

Two new Early Pliocene species of the crab genus *Hyas* Leach, 1814 (Majoidea, Oregoniidae) from northeast Japan

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Two new species of the oregoniid crab genus *Hyas* are described from the Lower Pliocene of northern Japan, *H. chippubetsuensis* sp. nov. from the Chippubetsu Formation exposed along the Tadoshi River (Fukagawa City, central Hokkaido) and *H. tentokujiensis* sp. nov. from the Tentokuji Formation at Daisen City (central part of Akita Prefecture). These two new taxa both have a densely tuberculate carapace and strongly vaulted dorsal regions. Another extinct congener in the northeast Pacific region, *Hyas tsuchidai* Imaizumi, 1952, from the Upper Miocene Wakkanai Formation of northern Hokkaido, Japan.

The earliest fossil record of the genus *Hyas* is from the 'lower Badenian' (Langhian, early Middle Miocene) of Austria. If *Hyas* originated in the Paratethys prior to the Middle Miocene, descendants migrated into the Pacific region by the Late Miocene and diversified during Late Miocene to Pliocene time in cool-water environments. The dispersal route of the genus might be linked to palaeobiogeographical constraints imposed by the timing of the opening of the Bering Strait.

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Introduction

The oregoniid crab genus *Hyas* Leach, 1814 comprises five extant species (Ng *et al.*, 2008) in middle- to high-latitude, shallow-marine to upper bathyal environments in the northern hemisphere. They occur mainly in the northeast and northwest Atlantic, along the coasts of central to northern Europe, in the North Sea, Arctic Ocean, the North Pacific from northern Japan to Oregon through the Aleutian Islands and Alaska, the Bering Sea, the Sea of Okhotsk, the Sea of Japan and the East China Sea southwards to Shanghai (Rathbun, 1925; Sakai, 1976; Williams, 1984).

Despite the wide geographical range of the modern species, the fossil record of the genus is sporadic. Except for records of fossil representatives of extant *Hyas araneus*

(Linnaeus, 1758) from the Pleistocene of England and Norway (Danielsen, 1909; Bell, 1921), extinct species of the genus include *H. meridionalis* Glaessner, 1928 from the 'Badenian' (= lower Langhian) of Austria, *H. oranensis* Van Straelen, 1936 from the Upper Miocene of Algeria and *H. tsuchidai* Imaizumi, 1952 from the Upper Miocene of Japan. Other fossil examples include fragments of chelae (Collins & Portell, 1998; Todd & Collins, 2006; Collins *et al.*, 2009a, b).

Recently, two additional species have been recovered from the Pliocene of northeast Japan (Fig. 1) in association with molluscan and decapod crustacean species that are indicative of cool-water environments. The aim of the present study is to describe these two new oregoniid taxa and to discuss their palaeobiogeographical implications. In order to determine their age in terms of diatom biochronology, diatom analyses were performed on matrix of specimens of the Tentokuji Formation and of the holotype of *H. tsuchidai*.

