

STRANDED JELLYFISH IN THE LOWERMOST CAMBRIAN (CORDUBAN) OF SPAIN

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ABSTRACT

Ninety discoid structures of big size occurring on a bedding plane of Nemakit-Daldynian to Tommotian sandstones (i.e. Corduban in the Spanish scale of Cambrian stages) from south-western Spain are described. Cross-cutting relationships between discoid structures and associated trace fossils, as well as evidence for penecontemporaneous deformation of sediment laminae below the discoids, permit to interpret these structures as impressions of ancient, soft-bodied marine organisms. Taphonomic, biometric, and morphological studies suggest that they are outer moulds of both sides, subumbrellar and exumbrellar, of ancient jellyfish of hydrozoan coelenterates, whose canals resemble the modern genus *Aequorea*. With diameters up to 88 cm, *Cordubia* was a giant by hydromedusae standards. Palaeoichnological, lithological and sedimentological features suggest an extremely shallow, marine environment, where these organisms stranded during a single event.

Cordubia gigantea gen. et sp. nov. is the oldest record of unquestionable jellyfish. The palaeontological site described here is outstanding, also because its anomalous record of hydrozoans in coarse siliciclastic rocks and the high number of specimens on a single top bedding plane of ca. 120 m². Since soft-bodied biotas of Nemakit-Daldynian to Tommotian ages are very scarce, this site may provide a better understanding of the important taphonomic and biological events across the Neoproterozoic/Phanerozoic transition, particularly the evolution of hydrozoans.

Key words: Soft-bodied fossils, jellyfish, Torreárboles Formation, Spain, Corduban, Lower Cambrian.

RESUMEN

Se describen noventa estructuras discoidales de gran tamaño, registradas en un plano de estratificación de areniscas de edad Nemakit-Daldyniense a Tommotiense (es decir, de edad Cordubiense en la escala española de pisos cámbricos) procedente del suroeste de España. Las relaciones de corte entre las estructuras discoidales y los icnofósiles asociados, así como las evidencias de deformación penecontemporánea de las láminas sedimentarias presentes debajo de los discoides, permiten interpretar estas estructuras como impresiones de antiguos organismos marinos de cuerpo blando. Los estudios tafonómico, biométrico y morfológico sugieren que se trata de moldes externos de las superficies subumbrelar y exumbrelar de medusas fósiles de celentéreos hidrozoos, cuyos canales se asemejan a los del género actual *Aequorea*. Con diámetros de hasta 88 cm, *Cordubia* fue un gigante para los estándares de las hidromedusas. Los rasgos paleoicnológicos, litológicos y sedimentológicos indican un medio marino extremadamente somero, donde estos organismos quedaron varados durante un único evento.

Cordubia gigantea gen. et sp. nov. constituye el registro más antiguo de medusas fósiles incuestionables. El yacimiento paleontológico aquí descrito es relevante no sólo por ello, sino también por constituir un registro

anómalo de hidrozoos en rocas siliciclásticas groseras y por el gran número de especímenes registrados en un sólo plano de estratificación de unos 120 m². Dado que las biotas de cuerpos blandos de edad Nemakit-Daldyniense a Tommotiense son muy escasas, este yacimiento puede ayudar a comprender mejor los importantes eventos tafonómicos y biológicos que ocurrieron durante la transición entre el Neoproterozoico y el Fanerozoico, particularmente en cuanto a la evolución de los hidrozoos.

Palabra clave: Fósiles de cuerpos blandos, medusas, Formación Torreárboles, España, Cordubiense, Cámbrico Inferior.

