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A new Middle Devonian chitinozoan assemblage from northern Iberia

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ABSTRACT

Chitinozoans were recovered from the Naranco, Huergas and Gustalapiedra formations of northern Spain, which yielded a diverse assemblage including 29 taxa in 9 named genera. The deposits are of early Givetian age, a time when Iberia was isolated from large continents as part of the Armorican Terrane Assemblage. The formations studied here consist of a large clastic unit interrupting carbonate deposition, with large limestone formations positioned above and below the formations analyzed here. This clastic unit includes the Kačák Event, an important global extinction event associated with anoxia in the marine realm. In this paper, the relatively well-preserved chitinozoan assemblage is described and considered from a biogeographical and stratigraphical perspective. The chitinozoan community was deposited in a short space of time and includes various taxa not previously known from the Middle Devonian, though the assemblage as a whole is attributable to the period. Only moderate similarity is seen with assemblages reported from Laurussia and Gondwana, with a slight bias towards the latter. This report adds to our knowledge of chitinozoan paleobiogeography and to other recent studies of Middle Devonian palynology in northern Iberia.

1. Introduction

While the chitinozoan record of the Silurian and Early Devonian of northern Spain is relatively well-known, with over one hundred taxa described from the area (Cramer, 1964, 1966a, 1966b; Cramer and Díez, 1978; Díez and Cramer, 1978; Richardson et al., 2001), the Middle Devonian strata has received next to no formal study. Only one paper, concerned more with land plant spores, has been written, which figured, but did not describe, three specimens of "*Ancyrochitina* sp." (Cramer, 1969). See Section 4 for the present authors' opinion of the attribution of these specimens. This is not for lack of suitable deposits or geological information; the lithostratigraphy has received extensive study, and units are often well exposed and present various features of interest. These deposits consist of a clastic unit sandwiched between thick carbonate deposits, representing a marine onshore–offshore transect, and are very well described sedimentologically, while they are also well age-constrained by conodont and land plant spore biostratigraphy. The sequence is known to have been deposited around a group of small islands isolated from the supercontinents of Laurussia and Gondwana (Torsvik and Cocks, 2013) and also spans the Kačák Event (García-Alcalde, 1998; Askew and Wellman, 2018), a major global extinction event with no definite cause. The present study aims to comprehensively describe the chitinozoan taxa from this sequence for the first time, comment on the assemblage's biogeographical similarities/differences with contemporary assemblages and add to other recent studies concerning the palynology of this sequence.

2. Geological setting

The present study utilizes the same samples as Askew and Wellman (2018) and the geological setting of the material is described in detail therein. In short, the Naranco, Huergas and Gustalapiedra formations, the subjects of the present study, are laterally equivalent and are found in the Asturias, León and Palencia provinces, respectively. Limestone formations occur stratigraphically below (the Moniello, Santa Lucía and Polentinos formations) and above (the Candás, Portilla and Cardaño formations) and again are all lateral equivalents (Fig. 1). The Naranco, Huergas and Gustalapiedra formations represent a disruption of carbonate deposition, replacing it with clastic sediment. The formations comprise a coarse, sandstone lower unit and a more mixed upper unit with interspersed beds of sandstone and siltstone (with occasional limestone beds), indicating that clastic input was reduced to some extent as compared with the lower unit. Detailed descriptions and environmental interpretations of the variety of facies present can be found in García-Ramos (1978), while Gibbons and Moreno (2002) provide a useful overview of the geology of this region.

Remains of the marine macrofauna of the Naranco, Huergas and Gustalapiedra indicate an Eifelian–Givetian age (García-López et al., 2002), which can be refined by conodont faunas recovered from the surrounding limestones. These indicate an age range for the formation from the *Polygnathus costatus costatus* zone (middle Eifelian; ca.

