A new inachid crab (Brachyura, Majoidea) from the Middle Eocene of the provinces of Barcelona and Girona (Catalonia, Spain)

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Marls assigned to the Coll de Malla Formation (Lutetian) in the area of Vic (Barcelona) and Sarrià de Ter (Girona) have yielded several specimens of a new brachyuran that can be assigned with confidence to the superfamily Majoidea. General carapace shape, the produced and bilobed front, with two longitudinal rounded ridges, the construction of the orbits, the gently arched posterior margin, as well as the strong conical protuberances in the dorsal regions, favour placement in the family Inachidae. The construction and distribution of the axial and branchial regions confirms assignment to the genus *Planobranchia*. Distinct features seen in the new material, such as the arched epibranchial ridges bounding the urogastric region, the gently arched posterior margin, and stronger protuberances in the dorsal regions permit the erection of a new species, *Planobranchia palmuelleri*. The excellent preservation of the anterior portion of the carapace in this new species adds to our knowledge of the genus, the diagnosis of which is emended.

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Introduction and geological setting

Via (1959, 1969) documented a large assemblage of decapod crustaceans from marly layers of Lutetian age in the provinces of Girona and Barcelona (Catalonia, Spain), the commonest crab being the portunoid *Colneptunus hungaricus* Lőrenthey *in* Lőrenthey & Beurlen, 1929, of relatively large size. Other crabs recovered include *Montezumella amenosi* Via, 1959, *Typilobus boscoi* Via, 1959, *Typilobus modregoi* Via, 1959, *Dromilites vicensis* Barnolas, 1973; in addition, the paguroid anomuran *Eocalcinus eocenicus* Via, 1959 occurs.

At the time, Via noted that the richest sites for this decapod fauna (see Via, 1969, table 6) were in the area of Sarrià de Ter (Girona), while outcrops in the Vic area (Barcelona) presented rarer and less diverse decapod faunas. Later, Barnolas (1973) described a new dromiid from the same region and reported, on the basis of extensive fieldwork, that the Vic area yielded both a greater abundance and species diversity. All the sites from which the new dromiid was collected were described in detail (Barnolas, 1973, p. 7), most of them in the villages of Tavèrnoles, Folgueroles and Tavertet (Vic area, Barcelona).

Revision of material from old collections, housed at the Museo Geologico del Seminario de Barcelona (MGSB), has resulted in the discovery of a majoid brachyuran that is here described as a new species. The more or less complete carapaces were collected from localities mentioned by Barnolas (1973).

The strata have always been considered Lutetian in age, but assignment to lithostratigraphical units has been slightly controversial. Via (1959, 1969) considered the crabbearing levels to belong to the Margas de Bañolas Formation (Almela & Ríos, 1943), while more recent studies (Serra-Kiel *et al.*, 2003, pp. 210, 211) have confirmed that the marly beds should be assigned to the Coll de Malla Marl Formation (Clavell *et al.*, 1970).

According to Serra-Kiel *et al.* (2003, pp. 201, 211), the strata correspond to a transgressive cycle. The base consists of a bioclastic sandstone interval, interpreted as a condensation level, rich in molluscs, some echinoids and a few crabs. The overlying levels mostly comprise marls, more or less fossiliferous, with at least two intervals of faunal condensation. Molluscs such as *Cardita, Chlamys* and *Cipraeovula* are very common in the marls, as are some echinoids and occasionally crabs. All specimens of the new brachyuran described herein were collected from these marly strata.

Systematic palaeontology

Infraorder Brachyura Latreille, 1802 Superfamily Majoidea Samouelle, 1819 Family Inachidae MacLeay, 1838 Genus *Planobranchia* Schweitzer & Feldmann, 2010

Type species – Micromaia laevis Lőrenthey, 1909, by original designation of Schweitzer & Feldmann (2010, p. 407).

Included species – Micromaia laevis, Micromaia simplex Remy in Gorodiski & Remy, 1959 and P. palmuelleri n. sp.

