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Cambrian origins and affinities of an enigmatic fossil group of arthropods

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Euthycarcinoids are one of the most enigmatic arthropod groups, having been assigned to nearly all major clades of Arthropoda. Recent work has endorsed closest relationships with crustaceans¹ or a myriapod–hexapod assemblage², a basal position in the Euarthropoda³, or a placement in the Hexapoda⁴ or hexapod stem group⁵. Euthycarcinoids are known from 13 species ranging in age from Late Ordovician or Early Silurian to Middle Triassic, all in freshwater or brackish water environments⁶. Here we describe a euthycarcinoid from marine strata in Argentina dating from the latest Cambrian period, extending the group's record back as much as 50 million years. Despite its antiquity and marine occurrence, the Cambrian species demonstrates that morphological details were conserved in the transition to fresh water. Trackways in the same unit as the euthycarcinoid strengthen arguments that similar traces of subaerial origin from Cambro-Ordovician rocks were made by euthycarcinoids^{7,8}. Large mandibles in euthycarcinoids^{6,9} are confirmed by the Cambrian species. A morphology-based phylogeny resolves euthycarcinoids as stem-group Mandibulata, sister to the Myriapoda and Crustacea plus Hexapoda.

Mandibulata Snodgrass, 1938

Euthycarcinoidea Gall and Grauvogel, 1964

Euthycarciniformes Starobogatov, 1988

Apankura gen. nov.

Etymology. *Apankura* (Quechua), meaning crab.

Type species. *Apankura machu* gen. et sp. nov.

Diagnosis. Euthycarciniform with large mandibles that occupy most of the space beneath the posterior cephalic tergite; anterior two pairs of pre-abdominal limbs smaller than the posterior nine pairs; limbs markedly taper distally, composed of about ten podomeres, distal podomeres are shorter, large setae are absent; at least six post-abdominal segments; post-abdominal tergites are each about 2.5-times wider than they are long.

Apankura machu sp. nov.

Etymology. Genus as above; *machu* (Quechua), meaning grandfather.

Holotype. Museo de Geología, Mineralogía y Paleontología, Universidad Nacional de Jujuy (JUY-P 24; Fig. 1).

Locality and horizon. Bed of Río Huasamayo, Garganta del Diablo, near Tilcara, Jujuy Province, Argentina. The holotype (the only known specimen) is in greenish-grey mudstone from the Casa Colorada Member, Santa Rosita Formation. The trilobites *Neoparabolina frequens argentina* and *Plicatolina scalpta* on the same slab indicate a latest Cambrian age (lower part of *Neoparabolina frequens argentina* zone)¹⁰. Green shales of the Casa Colorada Member represent lower offshore deposition in an open marine facies¹¹.

Diagnosis. As for genus.

The holotype is 38 mm long, including the head, pre-abdomen and six segments of the post-abdomen. The maximum width of the pre-abdominal tergites is 16 mm. As in other euthycarcinoids^{2,12}, the head is composed of a short anterior tergite and a longer, wider posterior tergite. The latter is trapezoidal, with gently curved lateral margins. The antenna is uniramous, with at least nine short articles. Large, well-defined spheroidal processes¹³ are at the lateral margin

of the head just in front of the juncture between the cephalic tergites. These processes are transversely ovoid, about as long as the anterior cephalic tergite. A pair of large, subquadrate appendages that occupies much of the space beneath the posterior cephalic tergite is interpreted as the mandible. Dark pigmentation at their inner margins suggests enhanced sclerotization and possibly dentition on the gnathal lobe. The mandible shows no evidence of subdivision of its gnathal lobe, and a palp is lacking. Immediately posterior to the mandible, patches of dark pigmentation are concentrated medially, probably corresponding to pigment strips called a buccal complex in *Euthycarcinus*⁹. In the latter, this complex resembles a setose hypopharynx. No post-mandibular oral appendages can be discerned.

The pre-abdomen has five tergites of varying length and width; the lengths increase in size from T1 to T4, with T5 about as long as T2. Their posterolateral corners appear to be blunt angulations, without spinose posterior projections. The pre-abdominal limbs are uniramous, with the posterior nine extending distally well beyond the tergal margins after flattening; anterior to these are two pairs of shorter appendages of similar form. A total of 11 pre-abdominal limbs matches other Euthycarciniformes^{9,13,14}. The limbs markedly taper distally, terminating in a spinose tip, with at least nine podomeres discerned in the best-preserved limb. The total number including the coxa may be as few as ten. The podomeres shorten distally, none of them bearing robust setae as known in some other euthycarcinoids^{6,9,13,14}. Eleven pairs of elongate, curved apodemal rods^{2,9} are preserved as dark pigment, originating near the limb