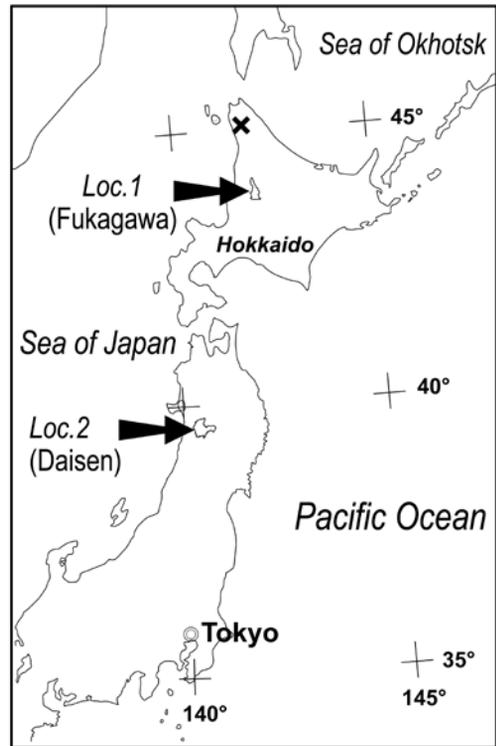


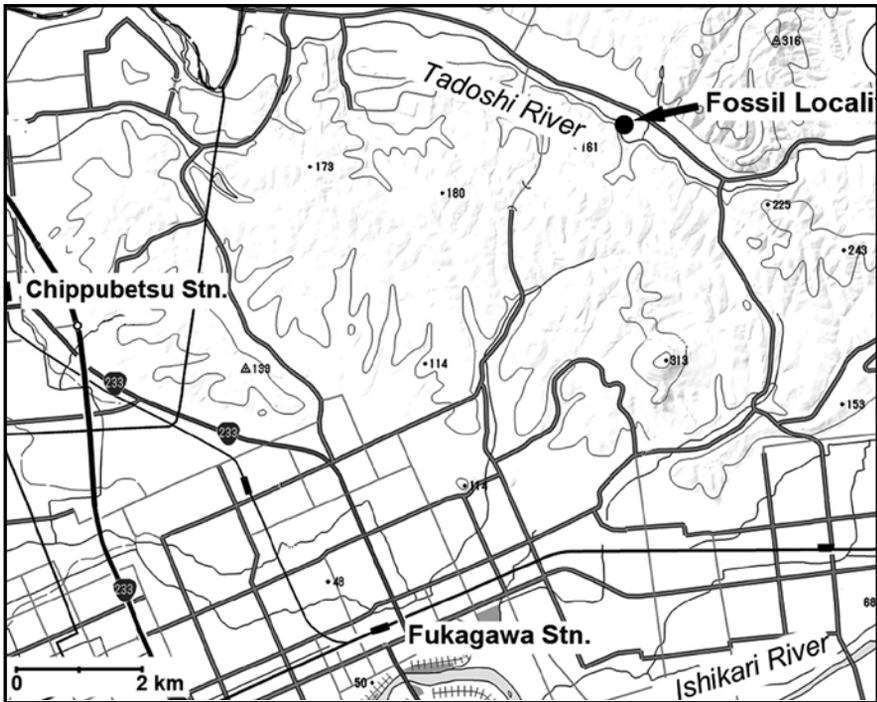
Fig. 1. Locality map showing extinct *Hyas*-bearing localities in northeast Japan; x indicates the type locality of *Hyas tsuchidai*.

Stratigraphical setting

(by H. Kato, Y. Yanagisawa & R. Nakashima)

Chippubetsu Formation – Three carapaces, chelae and ambulatory legs of *Hyas* were obtained from the silty sandstone in the lower part of this unit, as exposed along the Tadoshi River, Fukagawa City, central Hokkaido (Fig. 2A). This locality is the same as locality 5 of Nakashima (2002), from where the bivalve *Fortipecten takahashii* (Yokoyama, 1930) has been recorded. The Pliocene Chippubetsu Formation (Fukagawa Group) is distributed around Chippubetsu Town and Fukagawa City (central Hokkaido, northern Japan). It rests unconformably on the Middle Miocene Horoshin Formation (Nishitoppu Group), and is conformably overlain by the Ichhan Formation (Fukagawa Group) (Wada *et al.*, 1985). The Chippubetsu Formation is divided into a lower and an upper part. The decapod-bearing lower part is composed of massive, fine-grained, silty sandstone containing abundant boreal, shallow-marine bivalves such as *Fortipecten takahashii*, *Anadara amacula elongata* Noda, 1966, *Serripes groenlandicus* (Mohr, 1786), *Macoma calcarea* (Gmelin, 1791) and others. It is noteworthy that the new species of *Hyas* from this formation co-occurs with the cancrioid crab *Metacarcinus minutoserratus* (Nagao, 1941), as well as with bivalve species that are indicative of cool-water environments,

