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A unique winged euthycarcinoid from the Permian of Antarctica

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Abstract.—Euthycarcinoid arthropods (Cambrian–Triassic) were likely the first animals to transition from oceanic to freshwater and emergent environments. Although their basic bauplan is well known, they have a poor fossil record because their non-sclerotized exoskeleton was rarely preserved. Euthycarcinoids' unusual morphology (varying numbers of body segments, seemingly dichotomous possession of either mandibles or a labrum, specialized or generalized limbs, and possession by some euthycarcinoid species of sternal pores—structures possibly analogous to coxal vesicles in myriapods) contribute to uncertainty regarding their relationship to other arthropod groups; while their poor fossil record masks the evolutionary transitions within and between the separate realms they inhabited (marine, freshwater, emergent). A new euthycarcinoid from a Permian polar proglacial lake is described herein that is morphologically unlike all other euthycarcinoids, and interpreted as being well adapted for a nekton-benthic lifestyle. *Antarcticarcinus pagoda* n. gen. n. sp. possesses a pair of large wing-like processes that project laterally from the preabdominal dorsal exoskeleton. A trace fossil from the overlying Mackellar Formation, cf. *Orbiculichnus*, which was previously interpreted as having been produced by insects taking off or landing on wet sediments, is reinterpreted herein as being produced by *A. pagoda* n. gen. n. sp. due to the high degree of morphological similarity between traces and body fossils. This occurrence indicates that euthycarcinoids were able to adapt to life in temperate freshwater environments, while possible subaerial adaptations hint at an ability to breathe air. Indeed, if euthycarcinoids could breathe air, Cambrian terrestrial forays and rapid transition (by the Ordovician) into freshwater environments might be explained.

Introduction

Euthycarcinoids have suffered the indignity of many poorly known fossil groups—they have been shuffled from group to group as more taxa, and hence more characters, have been discovered. This is due to their extremely limited diversity (only 18 taxa distributed from Cambrian to Triassic deposits), low fossilization potential within their preferred habitats, their unusual morphology, seemingly dichotomous possession of either mandibles or a labrum (Schram and Rolfe, 1982; Edgecombe and Morgan, 1999; Racheboeuf et al., 2008), specialized or generalized limbs (Schram and Rolfe, 1982; Vaccari et al., 2004; Collette and Hagadorn, 2010), and possession by some taxa of sternal pores—structures possibly analogous to coxal vesicles in myriapods (Edgecombe and Morgan, 1999). Euthycarcinoids are of particular interest from an evolutionary perspective because they are morphologically similar to many enigmatic stem-group arthropods such as *Pisinnocaris subconigera* from the lower Cambrian Chengjiang Biota and, particularly, ?*Pisinnocaris* from the Hongjingshao Formation of Kunming, Yunnan Province, China (Hou and Bergström, 1998); because they transitioned from nearshore marine to freshwater environments (Racheboeuf et al., 2008); and because they may have been the first animals to make forays onto dry land in the Cambrian (MacNaughton et al., 2002; Collette and Hagadorn, 2010; Collette et al., 2010; Hagadorn et al., 2011). Recent hypotheses regarding euthycarcinoid relationships range from a close affinity with the Uniramia (= Myriapoda + Hexapoda [Edgecombe and Morgan, 1999]), the Myriapoda (McNamara and Trewin, 1993), the Branchiopoda (Wilson and Almond, 2001), or with the Hexapoda (Legg et al., 2013). While the genus- and species-level characters that define euthycarcinoid taxa vary substantially, grossly exaggerated or highly modified exoskeletal features have not thus far been reported, with the possible exception of *Arthrogyrinus platyurus*, a probable euthycarcinoid from the Permian that possesses a paddle-like, highly modified telson (Wilson and Almond, 2001). *Antarcticarcinus pagoda* n. gen. n. sp. is thus strikingly different from all other euthycarcinoid taxa in that it possesses a pair of large wing-like processes that project laterally from the preabdominal dorsal exoskeleton (see Fig. 1). Trace fossils from the overlying Mackellar Formation attributable to *A. pagoda* n. gen. n. sp. indicate that this taxon may have been nektonic, and that its stratigraphic range may include the entirety of the Pagoda

