 1993, which likewise has vertical shafts and horizontal branching networks and can intergrade with *Thalassinoides* (Zonneveld et al., 2000). The Strzelecki specimens, however, apparently lack external features diagnostic of *Camborygma*, such as scratch marks, body impressions, knobby surfaces, and thickened walls (Hasiotis and Mitchell, 1993; Hasiotis et al., 1999), although some Otway specimens have thickened walls and thus more closely resemble that ichnogenus

(Fig. 2C–D). Both the Otway and Strzelecki specimens exhibit extensive horizontal branching, blind chambers, and large horizontal chambers that interconnect with vertical and horizontal components, making the specimens more complex in overall geometry than parastacid trace fossils recently interpreted from the Late Jurassic–Late Cretaceous of Patagonia, Argentina (Bedatou et al., 2008).

Table 2

Measurements of burrow structures at Marengo Beach (Marengo), Otway Group

(A)				
Specimen #	Width 1	Width 2	Horizontal	Vertical
1	7.3		X	
2	7.1		X	
3	8.4		X	
4	7.3		X	
5	8.1		X	
6	8.2		X	
7	8.2		X	
8	5.8		X	
9	9.5		X	
10	9.1		X	
11	9.8		X	
12	8.2		X	
13	9.3		X	
14	7.1		X	
15	6.5		X	
16	6.1		X	
17	10.1		X	
18	7.3		X	
19	6		X	
20	6.1		X	
21	8.1	8.1		X
22	7.3	7.3		X
23	7.6	8.5		X
24	7.7	7.7		X
25	5.3	7.1		X
26	6.9	6.9		X
27	6.5	7.3		X
28	7.5	7.5		X

(B)			
Specimen #	Width 1	Width 2	Ratio
21	8.1	8.1	1.00
22	7.3	7.3	1.00
23	7.6	8.5	0.89
24	7.7	7.7	1.00
25	5.3	7.1	0.75
26	6.9	6.9	1.00
27	6.5	7.3	0.89
28	7.5	7.5	1.00

(A) Measurements from this locality of horizontal and vertical expressions of burrows. Specimens with a single measurement (Width 1) are of horizontally oriented burrows (tunnels), with Width 1 as the maximum diameter normal to the horizontal length. Specimens with two widths (Width 1, 2) are cross-sections of vertical burrows (shafts), where Width 1 is the least diameter of the cross-section and Width 2 is perpendicular to this width; these measurements were taken normal to the vertical axis of the burrows. Measurements were ordered with horizontally oriented specimens first (1–20), then vertically oriented specimens (21–28). All measurements are in centimeters. (B) Measurements of mutually perpendicular cross-sections from vertically oriented burrows (shafts) used for calculations of circularity ratios, where Width 1/Width 2=circularity (with 1.0 as a perfect circle). Specimen numbers correspond to those in (A).

4. Discussion

4.1. Paleontological significance of Australian parastacid body and trace fossils

Anatomical traits of the Otway body fossils, coupled with their occurrence in freshwater facies, rule out every decapod clade except Astacoidea. Additionally, morphological features of the trace fossils from the Strzelecki and Otway Groups are consistent with those of modern and fossil burrow networks attributed to decapods, and their occurrence in freshwater facies implies freshwater crayfish tracemakers. These body and trace fossils thus comprise independent lines of evidence supporting a presence of freshwater parastacid crayfish during the Early Cretaceous in southeastern Australia. The oldest previous parastacid body fossil was a single chela from the Paleocene of Queensland (Sokol, 1987), and parastacid trace fossils had been interpreted only very recently from the Late Jurassic–Late Cretaceous of Argentina (Bedatou et al., 2008). Our results thus more than double the minimum geologic range of parastacid crayfish body fossils to 106 Ma, and extend the geographic range of their trace fossils in Gondwana to Australia.

The Otway body fossils have well-defined propodal and dactylar spines, dorsolateral abdominal spines, and probable longitudinal carinae on the uropods, indicating that these are assignable to Parastacoidea and Parastacidae (Horwitz, 1990; Morgan, 1997). These body fossils represent the oldest known examples in Australia and any other former Gondwanan landmass. The presence of three body fossils, presumably from three separate individuals, also bodes well for future finds of more such body fossils in the Otway Group, particularly with these serving as new search images in strata that previously were the focus of vertebrate paleontology (Vickers-Rich et al., 1988; Rich and Vickers-Rich, 1989; Rich et al., 1997, 2002, 2005).

