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Tavernolesia, new genus (Crustacea, Decapoda, Brachyura), from the Eocene of the Iberian Peninsula

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ABSTRACT- Some new fossil brachyurans from Middle Eocene (Middle Lutetian) strata in the Provinces of Barcelona and Girona (Catalonia, Spain), discovered in old collections housed in the Geological Museum of Barcelona Seminary (= MGSB), assigned until now to the genus *Stenodromia*, present after accurate preparation, extraordinary fairly complete female ventral portions, complete attached chelipeds, and complete dorsal features. The main ventral characters of a unique specimen, such as the narrow, subtriangular female abdomen, with all abdominal segments free, not totally covering the narrow sternum, and the complete attached chelipeds, permit detailed and more confident comparison with closer fossil and extant genera. The unique assemblage of characters, mainly the peculiar frontal and orbital construction, the dorsal rows of discrete tubercles, the absence of deep dorsal grooves, together with the conspicuously long mesobranchial spines, warrants the erection of a new genus, *Tavernolesia* n. gen. The completeness of the new specimens, permit more detailed diagnosis, and the placement in the superfamily Calappoidea is confirmed.

RESUMEN - La cuidadosa preparación de algunos crustáceos decápodos, procedentes de antiguas colecciones, actualmente depositados en el MGSB, presenta una extraordinaria conservación de los quelípedos, así como de porciones dorsales y ventrales del caparazón. Estos decápodos, recuperados de estratos del Eoceno medio de las Provincias de Barcelona y Girona, estaban asignados hasta ahora al género *Stenodromia*. El conjunto de caracteres ventrales de un espécimen único, tales como un abdomen hembra, estrecho y subtriangular, con todos los segmentos libres, y los completos quelípedos, permite una detallada y más rigurosa comparación con los taxones más próximos, tanto fósiles como actuales. Este conjunto de caracteres únicos, especialmente la peculiar construcción orbital y frontal, las hileras dorsales constituidas por sutiles tuberculaciones, la ausencia de surcos dorsales profundos, junto con las extensas espinas mesobranquiales, garantizan el registro de un nuevo género, *Tavernolesia* n. gen. La completa preservación de los nuevos ejemplares, permite una diagnosis detallada y precisa, y se confirma el emplazamiento en la superfamilia Calappoidea.

KEYWORDS - Palaeontology. Crustacea. Decapoda, Calappoidea, new genus, Middle Lutetian, Catalonia, Spain.

INTRODUCTION

Only two species have been traditionally assigned to the genus *Stenodromia* Milne-Edwards in Bouillé, 1873 (Schweitzer *et al.* 2010). The type species, *S. gibbosa* was recorded on the basis of an isolated specimen, recovered from the Oligocene layers of the Southwest of France. The sole specimen consists of a not complete and badly preserved carapace, to the point that was assigned to the superfamily Dromioidea.

A new species, *S. calasanctii* Via, 1959, collected from Eocene layers in the Barcelona and Girona Provinces (Catalonia, Spain), was recorded with the description of several specimens, only carapaces, but some few in a reasonable degree of preservation (Via 1959, 1969). After this long period of time, only recently, a new species was added to the genus. In a recent general revision of the fossil genus *Calappilia* A. Milne-Edwards in Bouillé, 1873, the species *C. mainii* Allasinaz, 1987 was moved to Stenodromia (Busulini et al., 2014, p. 206). Thus, the geological and geographical distribution appears to be extremely reduced, only three species recorded in Oligocene and Eocene strata from Europe according to the authors indicated above. Nevertheless, the consistency of the genus does not seem warranted, mainly due to the poor preservation of the specimens described to date.

Via (1959) assigned *S. calasanctii* to the family Calappidae De Haan, 1833, and included it in the same genus on the basis of several specimens more or less well preserved and several remains of isolated chelipeds. According to this, the general outline of the carapace, dorsal granulation, distribution and shape of dorsal regions, orbitofrontal construction and chelipeds perfectly fits into the superfamily. The revision of the new material housed in the MGSB permits still a more confident assignation to the Calappoidea.