Emended diagnosis – Carapace of medium size, pyriform, about as wide as long, convex in both directions, maximum width at level of mesobranchial region; front produced, bifid, the two frontal spines continuing onto the carapace as longitudinal rounded ridges; orbits small, laterally situated, with a strong subtriangular outer-orbital tooth; dorsal regions fairly distinct, swollen, bounded by marked grooves; hepatic region with lateral spine and swollen posterior portion; anterolateral margins with subtriangular tooth between outer-orbital and hepatic nodes; mesogastric region narrow, bearing conical protuberance; anterior portion of mesogastric region very narrow, elongated, ridged, bounded by two elongated ridges that end in two frontal spines; protogastric region bearing subtle protuberance on either side; metagastric region narrow, V-shaped; urogastric region notably narrow, bounded by branchial regions; epibranchial regions de-

pressed, situated in lower plane; cardiac region subrhomboidal, with fairly elongated posterior portion, axial side bearing conical protuberances; intestinal region narrow, elongate; posterior margin convex, very broad, notably rimmed.

Remarks – The pyriform shape of the carapace, the anteriorly directed and produced front, with two rounded longitudinal ridges terminating in short spines, the construction of the orbits, the narrow axial portions, and the swollen branchial regions, place *Planobranchia* in the superfamily Majoidea. We tentatively refer the new taxon to the family Inachidae. The advanced front with straight lateral margins, the rounded longitudinal frontal ridges, the laterally situated orbits, with a strong outerorbital subtriangular tooth, and the conical spines or protuberances in the dorsal regions favour assignment to this family. Inachids are characterised (Zariquiey, 1968, p. 444) by a peculiar orbital construction, the supraorbital margins without strong spines or teeth, but the outer-orbital node with a very well-developed lobe; the front produced, with short rostral spines that are close and parallel. The dorsal regions are swollen, fairly well differentiated, with notable dorsal grooves, and some regions bear strong tubercles that may end in acute spines, the dorsal surface with weak ornament (Zariquiey, 1968, pp. 467-474).

Planobranchia was included in the subfamily Majinae by Schweitzer & Feldmann (2010, p. 407). Members of that subfamily are distinguished (Feldmann *et al.*, 2011, p. 330) by long and divergent rostral spines, orbits with a well-developed supraorbital eave, characterised by notable preorbital spine, strong postorbital spine and an intercalated supramarginal spine. The dorsal regions are weakly differentiated in the Majinae, with weakly marked grooves, and the dorsal surface is usually covered by dense granules. This assemblage of characters confirms that *Planobranchia* cannot be assigned to the Majinae.

Planobranchia palmuelleri n. sp. Pl. 1.

Diagnosis – Carapace of medium size for family, pyriform, about as wide as long, convex in both directions, maximum width in lateral portions of mesobranchial region; front produced, bifid; rounded longitudinal ridges diverge towards rear of carapace, parallel in distal portions; orbits small, laterally situated, with strong outer-orbital sub-triangular tooth; dorsal regions swollen, distinct, bounded by marked grooves; hepatic region with notable lateral spine and strongly swollen posterior portion; anterolateral margins with notable subtriangular tooth between outer-orbital and hepatic nodes; mesogastric region narrow, bearing strong, salient, conical protuberance; anterior extension of mesogastric region notably narrow, elongated, fairly ridged, bounded by two elongated ridges that end in two frontal spines; protogastric region narrow, V-shaped; urogastric region narrow, bounded by two narrow arched swellings, both fairly elongated; epibranchial, mesobranchial and metabranchial regions clearly differentiated; epibranchial, mesobranchial and metabranchial regions clearly differentiated; epibranchial region obliquely disposed, with posterior (axial) portion arched; cardiac region subrhomboidal, bearing strong conical protuberance on axial side and two nodes in

distal portions; intestinal region narrow and elongated; posterior margin very broad, merging with posterolateral margin, gently arched and clearly defined by notable rim. Dorsal regions covered by dense small pits.

Derivation of name – In honour of Pál Müller, prolific Hungarian palaeocarcinologist who significantly contributed to our knowledge of fossil decapod crustaceans.

Material, locality and stratigraphic level – Holotype is MGSB 79782; paratypes are MGSB 79783a-c, 79784a-b and 79785; all nearly complete carapaces. Additional material is MGSB79786a-c. Maximum length and width of holotype approximately 23 and 19 mm, respectively. All specimens, with the exception of MGSB 79785, are from outcrops situated in the Vic area (municipalities of Tavèrnoles, Folgueroles and Tavertet); MGSB 79785 is from Sarrià de Ter. All material from the Coll de Malla Formation (Lutetian, Middle Eocene).