A



B

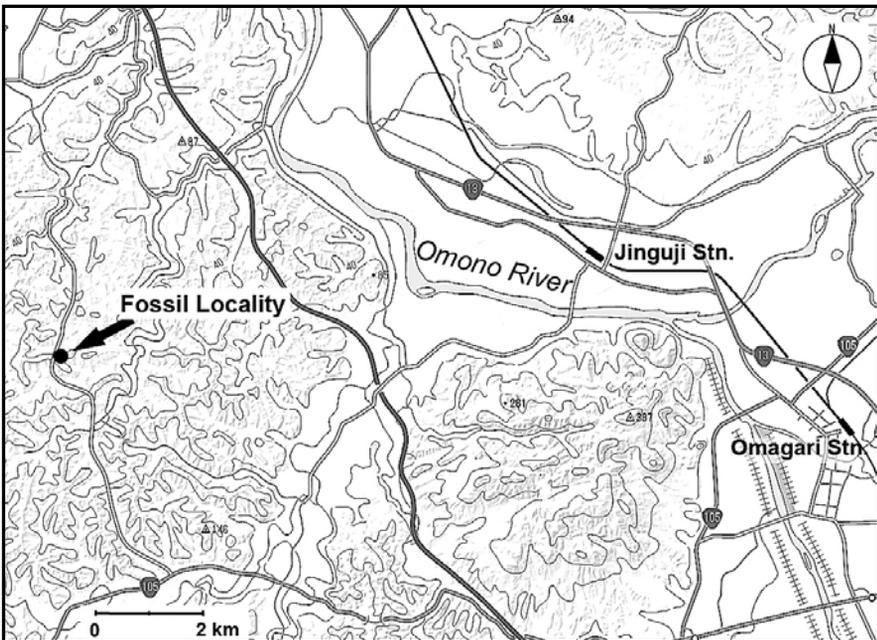


Fig. 2A, B. Map of decapod-bearing outcrops of the Chippubetsu and Tentokuji formations, respectively. Background maps are based on the Web GSI, Densi Kokudo (Digital Japan) provided by the Geospatial Information Authority of Japan.

such as *Fortipecten takahashii* and *Serripes groenlandicus*. The upper part of the formation consists of fine- to coarse-grained tuffaceous sandstone including granule- to pebble-sized conglomerate.

According to Wada *et al.* (1986) and Nakashima (2002), the present section of the Chippubetsu Formation can be assigned to the Early Pliocene *Thalassiosira oestrupii* Subzone (NPD7Bb; 5.6-3.5 Ma) in the Neogene North Pacific diatom zonation of Yanagisawa & Akiba (1998) (see Fig. 3).

Tentokuji Formation – Two specimens of *Hyas* were collected from the Pliocene Tentokuji Formation at a road construction site in Osawago-syuku, Daisen City (Akita Prefecture; Fig. 2B). This unit is distributed in the central part of the Akita Prefecture, northeast Japan. In the study area, the formation conformably rests on the Upper Miocene Funakawa Formation and is in turn overlain by alluvial and terrace deposits (Usuda *et al.*, 1978). Specimens of *Hyas* were found in calcareous nodules of tuffaceous sandy siltstone of the lower part of the Tentokuji Formation which is stratigraphically situated around the K-7 tuff layer of Usuda *et al.* (1978).

The molluscan fauna of this formation is characterised by species that are referable to the Omma-Manganji Fauna, which is a cool-temperate assemblage from the Pliocene of the Sea of Japan side (Ogasawara, 1994; Amano *et al.*, 2000), and which, in part, contains warm-water inhabitants. Recent studies of molluscan and ostracod assemblages have revealed warm-water influxes in the basal and middle parts of the formation (Shimamoto & Koike, 1986; Irizuki, 1996; Amano *et al.*, 2000). Although there are no molluscs associated, similar-looking calcareous nodules obtained from near the present locality, do contain molluscan species, including the cool-water inhabitant *Serripes groenlandicus* (see Sato *et al.*, 2002).

The matrix of the nodules with the new crabs was screened for diatoms, but age-diagnostic marker species were not found. However, the decapod fossils can be dated by combining data of diatoms and planktonic foraminifera that have been recorded previously from the Tentokuji Formation in this area (Fig. 3). Diatom assemblages assigned to the *Thalassiosira oestrupii* Subzone (NPD7Bb; 5.6-3.5 Ma) were described from near the base of the formation (Tsuchiya & Yoshikawa, 1994), which indicates the decapod fossils to be younger than 5.6 Ma. Planktonic foraminifera documented from several outcrops exposing the upper part of the Tentokuji Formation (Usuda *et al.*, 1979) suggest that the boundary between zones PF6 and PF7 (3.3 Ma; see Miwa *et al.*, 2004) of Maiya's (1978) regional planktonic foraminiferal zonation lies above the level which yielded the decapod fossils. This implies that the latter are older than 3.3 Ma. Thus, available biostratigraphical data yield an Early Pliocene date, between 5.6 and 3.3 Ma, for the present decapods. Although Kato & Nakashima (2013) noted the stratigraphical age of *Hyas* from this locality to be Middle Pliocene, this must now be amended to Early Pliocene, as based on these biostratigraphical data.