With regard to the trace fossils, decapods are interpreted as the probable tracemakers of *Thalassinoides* or similar fossil burrows in nearly every example from Mesozoic or Cenozoic deposits (Frey et al., 1984; Goldring et al., 2007). Moreover, *Thalassinoides*- or *Camborygma*-like burrow systems in freshwater environments are credited specifically to crayfish tracemakers (Kowalewski et al., 1998; Hasiotis et al., 1999; Zonneveld et al., 2000; Miller et al., 2001; Kim and Pickerell, 2002; Bedatou et al., 2008), hence we conclude that freshwater crayfish were the makers of the Otway and Strzelecki trace fossils.

Other than crayfish, the most likely alternative tracemakers for the Strzelecki and Otway trace fossils would have been similarly sized vertebrates, such as lungfish or tetrapods. For example, lungfish burrows are vertically oriented, can have enlarged terminations at their deepest points, and burrow diameters can overlap with those of crayfish (Hasiotis, 1990; Kowalewski et al., 1998; Hasiotis et al., 1999; Miller et al., 2001; Gobetz et al., 2006). This ichnological dilemma was encountered in a previous study relating to possible fossil evidence of Gondwanan crayfish, wherein Permian and Triassic trace fossils in Antarctica were interpreted initially as “crayfish burrows” (Babcock et al., 1998). These structures, however, were later evaluated as probable

therapsid burrows (Hasiotis et al., 1999; Miller et al., 2001). Consequently, we used previously outlined criteria for distinguishing crayfish-like or other invertebrate burrows from vertebrate burrows (Hasiotis et al., 1993, 1999; Miller et al., 2001; Groenewald et al., 2001; Hasiotis et al., 2004) and note that the Strzelecki and Otway trace fossils have: (1) two or more vertical shafts connecting to upper openings, sometimes forming a U-shape (e.g., Fig. 3C); (2) interconnecting vertical and horizontal components; (3) no spiraling in vertical components; (4) mostly horizontal branching; enlarged junctions between branches; (5) expanded chambers connected by smaller-diameter tunnels and shafts; (6) short, enlarged terminations in horizontal and vertical branches; and (7) near-circular cross-sections. Some decapod trace fossils (e.g., *Gyrolithes* de Saporta, 1884) and modern decapod burrows, however, spiral in vertical components (Goldring et al., 2007), but this trait is relatively more common in trace fossils interpreted as tetrapod burrows (Hasiotis et al., 2004, 2007; Varricchio et al., 2007). Moreover, tetrapod burrows normally have elliptical cross-sections; only one or (infrequently) two upper openings; are gently inclined (ramp-like) or spiraled; show little branching; and oftentimes have scratch marks representative of tetrapod appendages (Groenewald et al., 2001; Hasiotis et al., 2004, 2007). Lungfish burrows can also resemble those of crayfish or similar decapods in some respects, but these show no branching (Hasiotis, 1990; Hasiotis et al., 1993; Gobetz et al., 2006). In contrast, decapod burrows in general commonly have well-developed branching and expanded burrow junctions, a trait that also helps to distinguish these from burrows made by non-decapod invertebrates (Frey et al., 1984; Ekdale, 1992; Goldring et al., 2007). Lastly, Strzelecki and Otway Group strata also rarely show evidence of paleosols, with a few notable exceptions (Constantine et al., 1998), and most facies in each group likely represent braided-river and overbank deposits (Vickers-Rich et al., 1988; Rich et al., 1989; Rich et al., 1997). As a result, environments would have excluded many tetrapod burrows (Hasiotis et al., 2004, 2007), while being entirely appropriate for crayfish.

The Strzelecki and Otway trace fossils also overlap well in size and geometry with modern parastacid burrows. Most modern parastacids are primary or secondary burrowers, either staying in their burrows continuously or moving to construct burrows in accordance with seasonal changes (respectively); a few parastacids, however, are also tertiary burrowers, making burrows only when necessary (e.g., for breeding or during droughts) and staying above the water table (Richardson and Swain, 1980; Horwitz and Richardson, 1986; Hobbs, 1988; Hogger, 1988; Horwitz, 1990). Parastacid burrow systems range from the simple, unbranched tunnels of *Cherax destructor* Clark, 1936 to the branched and multi-chambered burrow systems made by *Cherax albidus* Clark, 1936 or species of *Engaeus* Erichson, 1846 or *Euastacus* Clark, 1936 (Richardson and Swain, 1980; Horwitz et al., 1985a,b; Horwitz and Richardson, 1986; Hobbs, 1988; Lawrence et al., 2001). Species of *Engaeus* can have two or more generations within the same burrow system, forming complex networks with interconnecting horizontal tunnels, vertical shafts, and expanded chambers (Richardson and Swain, 1980; Horwitz et al., 1985a,b; Horwitz and Richardson,

1986; Horwitz, 1990). Modern-day *Engaeus* systems are the most similar to the Strzelecki and Otway burrow systems.