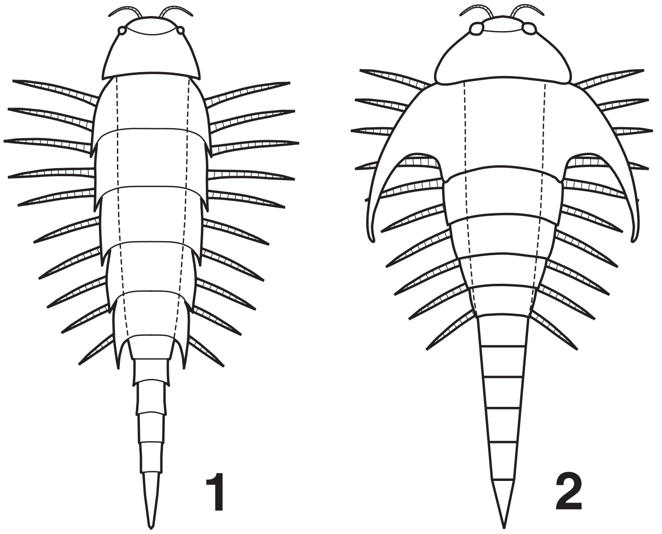

Figure 1. Generalized anatomy of euthycarcinoid arthropods and a comparison with morphology known of *Antarcticarcinus pagoda* n. gen. n. sp. (**1**) Generalized morphology of a euthycarcinoid based on the Devonian taxon *Heterocrania rhyniensis* (Anderson and Trewin, 2003) provided here for comparison with *A. pagoda* n. gen. n. sp. (**2**) Reconstruction of *Antarcticarcinus pagoda* n. gen. n. sp. based on material described herein.

and Mackellar formations. Discovery of *A. pagoda* n. gen. n. sp. is significant because it places euthycarcinoids among conchostracans and ostracodes as one of the earliest freshwater, lake-dwelling macroscopic animals known from high southern latitudes, and because it has interesting paleoecologic, paleoenvironmental, and taphonomic implications.

Locality and stratigraphy

Described specimens were collected during 1995 and 1997 from the lower Pagoda Formation along an arête extending east-northeast from the Mt. Butters massif, Shackleton Glacier area, central Transantarctic Mountains, Antarctica. In the central Transantarctic Mountains, the Pagoda Formation consists predominantly of massive diamictite beds (Isbell et al., 2001). In the lower Pagoda Formation at Mt. Butters, weakly stratified diamictite beds, clast-supported breccia beds, siltstone and sandstone beds, and lonestone-bearing fine-grained units are also present. Stratified diamictites and breccias are of inferred settling from suspension, ice-rafted debris and mass-flow origin (Miller, 1989; Miller and Collinson, 1994; Isbell et al., 2001). Siltstone and sandstone beds contain cross-laminations, symmetrical and interference ripples, and are interpreted to have been deposited in a shallow-water lacustrine environment (Isbell et al., 2001), while ice-crystal casts indicate syndepositional freeze-thaw cycles in the Pagoda Formation (Miller, 1989). Collectively, lithofacies evidence suggests that deposition of the lower part of the Pagoda Formation at Mt. Butters occurred in a glacially fed or ice-contact lake that developed approximately coevally with the late Paleozoic initial advance of the Gonwanide glaciers over the present day Shackleton Glacier area (Isbell et al., 2001).

The age of the Pagoda Formation at Mt. Butters is poorly constrained; the lower part of the formation could be latest Carboniferous (Gzelian) to earliest Permian (Asselian) (Babcock et al., 2002). Palynologic samples, including plant spores and pollen, recovered from a diamictite in the upper Pagoda Formation in the Nimrod Glacier area, Antarctica, indicate an early Permian age (Asselian–Tastubian) (Askin, 1998). The glacigenic Pagoda Formation is conformably overlain by late Permian interbedded shales and fine-grained sandstones of the post-glacial lacustrine Mackellar Formation (Miller and Collinson, 1994).

Pagoda Formation lacustrine biota

The euthycarcinoid described herein is a rare component of a low-diversity conchostracan-dominated lacustrine biota that occurs within the Pagoda Formation (Babcock et al., 2002). Euthycarcinoid remains co-occur with the conchostracan *Cyzicus* (*Lioestheria*) *shackletonensis* (Babcock et al., 2002, figs. 3, 4) in siltstone beds that comprise a series of coarsening-upward (siltstone to sandstone) sequences that are 0.75–2 m thick. Other fossils from this interval include small ostracodes and coalified wood fragments (Babcock et al., 2002). Trace fossils, predominantly shallow surface burrows and bilobed traces, typically extend subparallel to bedding (Isbell et al., 2001). Traces in the Pagoda Formation have a patchy lateral distribution, and include both small, bilobed traces with scratch marks (Miller and Smail, 1996) consistent with disruption of the sediment by conchostracans (Tasch, 1964), and slightly larger, *Palaeophycus*-like traces consistent with construction by vermiform animals (Isbell et al., 2001).