INTRODUCTION

The discovery of soft-bodied biotas (including trace and body fossils) at the transition from Neoproterozoic to Phanerozoic eons is essential for understanding the emergence of body plans, the ongoing evolutionary patterns and the changes in ecosystems during that time. The worldwide Ediacara-type biotas include soft-bodied fossils of controversial affinities (Gehling, 1991; Seilacher, 1992; Fedonkin, 1992; Runnegar, 1995) preserved mainly as concave hyporeliefs (i.e. outer moulds) in high-energy sandstones (Glaessner, 1984; Fedonkin, 1985). Associated trace fossils in late Neoproterozoic rocks are simple forms which reflect peculiar ethologies of small bilaterians exploiting a thin column of sediment (Crimes, 1994; "under mat miners" of Seilacher and Pflüger, 1994). Ediacara-type biotas range from late Neoproterozoic (ca. 600 Myr BP) to the lowermost Cambrian (Nemakit-Daldynian, ca. 540 Myr BP; Jensen *et al.*, 1998). Soft-bodied Burgess Shale-type biotas include representatives of many eucoelomata phyla, which were delicately preserved in fine-grained rocks under low-energy conditions (Conway Morris, 1998). Since the oldest Burgess Shale-type biotas occur in Atdabanian rocks (Early Cambrian), a remarkable record gap exists for most Nemakit-Daldynian and Tommotian soft-bodied animals. The discovery of ninety specimens of giant discoid fossils on a bedding plane of Nemakit-Daldynian to Tommotian sandstones in southwestern Spain provides new insights into the Early Cambrian life scenario.

GEOLOGIC SETTING

This unique palaeontological site is near the village of Constantina, Sierra Morena, 91 km north of Seville, Spain (Fig. 1a). The terminal Neoproterozoic is represented here by the marine Volcanic-Sedimentary Complex (Liñán Guijarro, 1978). Its uppermost part is composed of andesites, lutites and fine sandstones of the San Jerónimo Formation, which contain cyanobacteria (Liñán and Palacios, 1983) and trace fossils (Fedonkin *et al.*, 1985) suggestive of a Vendian age. The Lower Cambrian comprises the Torreárboles Formation, the Campoallá series and the Alanís beds. The Campoallá series contains

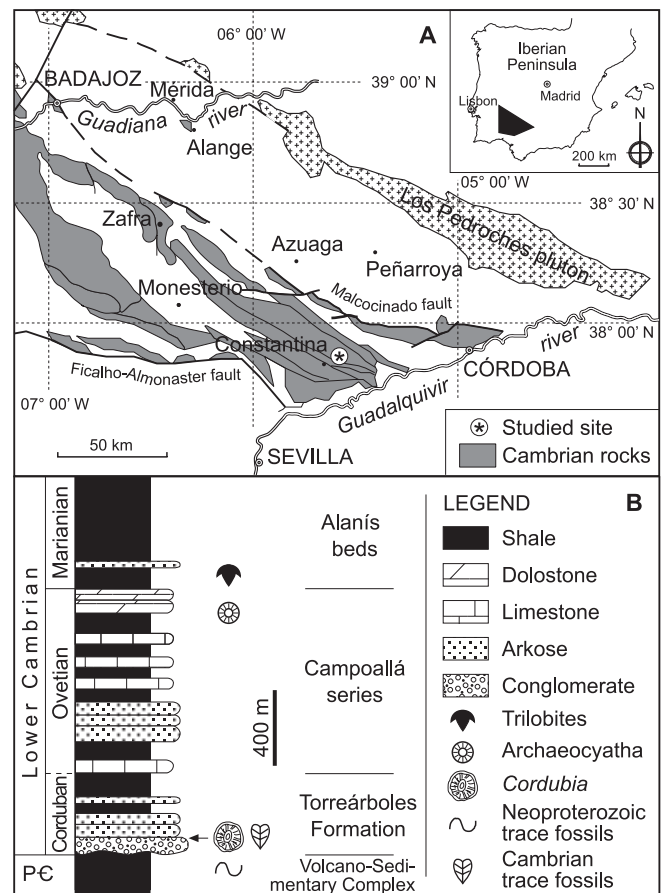


Figure 1. a: Geological sketch map with location of the palaeontological site. b: Synthesis of the stratigraphy of the area.

Ovetian (i.e. Atdabanian) archaeocyatha (Perejón, 1986) and the Alanís beds yielded Marianian (i.e. Botoman) trilobites of the *Saukianda* fauna (Richter and Richter, 1940; Sdzuy, 1962).