Although some species of parastacids build burrows above the water table, the Strzelecki and Otway burrows were likely constructed below it, based on their predominantly horizontal elements (Horwitz et al., 1985a,b; Horwitz and Richardson, 1986; Hasiotis et al., 1999). Modern parastacid burrows can be classified as Type 1, 2, or 3 burrows; this classification is based on their occurrences in or near permanent water bodies, below the water table, or emergent environments, and corresponds with primary, secondary, and tertiary burrowers, respectively (Horwitz and Richardson, 1986). The interpretation of seasonally high-energy fluvial facies and overall humid paleoenvironments in the Strzelecki and Otway Groups (Vickers-Rich et al., 1988; Constantine et al., 1998; Tosolini et al., 1999; Rich et al., 2002) implies that crayfish burrows in such environments likely would have been either Type 1 or 2, depending on seasonality. In terms of their preservation, burrows at both Flat Rocks and Marengo were subjacent to lenticular sandstones and filled with sand connected directly to those beds, suggesting passive filling from above. Scouring of braided-stream bottoms likely eroded and exposed open burrows, which expanded burrow tops and allowed for easier filling. Sediment fills by fluvial channel and overbank sands thus probably preserved only the deepest parts of burrow networks; chimneys or other upper parts of burrows accordingly would have had low preservation potential. These lenticular sandstones and associated fine-grained muddy sandstones likely indicate edges of braided-river channels intergrading with overbank facies, which also would have been probable locations for parastacid burrows (Horwitz and Richardson, 1986).

4.2. Evolutionary and paleoecological significance of Australian body and trace fossils

Southeastern Australia represents the center of parastacid crayfish biodiversity (Riek, 1972; Hobbs, 1988; Crandall et al.,

2000), biogeographically connecting the Victorian body and trace fossils to parastacid phylogeny. An Early Cretaceous parastacid presence in Australia follows the oldest known astacoidean body fossils from the Late Jurassic of Laurasia (Taylor et al., 1999; Shen et al., 2001), the oldest interpreted parastacid trace fossils from the Late Jurassic of Argentina (Bedatou et al., 2008), and initial separation of Gondwanan landmasses, including Australia (Veevers et al., 1991; Miller et al., 2002). These Early Cretaceous parastacids in Australia, however, precede the complete splitting of Antarctica from Australia later in the Cretaceous (Veevers, 2006). Interestingly, the separation of Africa and India from Australia–Antarctica–South America, estimated at 132 Ma (Veevers, 2006), nearly coincides with the predicted radiation time of parastacids (134 Ma), the latter based on molecular phylogenies (Porter et al., 2005; Fig. 4). Present-day parastacids are absent from India and Africa (excepting Madagascar), which implies that parastacid radiation and dispersal may have happened in other Gondwanan landmasses through vicariance soon after separating. The evidence presented here does not necessarily confirm a parastacid origin in Victoria; nonetheless, other evidence, such as biogeography, biodiversity, and molecular-based phylogenies, also point toward this area as a long-time locus for this clade (Huxley, 1879; Riek, 1972; Austin, 1995; Crandall et al., 2000; Rode and Babcock, 2003; Ah Yong and O’Meally, 2004; Porter et al., 2005). In short, the Otway and Strzelecki fossil evidence fills a significant gap in the evolutionary history of freshwater crayfish in the Southern Hemisphere, and provide more evidence pertaining to hypotheses for crayfish dispersal through freshwater ecosystems in Gondwana before the complete separation of its landmasses.

