

# Medusoid Cnidarians from the Montral-Alcover Lagerstätten (Triassic), Northeastern Spain

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**ABSTRACT**—We present a number of specimens of medusoid cnidarians, all of which are the first ever described from the Spanish Ladinian. *Tarracodiskus viai*, *T. villaltai*, and *Heliobranchia catalaunica* are described as new genera and species. These specimens present a number of systematic challenges due to our lack of knowledge with regard to their life cycle, soft anatomy, phenotypic plasticity, convergent characters, and paucity in the fossil record. Their mode of preservation is consistent with that of other fauna from the Montral-Alcover locality.

**KEY WORDS**— Medusoid cnidaria. Fossil impressions. Upper Muschelkalk Ladinian, NE Spain.

**RESUMEN**— En este trabajo presentamos varias impresiones fósiles de cnidarios, que son nuevos para el Ladiniano español. Tres de ellos, *Tarracodiskus viai*, *T. villaltai* y *Heliobranchia catalaunica*, se describen como géneros y especies nuevas. Todos estos especímenes representan un reto para su clasificación dado que desconocemos el ciclo de su vida, carecemos de una descripción de sus órganos internos, y también debido a la plasticidad fenotípica, la posible presencia de caracteres convergentes y su rareza tanto en el registro fósil como en el presente. La manera como estas impresiones se preservaron, concuerda con la de otra fauna previamente descrita de esta formación geológica y de esta localidad.

## Introducción

The Montral-Alcover locality in the Province of Tarragona, Catalonia, NE Spain, has yielded and continues to yield exceptionally well-preserved Triassic fossils. Taxa recovered to date from Montral-Alcover include mollusks (Seguí, 1999; Seguí, 2000), limuloids (Vía & Villalta, 1966; Romero & Vía, 1977; Vía, 1987a), crustaceans (Vía, 1971; Vía & Villalta, 1975; Calzada & Urquiola, 1994), insects (Vía & Calzada, 1987), holothurians (Cherbonnier, 1976), fish (Villalta & Vía, 1966; Beltan, 1972), reptiles (Ellenberg & Villalta, 1974; Sanz et al., 1993; Rieppel & Hagdorn, 1998), and the enigmatic Paleocyphonautidae (Vía & Romero, 1978; Romero et al. 2005). The majority of these taxa are nektonic, and several specimens are preserved in exquisite detail as soft-bodied impressions. This paper focuses on the medusoid cnidarians from Montral-Alcover. The three new species described in this report are the first ever reported from the Triassic of Spain.

## Geological setting

The Montral-Alcover area is situated about 100 km SW of Barcelona, in the Province of Tarragona (ca. 41° 10'N 1°10'E) (Map Datum NAD83/WGS84 "Zone: 30 Easting: 653801, Northing: 4558879").

The quarry that yielded the cnidarian fossils is owned by Mr. Fernando de Lucas. All specimens referred to in this report are either deposited at the Geological Museum of the Seminary of Barcelona, Spain, or privately owned by Julio Seguí.

Fossiliferous strata at Montral-Alcover consist of laminated dolomicrite (locally known as "Pedra de Alcover" or Alcover Stone) interpreted to correlate with the Upper Muschelkalk of northeastern Spain, which is of late Ladinian age (Rieppel & Hagdorn, 1998). Strata of the Upper Muschelkalk that crop out in the region accumulated on a homoclinal ramp characterized by extensive barrier complexes and/or localized buildups. The fossil-bearing interval, known as the "Alcover Unit," is part of Depositional Sequence 5 of the Triassic Supercycle in the Catalan Coastal Ranges. Depositional Sequence 5 has an average thickness of 50 m and is divided into

three sub-units. The middle sub-unit, which has yielded virtually all of the fossils found to date, is comprised of several coarsening- and thickening-upward cycles with laminated dolomicrites at their bases. The middle sub-unit shows a general shallowing trend from anoxic to intertidal-supratidal deposits and has been interpreted as part of an early highstand systems tract reflecting transgression along the northwestern coast of the southern branch of the Neotethys (Calvet & Tucker, 1995).