The fossils reported here occur in the Torreárboles Formation. It unconformably overlies the terminal Neoproterozoic basement, which uplifted in SW Iberia during the final Cadomian phases; strong palaeoreliefs appeared and were subsequently covered by the Torreárboles siliciclastics, which represent the onset of the general Cambrian transgression on SW Iberia (Liñán and Gámez-Vintaned, 1993). The Torreárboles Formation is 0-400 m thick and consists of conglomerates and sandstones of the lower La

Tierna Member and reddish shales and sandstones of the upper Julia Member. Sedimentary environments evolved from terrestrial and littoral conditions in the lower member to sublittoral settings in the upper. Trace fossils (Fedonkin *et al.*, 1985; Liñán, 1984) suggest a Corduban age (a north-western peri-Gondwanan stage equivalent to the Nemakit-Daldynian plus the Tommotian; Liñán and Gámez-Vintaned, 1993) for this formation. The biota studied here occurs at the lower part of the La Tierna Member, dated as the earliest Cambrian zone (Gámez Vintaned and Liñán, 1996) (Fig. 1b).

Site description

This palaeontological site displays one of the highest concentrations of discoid soft bodies known from the Phanerozoic fossil record. Ninety specimens of discoid fossils up to 88 cm in diameter are recorded on a single, well exposed top bedding plane of ca. 120 m² (15 m x 8 m) dipping 20° south. Because of the hardness of the conglomerates and sandstones of the La Tierna Member, naturally-exposed large bedding planes are rarely found in the extensive outcrops in Spain and Portugal. This leads us to suspect that the present bedding plane was artificially exposed in a quarry between the eighteenth and twentieth centuries, when the so-called “house of the written stone” (which led to the popular interpretation of the fossils as petroglyphs) was built in the vicinity using blocks from La Tierna Member.

Lichen colonisation and water run-off cause damage to the fossils at a high rate. The joints system affecting the bedding plane also favour slow collapse of the part next to a cliff. This call for urgent measures to this exceptional palaeontological heritage.

TAPHONOMY AND ASSOCIATED TRACE FOSSILS

Ediacara-type preservation in coarse-grained siliciclastics is a common feature of Neoproterozoic soft-bodied biotas, but is known in Cambrian rocks only from fine-grained sandstones of the Early Cambrian Uratanna Formation in South Australia (Jensen *et al.*, 1998) and from medium-grained sandstone surfaces of the Upper Cambrian Mt. Simon Formation in Wisconsin, U.S.A. (Hagadorn *et al.*, 2002). The Spanish fossils are preserved at the top of a one-centimetre layer of medium-grained, arkosic greywacke with parallel lamination, which covers a thick bed of conglomerate. Small-scale oscillation ripples with straight crests overprint the greywacke layer and are, in turn, interrupted by the fossils, which are preserved as gently-dipping, shallow furrows wider than deep; Fig. 2a). Some specimens show complete or partial overlapping with others (Fig. 3a; specimens 50A and B) and many are elongated parallel to the ripple marks. In cross section, the

horizontal, parallel lamination is shown to be depressed underneath the furrows (Fig. 2d). Small endogenous burrows (*Planolites montanus* Richter, 1937; Fig. 2b) and trails (*Cochlichnus* ichnosp.) occasionally overprint both circular and radial fossil furrows. The ichnogenera *Circulichnis* Vyalov, 1971 and *Monomorphichnus* Crimes, 1970 are also present on the bedding plane. Tectonic joints sharply intersect the furrows, causing short offsets in a few specimens, indicating that joints originated later and than the furrows can not be petroglyphs.

The ichnofossils indicate a marginal marine fauna bioturbating a soft, sandy substratum. Small-scale oscillation ripples suggest low-energy and extremely shallow water. Thus the most likely scenario is the massive accumulation of pelagic organisms stranded on the sea shore during a single event (probably because of mass mortality). The carcasses were rapidly buried and endobenthic fauna started bioturbation. This view is supported by (1) the overlapping of specimens; (2) the interruption of ripple marks; (3) the deformation of parallel lamination below the fossils (under the thickest part of the bodies when the sediment was still soft); (4) the elongation of some specimens parallel to the ripples (deformed at the moment of deposition); (5) fairly good preservation for a coarse siliciclastic sediment, and (6) trace fossil overprints.

The features noted above also disprove an ancient, anthropological origin as petroglyphs. In turn, it seems more rational that palaeontological sites like this could have been a source of inspiration for primitive cultures, because the circular markings may have been conceived as confirmation of the universal myth of the mother Earth-father Sun relationship.

