

Pristinaspinidae, a new family of Cretaceous kiwaiform stem-lineage squat lobster (Anomura, Chirostyloidea)

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Key words – Squat lobster, *Kiwa*, Kiwaidae, *Pristinaspina*, fossil.

The chirostyloid squat lobster *Pristinaspina gelasina* from the Upper Cretaceous of Alaska is most closely related to members of the genus *Kiwa* (Kiwaidae) as indicated by the presence of supraocular spines, a medially carinate rostrum and similar carapace groove patterns. Evidence from morphology, stratigraphic position and molecular divergence estimates of extant chirostyloids supports its position in the stem of Kiwaidae. *Pristinaspina*, however, also differs significantly from kiwaidae and is here assigned to a new family, Pristinaspinidae. The chief distinction between the free-living pristinaspins and vent- or seep-associated kiwaidae (and an important synapomorphy of the latter) is the enlargement of the metabranchial regions in kiwaidae, which meet in the mid-line and separate the cardiac region from the intestinal region. The enlarged metabranchial regions of kiwaidae may have improved respiration in poorly oxygenated, chemosynthetically affected waters. This appears to track a major shift in the deep-water ecology of kiwaiform squat lobsters, that is, the movement into chemosynthetic habitats.

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Introduction

The phylogeny of the Anomura has received a great deal of attention in recent years, resulting in significant changes to our understanding of the evolution of the group and to its classification, especially of the marine squat lobsters (Ah Yong *et al.*, 2009; Schnabel *et al.*, 2011; Tsang *et al.*, 2011; Bracken-Grissom *et al.*, 2013). Recent revisions of the squat lobster system (Schnabel & Ah Yong, 2010; Ah Yong *et al.*, 2011) recognise two major superfamilies: Galatheoidea Samouelle, 1819 and Chirostyloidea Ortmann, 1892. Moreover, the squat lobsters had long been considered a single, phylogenetically unified group, but the aforementioned phylogenetic studies have shown that the galatheoids and chirostyloids are not sister groups, but appear to have convergently evolved a similar body form. The Chirostyloidea, containing Chirostyliidae Ortmann, 1892, Eumunididae A. Milne-Edwards & Bouvier, 1900 and Kiwaidae Macpherson, Jones & Segonzac, 2005, is phylogenetically nearest to the aegloids and lomisooids.

Although the Recent chirostyloids are highly speciose (Baba *et al.*, 2008), the fossil record is presently poor, being known only from two species, *Pristinaspina gelasina* Schweitzer & Feldmann, 2000 (Upper Cretaceous of Alaska) and *Eouropytychus montemargensis* De Angeli & Ceccon, 2012 (Eocene of northern Italy). *Eouropytychus* corresponds to the current concept of Chirostylidae, but the position of *Pristinaspina* is less clear. *Pristinaspina* was originally and appropriately placed in Chirostylidae (Schweitzer & Feldmann, 2000) under the prevailing concept of the family. With the revised understanding of the Chirostylidae, however, *Pristinaspina* cannot be readily accommodated there, with its supraorbital spines, broad, medially carinate rostrum and well-marked branchiocardiac grooves with well-defined branchial regions. Chirostylids always lack supraocular spines and a median carina on the rostrum. Unlike eumunidids, *Pristinaspina* has neither a spiniform rostrum nor a transversely striated carapace. The broad, carinate rostrum, presence of supraocular spines and well-defined branchiocardiac grooves of the carapace of *Pristinaspina*, however, are shared by members of the Kiwaidae. Although *Pristinaspina gelasina* is closest to the kiwaidae, it nevertheless has important differences in carapace groove patterns. A new family is recognised herein to accommodate *Pristinaspina*. We are pleased to dedicate this study to Pál Müller (Budapest), in recognition of his major contributions to the palaeontology of decapod crustaceans.

Systematic palaeontology

Superfamily Chirostyloidea Ortmann, 1892

Family Pristinaspinidae nov.

Type genus – *Pristinaspina* Schweitzer & Feldmann, 2000.

Stratigraphic range – Late Cretaceous (Cenomanian-Maastrichtian).

Diagnosis – Carapace elongate, margins broadly tapering, widest at metabranchial regions; surface regularly dimpled, without transverse striae or dorsal spines, regions clearly defined. Rostrum well developed, triangular, with distinct median carina. Supraorbital spines slender, well developed. Carapace margins spinose, with 3 hepatic marginal spines posterior to supraocular spines, 2 spines on anterior epibranchial margins, 1 metabranchial spine at base of branchiocardiac groove. Cervical groove well defined, demarcating gastrohepatic region. Metagastric region subquadrate, anterior concave. Branchiocardiac grooves well marked, clearly defining wide, swollen metabranchial regions. Anterior part of branchiocardiac groove subparallel to cervical groove, between them enclosing triangular mesobranchial and epibranchial regions; epibranchial region slightly larger and more swollen than mesobranchial region. Cardiac and intestinal regions fused, hourglass shaped, anteriorly as wide as metagastric region, separating metabranchial regions.