The fossils of Montral-Alcover are preserved in laminated dolomicrites that accumulated in small basins situated between dasycladacean mud-mound reefs (Esteban et al., 1977; Sanz et al., 1993). Fossils are generally intact and articulated, and show little evidence of post-mortem disturbance. This may reflect the inhibition of benthic marine scavengers in a low-energy, oxygen in a depleted inter-reef environment (Vía, 1987b). Based on the composition of the taxa it is reasonable to speculate that a significant fraction of the Montral-Alcover assemblage is allochthonous and was passively transported to the site of burial (Vía et al., 1977).

## Materials and preliminary remarks

*Material examined:* Specimens studied include 53614, 53616, 63612, 53615 and 53619, housed in Geological Museum of Seminary of Barcelona and MA-51, MA-52, MA-53, and MA-54 kept at the Julio Seguí private collection. Anatomical observations were made with a NIKON SMZ 1500 dissecting microscope. Anatomical features were measured to the nearest 1 mm using a digital caliper (Fowler NSK Pro-Max).

One could question whether the medusoid specimens described in this paper are trace fossils. Häntzshell (1975, p. W144) discussed this issue when substantially modifying some of the descriptions made by Harrington & Moore (1956) regarding certain medusoid impressions that he considered just as trace fossils or medusae incertae sedis. Yet, we consider the material studied herein as true fossil medusoid impressions given their excellent preservation and its clear differentiation from the surrounding sediment. This is consistent with many other fossils of the same locality that are not trace fossils. Interestingly a work in press (Carrasco 2011) does describe the first trace fossil for this locality (*Asteriacites*) where the contours are unclear and/or undefined.

Häntzshell (1975, p. W144) also points out that the uncertain jellyfishes derive from flysch; however, the Alcover-Montral sedimentation is not flysch.

Therefore, assigning the fossils described in this paper to free-living cnidaria is reasonable given their morphology and their parallelism to living taxa. Further findings could provide additional information to finally clarify this issue.

Cnidarians in general and medusoids in particular have long fossil records, with representatives from the Ediacaran fauna of the Late Proterozoic (Scrutton, 1979).

However, the medusoids, with their soft bodies, are only preserved under ideal circumstances (Vía, 1987b; Norris, 1989; Rieppel & Hogdorn, 1998). When the necessary conditions are met, the resulting specimen can show dramatic anatomical detail. However, there can still be problems related to classification. For example, the basic synapomorphy for the phylum Cnidaria is the presence of nematocysts, but such organs are virtually impossible to observe in fossil impressions. Moreover, cnidarian systematics cannot be fully understood unless we know the species life cycle (Lang Da Silveira & Carrara Morandini, 1997), which, in the case of fossils, is also virtually impossible to ascertain. Werner (1973) has warned about the utilization of purely morphological characters for classifying these organisms. Many fossil impressions that have been assigned to the order Scyphozoa, for example, lack any obvious resemblance to modern free-swimming types (Moore & Harrington, 1956). To complicate matters further, Thiel (1966) asserted that scyphozoans display a high degree of phenotypic plasticity. Despite the potential caveats, we have attempted to classify the Cnidaria from Montral-Alcover.

Several taxa have been previously interpreted as medusae, on the basis of having concentric rings and radial structures; however, they would be unlikely to be confused with our species. These differences bear some discussion.

In the enigmatic fossil genus *Eldonia*, characterized by concentric rings containing numerous radial structures, the radial structures appear pleated, compared with those of *Tarracodiscus viai* which are short and fine, those of *Catalanodiscus villaltai* which are spherical, and those *Heliobranchia catalaunica* which long and are sharply triangular. Originally described by Walcott (1911) as a free-swimming holothurian, this and subsequently-described related species have been variously interpreted as echinoderms (A. H. Clark, 1912, 1913; Durham, 1974), siphonophores (Madsen, 1962), medusae (H.L. Clark, 1912; Sun & Hou, 1987), medusiform lophophorates (Dzik, 1991, 1997; Chen et al., 1995; Zhu et al., 2002), and *incertae sedis* (Conway Morris & Robison, 1988; Alessandrello & Bracchi, 2003). One of us (LG) has studied Walcott's original material, and found Walcott's structural descriptions to be meticulous and accurate. Whilst a reinterpretation of *Eldonia* is beyond the scope of this paper, we can nonetheless state with confidence that none of our species could be easily confused with *Eldonia*.