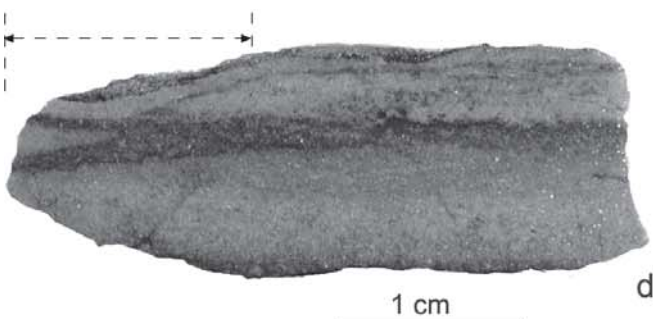
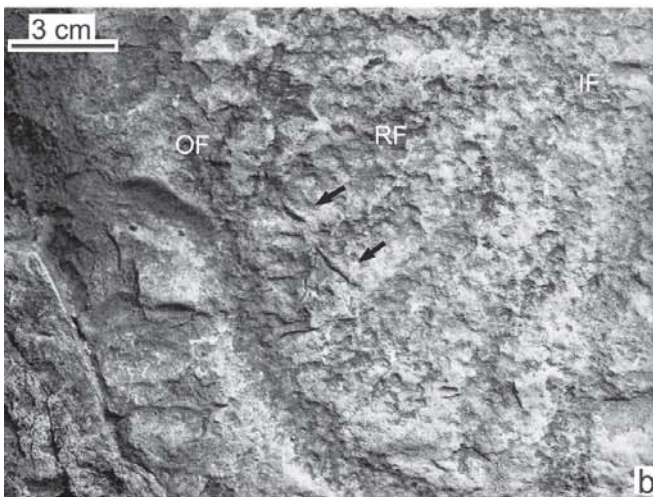
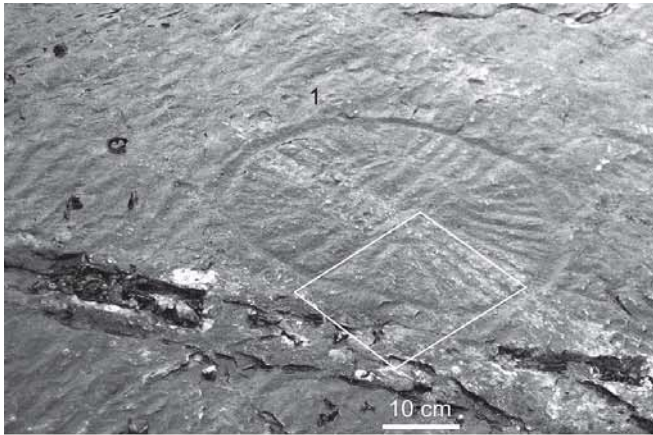
TAXONOMY AND DISCUSSION

Genus *Cordubia* gen. nov.

Type species: *Cordubia gigantea* gen. et sp. nov.

Derivation nominis: The name *Cordubia* derives from the Corduban Stage.

Diagnosis: Discoid, top-bedding impressions consisting of two circular or near-circular, concentric or eccentric furrows connected by straight radial furrows. This morphology, called morphotype A, is associated with another one consisting of a single circular to near-circular furrow (morphotype B). Both morphotypes are ornamented by densely disposed, millimetric pits (Figs. 2b, c). They are interpreted as subumbrellar and exumbrellar impressions of the same type of jellyfish. The entire area encircled by the outer furrow is generally flat, but slightly convex in some specimens of type A (e.g. specimen 37; Fig. 4) and slightly concave in a few type B specimens.