Materials and methods

Euthycarcinoid body fossil specimens described herein were immersed in ethanol and photographed through a Nikon SMZ800 stereomicroscope. Image acquisition was done with a Nikon D3100 digital SLR camera mounted to a Nikon P-IBSS2 camera mount. A circular polarizer was attached to the bottom of the objective lens. Illumination was provided by a studio strobe and fiber-optic illuminator that was equipped with a polarizing filter. Camera lucida drawings were done using a Nikon drawing tube attachment. Camera lucida drawings were scanned and traced in Adobe Illustrator. *Orbiculichnus* traces figured herein were supplied by Derek Briggs.

Repositories and institutional abbreviations.—Specimens described and illustrated here are housed in collections of the Paleontological Research Institution (PRI), Ithaca, New York; and the Burke Museum of the University of Washington (UWBM).

Systematic paleontology

Class Euthycarcinoidea Gall and Grauvogel, 1964
Genus *Antarcticarcinus* new genus

Type species.—*Antarcticarcinus pagoda* n. gen. n. sp. by monotypy.

Diagnosis.—Euthycarcinidea with a pair of dorsally located, long, laterally directed extensions of the anteriormost dorsal tergite.

Etymology.—Antarctica, referring to the discovery location; *carcinus*, from *karkinos* (Gr.), meaning crab.

Antarcticarcinus pagoda new species
Figures 2, 3

Holotype.—PRI 68571.

Diagnosis.—As for genus.

Etymology.—*pagoda*, referring to the Pagoda Formation, from which these specimens were recovered.

Occurrence.—Gray siltstone beds in the lower part of the Pagoda Formation (upper Carboniferous?–lower Permian) 4–4.5 m above the base of the Pagoda Formation (section F of Isbell et al., 2001), exposed adjacent to Mt. Butters, Shackleton Glacier area, central Transantarctic Mountains, Antarctica (84°51.7'S, 177°19.1'W).

Description.—Holotype 43.7 mm long, including head and preserved part of preabdomen, maximum width 45.2 mm. Head 10.8 mm long, 25.0 mm wide. Outline of head semicircular to subtrapezoidal; an inflection of head outline and possible sclerite posterior margin on holotype specimen indicate head may be composed of two sclerites. Posterolateral margins of presumed posterior cephalic tergite (PCT) acutely rounded. A pair of semi-circular eyes present near inferred junction of anterior cephalic tergite (ACT) and PCT. An axially oriented structure extends from anterior margin of ACT posteriorly, terminating in a bifurcation. A pair of mandibles (M in Fig. 2.2) appears to be present, defined by very low ridges of darker sediment. These structures are approximately square in outline, are distinctly separated along the ventral midline of the animal, and narrow slightly posterolaterally.

Number of dorsal tergites unknown; at least 3–4 preserved. Anteriormost dorsal tergite (T1) with large, prominent lateral processes (LP). Lateral processes long (axially) where they extend from T1, narrowing distally and posteriorly; anterolateral margins gently rounded, becoming nearly straight medially. Fragmentary specimens of LP indicate distal end slightly curved inward toward body, termination acuminate. Surface of LP covered with parallel, linear, closely spaced ornamentation. Posterolateral margin of T1 near 90°; extends anteriorly and adaxially in arcuate outline forming LP of T1.

At least five ventral sternites preserved in holotype specimen. Sternite 1 (S1) substantially longer (axially) than posterior sternites; sternites decrease in width posteriorly. Posterolateral sternal margins acutely rounded. Sternal pores not apparent.