The numerous species assigned to the genus Calappilia, actually 23, according to the last studies (Rumsey et al., 2016), have always been considered controversial (Via, 1969; Williams et al., 1988; Busulini et al., 2014), to the point that the genus embraces a high degree of variation in the main characters. The general outline of the carapace presents a strong variety. Concerning to the distribution and shape of dorsal regions and grooves, there is also a high degree of morphological distinctions. The dorsal surface is very diverse as well, being considered from nearly smooth to highly tuberculate. Thus, it seems that a severe revision should be done. Only C. mainii, as mentioned above, was moved to the genus Stenodromia (Busulini et al., 2014).

The perfectly preserved attached chelipeds, dorsal and ventral regions in the new specimens, assigned until now to *S. calasanctii*, permit more detailed comparisons with extinct and extant forms, and a separation in a new genus, *Tavernolesia* n. gen. The new material can also contribute to the general understanding for a placement in the appropriate family. Better preserved new material of the different fossil genera could confirm placement in a differentiated fossil family within the Calappoidea.

MATERIAL, LOCALITIES AND STRATIGRAPHY

Middle Lutetian fossil crustaceans were relatively common in the marly layers exposed in the outcrops of the Vic, Berga, and Girona areas (Catalonia, Spain). Concerning to the species of small size, most of them consist of not complete or disarticulated exuviae. Within the large assemblage of crustacean fauna recorded by Via (1959, 1969) and Barnolas (1973) the numerous species discovered were intensively collected, but generally, the ventral portions appear to be very rare. In some cases, only recently, *i.e. Tavernolesia boscoi* (Via, 1959), have been described (Artal & Hyžný, 2016). Most of this large and diverse crustacean fauna was recovered from the villages of Tavèrnoles, Folgueroles, Tavertet and Vilada, in the Barcelona Province, and Sarrià de Ter in the Province of Girona (Barnolas, 1973, Artal et *al.*, 2014, Artal & Hyžný, 2016).

The accurate preparation of material from old collections, nowadays housed in the Museo Geológico del Seminario de Barcelona (MGSB), permits examination of perfectly preserved dorsal carapaces, female ventral portions, and complete chelipeds. A unique specimen, with complete attached chelipeds, and very well preserved dorsal and ventral primary characters, was recovered from Tavèrnoles, the name of the village that honours the new genus.

The age of the layers is confirmed as Middle Lutetian (Serra-Kiel *et al.*, 2003), and belong to the Coll de Malla Marl Formation (Clavell *et al.*, 1970). This lithological and stratigraphical unit has been considered in most recent studies (Serra-Kiel *et al.*, 2003) as corresponding to transgressive and regressive cycles, with sediments from the Middle Lutetian to the Late Lutetian. The firs portion, the transgressive cycle, contain sediments about 35 metres thick, bearing the most diverse decapod fauna. In the upper sediments, the big sized portunoid *Colneptunus hungaricus* Lörenthey in Lörenthey and Beurlen, 1929, is relatively common in a brown coloured sandstone interval.

Concerning to the transgressive cycle, the widespread exposed strata of the study area, always present three very-well differentiated levels in which the crustaceans occur. According to Serra-Kiel et al. (2003), the base is characterized by thin bioclastic sandstone interval, interpreted as a condensation level. This first level contains abundant foraminifers, bryozoans, molluscs, some echinoids, disarticulated chelipeds of callianasids and very few crabs. The presence of T. calasanctii was always scarcely collected in this thin bioclastic level. The overlying strata are mostly constituted by marls, thick horizons with scarce fossil fauna and low number of collected specimens of the new genus. The highest levels, with at least two thin intervals of fauna condensation, few separated, were interpreted as levels of tempestites (A. Barnolas per. comm.). In the condensation levels abundant molluscs occur, some echinoids, and some few crabs. Most of the specimens of the new genus were collected in the condensation horizons of the marly strata. The uppermost levels of the transgressive

cycle, consists of brown coloured sandstones, in which the diverse crustacean fauna tends to disappear.