Discussion: *Cordubia* is distinct from all “medusoid” fossils in that the spacing of the radial furrows is very similar to furrow width. *Cordubia* differs from the epireliefs of the Neoproterozoic genera *Bonata* Fedonkin, 1980 and *Irridinitus* Fedonkin, 1983 in that it lacks a central, raised area and has an inner furrow. The Neoproterozoic genus *Nadalina* Narbonne and Hofmann, 1987 shows an inner ring of millimetric pits, but lacks radial structures. Properly, the forms preserved at the top of bedding planes can be compared with *Cordubia*; the assumption that most Neoproterozoic and Palaeozoic forms were non-resistant organisms (Wade, 1968) allows some comparison between both genera. *Cordubia* also differs from the Neoproterozoic genera *Aspidella* Billings, 1872, *Cyclomedusa* Sprigg, 1947, *Ediacaria* Sprigg, 1947, and *Mawsonites* Glaessner and Wade, 1966, and from the Neoproterozoic to Lower Cambrian genus *Kullingia* Glaessner *in* Føyn and Glaessner, 1979, in having only two concentric rings. The three-dimensional *Protolyellia* Torell, 1870 of the Lower Cambrian differs from *Cordubia* in having either incomplete, bifurcating, irregular or anastomosing radial furrows and very small near-circular furrows; it has also been interpreted as psammocorallia (Seilacher, 1992). The Lower Cambrian genera *Stellostomites* Sun and Hou, 1987 and *Yunnanomedusa* Sun and Hou, 1987 lack thick concentric rings and show thin, either simple or outwards-trifurcating radial ridges. In contrast to all these fossils, the size of *Cordubia* (ranging from 18 to 88 cm in diameter) is only paralleled by Upper Cambrian and Upper Jurassic medusae. Upper Cambrian medusae from Wisconsin (U.S.A.) (Hagadorn *et al.*, 2002) differ from *Cordubia* in that they lack radial features and display top-bedding annular ridges. Upper Jurassic subumbrellar impressions of *Rhizostomites* Haeckel, 1866 show very thin, densely spaced concentric features in the outer area and tetramerous gonadal impressions in the centre.

Figure 2. a: Specimen 1 (morphotype A, holotype; MPZ 2002/11) interrupts small-scale oscillation ripples (except in the central area). White rhomboid defines area shown in figure 2b. (Field photograph). b: Partial view of the holotype of *Cordubia gigantea* gen. and sp. nov. (specimen MPZ 2002/11). Burrows of *Planolites montanus* overprint radial furrows and areas inbetween (black arrows). Note that ornamentation of millimetric pits are also present on the areas between radial furrows. OF: Outer furrow; RF: Radial furrow; IF: Inner furrow. (Field photograph). c: Specimen 43, morphotype B, ornamented by pits (field photograph). d: Cross section of sediment and the outermost part of specimen 61, morphotype B. The horizontal, parallel lamination has become depressed underneath the furrow of the fossil (between arrows). (Lighting in a and c is from the upper left corner, and from the upper right in b).

Cordubia gigantea gen. and sp. nov.

Figs. 2-4

Derivatio nominis: The specific name refer to the large size of the specimens.

Diagnosis: The ratio outer furrow width/ outer diameter (OFW/OD) ranges approximately from 1/10 to 1/20 (Table 1); the ratio outer furrow width/ inner furrow width (OFW/IFW) ranges from 1/1.0 to 1/2.1; the width of radial furrows increases toward the outer margin and is very similar to the their spacing.

Material: Twenty specimens of morphotype A and seventy of B have been identified. The specimen designated as the holotype (Figs. 2a, 3a) is of type A. The type material remains in the field;

replicas of the holotype (MPZ 2002/11), the paratypes (MPZ 2002/12-MPZ 2002/18) and others (MPZ 2002/953-MPZ 2002/956) are housed in the Museo Paleontológico de la Universidad de Zaragoza (Spain). A core containing host rock and part of specimen 61 (MPZ 2002/19) was sampled. A replica of one paratype is in the Museo de Geología de la Universidad de Sevilla (MGUS-2100).

Measurements on the best-preserved specimens (Table 1) are compatible with allometric growth, as typical of animals: the outer furrow width (OFW) increases as does the outer diameter (OD), and the ratio OFW/OD decreases as the body size grows (see insert in table 1). Furthermore, the order of radial symmetry increases with body size.

The presence of only two morphotypes among ninety identified specimens points to an unique, two-sided animal. Type B specimens totally interrupt the ripple marks placed below, while there are some ripples preserved in