Remarks – Pristinaspinidae fam. nov. and Kiwaidae are unique among chirostyloids in having swollen branchial regions with well-defined branchiocardiac grooves and a broad, medially carinate rostrum. In other chirostyloids, the branchial regions are flat and ill- or undefined, and the rostrum lacks a median carina. The overall carapace re-

gionalisation of pristinaspinids and kiwaid is similar, albeit somewhat less pronounced in the latter. The chief distinction between pristinaspinids and kiwaid (and an important synapomorphy of the latter) is the great proportional width of the metabranchial regions in kiwaid, which are more expanded and meet in the midline, separating the cardiac region from the intestinal region. Conversely, the metabranchial regions in pristinaspinids, although wide, are clearly separated by the fused cardiac and intestinal regions. Pristinaspinidae further differs from Kiwaidae in having subparallel, rather than strongly divergent cervical and branchiocardiac grooves; mesobranchial regions slightly smaller, rather than markedly smaller than the epibranchial regions; and prominently spinose rather than unarmed lateral carapace margins. For comparison with Pristinaspinidae, a parallel diagnosis of Kiwaidae based on dorsal carapace characters is given below.

Shared morphological features between pristinaspinids and kiwaid, along with stratigraphic position of *P. gelasina* (Pl. 1, fig. 1), support placement of Pristinaspinidae in the stem-lineage of Kiwaidae, although a position in the chirostylid + kiwaid stem would also be possible (Ahyong *et al.*, 2011). Divergence-time estimates based on multi-gene phylogenetic analysis, however, suggest that the common ancestor of Chirostylidae and Kiwaidae diverged during the Early to mid-Cretaceous, predating the first appearance of Pristinaspinidae, and estimated divergence times of Kiwaidae are post-Cretaceous (Roterman *et al.*, 2013). Thus, combined evidence from morphology, stratigraphy and molecular divergence best places Pristinispinidae in the stem-lineage of Kiwaidae, supporting a kiwaiform clade. The former presence of *Pristinaspina* in deep water along the North Pacific Rim, in combination with the present distributions of the majority of extant species of *Kiwa*, suggests that kiwaid may have evolved in deep water along the eastern Pacific margin during the late Paleogene or early Neogene (Roterman *et al.*, 2013).

Pristinaspina gelasina was recovered from Upper Cretaceous (Cenomanian-Maastrichtian) non-chemosynthetic, siliciclastic deposits in Alaska. These deposits from the deep continental slope have associated thalassinidean remains but no corals, indicating that the palaeohabitat was a soft substrate, probably sand or mud (Schweitzer & Feldmann, 2000). Thus, *P. gelasina* was probably free living, neither associated with live coral, like chirostylids and eumunidids (Kilgour & Shirley, 2008; Le Guilloux *et al.*, 2010), nor chemosynthetic habitats, like modern kiwaid (Roterman *et al.*, 2013). The relatively swollen branchial regions of Pristinaspinidae compared to most other squat lobsters (apart from Kiwaidae and the munidids, *Cervimunida* and *Pleuroncodes* in the eastern Pacific), however, could indicate that the kiwaiforms may already have been more tolerant of less oxic conditions prior to the move by kiwaid to chemosynthetic habitats, such as those found at continental slope oxygen minimum zones, which today are widespread in the East Pacific (Levin *et al.*, 2010).

All known species of *Kiwa* (Pl. 1, figs. 2-5) occur in chemosynthetic habitats, whether cold methane seeps or hydrothermal vents, and have fields of specialised setae used to 'farm' sulfur-reducing bacteria on which the animal feeds (Thurber *et al.*, 2011). The phylogeny of the few known species of *Kiwa* is consistent with a possible transition from cold seep to hydrothermal vents. Together with identification of the free-living Pristinaspinidae as part of the kiwaid stem, the ecological transition from soft sediment (Pristinaspinidae) to chemosynthetic habitat (Kiwaidae), with a seeming progression

from cold seep to hydrothermal vent, is plausible and parallels patterns seen in vestimentiferan tubeworms and mytilid bivalves (Halanych, 2005; Jones *et al.*, 2006). Whether kiwaidids did move from seep to vent, or *vice versa*, however, remains to be tested through discovery of additional species of *Kiwa*, although the distinction between seep and vent endemism may be less well defined in this family, based on the similarity in ectosymbionts found on seep and vent kiwaidids (Goffredi, 2010; Thurber *et al.*, 2011). Regardless of the precise mode of transition, the late Paleogene/early Neogene radiation of Kiwaidae, possibly in the East Pacific, is contemporary with the subduction of active spreading ridges under the North American Plate (Meschede & Barckhausen, 2001; Madsen *et al.*, 2006; Schellart *et al.*, 2010), where methane seeps, hydrothermal vents and non-chemosynthetic continental slope habitats are likely to have been in very close proximity.