Wakkanai Formation – The type and sole specimen of *Hyas tsuchidai* originated from the siliceous shale of the Wakkanai Formation distributed in the north of the Toyotomi hot spring at Toyotomi Town (Teshio County, northern Hokkaido; see Fig. 1). The definition and age of the Wakkanai Formation are, however, still controversial. As Fukusawa (1985) and several other authors have pointed out, the Wakkanai and

overlying Koetoi formations had traditionally been divided solely by lithology, namely siliceous shale (hardshale) for the former and diatomite and diatomaceous mudstone for the latter. However, this lithological boundary occasionally does not match the chronostratigraphic boundary (Fukusawa, 1985). Although the Wakkanai Formation is rare in macrofossils, Ishida & Fujita (2001) documented an ophiuroid, *Ophiura sarsii sarsii* Lütken, 1855, from the same locality. This brittle star subspecies is also seen in the matrix of the holotype of *H. tsuchidai* (see Hatai, 1952, fig. 1).

Based on diatom evidence, Fukusawa (1985) dated the Wakkanai Formation as Middle Miocene and the Koetoi Formation as Late Miocene to Early Pliocene, respectively. In contrast, Sagayama (2000) assigned the Wakkanai Formation to the upper Middle to uppermost Miocene and the Koetoi Formation to the uppermost Miocene to Lower Pliocene, on the basis of diatom biochronology. More recently, Koshigai *et al.* (2012) have indicated that the Wakkanai Formation ranged from the uppermost Middle Miocene to lowermost Pliocene (in part).

In the present study, unfortunately, diatom fossils were not obtained from the matrix of the type specimen of *Hyas tsuchidai*; their absence can probably be ascribed to silica diagenesis. Thus, the proper age of *H. tsuchidai* cannot be determined directly. However, on the basis of previous studies of the Wakkanai Formation, the most plausible age of *H. tsuchidai* is here considered to be Late Miocene, although an Early Pliocene date cannot be ruled out entirely.

Systematic palaeontology
(by H. Kato & R. Nakashima)

Institutional abbreviations – APM, Akita Prefectural Museum, Akita City; CBM-PI, Natural History Museum and Institute, Chiba; IGPS, Institute of geology and Paleontology, Tohoku University, Sendai.

Superfamily Majoidea Samouelle, 1819
Family Oregoniidae Garth, 1958
Genus *Hyas* Leach, 1814

Type species – *Cancer araneus* Linnaeus, 1758, by original designation.

Remarks – The two new species described below exhibit a remarkably uneven, trilobed dorsal surface. However, the general carapace outline, including a hepatic expansion, a medially curved, bifid rostrum, flattened dorsal tubercles and orbits consisting of rounded supraorbital eaves and characteristic postorbital spines confidently place them in the genus *Hyas*. *Hyas tani* Hu, 1984, from the Upper Pleistocene of Taiwan, has subsequently turned out to represent an abdomen of a dromiid crab (Hu & Tao, 1996, p. 65).

Stratigraphical range – Middle Miocene to Recent.

***Hyas tsuchidai* Imaizumi, 1952**
Pl. 1, figs. 1, 2.

Material examined – IGPS 74001 (holotype).

Remarks – *Hyas tsuchidai* is a small species with acute hepatic spines and a small rostrum; it is characterised by transversely arranged granular tubercles on the proto- and mesogastric regions. As already noted by Imaizumi (1952), *H. oranensis* Van Straelen, 1936, from the ‘Sahelian’ (= Upper Miocene) of Algeria and *H. meridionalis* Glaessner, 1928 from the lower Langhian of Austria are also small in comparison with extant species. In contrast, *H. chippubetsuensis* sp. nov. and *H. tentokujiensis* sp. nov. described below are both moderately large species.

Stratigraphical age – Late Miocene.

***Hyas chippubetsuensis* sp. nov.**

Pl. 2, figs. 1-7, 9-11.

Material examined – The holotype, a carapace, is CBM-PI 0002811; paratypes are CBM-PI 0002812, a carapace; CBM-PI 0002813, a left cheliped; CBM-PI 0002814, a dactylus and fixed finger of a left chela; CBM-PI 0002815, a right palm; CBM-PI 0002816, a dactylus of a left cheliped; CBM-PI 0002817, a fixed finger of a left cheliped.

Etymology – After the Chippubetsu Formation.