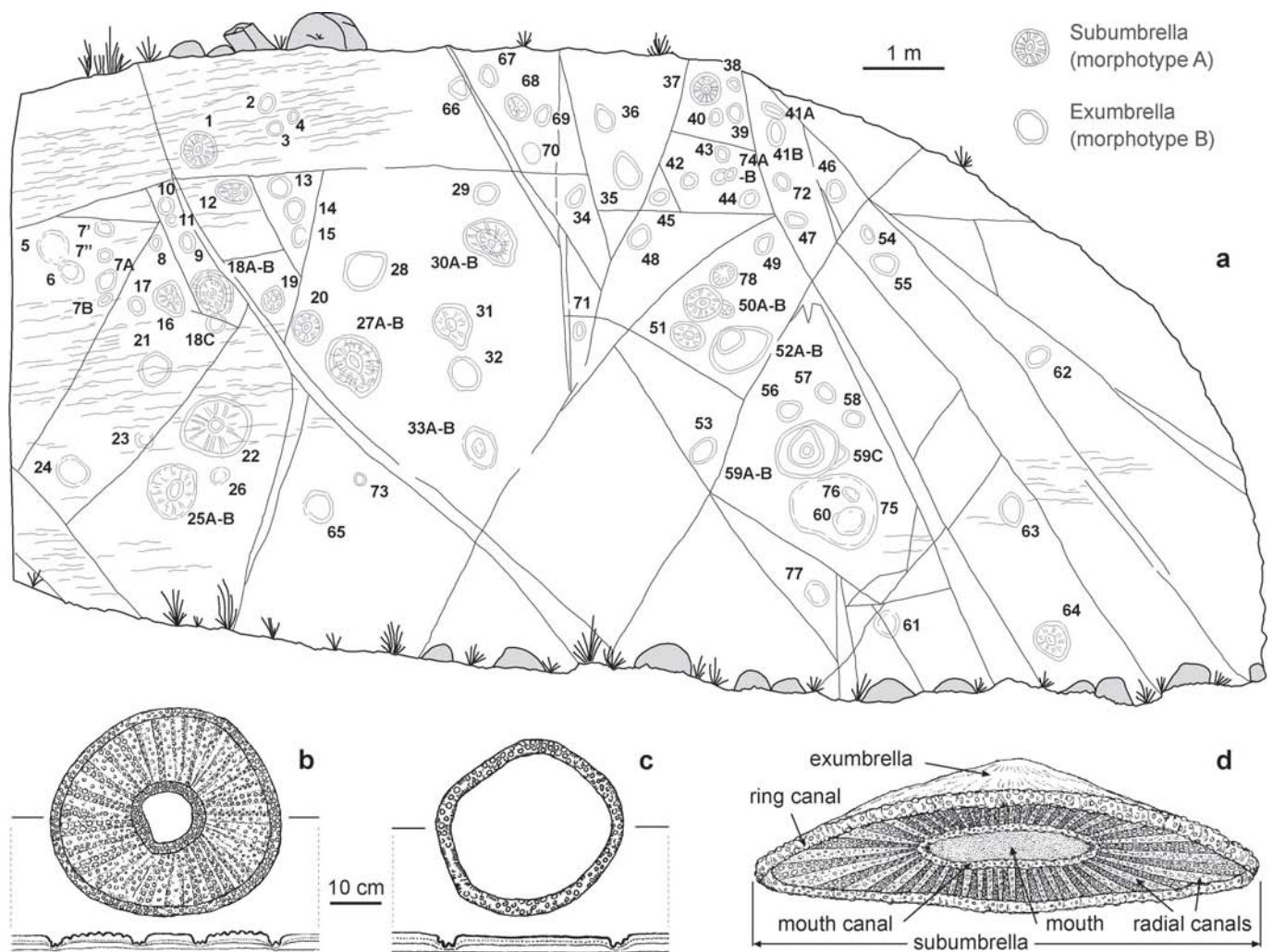


Figure 3. a: Sketch of the bedding surface showing *Cordubia gigantea* gen. and sp. nov., joints and oscillation ripples. Measurements of some well-preserved specimens are shown in table 1. Specimens 1 (MPZ 2002/11: holotype; 12 (MPZ 2002/12), 16 (MPZ 2002/13), 37 (MPZ 2002/14) and 50A (MPZ 2002/15): paratypes of morphotype A. Specimens 2 (MPZ 2002/16), 42 (MPZ 2002/17) and 43 (MPZ 2002/18): paratypes of morphotype B. The polished section shown in figure 2d belongs to specimen 61 (MPZ 2002/19). b, c: Sketches of morphotypes A and B and their preservation. d: Reconstruction of *Cordubia gigantea* gen. and sp. nov.

the central area of some type A specimens (Fig. 2a), suggesting that the topography was convex on “side B” and concave on “side A”. Type A specimens with convex-up central areas hint at a flattened bell shape for the organism. The fact that ca. 70% of specimens of type A have an eccentric inner furrow and that many of them are elongated parallel to the ripple marks, hints at soft bodies that became deformed when stranding on the sea shore.