Another fossil characterized by concentric rings and radial structures, *Peytoia*, also described by Walcott (1911), was originally described as a rhizostome scyphomedusa but later reinterpreted as the mouth-part of *Anomalocaris* (Whittington & Briggs, 1985). The radial structures of *Peytoia* are rounded triangular lobes, arranged side-by-side like a pineapple ring (Conway Morris & Robison, 1982), or a many-segmented citrus fruit in cross section; this morphology and arrangement is unlike any of our specimens.

Other medusoids characterized by concentric rings and radial features include those in the genera *Ediacaria* and *Cyclomedusa*, differing in presence of rings around the central nipple in *Cyclomedusa*, whereas these rings are lacking in *Ediacaria* (Sprigg, 1947; Sprigg, 1949). Gehling et al. (2000) regarded these and many other named Ediacaran medusoids as preservational morphs of *Aspidella terrinovica* Billings, 1872.

## Taxonomy

Phylum CNIDARIA Hatschek, 1888  
Class HYDROZOA Owen, 1843  
Order LEPTOMEDUSAE Haeckel, 1866  
Family AEQUOREIDAE Eschscholtz, 1829

*Tarracodiscus* gen. nov.

Type species: *Tarracodiscus viai* sp. nov.

**Diagnosis** – Essentially a perfect disk, completely flat, divided into four concentric disks (from the center to the exterior) similar to that observed in Recent hydrozoan medusae (e.g., *Aequorea* spp.): the external disk which is presumably the bell margin, with numerous centripetal grooves or spherical-shaped small circles.

**Description** – Essentially a perfect disk, completely flat, not divided by projecting ridges or partitions, margin of bell entire, divided into four concentric disks (from the center to the exterior) similar to that observed in Recent hydrozoan medusae (e.g., *Aequorea* spp.): (a) a central, somewhat elliptical disk, about 20% of the diameter, without any markings and clearer than the other disks, corresponding to the area of the manubrium; (b) larger, intermediate, darker disk, about 60% of the total diameter, perfectly round in its external circumference but somewhat elliptical in its internal one; (c) a smaller intermediate disk with irregular defts that corresponds to about 20% of the total diameter, and, (d) an external disk which is presumably the bell margin with numerous centripetal grooves. These grooves are similar to those found in *Hydrocraspedota mayri* (Kolb, 1951) (see Harrington & Moore, 1956, p. F75, fig. 61, 1c.).

**Etymology** – Tarraco (L.) = Latin name for Tarragona, the Spanish province in which it was found; discus (L.) = disk, because of the perfect wheel-shape of the body.

**Remarks** – The genus *Tarracodiscus* has been assigned to the suborder Leptomedusae because it shares a distinctive pattern of concentric zones and radial structures with the genus *Aequorea*. We recognize that such resemblance may be the result of convergent evolution.

*Tarracodiscus viai* sp. nov.

**Taxonomical data** – The holotype is housed at the Geological Museum of Seminary of Barcelona with the number 53619. It comes from Mr. Fernando de Lucas quarry, near the Alcover-Montral road, Tarragona province, NE Spain. Sheet 445, Cornudella. Stratum typicum

Upper Ladinian. Named after of Dr. Luis Vía in his birth centenary (1910-1991) and one of the pioneer researchers of the Montral-Alcover fauna.

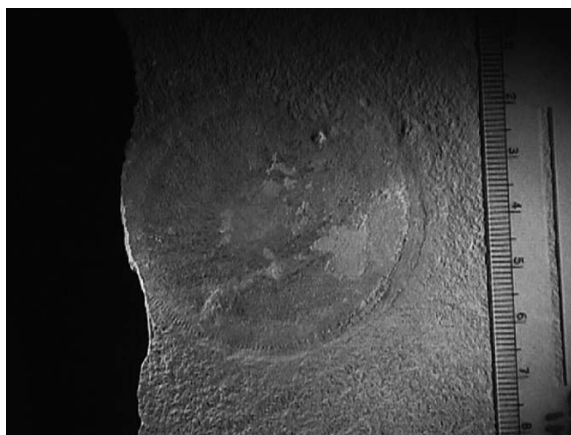


Fig. 1. *Tarracodiscus viai* gen. nov., sp. nov. (MA-51, paratype).