The following abbreviations are used to denote the repositories of material illustrated or referred to in the text: MGSB: Museo Geológico del Seminario de Barcelona, Barcelona, Spain. MNHN: Muséum national d'Histoire naturelle, Paris, France.

SYSTEMATICS

Infraorder Brachyura Latreille, 1802 Section Eubrachyura Saint Laurent, 1980 Subsection Heterotremata Guinot, 1977 Superfamily Calappoidea De Haan, 1833 Family Calappidae De Haan, 1833

> *Tavernolesia* new genus Fig. 1, 2, 3.

Type species. Stenodromia calasanctii Via, 1959.

Diagnosis - Small-sized carapace, from subcircular to longitudinally ovate in outline, only slightly longer than wide; maximum width in anterior portion, at position of epibranchial region; carapace strongly convex in both directions; front scarcely projecting beyond orbits, narrow, clearly subtriangular from frontal view, also seen as triangular from dorsal view; orbits small, directed forward, with raised walls, small incisions in supra and infraorbital margins; anterolateral margins of carapace broadly arched, with six to seven small lobes; posterolateral margins of carapace nearly straight, converging backwards, wearing a long mesobranchial spine and a short spine in the middle; the mesobranchial spine is clearly directed upwards, backwards and laterally; posterior margin narrow, with three notable spines, the axial somewhat longer than the two in the corners; dorsal carapace surface with three notable subparallel longitudinal ridges and two faint lateral rows of small tubercles; dorsal regions with undifferentiated gastric and branchial areas; hepatic region small. subtriangular, elongated, with a slight inflation and two lateral small and spinuous lobes; cardiac region elongate, slightly swollen, with discrete tubercle; intestinal region depressed, small; dorsal grooves scarcely marked, nearly absent; female abdomen narrow, subtriangular, with all abdominal segments free, segments 6-1 decreasing in size posteriorly, long. subtriangular; sternum telson narrow, episternites arched, with nearly vertical margins; chelipeds stout, with curved thin fingers, upper margins bearing seven strong conical spines, external side of the hand with three rows of strong conical spines.



figure 1. *Tavernolesia calasanctii.* MGSB79789. Dorsal view. Tavèrnoles (Barcelona).

Etymology - From Tavèrnoles, the name of the village in the province of Barcelona (Catalonia, Spain) from where the fossil brachyurans with ventral portions preserved were recovered. This locality also has been one of the richest areas for the Lutetian crustacean faunas.

Remarks - The new genus differs from all extinct and extant members assigned to the Calappoidea (Ng *et al.*, 2008; Schweitzer *et al.*, 2010) in having a set of characters which are unique, not completely shared by other genera. The main differences, consists of a dorsal carapace with faint ridges and absence of deep dorsal grooves; dorsal surface of carapace smooth, bearing discrete rows of faint tubercles; a unique set of lateral spines, mainly a conspicuously long mesobranchial spine, raised, directed upwards, backwards and laterally; posterior margin bearing three spines. The set of characters makes different this genus from all others known.

Material examined The holotype, MGSB15928, dorsal carapace; complete а MGSB79789. complete female specimen; а MGSB79790, а completely preserved dorsal carapace of a big sized specimen; MGSB79791, a complete dorsal carapace of a juvenile specimen. All from the Middle Eocene (Middle Lutetian) in the Vic, Berga and Girona areas, (Catalonia, Spain). Maximum carapace width and length in MGSB79790 are 14,2 and 14 mm, respectively.



Figure 2. *Tavernolesia calasanctii* MGSB79789. Ventral view. Tavèrnoles (Barcelona).