Description - Carapace of medium size for the family, with pyriform outline, dorsal surface fairly convex in both directions, longer than wide, with maximum width at the level of the mesobranchial region; front produced, bilobed, with two short parallel spines and straight lateral margins; the frontal spines continue backwards, over the frontal region, as two longitudinal rounded ridges that are divergent posteriorly; orbits laterally situated, supraorbital margin with strong outer-orbital tooth; anterior portion of lateral margins fairly spiny; posterior portion of lateral margins without spines, broadly arched; hepatic region defined by a strong lateral spine and a strong posterior inflation; notable subtriangular tooth between the outer-orbital lobe and hepatic spine; mesogastric region relatively narrow, bearing a strong conical protuberance and a ridged anterior portion, bounded by two rounded frontal ridges; protogastric region weakly defined, bearing a low protuberance on either side; metabranchial region narrow, V-shaped; urogastric region bounded by two arched swellings; epibranchial region obliquely inflated, with posterior (axial) portion arched, bounding the urogastric region; mesobranchial region broadly inflated; metabranchial region less swollen, somewhat depressed; cardiac region transversely rhomboidal, with an elongated posterior portion, the axial portion bearing a strong conical protuberance; intestinal region smooth, weakly defined; posterior margin very broad, gently arched, merging with the posterolateral, together nearly occupying the maximum carapace width.

Discussion

The new species is assigned to *Planobranchia* because it shares with that genus the pyriform carapace, with a similar outline, conspicuously narrow axial regions, and similarly inflated mesobranchial regions. In particular, the new species is distinguished from congeners in showing a different anterior portion of the carapace, different epibranchial regions, stronger tubercles on the dorsal surface, and distinct posterior margins. *Planobranchia palmuelleri* n. sp. presents distinct hepatic regions, with the hepatic spine much more produced, and the posterior inflation much more marked and better developed than in *P. laevis*; the gastric regions bear notable protuberances, with the mesogastric region distinctly pronounced and salient; the anterior extension of the meso

ogastric region is ridged, and bounded by longitudinal narrow ridges that continue into short frontal spines. In the new species the urogastric region is bounded by fairly arched epibranchial posterior portions, which are very narrow and swollen, like oblique ridges; the mesobranchial region does not meet the urogastric region directly; the metabranchial region appears to be less depressed than in P. laevis; the mesogastric, protogastric, urogastric and cardiac regions bear one more or less strong conical protuberance that sometimes ends in an acute spine. These characters are clearly distinct from those of P. laevis and P. simplex, in which the posterior margin is broad and gently arched, defined by a thin rim that does not appear to be separated by strong depressions from the branchial regions. Planobranchia laevis is distinguished from P. palmuelleri n. sp. by an extremely narrow urogastric region, which is directly bounded by the axial portion of the mesobranchial region rather than by arched posterior portions of the epibranchial regions; the epibranchial regions appear to be more subdivided by oblique swellings and accentuated oblique or transverse depressions; the epibranchial and mesobranchial regions seem weakly differentiated, i.e., 'widest part of epibranchial and mesobranchial regions converge as angular projections toward urogastric region' (Schweitzer & Feldmann, 2010, p. 407). The cardiac region bears two small axial protuberances over a transverse ridge (Feldmann et al., 2011, p. 333), whereas in the new species the cardiac region bears only one, albeit much stronger, protuberance; the mesogastric region in *P. laevis* has a less accentuated axial protuberance. The front appears to be downturned, and despite the fact that it is not complete, the preserved portion does not seem to possesses a notably ridged anterior portion of the mesogastric region; the posterior margin is distinctly V-shaped. All differences indicated above are observed in the illustrations of Planobranchia laevis, being especially evident in oblique view (Feldmann et al., 2011, fig. 5/2). The differences from P. simplex are even more accentuated (Schweitzer & Feldmann, 2010, fig. 2A), and concern, in particular, the narrower urogastric region, bounded by extremely angular terminations of the branchial regions and the strongly V-shaped posterior margin.