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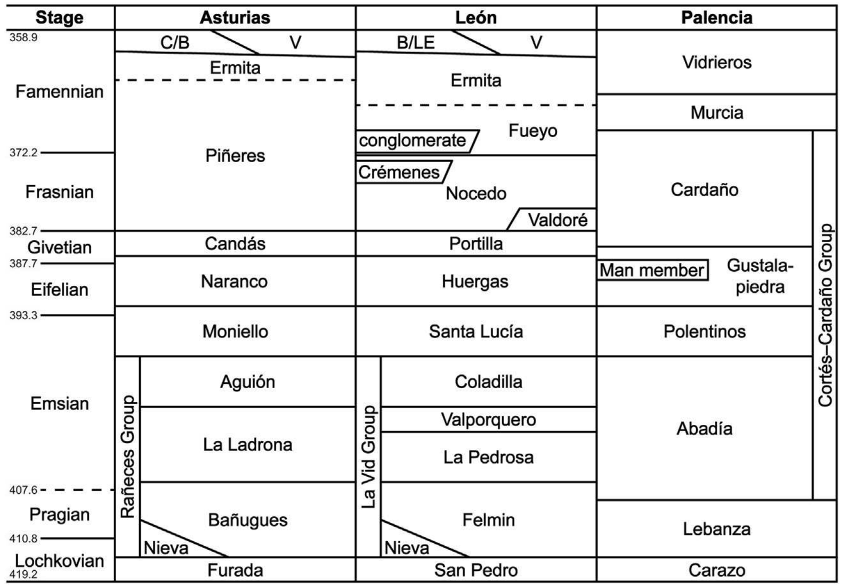

Fig. 1. Age and correlation of Devonian strata in several Iberian areas. Dashed boundary lines indicate uncertainty. Absolute ages of stage boundaries are given in Ma, taken from Becker et al. (2012). Diagram not to scale. Abbreviations for uppermost Famennian units: B, Baleas; C, Candamo; LE, Las Ermitas; V, Vegamián. Redrawn from García-Alcalde et al. (2002).

391–392 Ma) to the lower *Polygnathus varcus* zone (early, but not earliest, Givetian; ca. 386–387 Ma) (Becker et al., 2012; García-López et al., 2002; García-López and Sanz-López, 2002). The dispersed spore assemblage described in Askew and Wellman (2018) supports this, though suggests the palynomorph-bearing deposits were deposited within a short interval of a little over 1.5 million years (ca. 386–387.7 Ma), entirely within the early Givetian *lemurata-langii* Assemblage Zone (*Geminospora lemurata* Interval Zone) (Breuer and Steemans, 2013).

See Fig. 2 for the locations of this study's sample sites within northern Spain. Details of the 30 localities used and samples taken for this study are given in Askew and Wellman (2018).

3. Material and methods

Two periods of field work were undertaken, in which 130 rock samples were collected, covering the outcrop area of the Naranco, Huergas and Gustalapiedra formations. Dark, fine-grained beds of siltstone and mudstone, interspersed within the layers of sandstone that dominate