Diagnosis – Moderate-sized species of *Hyas* with dense cover of tubercles and nodes of various sizes, on highly elevated dorsal regions; strong hepatic expansion with rounded posterolateral angle; anterolateral margin of carapace strongly constricted posterior to hepatic lobe; mesogastric, branchial and cardiac regions markedly swollen.

Description – Carapace pyriform, convex both longitudinally and transversely, length slightly exceeding width; widest posteriorly. Rostrum triangular, bifid, slightly curved inwards, two longitudinal rows of tubercles from each spine continuing to protogastric region. Supraorbital eave rounded, thickened, bearing dense granules. Eye stalk short, thick; abruptly tapering distally. Postorbital spine triangular with concave anterior surface; tip projecting nearly same distance as longitudinal mid-point of orbital eave; continuing lateral expansion of hepatic region. Dorsal regions strongly elevated with dense flattened tubercles and nodes of various sizes; clearly divided by deep and broad grooves. Hepatic region depressed, remarkably expanded anterolaterally; lateral margin concave medially; posterolateral angle rounded. Medial longitudinal regions highly convex. Protogastric region strongly vaulted with longitudinal rows of tubercles and scattered granules medially. Mesogastric region strongly swollen; two conical nodes arranged longitudinally, posterior one largest on dorsal surface. Metagastric region swollen, covered with conically clustered tubercles. Urogastric region broad, less elevated with flattened tubercles and granules. Cardiac region highly elevated with inconspicuous tubercles. Anterolateral margin of carapace strongly constricted posterior to hepatic region, forming deep and broad inlet. Branchial region extremely vaulted with dense, various-sized tubercles and nodes; rugose posteriorly. Sinuous swelling along branchiocardiac groove. Intestinal region narrow, rugose. Posterior margin rimmed, tip projecting posteriorly.

Cheliped stout. Carpus with large, pointed tubercles on dorsal and ventral margins and lateral surface. Palm long; length about twice length of fingers; dorsal and ventral margins nearly parallel; coarse tubercles aligned along dorsal margin proximally; ventral margin with granules; lateral surface gently convex with longitudinal short slits along ventral margin and transverse short slits near distal margin. Dactylus stout; lateral surface bearing a longitudinal broad groove medially, irregular shaped large excavations arranged longitudinally within; upper margin with rows of setal pits; medial surface bearing longitudinal groove with sparse setal pits. Prehensile margin of dactylus with a blade-shaped, large tooth on slightly proximal of longitudinal midpoint. Fixed finger stout, faintly curved upwards; lateral surface also with longitudinal medial groove with irregularly shaped and aligned excavations; medial surface bearing a longitudinal groove with row of pits. Prehensile margin with conical tooth proximally.

Remarks – The present species resembles *H. tentokujiensis* sp. nov. (see below) in having strongly elevated dorsal regions and a densely tuberculate dorsal ornament. In the former, however, flattened tubercles and nodes on the rostral, protogastric and branchial region are remarkably coarser and densely clustered. On the other hand, the tuberculate urogastric region of *H. chippubetsuensis* sp. nov. is less elevated than the longitudinally elevated ridge in *H. tentokujiensis* sp. nov. These differences of dorsal surfaces were confirmed not only in the fossil carapace but also in the plaster cast from the external mould of *H. tentokujiensis* sp. nov., which displayed an episkeletozoan (serpulid worm; Pl. 3, fig. 1). The hepatic expansion of the former is clearly broader, and the constriction of anterolateral margin between the hepatic expansion and branchial region is stronger than the latter. Moreover, protogastric regions are notably narrow in comparison with the broad and strongly vaulted ones in *H. tentokujiensis* sp. nov.

In addition to its small size, *Hyas tsuchidai* differs clearly from the present new species by having a transverse row of tubercles on the protogastric region. *Hyas chippubetsuensis* sp. nov. is easily distinguished from *H. meridionalis* by its strongly tuberculate and deeply demarcated dorsal carapace surface. *Hyas oranensis*, which has a granulated dorsal carapace and well-divided dorsal regions, differs from *H. chippubetsuensis* sp. nov. in that the latter has strongly vaulted protogastric and tumid dorsal medial regions. Among extant species, *H. alutaceus* Brandt, 1851, from the northern and eastern North Pacific and the seas of Okhotsk and Japan (Takeda *et al.*, 2011) comes closest, but both of the present new species are apparently distinguished by having densely tuberculate dorsal regions, extremely vaulted branchial regions and a strongly dilated hepatic expansion.