Two or three partial limbs are preserved (LMB in Fig. 2.2). Limbs composed of 4–5 similarly sized box-like to irregularly shaped podomeres. Limbs appear uniramous, and appear to insert close to the ventral midline of trunk (Fig. 2.2). A possible disarticulated limb or antenna (ANT? in Fig. 2.2) is located adjacent to the posterior cephalic tergite; this appendage is composed of smaller, more gracile, boxlike elements. A possible

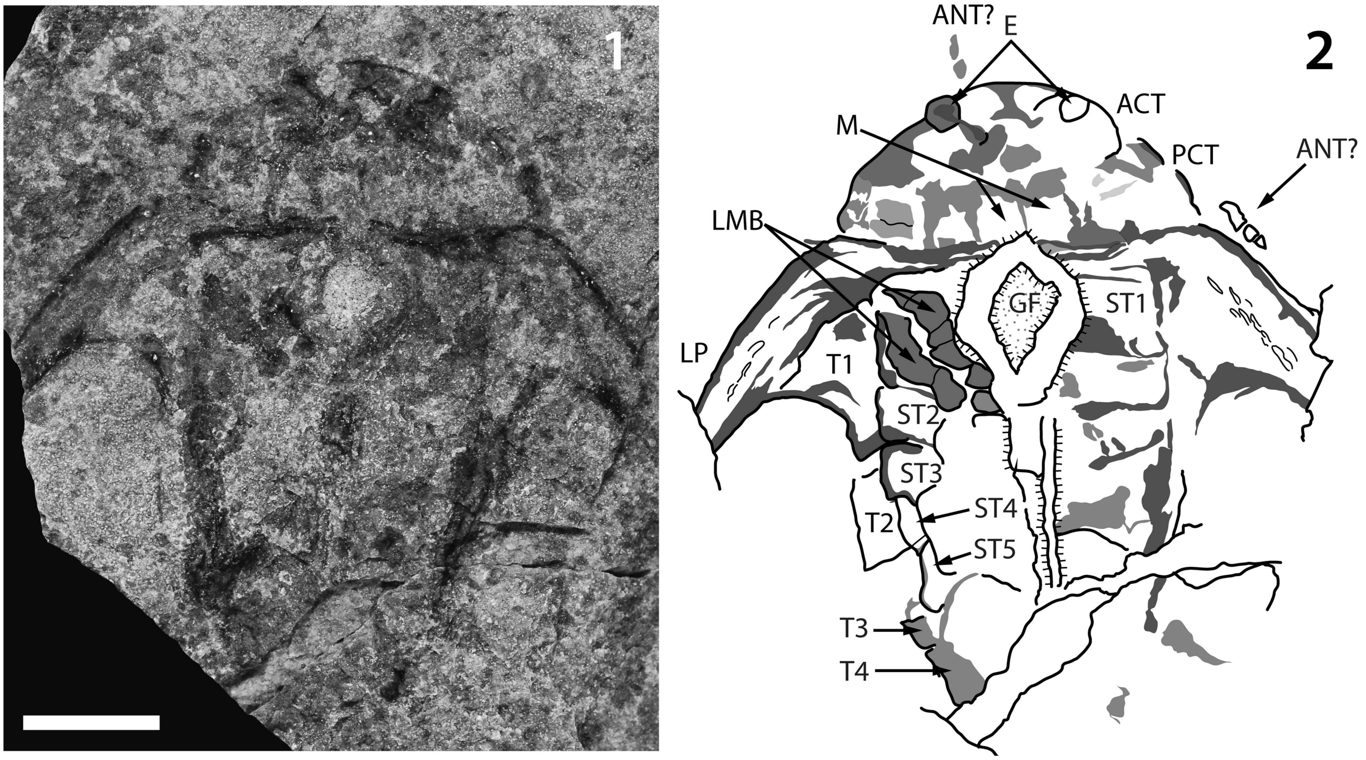

Figure 2. Holotype of *Antarcticarcinus pagoda* n. gen. n. sp. (**1**) PRI-68571, photographed immersed in ethanol under polarized light. Scale bar = 1 cm. (**2**) camera lucida drawing of PRI-68571. ANT? = possible antenna; LP = lateral process; E = eye; GF = gut fill; LMB = limb; M = possible mandibles; ST = ventral sternites; T = dorsal tergites.

antenna extends forward from the anterior cephalic tergite. No limb setae have been observed.

Raised, elliptical structure present immediately posterior to PCT; widest part of structure coincides with S1, narrows posteriorly; infill coarser than surrounding matrix. Postabdomen not preserved; holotype preserved in ventral aspect.