bases, and are directed posteromedially with variable degrees of rotation. Transverse anterior and posterior margins of sternites are defined across the medial third of the pre-abdomen. The lateral margins of the sternites are obscure, but given the equivalent widths of the pre-abdominal sternites and the post-abdominal segments in other euthycarcinoids, the widths of the sternites of *Apankura* are on average about 3.3 times greater than the lengths. The post-abdomen lacks appendages, and gently narrows in width posteriorly. Six segments are preserved, the width of each being about 2.5 times greater than the length. The post-abdomen is incompletely preserved posteriorly, and we infer the presence of a telson. The gut is preserved in the post-abdomen as a narrow tube with fine black fill. A band of gut filling at the posterior end of the specimen may be expelled faecal matter. A circular structure slightly offset from mid-width of the second post-abdominal segment is of uncertain identity, although a gonopore is a possibility.

Members of the Euthycarcinoidea have the following characters shared with *Apankura*: spheroidal processes at the lateral edge of the articulation between a short anterior cephalic tergite and longer posterior cephalic tergite; mandibles beneath the posterior cephalic tergite, with the mandible apparently lacking a palp; trunk tagmosis into a pedigerous pre-abdomen and a narrow, limbless post-abdomen; multiple wide sternites associated with each pre-abdominal tergite, where the ratio of sternites per tergite increases posteriorly, with decoupling of the tergal and sternal segmentation; antenniform pre-abdominal limbs with short segments; a slender, curved apodeme originating near each pre-abdominal limb base.

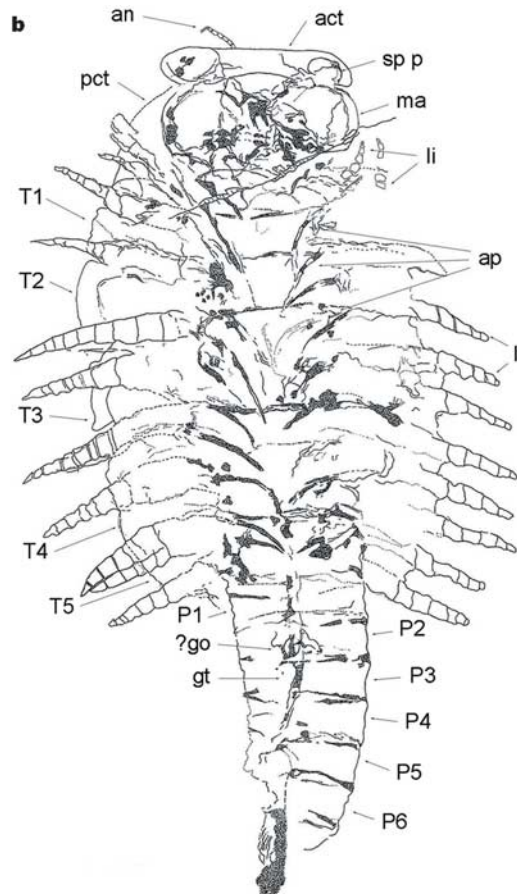


Figure 1 Holotype of *Apankura machu*. **a**, JUY-P24. Scale bar, 5 mm. **b**, Interpretative drawing of JUY-P24. act, anterior cephalic tergite; an, antenna; ap, apodemal rod; ?go, possible gonopore; gt, gut; li, limbs; ma, mandible; pct, posterior cephalic tergite;

sp p, spheroidal process; T1–T5, pre-abdominal tergites 1–5; P1–P6, post-abdominal segments 1–6.

Eleven pre-abdominal sternites, legs and apodemes and five pre-abdominal tergites are shared with other Euthycarciniformes^{9,13}. *Apankura* is unique in having reduced anterior pre-abdominal limbs, relatively few podomeres in the limbs, and at least six post-abdominal segments, versus five in the Devonian/Carboniferous Kottyxerxidae and four in the Carboniferous/Triassic Euthycarcinidae.

The presence of mandibles as the sole gnathal appendage in euthycarcinoids is indicated by the Devonian *Heterocrania*⁶ and the Carboniferous/Triassic *Euthycarcinus*^{9,14}. The mandibles of *Apankura* are of the same size as those reconstructed for *Heterocrania*⁶, and similarly occupy most of the posterior cephalic tergite (Fig. 2). A single mandibular origin in myriapods, hexapods and crustaceans (the Mandibulata) is supported by similarities in morphology and gene expression^{15,16}. Molecular data variably either support monophyly of Mandibulata¹⁷, and implicitly the homology of mandibles, or unite myriapods with chelicerates rather than with hexapods and crustaceans^{18,19}.