The genus *Planobranchia* was assigned to the subfamily Majinae (Schweitzer & Feldmann, 2010, p. 407) rather than to the Inachidae, probably because of the incompletely preserved anterior carapace portions in all species assigned at the time (see Feldmann *et al.*, 2011). It was diagnosed and described without distinct frontal and orbital characters, and the orbital construction was interpreted erroneously, as bearing a supramarginal eave with three spines, probably due to poor preservation. Because of the original assignation of the two species to the genus *Micromaia*, *Planobranchia* was compared mainly with the former genus, and both genera were placed in the Majinae (Feldmann *et al.*, 2011, p. 330). The produced front with straight lateral margins in the new species, and the smooth supraorbital margin with a strong outer-orbital triangular tooth, compare to a similar disposition in *Inachus* Weber, 1795.

Van Straelen (1933) recorded a new genus, *Eoinachoides*, from the Eocene of Venezuela which at first view looks rather similar to *Planobranchia palmuelleri* n. sp. Of special interest is the fact that this majoid also possesses a narrow urogastric region bounded by clear arched ridges that correspond to the epibranchial region. The carapace shape, the superficially similar distribution of regions, in particular the swollen branchial regions, indicates that both forms are related, but the much wider axial regions in *Eoinachoides* (Van Straelen, 1933, fig. 3), and the near-circular outline of the carapace preclude assignment to that genus. A detailed study of the regions and main characters confirm two clearly different genera. Much later, Aguilera *et al.* (2010, fig. 6.3) illustrated two similarly sized forms which were assigned to *Eoinachoides*, from two different localities in Venezuela, from beds of Eocene and Miocene age, respectively. *Eoinachoides* was placed by Van Straelen (1933) in the Inachinae, then considered to be a subfamily of the Majidae. The size of *Eoinachoides senni* appears to have been very small, based on Van Straelen's (1933) figure, but this is not indicated. Illustrations provided by Aguilera *et al.* (2010), under the names of *Eoinachoides senni* and *Eoinachoides* sp., confirm that these are similar in size to *Planobranchia palmuelleri* n. sp.

Planobranchia palmuelleri n. sp. could be an intermediate between *Eoinachoides* and *Planobranchia laevis*. With regard to the general carapace shape, *Eoinachoides* is nearly subcircular, *Planobranchia palmuelleri* n. sp. being somewhat more elongated, but much less so than *P. laevis*. The posterior margin in *Eoinachoides* appears to be nearly straight in the axial portion, and less broad than in *Planobranchia palmuelleri* n. sp., which possesses a gently arched posterior margin. In *Planobranchia laevis* the posterior margin is distinct, being strongly V-shaped, less rimmed and depressed by the branchial regions. In the absence of preserved ventral portions, the three forms can only be tentatively assigned to the Inachidae. Better-preserved material, preferably with ventral portions or more complete frontal regions, for both *Eoinachoides* and all species currently assigned to *Planobranchia* are needed for a more rigorous assessment.

Comparison of the new species with extant forms confirms that there is no species with the same set of characters. Nevertheless, it does reveal some similarities to the extant genus *Inachus*: the frontal region is very similar, as are the construction and disposition of the orbits, the broad, gently arched posterior margin, and the conical protuberances in the dorsal regions. In *Inachus* the front is bilobed, with short rostral spines, with two rounded longitudinal ridges and straight lateral margins (Zariquiey, 1968, figs. 158a, 159a), as it is in the new species; the orbits are laterally disposed, without preorbital and supraorbital spines, with a strong subtriangular outer-orbital tooth. The hepatic region is very similar as well, being strongly swollen. However, the posterior portion of the carapace presents clear differences, in the distribution of the branchial, cardiac and intestinal regions, which are less elongated in *Inachus*. The new taxon is also clearly distinct in having a lower number of dorsal conical protuberances, which are also less prominent. *Planobranchia* seems best placed in the family Inachidae as indicated above.

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Plate 1

Planobranchia palmuelleri n. sp., Coll de Malla Formation (Middle Eocene, Lutetian), Vic area (municipalities of Tavèrnoles, Folgueroles and Tavertet, Barcelona). Scale bar equals 10 mm.

- Fig. 1. Holotype, dorsal view, MGSB 79782.
- Fig. 2. Paratype, dorsal view, MGSB 79783a.
- Fig. 3. Holotype, lateral view, MGSB 79782.
- Fig. 4. Paratype, dorsal view, MGSB 79784a.