Either way, the ecological transition into arguably more extreme habitats might account for the further expansion of the branchial regions in kiwaidids as a means of improving respiration in poorly oxygenated chemosynthetically affected waters. Thus, the key morphological synapomorphy that separates Pristinaspinidae from Kiwaidae appears to track a major shift in the deep-water ecology of these animals, that is, the movement into chemosynthetic habitats. It is worth mentioning that the late Paleogene/early Neogene radiation of Kiwaidae (Roterman *et al.*, 2013) coincides with a dramatic drop in the carbonate compensation depth in the equatorial Pacific at the Eocene/Oligocene transition (Pälike *et al.*, 2012), possibly indicating that prior to this event, there may have been insufficient ambient oxygen levels in the Pacific deep-sea for Kiwaidae to inhabit vent and seep habitats. It has already been suggested that the Paleocene/Eocene Thermal Maximum (PETM), a period characterised by a poorly ventilated deep-sea may have been responsible for the widespread extinction of vent and seep-associated megafauna, with present-day diversity the consequence of subsequent radiations (Vrijenhoek, 2013). The radiation of Kiwaidae ~ 17 million years after this event (Roterman *et al.*, 2013), possibly later than other vent and seep endemic faunas such as vestimentiferan tubeworms (Vrijenhoek, 2013) may signify a greater sensitivity of kiwaidids to ambient oxygen levels than many other chemosynthetic taxa, as evidenced by the morphological adaptations that differentiate Kiwaidae from Pristinaspinidae. Indeed, the indication, based on molecular divergences, that the other vent and seep-endemic decapod crustaceans (Bresiliidae and Bythograeidae) may also have radiated in these habitats more recently than many other taxa (Shank *et al.*, 1999; Vrijenhoek, 2013) raises the possibility that decapods as a whole are possibly evolutionarily constrained by the internal placement of their branchiae under the carapace, thus limiting the potential surface area for efficient gas exchange required in poorly oxygenated conditions.

At present, the fossil record of clades neighbouring the chirostyloids is sparse. Lomisoids, endemic to southeastern Australia, have no known fossil record. Along with *Pristinaspina*, however, aegloid fossils are all from modern Pacific localities. Just as many other decapods originated at high latitudes during the Cretaceous (Feldmann & Schweitzer, 2006), pristinaspinids and aegloids may have high-latitude origins in the north and south, respectively. That both pristinaspinids and aegloids have Cretaceous fossil records only from modern Pacific localities points to a palaeo-Pacific rather than Tethyan origin for the chirostyloid-aegloid-lomisoid clade (Ahyong *et al.*, 2011).

Kiwaidae Macpherson, Jones & Segonzac, 2005

Type genus – *Kiwa* Macpherson, Jones & Segonzac, 2005, by original designation (monotypy).

Stratigraphic range – Recent.

Diagnosis – Carapace elongate, margins broadly tapering, widest at metabranchial regions; surface smooth or pitted, without transverse striae or dorsal spines, regions defined. Rostrum well developed, triangular to linguiform, with median carina. Supraorbital spines short. Carapace margins unarmed. Cervical groove well defined, demarcating gastrohepatic region. Metagastric region subtrapezoid, anteriorly and posteriorly concave. Branchiocardiac grooves well marked, defining wide, swollen metabranchial regions; transverse or slightly inclined anteriorly either side of midline, always oblique to cervical groove. Subtriangular mesobranchial and polygonal epibranchial regions. Epibranchial region markedly larger than mesobranchial region. Cardiac region subtriangular, as long as or longer than wide, anterior margin convex; intestinal region triangular, markedly wider than long. Cardiac and intestinal regions separated by medially confluent metabranchial regions.

Remarks – This family contains only the type genus, *Kiwa*, with two described species, *K. puravida* Thurber, Jones & Schnabel, 2011 (Galapagos Rift; Pl. 1, fig. 2) and *K. hirsuta* Macpherson, Jones & Segonzac, 2005 (Pacific-Antarctic Ridge; Pl. 1, fig. 3), with one undescribed species from the East Scotia Ridge (Pl. 1, fig. 4; see Rogers *et al.*, 2012) and possibly another from the Southwest Indian Ridge (Pl. 1, fig. 5; see Roterman *et al.*, 2013).

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Plate 1

Pristinaspinidae

Fig. 1. *Pristinaspina gelasina* Schweitzer & Feldmann, 2000, line drawing of carapace based on the type lot from the Cenomanian-Maastrichtian of Alaska (after Schweitzer & Feldmann, 2000, fig. 9).

Kiwaidae

Fig. 2. *Kiwa puravida* Thurber, Jones & Schnabel, 2011, male holotype.

Fig. 3. *Kiwa hirsuta* Macpherson, Jones & Segonzac, 2005, male holotype (A. Fifis/IFREMER, courtesy of M. Segonzac).

Fig. 4. *Kiwa* sp., East Scotia Ridge.

Fig. 5. *Kiwa* sp., southwest Indian Ridge.

Scale bars equal 2 mm (Fig. 1) and 10 mm (Figs. 2-5).