Occurrence – Lower part of Chippubetsu Formation (Fukagawa Group).

Stratigraphical age – Early Pliocene.

Measurements (in mm) –

Specimen no.	Carapace width	Carapace length	Width between postorbital spines	
CBM-PI 0002811 (holotype)	45.4	>53.2	22.1	
Specimen no.	Carpus width	Carpus length	Palm width	Palm length
CBM-PI 0002813 (paratype)	14.9	25.2	17.7	>55.9

Hyas tentokujiensis sp. nov.

Pl. 3, figs. 1-4.

Material examined – The holotype is APM 744-47, a carapace and appendages; the single paratype is APM 744-48, a carapace.

Etymology – After the Tentokuji Formation.

Diagnosis – Moderate-sized species of *Hyas* with strongly vaulted branchial regions. Strongly elevated dorsal regions defined by deep grooves. Hepatic region broadly dilated laterally; posterolateral corner gently convex. Moderate post-hepatic constriction on anterolateral margin of carapace.

Description – Carapace pyriform; longer than broad; widest posteriorly. Rostrum triangular, bifid, converging anteriorly. Orbital eave rounded, granulated dorsally. Postorbital spine projecting anteriorly nearly at same distance as longitudinal mid-point of orbit. Fissure between orbital eave and postorbital spine deep, narrow. Hepatic expansion broad; dilated laterally, separated from branchial region by broad, deep sinuous depression; posterolateral corner gently convex. Two longitudinal rows of tubercles arise from base of each rostral spine on frontal region. Proto-, meso- and metagastric regions strongly vaulted; tubercles of various sizes scattered over median longitudinal area. Groove between meso- and metagastric regions curved anteriorly at small, crescent-shaped node. Urogastric region forming elevated longitudinal ridge, but lower than other regions. Cervical groove deep and broad. Branchial region covered with scattered tubercles. Meso- and metabranchial regions strongly vaulted. Cardiac region highly elevated. Intestinal region with close-set tubercles. Posterior margin rimmed, without pointed tip projecting posteriorly

Merus of cheliped triangular in cross section; large tubercles aligned on upper margin.

Remarks – The present species is easily distinguished from *H. meridionalis* in having a deeply demarcated dorsal surface of carapace. In comparison with *H. oranensis*, the new species exhibits more nodose, vaulted dorsal regions. Among extant congeners, the new species resembles *H. alutaceus* and *H. coarctatus* Leach, 1814, in having a relatively longer carapace and broad hepatic expansion without distinct posterolateral angle. However, *H. tentokujiensis* sp. nov. can be differentiated from those forms in having strongly elevated dorsal regions, especially the protogastric, branchial and cardiac regions, and deep and broad cervical and branchiocardiac grooves. The urogastric region of the present species forms a distinct medial longitudinal ridge. In addition, the posterior part behind the metabranchial and intestinal regions in the new form is remarkably rugose. As a whole, the dorsal carapace surface in *H. tentokujiensis* sp. nov. presents a more rugged dorsal surface by the elevated regions and the deep grooves, similar to *H. chippubetsuensis* sp. nov.

Occurrence – Lower part of the Tentokuji Formation.

Stratigraphical age – Early Pliocene.

Measurements (in mm) –

Specimen no.	Carapace width	Carapace length	Width between postorbital spines
APM 744-47 (holotype)	38.6	54.2	24.4
APM 744-48 (paratype)	43.6	59.1	26.3

Discussion

Morphologically, the new species described herein are close in general shape and dorsal carapace ornament. The late Miocene *H. tsuchidai* differs in having a small, relatively flattened carapace with granular tubercles on the dorsal surface.

The early Middle Miocene *H. meridionalis* from Austria and the Late Miocene *H. oranesis* from Algeria are also smaller than the present two new species. Assuming that all other Neogene species and extant forms are congeneric, the dispersal route of the genus in the North Pacific might be linked to the palaeobiogeographical constraint concerning to the opening of the Bering Strait.

Extant species of *Hyas* are generally considered to be cool-water inhabitants, in particular *H. araneus*, which is regarded as a cold eurythermal species (Walther *et al.*, 2010) or a Boreo-Arctic species (Węsławski, 1987). In other words, *Hyas coarctatus* and *H. araneus* are regarded as boreal and subarctic species, respectively (Anger, 1984).