CONCLUSIONS

The taphonomic study of discoid fossils, together with their morphology and ontogeny, allow them to be interpreted as outer moulds of ancient jellyfish of hydrozoan coelenterates similar to the extant genus *Aequorea*; the radiate morphology A corresponds to the subumbrellar and the simpler morphology B to the exumbrellar side of the same organism. The outer furrow represents the ring ca-

MORPHOTYPE B			MORPHOTYPE A							
Specimen	D	FW	Specimen	OD	OFW	NRF	ID	IFW	RFS	IFP
25A	64 x 67	---	1	43 x 50	2.5	36	15 x 15	1-1.5	1.5-2	C
28	51 x 59	2.5-3	12	30 x 33	2	24-25	10 x 12	1	---	E
29	35 x 40	3	16	35 x 37	1-1.5	25	16 x 18	1	0.7	E
34	28 x 28	1.5	22	80 x 88	3-3.5	40	17 x 19	1.5	1	E
35	45 x 45	1.5	27A	55 x 67	2.5-3	40	19 x 21	2	---	E
36	49 x 49	1.5	30A	56 x 60	2.5-3	40	28 x 26	2	1	E
48	27 x 29	2.5	37	34 x 36	1.5	25	15 x 15	1-1.5	0.7-1	E
49	25 x 26	3-4.5	50A	35 x 37	2	25	13 x 13	1	---	E
52A	26 x 31	1.5	50B	18 x 18	2	> 9	5 x 7	1	---	C
53	25 x 28	2.5	51	28 x 27	1.5	> 16	9 x 11	1.5	---	C
56	25 x 26	3								
57	21 x 23	2.5								
58	23 x 26	3								
59 A	66 x 73	3.5-5								
59 B	30 x 41	2.5								
65	55 x 56	---								
66	29 x 32	2.6								
67	20 x 23	1.9								
68	32 x 34	2.3								
69	23 x 25	2								
70	20 x 23	---								
71	18 x 21	---								

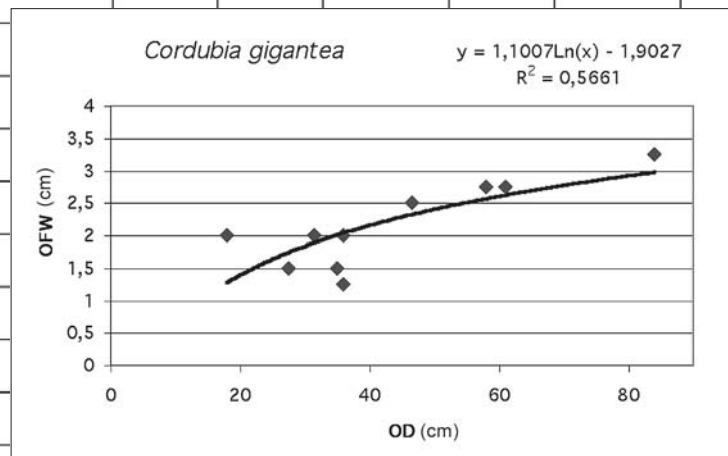


Table 1. Biometric parameters for morphotypes A and B of *Cordubia gigantea* gen. et sp. nov.

Note. D: diameter; FW: furrow width; OD: outer diameter; OFW: outer furrow width; NRF: number of radial furrows; ID: inner diameter; IFW: inner furrow width; RFS: radial furrows spacing; IFP: inner furrow position (C: central; E: eccentric). All measures are in centimetres.