Remarks.—*Antarcticarcinus pagoda* n. gen. n. sp. is assignable to the Euthycarcinoidea by possession of a greater number of ventral sternites than dorsal tergites, uniramous appendages, possession of anterior and posterior cephalic tergites with a pair of spherical eyes located near the juncture of these plates, and a pair of mandibles. However, a direct comparison with other euthycarcinoid taxa is extremely difficult owing to the incomplete nature of the holotype of *A. pagoda* n. gen. n. sp. Overall, *A. pagoda* n. gen. n. sp. bears the greatest gross similarity with members of the family Euthycarcinidae Handlirsch, 1914 (i.e., genera *Euthycarcinus*, *Kottixerxes*, *Schramixerxes*, *Smithixerxes*, and *Synaustrus*). Problems with this placement include preservation of apparently only four dorsal tergites (T1–T4 in Fig. 2.2), although this is likely due to the incomplete nature of the holotype. Apparent limb podomeres beneath the preabdomen (LMB in Fig. 2.2) appear to be flattened; whether this flattening is due to taphonomy or to original morphology cannot be determined. Additionally, no limb setae have been observed. Within the family Euthycarcinidae, all members of the genera *Euthycarcinus*, *Kottixerxes*, and *Synaustrus* have slender, non-flattened, antennaeform appendages with setae (Gall and Grovagel, 1964; Schram and Rolfe, 1982; Schneider, 1983; Schultka, 1991; Edgecombe and Morgan, 1999). Of the remaining genera currently within Euthycarcinidae, *Schramixerxes* possess no setae on the limbs (Racheboeuf et al., 2008) and no information on limbs exists for *Smithixerxes* (Schram and Rolfe, 1982). Without any postabdominal information, and considering the incomplete nature of the holotype, we prefer to retain *Antarcticarcinus pagoda* n. gen. n. sp. in open nomenclature within the class Euthycarcinoidea.

Antarcticarcinus pagoda n. gen. n. sp. was originally described and interpreted as a freshwater decapod crustacean (crayfish) by Babcock et al. (1998). This attribution was based largely upon the texture of the single specimen that was known at that time (a single lateral processes as interpreted herein, PRI 68572, Fig. 3.1, 3.2) that was interpreted as a crayfish propodus or fixed finger (Babcock et al., 1998). Those authors further based their attribution upon burrows that were interpreted as having been constructed by crayfish that occur in the lower Triassic Fremouw Formation, which occurs several formational units above the Pagoda Formation (Babcock et al., 1998, fig. 2). Moreover, Fremouw traces occur in a completely different depositional setting—crevasse splay deposits laterally adjacent to floodplain deposits (Babcock et al., 1998).

Babcock et al. (1998) dissected crayfish and interpreted the rod-like, or closely spaced linear texture of the fossil lateral processes (Fig. 3.1, 3.2) as being similar to the cuticle of the modern crayfish genus *Procambarus*, but they did not indicate if further dissections were done with other groups of claw-bearing arthropods. Also, there was no indication in PRI 68572 of the 'teeth' mentioned in Babcock et al. (1998) when examined under a stereomicroscope, but the margin of the preserved portion of the cuticle does appear to have an irregularly fractured edge. Because of the articulated state of the anterior portion of the holotype of *A. pagoda* n. gen. n. sp. (PRI 68571), including the lateral processes, the decapod crustacean interpretation of the single isolated specimen (Babcock et al., 1998, fig. 3A) is no longer supported, and that specimen is transferred to *A. pagoda* n. gen. n. sp. herein.