**Diagnosis** – Essentially a perfect disk, completely flat, divided into four concentric disks (from the center to the exterior): the external disk that is presumably the bell margin, with numerous centripetal grooves.

**Description** – The same as the diagnosis.

**Material and measures** – Three specimens: The holotype and 2 paratypes. Holotype: 53619 (Fig. 3). Dimensions: Total diameter = 39 mm; disk (a) = 13 mm (widest) to 7 mm (narrowest), disk (b) = 38 mm (widest) to 30 mm (narrowest), disk (c) = 4 mm on average and disk (d) = 3 mm on average.

Paratype MA-51 (Fig. 1). Dimensions: Total diameter = 51 mm. Disk (a) = 14 mm (widest) to 1 mm (narrowest); disk (b) = 42 mm (widest) to 33 mm (narrowest); disk (c) = 5 mm on average; disk (d) = 3 mm on average. Paratype MA-53 (Fig. 2). Dimensions: Total diameter = 49 mm. Disk (a) = 14 mm (widest) to 1 mm (narrowest); disk (b) = 42 mm (widest) to 33 mm (narrowest); disk (c) = 5 mm on average; disk (d) = 3 mm average.



Fig. 2 - *Tarracodiscus viai* gen. nov., sp. nov. (MA-53, paratype).

Variations between these specimens. MA-53 (Fig. 2) is very similar to MA-51, although it is not so well preserved. Unlike the specimen MA-51, differentiations between disks (a) and (b) are not apparent. However, the clefts of disk (c) and the coronal margin of disk (d) are comparable to the specimen MA-51. Specimen 53619 (Fig. 3) is also very similar in gross morphology to MA-51, but the anatomical details are even less conspicuous than for MA-53. MA-53 (Fig. 4) is also similar to the specimen MA-51, although the clefts of disk (c) are much more pronounced. This may reflect differential fossilization processes.

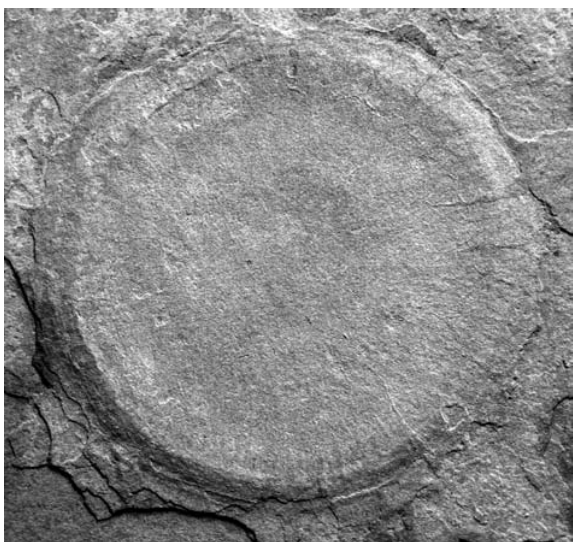


Fig. 3 - *Tarracodiscus viai* gen. nov., sp. nov. (53619, holotype). Measures in text.

**Remarks** – No similar medusae have been described from Triassic. *Tarracodiscus viai* bears a striking resemblance to hydromedusae in the Recent genus *Aequorea* Péron & Lesueur, 1810. Like *Aequorea*, *T. viai* has four dissimilar concentric rings, one of which is a zone of radial structures. In *Aequorea*, these radial structures are the internal radial canals and corresponding external gonads (Russell, 1953). These radial structures are also similar to the radial grooves found in the Jurassic species *Hydrocraspedota mayri* (Kolb, 1951); however, the internal structures that are so conspicuous in *H. mayri* are not evident in *T. viai*.

*Tarracodiscus villaltai* sp. nov.