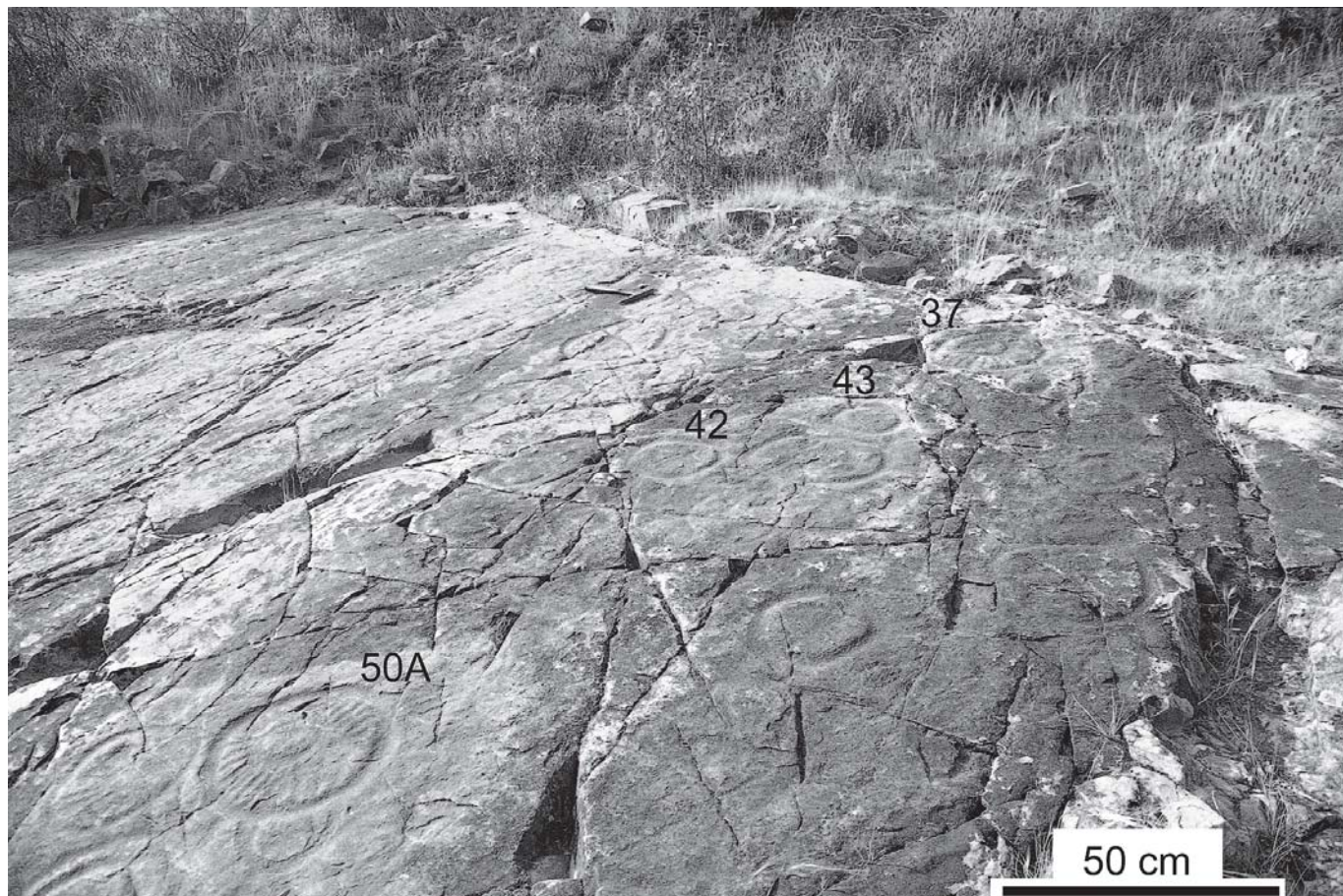


Figure 4. Partial view of the site. The bedding surface dips towards the left. Paratypes of morphotype A (37, 50A) and morphotype B (42, 43) are indicated. (Field photograph. Lighting is from the upper left corner).

nal, the inner furrow the mouth canal and the radial furrows the radial canals (Fig. 3d). Massive death of jellyfish, triggered by events of ecological stress, and followed by accumulation on beaches (mainly with the exumbrellar side down, as in the present case; Bruton, 1991) are common in modern environments.

The scarcity of earliest Cambrian soft-bodied fossils, the anomalous record of hydrozoans in coarse siliciclastic rocks, and the high number of specimens found reveal this Spanish palaeontological site as exceptional for a better understanding of the important taphonomic and biological events across the Neoproterozoic/Phanerozoic transition, particularly the evolution of hydrozoans.

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