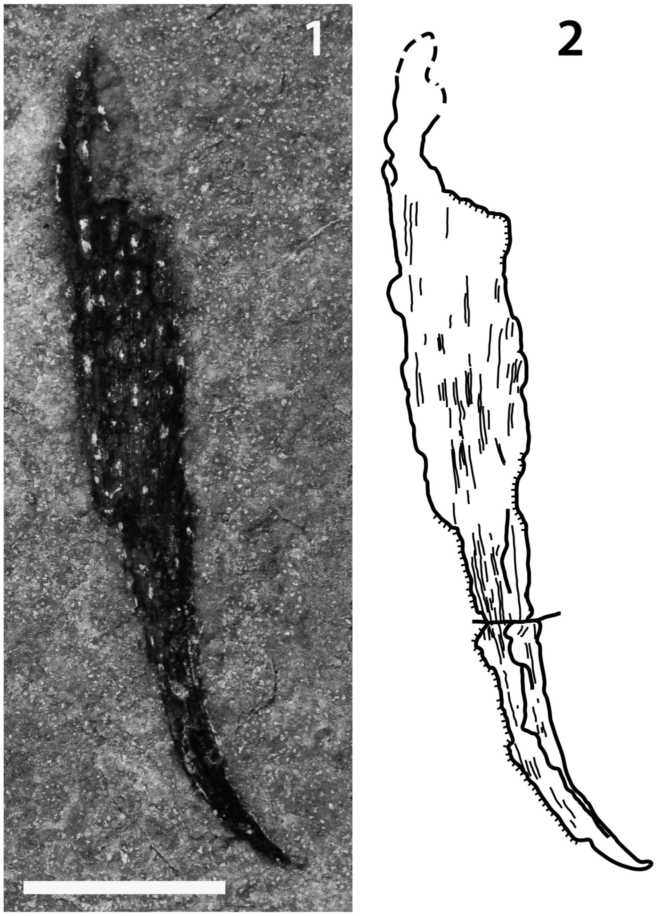

Figure 3. Disarticulated and isolated lateral process of *Antarcticarcinus pagoda* n. gen. n. sp. This specimen, which occurs on a small slab with no other remains present, was previously interpreted by Babcock et al. (1998) as a crayfish claw; compare with lateral process (LP) in Figure 2. (**1**) PRI-68572, showing texture. Photographed immersed in ethanol under polarized light. Scale bar = 1 cm. (**2**) interpretive drawing of PRI-68572.

Antarcticarcinus pagoda n. gen. n. sp. appears to have been well adapted for a lacustrine environment, with gross morphology consistent with a nektobenthic lifestyle. The large wing-like processes extending laterally from the trunk dorsal surface may have aided in stabilizing the animal on soft muds at the sediment-water interface, or in swimming for steering or lift rather than propulsion. Although many other euthycarcinoid taxa possessed spine-like extensions of the dorsal segments (McNamara and Trewin, 1993; Wilson and Almond, 2001; Racheboeuf et al., 2008), no other taxon has advancement of these features forward of the posterolateral corner of tergite, or the greatly exaggerated size of the lateral processes in *A. pagoda* n. gen. n. sp. A probable three-dimensional gut trace in the holotype is partially filled with sediment coarser than the surrounding matrix, indicating a possible deposit-feeding lifestyle.

Other material examined.—PRI 68572–68576: fragmentary remains including isolated lateral processes and unidentified sclerites. All specimens reposited at the Paleontological Research Institute, Ithaca, New York.

Paleoecology

Trace fossils from the Pagoda Formation are low diversity and relatively uncommon, but can be abundant on some bedding surfaces (Isbell et al., 2001). Arthropod-produced traces are represented by a single ichnogenus—*Isopodichnus*, which is a feeding trace generally attributed to concostracan crustaceans (Pollard, 1985). No arthropod-produced walking trails have been reported from the Pagoda Formation. However, *Diplichnites* and arthropod-produced resting traces attributed to cf. *Orbiculichnus* have been reported from the overlying Mackellar Formation at nearby Mt. Weeks (Briggs et al., 2010). The lower Permian Mackellar Formation is interpreted as representing a large post-glacial lake or lake complex, deposited in a basin that gradually filled as early Permian continental glaciers retreated (Lindsay, 1970; Miller and Collinson, 1994). Mackellar resting traces (Fig. 4) bear a distinct morphological resemblance to *A. pagoda* n. gen. n. sp. The anterior of cf. *Orbiculichnus* traces are rounded, corresponding with the head of *A. pagoda* n. gen. n. sp. (Fig. 4). The other traces are approximately T-shaped, with long, straight or slightly curved longitudinal axes.

Orbiculichnus traces were originally interpreted as having been produced by an insect jumping off of wet sediment surfaces (Briggs et al., 2010). Euthycarcinoids were considered as plausible tracemakers for Mackellar resting traces, but discounted because no euthycarcinoid was then known with morphology capable of producing the transverse structures of the resting traces (Briggs et al., 2010). Although no euthycarcinoid remains are currently known from the Mackellar