Description. Carapace small-sized; from subcircular to longitudinally ovate in outline; only slightly longer than wide, widest anteriorly, at the level of the epibranchial region; dorsal surface strongly convex in both directions. Front few projected, narrow, with the apex strongly downturned, fairly subtriangular when seen from frontal view, with slight incisions and depressions before orbits. Orbits small, subcircular, anteriorly directed, with raised walls; supraorbital margin with two small incisions, infraorbital margin with one small incision; the orbits appear to be inclined and subelliptical in shape when seen from frontal view. Anterolateral margins broadly arched, wearing six to seven small lobes, some of them with small tooth. Posterolateral margins nearly straight, converging backwards, wearing а conspicuously long mesobranchial spine and a short lateral spine in the middle. Posterior margin short, with three small spines: the axial spine somewhat longer that the two situated in the corners. Dorsal carapace surface bearing three longitudinal inflations and two lateral rows of week tubercles; the vertical ridges, covered with small tubercles, the surface between ridges smooth. Gastric regions undifferentiated, only the posterior portion of the mesogastric region is defined by a small tubercle, some specimens insinuating protogastric lobes. Hepatic region small, elongated, slightly swollen, bearing a faint inflation. Cardiac region defined by an elongated inflation, with an axial swelling. Branchial regions large, scarcely differentiated, bearing two longitudinal ridges, the central ridge being more swollen, bearing three small but well-marked tubercles in the posterior portion, the lateral ridge scarcely inflated, bearing three weak tubercles in the anterior portion. From the mesobranchial region, a long spine is directed upward, backwards and laterally. Intestinal region small, flat. Dorsal grooves not well defined, only smooth depressions between the ridges are more or less defined in the posterior portion of the carapace. Dorsal carapace surface densely and uniformly covered by diminutive, nearly imperceptible, pits and granules. Sternum narrow, longitudinally oval, lateral margins nearly vertical. Episternites long, arched, with nearly vertical margins. Female abdominal segments subtriangular, narrow, not totally covering the lateral sides of the episternites, all segments free. Female telson triangular, long, longer than other segments; segment 6 transversely subrectangular, longer that the posterior ones; segments 2-5 decreasing in size posteriorly, bearing three longitudinal rows of faint tubercles; segment 3 is the broader; all segments free. Chelipeds stout, dorso-ventrally flattened, the upper margin of the palm bearing seven notable conical spines, and the lower margin ridged, bearing small tubercles; inner side of the palm flat, to be adapted to the body; fingers of the propodus short, thin and notably curved; outer side of the palm conspicuously convex, bearing three transverse rows of strong conical spines. Carpus large, subtriangular. Merus long dorso-ventrally flattened. Pereiopods long, flattened.



Figure 3. *Tavernolesia calasanctii* MGSB79791. Dorsal view. Tavèrnoles (Barcelona).

Discussion. The dorsal and ventral features, together with the attached chelipeds of *Tavernolesia* n. gen. exhibits primary characters that permit assignment to the superfamily Calappoidea (Williams & Child, 1988; Ng *et al.*, 2008, pg 48; Schweitzer *et al.*, 2010). The main features of the carapace, such the

general carapace outline, shape and distribution of dorsal regions; presence of lateral and posterior spines, well-defined longitudinal ridges bearing small tubercles; a narrow, subtriangular, and scarcely projected front; and small, subcircular orbits, confirms placement in the superfamily. The general ventral morphological features, such the narrow sternum, the subtriangular female abdomen with all segments free, and the characteristic construction of the chelipeds also warrant assignment to the superfamily. Usually, the male and female abdomens are narrow and few differentiated, the female bearing three rows of elongated swellings (Willaims and Child, 1989). However, a set of distinctive features in the new genus, such the slightly elongate carapace with three notable spines in the posterior margin, the narrow and few projecting front, being triangular even from dorsal view, small orbits with raised walls and three incisions, five subparallel longitudinal grooves bearing discrete tubercles, dorsal surface without grooves, two posterolateral spines, the first notably salient, directed upwards, backwards and laterally, distinguish Tavernolesia from all other genera. The exclusive assemblage of characters, but mainly the mesobranchial spines, in Tavernolesia, are a definitive feature to exclude the new genus from all extinct and extant genera assigned to the family Calappidae.