The phylogenetic position of euthycarcinoids in the Arthropoda was evaluated by means of a matrix of 337 morphological characters (see Supplementary Information), of which euthycarcinoids can be scored for 70. Analysis with equal weights resolves euthycarcinoids either as a sister group to extant Mandibulata or as a sister group to Crustacea or Hexapoda within the Tetraconata (that is, Crustacea + Hexapoda)²⁰. Successive approximations²¹ and implied²² weighting select a subset of the equally weighted cladograms in which euthycarcinoids form a sister group with Myriapoda and Tetraconata (Fig. 3). With this hypothesis, crown-group mandibulates are united by having the post-mandibular appendage modified as a first maxilla. The stem-group mandibulate clade that includes euthycarcinoids is united by the mandible. Characters shared by myriapods and euthycarcinoids, such as palpless mandibles and coxal–sternal articulation of the trunk limbs, map basally for Mandibulata. Other apomorphies of Mandibulata, such as a four-celled crystalline cone and inter-ommatidial pigment cells²³, cannot be evaluated in fossils, and whether they define the

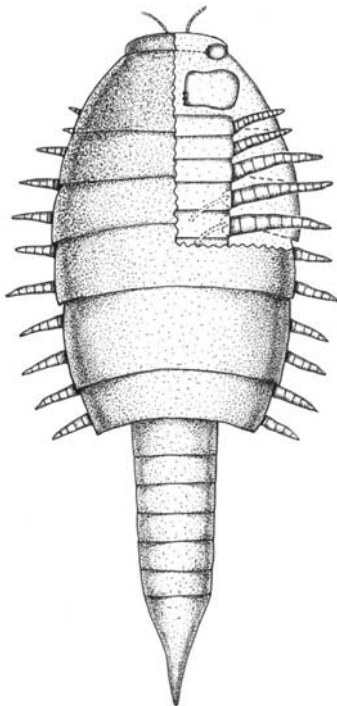


Figure 2 Reconstruction of *Apankura machu* in dorsal view, with ventral structures exposed in a cutaway view of the right side.

mandibulate crown-group or also include the stem-group is unknown.

Although *Apankura* provides by far the oldest body fossil record of euthycarcinoids, trace fossils from Late Cambrian or Early Ordovician aeolian sandstones have been ascribed to an amphibious arthropod, possibly a euthycarcinoid⁷. Traces similar to the “type 2” trackway⁷ attributed to euthycarcinoids occur in the same unit as the holotype of *Apankura machu* (the Casa Colorada Member, at Quebrada Ruspasca; Fig. 4). The trackways are found in a mudstone and combined-flow rippled sandstone facies deposited in an upper offshore setting¹¹. The maximum preserved extent of the trackways is 12 cm long and up to 4 cm wide. At its deepest impression, the external width of the trackway is 35 mm, with its internal width²⁴