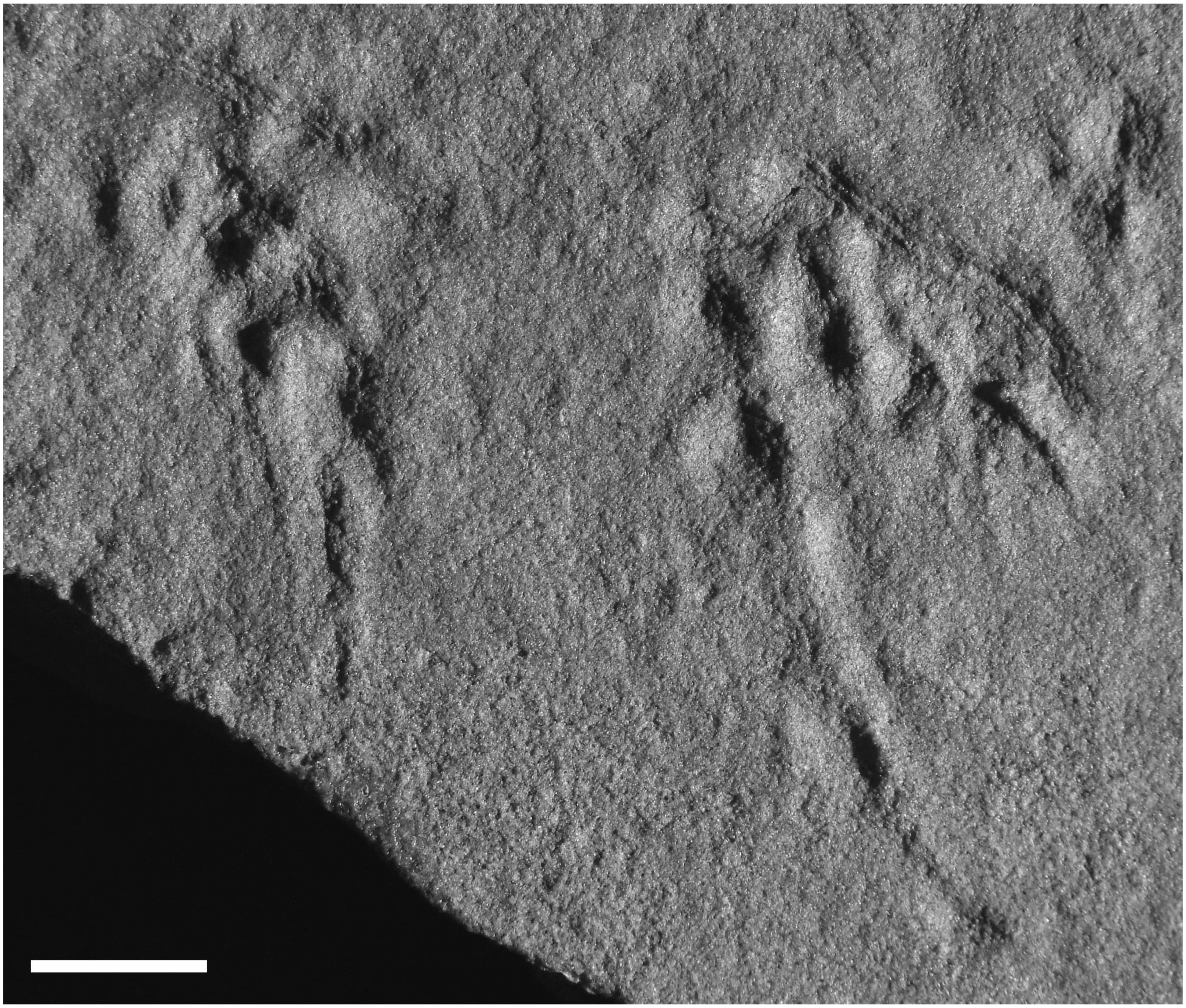

Figure 4. UWBM 98803, cf. *Orbiculichnus*, trace fossils interpreted to be produced by the euthycarcinoid *Antarcticarcinus pagoda* n. gen. n. sp. Scale bar = 1 cm. Photograph courtesy of Derek Briggs.

Formation, the very strong morphological similarities between trace and inferred tracemaker are striking. We thus reinterpret these impressions as having been produced by the long lateral T1 processes of *A. pagoda* n. gen. n. sp., while the long, posterior longitudinal groove would have been produced by the legless postabdomen and telson of *A. pagoda* n. gen. n. sp. (compare Figs. 1, 3 with the reconstruction of *A. pagoda* n. gen. n. sp. in Fig. 1). Additionally, the *Protichnites* and *Diplichnites* trackways on the surface figured in Briggs et al. (2010, fig. 3a) may have been produced by *Antarcticarcinus* n. gen. walking on the sediment surface because these ichnogenera have been associated with eutycarcinoids (MacNaughton et al., 2002; Collette et al., 2012).