**Taxonomical data** – The holotype is housed provisionally in the private collection of Mr. J. Seguí with the number MA-52 (Fig. 4). It was found at the Mr. Fernando de Lucas quarry, near the Alcover-Montral road, Tarragona province, NE Spain. Sheet 445, Cornudella. Stratum typicum Upper Ladinian. Named after Dr. J. Fernández de Villalta, (1913-2003) prominent Spanish paleontologist and with Dr. Via, one of the pioneer researchers of the Montral-Alcover fauna.



Fig. 4. *Tarracodiscus villaltai* sp. nov. (MA 52, holotype) Measures in text.

**Diagnosis** – Essentially a perfect disk, completely flat, divided into four concentric disks (from the center to the exterior), with 30 spherical-shaped circles on the external disk, arranged in a band near the margin of the disk. Fig. 4

**Description** – The same as the diagnosis.

**Material and dimensions** – The sole specimen known is the holotype. Its dimensions are: Total diameter = 50 mm; external ring = 6 mm.

**Remark** – The unique morphology of *T. villaltai* is analogous to that of several Recent and fossil medusae. Regular papillae of this nature are rare in the Recent medusae, and therefore are highly diagnostic for those species in which they occur. For example, in the hydrozoan family Aequoreidae, genera are characterized by the arrangement or absence of their subumbrellar papillae: in *Zygocanna* and *Rhacostoma*, the papillae are in rows between the radial canals; in *Aldersladia*, the papillae underlie the radial canals singly or in connected multiples; in *Gangliostoma*, the papillae are at the base of the manubrium; and in *Aequorea*, subumbrellar papillae are lacking (Gershwin, 2006). In the scyphozoa, exumbrellar warts, knobs and papillae occur in various taxa, but only in the family Cepheidae are the papillae arranged in diagnostic patterns of rows, whorls and regions, typically on or around the central hump (Kramp, 1961; Gershwin & Zeidler, 2008). However, none of these would be easily confused with *T. villaltai*, in which a single whorl is arranged around the periphery of the exumbrella.

In the fossil medusae, *Beltanella gilesi* Sprigg, 1947, from the Ediacaran of South Australia, is characterized by eight circular structures midway toward the margin; and *Bassaenia moreae* Renz, 1925, from the Upper Cretaceous of Greece, is characterized by two whorls of structures, elliptical in the outer whorl and round in the inner whorl. Neither of these would be easily confused with *T. villaltai*, which is characterized by 30 round structures in a peripheral band.

Unlike that of its congener *T. viai*, the unique morphology of *T. villaltai* has no parallel in the Recent medusae.

Class SCYPHOZOA Götte, 1887  
 Subclass CORONAMEDUSAE Calder, 2009  
 Order CORONATIDA Vanhöffen, 1892  
 Family HELIOBRANCHIIDAE nov. fam.

*Diagnosis* – Coronatida with triangular 12 lappets, arranged all over the external part of disk.

*Description* – This family includes coronomedusae distinguished by their sun-shaped margins.

*Etymology* – Helios after the greek name of the sun because of its radiant shape; *branchion* (G.) for arms because the lappets.

*Remarks* – No similar morphology is found in recent or fossil Coronatida; thus, it seems suitable to propose a new family, yet uncertain, better than to relegate the studied specimens in open nomenclature without family assignment. Additionally, the morphological features are consistent with those found in Coronatida.

Curiously the Naticidae (Gastropoda) have their eggs in a similar form: a disk with lappets (Dr. Abad, personal communication, 8.11.2010).

*Heliobranchia* gen. nov.

Type species: *Heliobranchia catalaunica*, sp. nov.

*Diagnosis* – Same as for the family.

*Description* – Same as for the family.

*Etymology* – For the genus: *Helios* (Gr.) = after the sun because of its radiant shape, *branchion* (Gr.) = arms; meaning with the arms (referring to lappets).

*Heliobranchia catalaunica* sp. nov.