The closer extant genera, appears to be *Paracyclois* Miers, 1886 and Cyclozodion Williams & Child, 1989. The subcircular and convex carapace of Tavernolesia, the narrow, triangular, only slightly produced front, the raised walls of orbits, bearing incissions; the undifferentiated gastric and branchial regions, the spines in the posterolateral margins, and the three spines in the posterior margin are shared, and very close characters to these seen in Paracyclois and Cyclozodion. The female abdomen present similar characteristics, pleomere 6 being the longer, 2-5 decreasing posteriorly, 3 the broader. However, in the genera Paracyclois and Cyclozodion the carapaces are much more big-sized, the general outline is clearly subcircular, less elongate, the dorsal surface usually smooth, without strong longitudinal ridges, and the external portions of the chelipeds are characterized by domed, pearl-like granules, without strong spines. Some species present a dorsal surface covered by numerous notable granules, not regularly distributed along the carapace (Williams & Child, 1989, Figs. 4,6). The lateral margin is characterized by the absence of a long mesobranchial spine (Williams & Child, 1989). The set of characters in Tavernolesia suggest an intermediate form, with some features being close to other different genera but absolutely distinguished from all of them. This concept was pointed by Williams and Child (1989, p. 120), suggesting a close relationship among the genus Calappa Weber, 1795, Calappilia, Paracyclois and Cyclozodion.

The extant genus Mursia Leach in Desmarest, 1823 presents some similar features. The dorsal surface is characterized by five rows of tubercles, with not deep grooves between the ridges; extremely long mesobranchial spine; similar frontal and orbital construction, the orbits raised, with incisions, the front narrow, downturned, but still seen as subtriangular from dorsal view; chelipeds stout, granular, with crested upper margins bearing strong conical spines (Galil, 1993; Galil & Takeda, 2004). Nevertheless, the genus Mursia exhibits a broader carapace, the outline being strongly ovate transversely; the dorsal surface with no parallel longitudinal rows of tubercles, being divergent backwards; the dorsal ornamentation is more dense, with much more numerous tubercles; the lateral spine is extremely long, usually directed laterally. The fossil species assigned to *Mursia* present similar characters (Rathbun, 1926, p. 82). Via (1959, p. 140) established *M. marcusana* Rathbun, 1926, as the closer species related to Tavernolesia. However, the subcirculat outline of the carapace, appearing to be somewhat elongate with the three posterior spines, the five subparallel dorsal ridges bearing discrete tubercles, the shape, direction and position of the mesobranchial distinguish spine perfectly Tavernolesia. All the assemblage of differentiated characters in the new genus permits the distinction from all the extant and fossil forms assigned to Mursia (Galil, 1993; Schweitzer et al, 2010, p. 84).

Tavernolesia calasanctii was related to the extinct genus Stenodromia A. Milne-Edwards in Bouillé, 1873 by Via (1959, 1969), according to the general descriptions and drawings of the type species, S. gibbosa. This genus is based in a scarcely complete and poorly preserved isolated carapace. The new species appeared to be close on the basis of superficial resemblance in the carapace outline, the frontal construction, distribution of dorsal regions, and the dorsal surface bearing longitudinal ridges. The accurate examination of the type species of Stenodromia confirms a bigger size of the carapace, and very distinctive characters such the salient front with a deep axial groove, the extremely deep axial grooves all along the carapace, bounding narrow and ridged gastric and oblique ridges all along the carapace. The holotype, housed in the MNHN confirms that it consist of a completely distinct genus (Busulini et al., 2014). T. calasanctii definitely presents a smaller size of the carapace, being somewhat longer than wide due to the three notable posterior spines, different orbito-frontal construction, with a triangular front when seen from dorsal view, and orbits with raised walls, the dorsal surface covered with five discrete ridges and without dorsal grooves, a long mesobranchial spine, features not seen in Stenodromia. Busulini et al. (2014) diagnosed Stenodromia as having a slightly protruding front, the cardiac and gastric regions defined by deep long

grooves, oblique keel from posterior branchial region to gastric regions (Busulini et al., 2014, p. 206). Via also mentioned a salient front in S. gibbosa, with a different orbitofrontal construction, the description of Milne-Edwards considers the front as snout-shaped. Busulini et al. (2014, p. 206), in the revision of the European species assigned to the genus Calappilia, moved C. mainii Allasinaz, 1987 to the genus Stenodromia. The specimens studied in order to erect the new species recorded by Allasinaz, as mentioned by Busulini et al. (2014) present notable differences, appearing to be a rather heterogeneous group. The holotype looks extreme, with weird deformations, but some other specimens appears to be rather close to the genus Tavernolesia (Allasinaz, 1987, P.1, Figs. 3, 5). To the moment, we could accept the possible inclusion in Tavernolesia, especially considering some specimens illustrated by Allasinaz, but new material is necessary to have a confident assignation.