All euthycarcinoid taxa except for the Middle Triassic *Synaustrus brookvalensis* occur from approximately 30°N to 30°S. Both *S. brookvalensis* and *A. pagoda* n. gen. n. sp. occur at approximately 85°S, but *S. brookvalensis* occurred during greenhouse Middle Triassic time, while *A. pagoda* n. gen. n. sp. inhabited an ice-dominated lake. As inhabitants of a polar lake supplied by seasonally introduced glacial meltwater, *A. pagoda* n. gen. n. sp. must have been capable of withstanding extremely cold temperatures. Abundant evidence shows that continental glaciation in southern Gondwana was extensive during the latest Paleozoic (Crowell, 1978, 1999, p. 28–39; Coates, 1986; Collinson and Elliot, 1986; Miller, 1989). Based on the inferred temperature tolerances of coexisting conchostracans (Tasch, 1964), water temperatures in the Pagoda lake may have reached approximately 10°C for several weeks each year. Trace fossils, whose margins are commonly indistinct, were probably constructed in soft, unfrozen muds (Miller and Smail, 1996). Wood fragments present in the Pagoda Formation at Mt. Butters imply the proximity of terrestrial vegetation requiring an environment that received enough sunlight and warmth seasonally to promote growth (Isbell et al., 2001). The occurrence of euthycarcinoids in low-diversity freshwater settings dominated by conchostracans is not unique to the Pagoda lake—*Euthycarcinus martensi* from Germany also co-occurs with conchostracans and few other animals (Schneider, 1983). Euthycarcinoids from the upper Carboniferous Mazon Creek (Schram and Rolfe, 1982) and Montceau-les-Mines (Rolfe et al., 1982; Schram and Rolfe, 1982; Schram and Rolfe, 1994) deposits co-occur with conchostracans, ostracodes, and numerous other taxa. Taken together, paleobiological and sedimentological evidence suggest periodic warming in high southern latitudes during the Permian (Isbell et al., 2001).

The extreme rarity of non-mineralized arthropod body fossils such as *A. pagoda* n. gen. n. sp. in these lacustrine deposits imply that: (1) difficult ecological conditions may have been limiting to many taxa, or (2) scavenging and/or microbial degradation proceeded rapidly due to limited resources. Remains of predaceous or scavenging animals are unknown from the Pagoda Formation, but trace-fossil evidence from the Mackellar Formation suggests that *A. pagoda* n. gen. n. sp. may not have been a rare animal because many cf. *Orbiculichnus* traces attributable to this taxon occur on a single small slab from Mt. Weeks (Briggs et al., 2010).

The occurrence of *Antarcticarcinus pagoda* n. gen. n. sp. in a polar lacustrine setting indicates that euthycarcinoids may have been more successful and geographically widespread than previously thought. All known euthycarcinoids occur in shallow, emergent, nearshore, or lacustrine environments (Racheboeuf et al., 2008), and with the exceptions of *A. pagoda* n. gen. n. sp. and *Arthrogyrinus platyurus* (Wilson and Almond, 2001) from the Carboniferous of the UK, most do not have adaptations specific to an aquatic lifestyle. Together with their dispersed paleobiogeographic distribution, and very limited number of occurrences, this begs the question of whether euthycarcinoids were truly aquatic organisms, or whether perhaps they may have been amphibious. A pair of ventral exoskeletal sternal pores per preabdominal sternite is closely associated with internal tube-like structures in many euthycarcinoid taxa (Schram, 1971; Edgecombe and Morgan, 1999; Anderson and Trewin, 2003, p. 482, text-fig. 12; Vaccari et al., 2004). Such an arrangement of external openings and internal tubes is strikingly similar to the respiratory system in millipedes where a pair of respiratory spiracles per segment opens internally to a branched tracheal tree for distribution of gasses to tissues (Clarke, 1973, p. 101). Others have posited that the sternal pores could be coxal vesicles associated with eversible sacs of the type present in myriapods (Edgecombe and Morgan, 1999), where these structures are associated with moisture uptake (Clarke, 1973, p. 56). Either of these interpretations for euthycarcinoid sternal pores argues for an amphibious or subaerial lifestyle. Considering these interpretations, together with abundant trace-fossil evidence indicating subaerial euthycarcinoid activity (McNamara and Trewin, 1993; MacNaughton et al., 2002; Vaccari et al., 2004; Collette and Hagadorn, 2010; Collette et al., 2012), the absence of euthycarcinoid remains in offshore deposits, it is possible that euthycarcinoids had developed the ability to breathe air by Cambrian time, and that they adopted an amphibious lifestyle thereafter.

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