The fact that the oldest record in the North Pacific region is from northernmost Japan, and in view of co-occurring molluscan and decapod crustacean species, plus the geographical location of the two new Pliocene species, an adaptation to cool-water environments similar to that of extant species is suggested.

According to recent studies (Marincovich & Gladenkov, 1999), the Bering Strait was closed by the latest Miocene, preventing marine invertebrates of the Atlantic Ocean from migrating into the Pacific via the Arctic Ocean. The earliest opening of the Bering Strait is documented by the migration of the bivalve genus *Astarte* from the Arctic Ocean into the North Pacific (Marincovich & Gladenkov, 1999). Gladenkov *et al.* (2002) dated the first opening of the Bering Strait at 5.4–5.3 Ma.

Although the precise stratigraphical age of *H. tsuchidai* could not be determined, the most plausible date is Late Miocene; this is inconsistent with the accepted first opening of the Bering Strait (Fig. 3). However, as indicated above, the possibility of an Early Pliocene age for *H. tsuchidai* cannot be ruled out entirely. Further attempts to obtain the precise age of *H. tsuchidai* are needed to resolve this inconsistency.

Other records of the genus *Hyas* comprise tentatively referred material (i.e., 'aff. *Hyas* sp.'), such as that from the Upper Miocene (lower Tortonian) Tuirá Formation of Panama (Todd & Collins, 2006), the Upper Pliocene Bowden Formation and the Upper Pleistocene Port Morant Formation of Jamaica (Collins & Portell, 1998; Collins *et al.*, 2009a) and the Upper Pliocene of Costa Rica and Panama (Collins *et al.*, 2009b). These examples are situated much further south from the southern limits of the recent distribution of the genus. In view of the fact that all of these records are based exclusively on isolated fingers and meri, additional material, and carapaces in particular, are called for to determine their status.

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Plate 1

Figs. 1, 2. *Hyas tsuchidai* Imaizumi, 1952; carapace (internal and external mould, respectively), IGPS 74001 (holotype). Scale bar equals 10 mm.

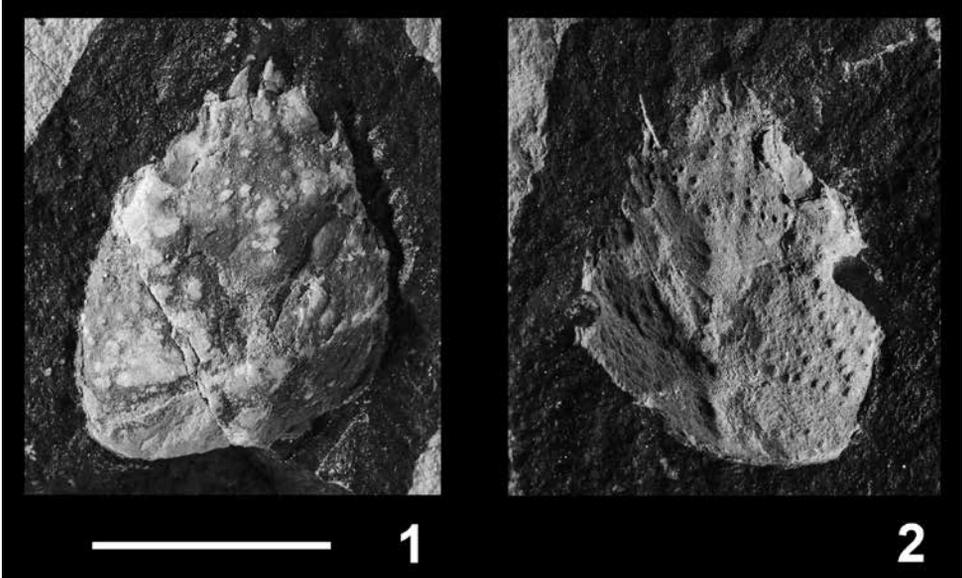


Plate 2

Hyas chippubetsuensis Kato & Nakashima, sp. nov. Scale bars equal 10 mm.

Figs. 1, 2. Palm of right cheliped, in medial and lateral views, respectively (CBM-PI 0002815; paratype).

Figs. 3, 4. Fixed finger of left cheliped, in medial and lateral views, respectively (CBM-PI 0002817; paratype).

Figs. 5, 6. Dactylus of left cheliped, in lateral and medial views, respectively (CBM-PI 0002816; paratype).

Fig. 7. Dactylus and fixed finger of left chela (CBM-PI 0002814; paratype).