The high-latitude settings of Early Cretaceous environments in the Otway and Gippsland Basins of Australia, as well as paleobotanical, sedimentological, and geochemical data, indicate mean annual air temperatures of -6 to $+5$ °C (Wagstaff and McEwen-Mason, 1989; Gregory et al., 1989; Veevers et al.,

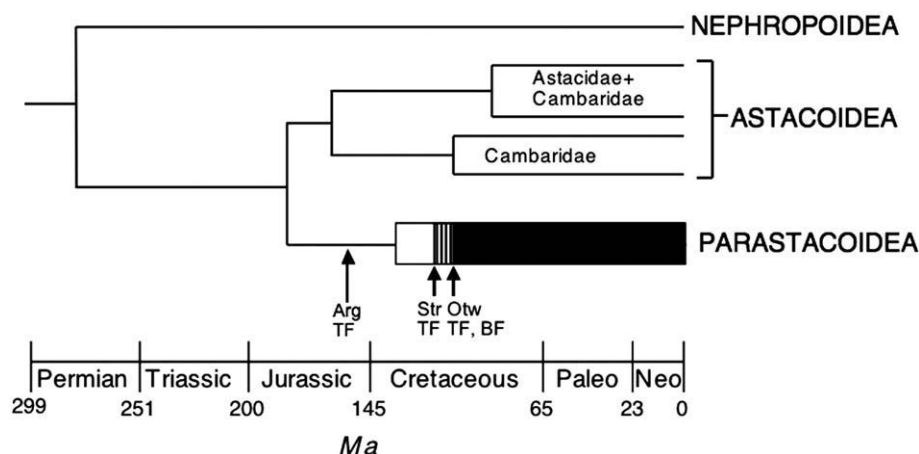


Fig. 4. Phylogeny of freshwater crayfish lineages incorporating new interpretation of minimum age for parastacoidean crayfish in Australia as Early Cretaceous, using fossil evidence (this study) in context of geologic time and inferred divergences and radiations. Radiation for Parastacoidea (Parastacidae) is interpreted as 134 Ma based on multi-locus phylogenetic analysis (Porter et al., 2005); Strzelecki Group trace fossils (Str TF) are estimated as 116 Ma, and Otway Group trace and body fossils (Otw TF, BF) are about 106 Ma, with dates based on palynological and fission-track analyses (Wagstaff and McEwen-Mason, 1989; Rich et al., 2005). In Parastacoidea lineage, vertical lines denote trace fossils and black indicates co-occurrence of body and trace fossils in Australia; oldest of Argentine trace fossils interpreted as parastacoidean burrows (Arg TF; Bedatou et al., 2008) are placed in Late Jurassic, before parastacid radiation.

1991), implying that crayfish in either basin must have been adapted for cold-water ecosystems. The parastacid trace fossils in this circumpolar setting indicate a potentially long history of burrowing in and otherwise living in cold-water ecosystems. Such adaptations are also seen in some modern species in southeastern Australia, parastacids elsewhere, and some Northern Hemisphere crayfish. For example, the astacid *Astacus astacus* Linnaeus, 1758, ranges as far north as 67°N in Finland, and some parastacid species live at about 46°S in New Zealand and Chile (Westman, 1973; Hobbs, 1988). *Austropotamobius pallipes* Lereboullet, 1858, also lives in streams at more than 1200 m elevation in Switzerland and France with winter temperatures of -2 to -4 °C (Laurent, 1988). *Pacifastacus leniusculus* Dana (1852), which lives in Lake Tahoe (Nevada, USA), occurs at nearly 1,900 m elevation (Goldman and Rundquist, 1977). Likewise, some parastacids (e.g., *Euastacus* and *Astacopsis* Huxley, 1878) are well established in cold-water rivers: *Euastacus* breeds in water temperatures of 5–10 °C and overwinters at below-freezing temperatures (Hogger, 1988). Furthermore, species of *Engaeus*, *Ombrastacoides*, Hansen and Richardson, 2006, and *Spinastacoides*, Hansen and Richardson, 2006, live in alpine Australia under seasonal snow cover at altitudes greater than 1000 m (Horwitz, 1990; Hansen and Richardson, 2006). Even in tropical regions, crayfish can be found in colder-water streams in alpine habitats: for example, species of the parastacid *Cherax* Erichson, 1846 occur at greater than 1500 m elevation in New Guinea (Hobbs, 1988).

As a result, the presence of parastacid body and trace fossils in a circumpolar setting during the Early Cretaceous is ecologically compatible with some modern species of crayfish. Bedatou et al. (2008) placed their interpreted parastacid burrows from the Late Jurassic–Late Cretaceous of Patagonia in a more temperate paleoenvironmental setting; moreover, the burrows they describe are mostly simple or Y-shaped vertical shafts, lacking the complex branching and large chambers exhibited by the Australian trace fossils. Hence the latter burrow systems may represent different burrowing strategies of Early Cretaceous crayfish in Australia, which also may reflect adaptations to cold-water climates. For example, crayfish burrows maintain narrower temperature ranges than at ground surfaces (Payette and McGaw, 2003), hence a burrowing habit could have aided survival during polar winters. Trace fossil assemblages from other formerly glaciated areas seemingly exhibit low ichnodiversity, further suggesting that infauna in some colder climates may have been limited by temperature-related factors (Bhattacharya and Bhattacharya, 2007).