*Taxonomical data* – The holotype is housed at the Geological Museum of the Seminary of Barcelona under number 53614. Figured (fig. 5). It was found at the

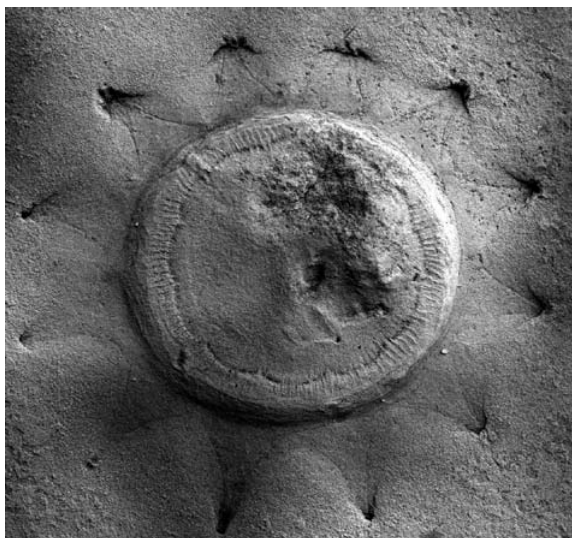


Fig. 5. *Heliobranchia catalaunica* gen. nov., sp. nov. (53614 MGSB, holotype). Measures in text.

Mr. Fernando de Lucas quarry, near the Alcover-Montral road, Tarragona province, NE Spain. Sheet 445, Cornudella. Stratum typicum Upper Ladinian. Toponym, named after Cataluña (NE Spain) (= in latin *Catalaunia*), where is the outcrop.

*Diagnosis* – Essentially a perfect disk, with 12 triangular and sharp pointed lappets.

*Material and dimensions* – Two specimens: The holotype: 53614 (Fig. 5). Dimensions: Total diameter = 49 mm; diameter of the central disk (i.e., excluding the lappets) = 29 mm; width of the coronal furrow = 3 mm on average; distance between the apical points of the lappets = 11 mm.

Paratype: 53616 (Fig. 7) is almost identical to the holotype, although the bell is poorly preserved. Two small clefts on the margin of the specimen could be the remains of a deflated bell. Dimensions: Total diameter = 54 mm; diameter of the central disk (i.e., excluding the lappets) = 48 mm; width of the coronal furrow = 3 mm on average (not very well defined in this specimen); distance between the apical points of the lappets = 17 mm.

*Description* – Body circular, with a prominent central disk (at least 5 mm high) and 12 conspicuous lappets. A clearly defined coronal groove separates the central disk from the peripheral zone of the body and lappets. The coronal groove is 'scalloped' rather than straight, with the scallops corresponding radially in alternation with the lappets. The coronal groove is further decorated with a series of very fine radial lines, some crossing the coronal groove like sewing stitches; whether these are homologous or analogous to pedalia is unknown. The body margin is about one-fourth the disc diameter, straight-sided peripherally, ending abruptly adjacent to the lappet zone. The twelve lappets are sharply triangular, about one-half as long as the disc diameter, deeply incised between, with smooth, well defined margins.



Fig. 6 – *Heliobranchia catalaunica* gen. nov., sp. nov. (53616 MGSB, paratype)

*Remarks* – The morphology of *Heliobranchia catalaunica* is spectacularly well preserved, but in need of discussion. The presence of numerous triangular radiating lappets has no equal in the Recent or fossil Medusozoa. We interpret these structures as stiff and of a solid consistency, due to the deep and sharp impressions that they have left. However, this leaves us to wonder about the structures and relationships of *H. catalaunica*.

Rather than leave *Heliobranchia catalaunica* as *incertae sedis*, or proposing a whole new higher taxon for it, we have conservatively assigned it to the order Coronatae on the basis of several shared characters, including: 1) a deep furrow (coronal groove) dividing the aboral surface (exumbrella) into a central disc and a peripheral zone; 2) the peripheral zone has radial thickening (pedalia), 3) lappet-like structures radiating from the body, and 4) marginal lappets have interspersed sense organs --- or: 4) sense organs in alternation with the lappets. It is worth noting that even the size of our fossil specimens is comparable to that of Recent adult members of this order (~50 mm). The placement of *Heliobranchia catalaunica* within a new family of Coronatae is justified on the basis of the unique shape of the pedalia and the scalloping of the coronal furrow.

## Acknowledgements

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