The extinct genus Calappilia A. Milne-Edwards in Bouillé, 1873 also shares some clearly distinctive features with Tavernolesia, such the general outline of the carapace, being usually subcircular, narrow orbits and front, dorsal surface at least with one axial longitudinal ridge embracing the gastric and cardiac regions, some posterolateral spines and similar constitution of chelipeds (Rumsey et al., 2016, Fig. 3). Nevertheless, the more recent diagnosis of the genus (Busulini et al., 2014, p. 196; Rumsey et al., 2016, p. 330), describes it as having deep longitudinal grooves separating gastric and cardiac regions from the branchial regions, and numerous large rounded tubercles all over the dorsal surface, notable characters not seen in Tavernolesia. A more or less heterogeneous group of species assigned to Calappilia present a subcircular outline, usually somewhat wider than long, a less elongated gastric region and the dorsal grooves are usually weakly marked. As mentioned by Williams & Child (1989, p. 120), all the species assigned to the genus Calappilia presents a considerable diversity in the dorsal ornamentation and the development of lateral spines along the margins. The coarse dorsal tubercles present an extreme diversity among the amount of species assigned to the genus, in total 23. The last studies (Busulini et al., 2014; Rumsey et al., 2016, p. 330), with excellent illustrations and descriptions confirm the extreme heterogeneity. The general outline of the carapace from clearly subcircular (C. perlata) to strongly ovate transversely (C. gemmata) or even subehexagoal (C. calculosa) presents an extraordinary variety of dorsal shape. The dorsal areolation presents as well a great diversity, with characters as densely tuberculate (C. dacica) to fairly smooth (C. gemmata). Posterolateral and posterior projections also exhibits a strong diversity, from strong subtriangular posterolateral spines (C. gemmata) to scarce, thin, acute posterolateral spines and three notable posterior spines

(C. tridentata). Posterior margin from narrow straight, without lobes (C. calculosa) to three notable posterior spines (C. tridentata). The deep grooves in C. calculosa presents a glass hour-like shape bounding the gastric and cardiac regions, and the dorsal surface was diagnosed as having five longitudinal ridges (Rumsey et al., 2016, p. 330). If we consider the illustrated drawings in Busulini et al. (2016, Pl.1, Figs. 3, 6, 9) the extreme diversity in the outline and general shape of the carapace is confirmed. Better preserved material and presence of well preserved ventral portions and chelipeds can confirm the assignment of various different genera. C. gemmata, for instance, if compared with the type species of the genus, in our view, directly deserves to be considered a new genus. So it seems that a severe revision is needed. If compared with the type species of the genus, C. verrucosa, exhibits a clearly circular outline of carapace, with continuous and strongly arched lateral margins without lobes or spines, only a small spine at the level of the postbranchial region, two very small posterior spines; dorsal surface densely, and more or less uniformly covered by large rounded tubercles; strong axial ridge embracing gastric, cardiac and intestinal regions; extremely deep grooves bounding the axial regions, defining a mesogastric and cardiac glass hour shape. Curiously, Via mentioned, but did not compare Tavernolesia with Calappilia, probably because the type species, C. verrucosa, exhibits a extremely ornamented carapace, with numerous large tubercles (Busulini et al., 2014, Fig. 1-3).

According to the assemblage of well-preserved dorsal features, together with the ventral characters and the rather complete chelipeds, the new taxon can be easily differentiated from all known extinct and extant forms. As usual when dealing on fossil species, material with more complete and better preservation is necessary to conclude about the definitive separation in different genera and for the possible record of new fossil families, but for now we confirm *Tavernolesia* as a new genus, clearly separated from *Stenodromia*.

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