One caveat in drawing such parallels with modern examples, however, is that milder global climates of the Early Cretaceous imply inexact correspondences between paleolatitudes and modern ranges of parastacid or other crayfish clades. The moderate fossil biodiversity of the Otway and Strzelecki Groups also connotes a faunal, floral, and paleoenvironmental situation that has no direct modern comparison (Rich et al., 2002). Nevertheless, our results supply another potential example of how circumpolar environments of Australia may have served as places of origin or sanctuaries for long-lived lineages once

shared with other Gondwanan landmasses during the Mesozoic (Vickers-Rich et al., 1988; Rich et al., 2002). Our conclusions also support similar proposals for high-latitude origins in the Southern Hemisphere for some invertebrate taxa, including decapods (Zinsmeister and Feldmann, 1984; Feldmann and Schweitzer, 2006), thus reinforcing the importance of high-latitude areas in evolutionary studies.

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Appendix A. Body fossil information

The body fossils are stored at the National Museum of Victoria (Melbourne) as NMV-P186041 (partial abdomen), NMV-P186042 (left chela), and NMV-P186009 (right chela). The specimens were originally collected in two field seasons at Dinosaur Cove, 1987 (NMV-P186009, NMV-P186041) and 1989 (NMV-P186042); they were catalogued and stored at the museum since their discovery. Unfortunately, no information was recorded about who specifically found each specimen, and inquiries with people who were on-site at Dinosaur Cove for each of those years did not yield any recollections.

Specimen labels associated with each read as follows: (1) “Specimen No. p.186009, Otway Group, Early Cretaceous, Slippery Rock East, Dinosaur Cove, Cape Otway, Victoria. Origin: T. Rich Exp. 1987, Field No. 287. 12-2-1987 [February 12, 1987]. (Cabinet 121), Loc. No. 2145”; (2) “Specimen No. p.186042 — arthropod (yabbie claws), Otway Group, Lower Cretaceous, Cross Tunnel, Slippery Rock site, Dinosaur Cove, Cape Otway, VIC. Loc. No. 2147. Origin: T. Rich Exp. 1989”;

(3) “Specimen No. p.186041 — arthropod (yabbie), Otway Group, Lower Cretaceous, Cross Tunnel, Slippery Rock site, Dinosaur Cove, Cape Otway, VIC. T. Rich Exp., 1987.” Examination of the specimens can be arranged by contacting either David Pickering or Rolf Schmidt, collection managers at the Museum of Victoria.

Measurements of some aspects of the body fossils were taken by AJM and related here. For NMV-P186041, the abdominal somites and telson have a combined length of 8.3 cm; hence the animal’s total body length was about 17 cm, assuming the abdomen represents half of this. The reconstructed width of somites 1–4 was consistently 1.8 cm, narrowing to 1.2 cm at segment 5. The single D–L spines on the abdominal segments were located in the last 1/3 (posterior portion) of somite lengths for somites 3 and 4, whereas the two D–L spines on somite 2 were equally spaced apart on somite 2. The telson is 19 mm long and 8 mm at its widest span, whereas the uropodal rami (exopod and endopod) together are 17 mm long and 8 mm at their widest (distal) ends (Fig. S8B). NMV-P186041 has a maximum length of 36.5 mm and width of 13.5 mm, where the propodus is 34 mm long and truncated slightly on its distal end, and the dactylus is 22.5 mm long and 2–5 mm wide. The cutting edges of the dactylus and propodus are separated distally by a gap of 5 mm. NMV-P186009 has a maximum length of 41.5 mm and length of 0.5 mm, and hence is more elongate than NMV-P186042. The dactylus is minimally 26 mm long and 2–6 mm wide, preserved in an open position, and thus forming a 4 mm-wide gap distally with the propodal finger.

Although NMV-P186041 and NMV-P186042 have sequential numbers, they are not thought to have come from the same individual animal. Indeed, their respective discoveries at Dinosaur Cove and subsequent cataloging were separated by two years. The numerical sequence is more likely related to their taxonomic similarity, which apparently was recognized by the person who did the original cataloging of the specimens, but unfortunately his or her identity is also not yet known.

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