Fig. 9. Left cheliped (CBM-PI 0002813; paratype).

Fig. 10. Carapace (CBM-PI 0002811; holotype).

Fig. 11. Carapace (CBM-PI 0002812; paratype).

Metacarcinus minutoserratus (Nagao, 1941).

Fig. 8. Carapace (CBM-PI 0002821).

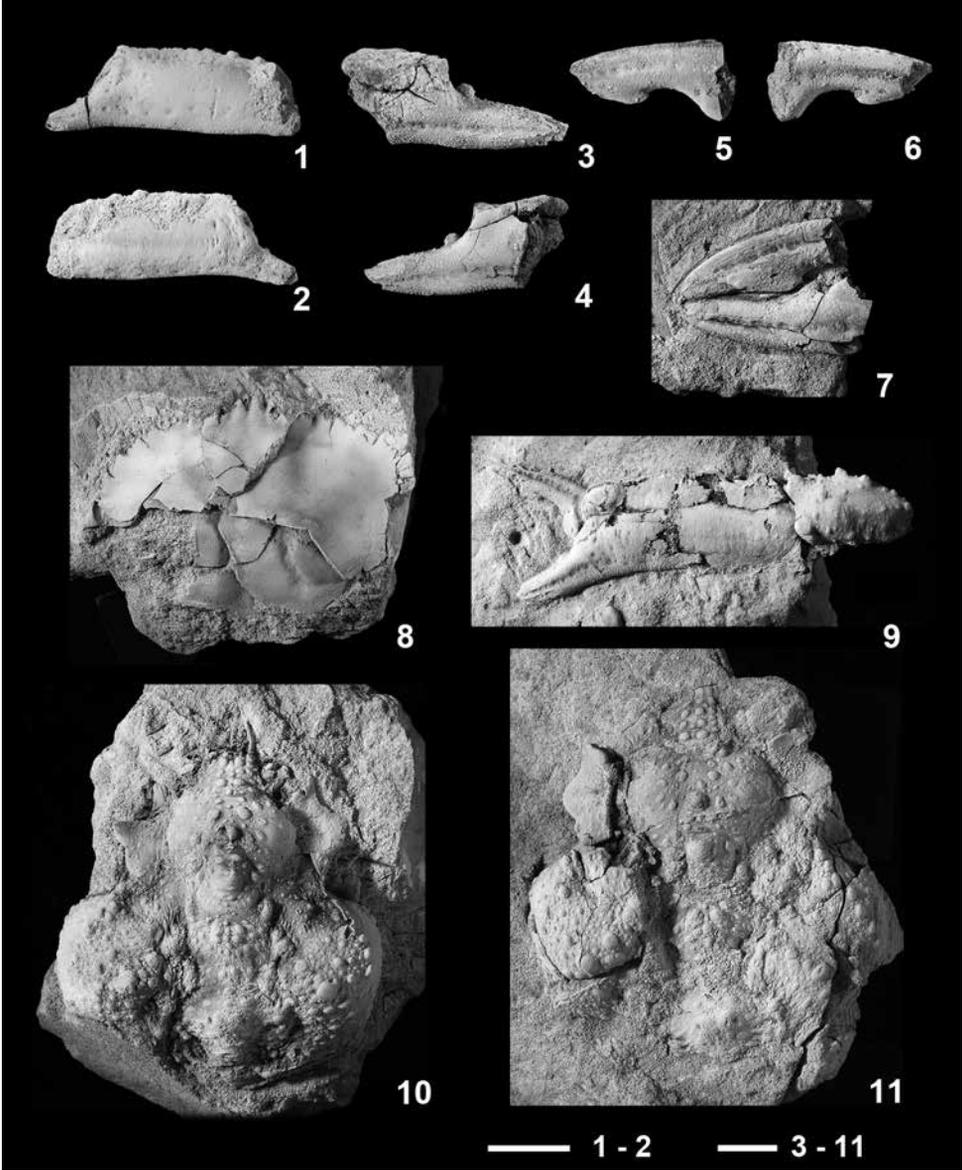


Plate 3

Hyas tentokujiensis Kato and Nakashima, sp. nov. Scale bar equals 10 mm.

Figs. 1, 2. Plaster cast of paratype (APM 744-48) and holotype carapaces (APM 744-47), respectively.

Figs. 3, 4. Carapace (APM 744-48; paratype) and carapace and appendages (APM 744-47; holotype), respectively.