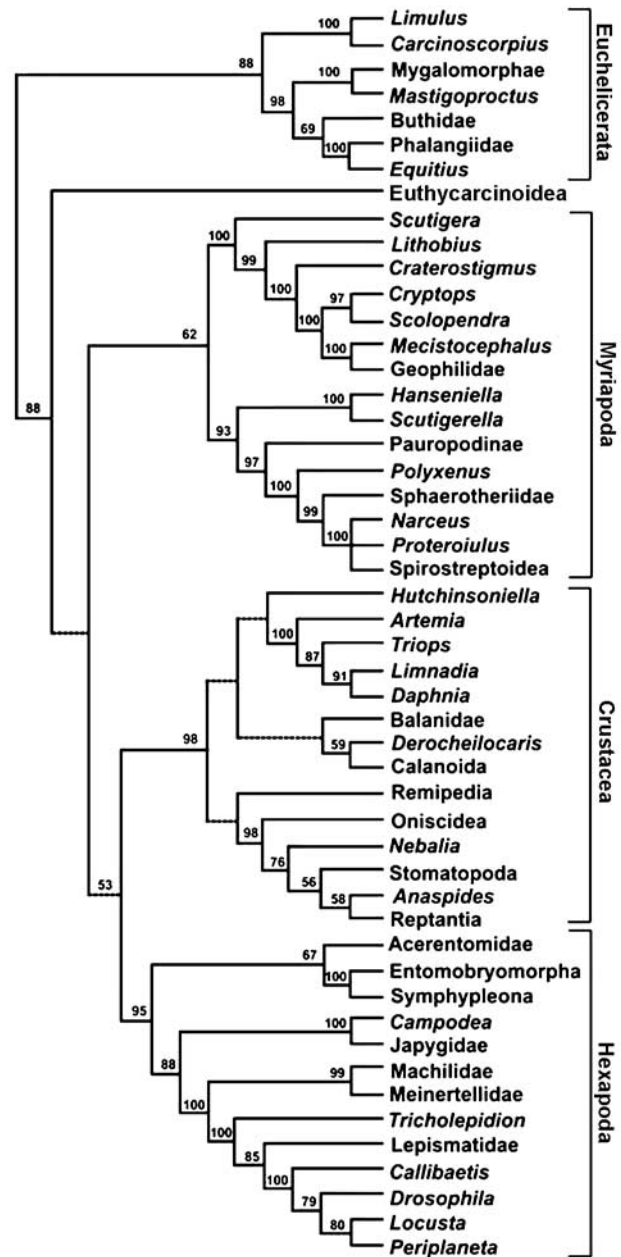


Figure 3 Strict consensus of the nine shortest cladograms for euthycarcinoids and extant Euarthropoda favoured by successive weights and implied weights for concavity functions $k = 1$ to $k = 6$. Internal nodes indicated by dashed lines are collapsed in some of the 297 shortest cladograms with equal weights (673 steps, consistency index 0.63, retention index 0.86). Numbers at nodes are jack-knife frequencies above 50% with equal weights.

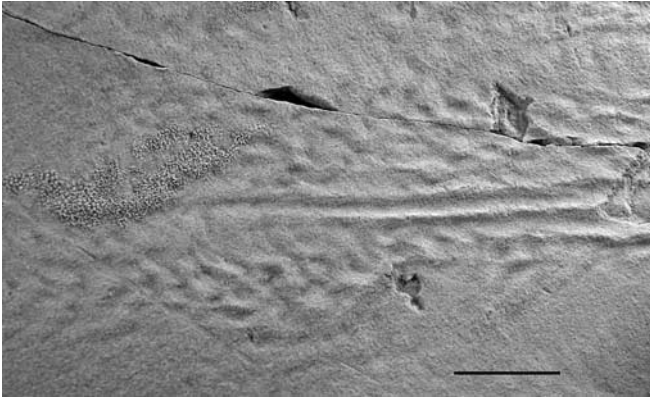


Figure 4 Trackway from the Casa Colorada Member, JUJ-P 25. Scale bar, 20 mm.

being 12 mm. Imprints are obliquely elongate and too diffuse to determine an imprint series. A well-defined internal continuous mark²⁴ 5 mm wide corresponds to the telson. The presence of euthycarcinoid body fossils in the Casa Colorada Member strengthens the case of a euthycarcinoid origin for this type of trackway. Arguments that other Cambro-Ordovician trackways of possible euthycarcinoid origin were made subaerially^{7,8} signal an important role for this group in arthropod terrestrialization. □

Methods

Phylogenetic analysis

Data include 337 characters from external morphology, internal anatomy, ultrastructure, gene order and gene expression (Supplementary Information) for 52 extant arthropod terminals and the extinct clade Euthycarcinoidea. Cladograms are rooted with tardigrades and onychophorans as out-groups to Euarthropoda. A heuristic search with PAUP*4.0b10 used 10,000 random stepwise addition sequences, saving five trees per replicate, with swapping on those trees with TBR branch swapping. Multi-state taxa were scored as variable. Successive approximations weighting was implemented using the rescaled consistency indices (RCI) from the equally weighted analysis, and subjected to the same heuristic search procedures. Implied weighting explored clade sensitivity across concavity functions $k = 1-6$, with a heuristic search. Node support was assessed by 1,000 parsimony jack-knife replicates using 33% deletion.

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Social parasitism by male-producing reproductive workers in a eusocial insect

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The evolution of extreme cooperation, as found in eusocial insects (those with a worker caste), is potentially undermined by selfish reproduction among group members^{1–3}. In some eusocial Hymenoptera (ants, bees and wasps), workers can produce male offspring from unfertilized eggs⁴. Kin selection theory predicts levels of worker reproduction as a function of the relatedness structure of the workers’ natal colony and the colony-level costs of worker reproduction^{5,6}. However, the theory has been only partially successful in explaining levels of worker reproduction^{7–9}. Here we show that workers of a eusocial bumble bee (*Bombus terrestris*) enter unrelated, conspecific colonies in which they then produce adult male offspring, and that such socially parasitic workers reproduce earlier and are significantly more reproductive and aggressive than resident workers that reproduce within their own colonies. Explaining levels of worker reproduction, and hence the potential of worker selfishness to undermine the evolution of cooperation, will therefore require more than simply a consideration of the kin-selected interests of resident workers. It will also require knowledge of the full set of reproductive options available to workers, including intraspecific social parasitism.

Bombus terrestris is a common Palaearctic bumble bee with an annual colony cycle, one queen per colony and single queen mating^{10–12}. Colony-level productivity costs of worker reproduction seem to be absent or low¹³. Under these conditions, kin selection theory predicts extensive male production by workers, as well as queen–worker and worker–worker conflict over worker reproduc-