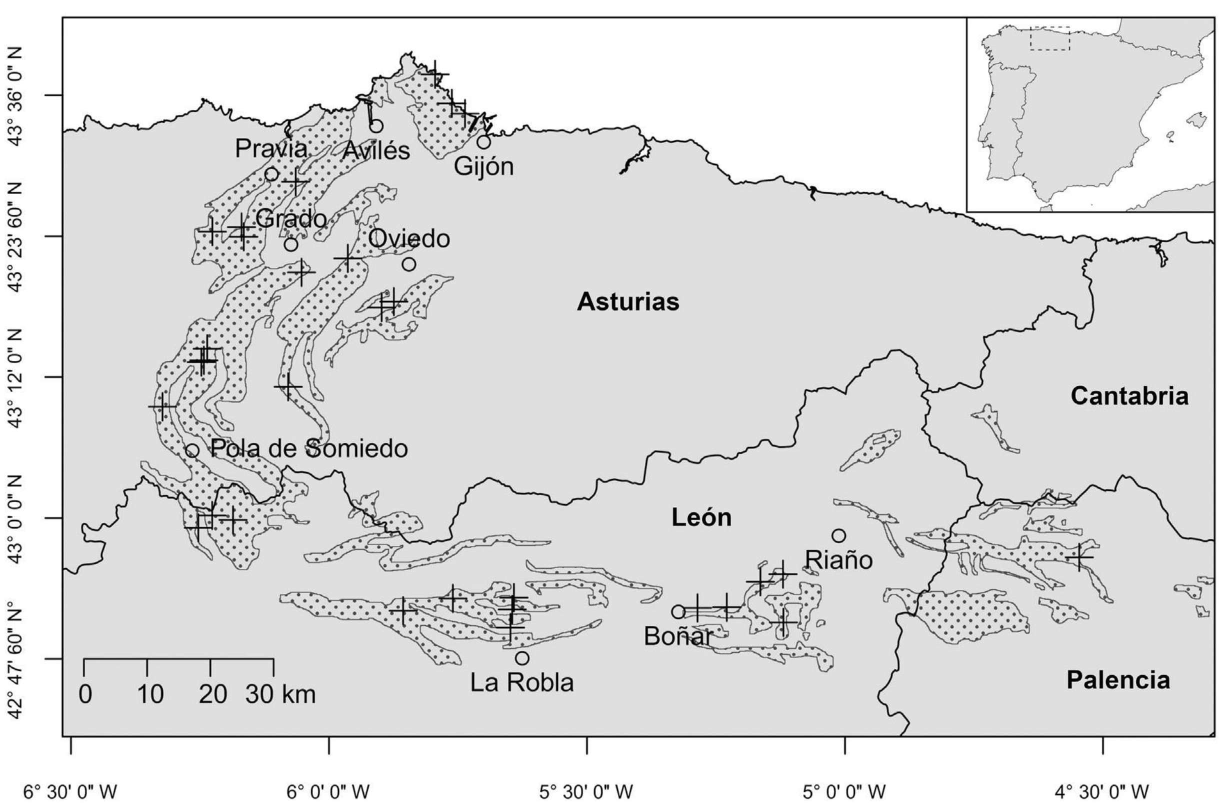

Fig. 2. Map of northern Spain with provinces labelled. Crosses indicate sites surveyed in this study. Outlined areas with dotted fill indicate the Devonian sediments' outcrop area.

the formations, were the focus of palynological sampling. Sample sites were mostly either single exposures or short sections which yielded a few consecutive samples. Three relatively long sections, measuring approximately 35, 70 and 330 m, were also analyzed, with samples taken at intervals throughout the exposure wherever good mud- or siltstone beds were seen. Sample details are given in Askew and Wellman (2018). Samples were processed using standard HCl–HF–HCl acid maceration techniques (Slater et al., 2015; Wellman, 2018a), followed by using a 15 μm sieve to remove some fine mineral residues. Heavy liquid centrifugation using $ZnCl_2$ removed any remaining mineral matter. Assessment of the resulting kerogen samples identified three barren samples and one very poorly preserved one; these were not processed further.

Preservation is generally good but thermal maturity is variable, with a TAI value between 2 and 4 (Traverse, 2008). Oxidization of all the samples was undertaken with Schulze's solution for 5–60 min, except four very thermally mature samples that were oxidized for around 19 h. Quantitative analysis was undertaken by spiking the samples with tablets containing modern *Lycopodium* spores at a ratio of one tablet per millilitre of organic residue. An equation derived from that given by Stockmarr (1971) then gives the number of palynomorphs per gram of processed rock, subject to the standard deviation given for the tablet batch (all tablets used here came from the same batch). Between two and four strew mounts were made for each sample, with 113 samples being counted using a standard 200 count. Once a total of 200 palynomorphs was reached, additional species were noted as rare. In cases where the slide did not contain 200 palynomorphs, every palynomorph was counted. Such slides are evident in the count data found in Askew (2019). Slides were examined using a light microscope and specimens photographed using a Meiji Techno Infinity 1-5C camera attached to a Meiji Techno MT5300H transmitted light microscope.

SEM materials were prepared in two ways; (i) picking individual chitinozoans for attachment to SEM stubs using carbon tabs and (ii) strew mounting. This involved fixing a glass cover slip to an SEM stub using Araldite® brand epoxy resin, before a palynomorph sample was strewn over it and dried. All stubs were gold-coated using an Edwards S150B sputter coater. All imaging was carried out using a Philips XL-20 SEM.

4. Systematic paleontology

The chitinozoans described below are arranged alphabetically by genera and treated as genera and species in accordance with the ICZN (1999), though the true origin of chitinozoans is not certain. Species with an uncertain identification are signified cf. or?, after Matthews (1973). A limited synonymy is provided for species recorded previously from the Naranco, Huergas and Gustalapiedra formations. This amounts to three specimens of *Ancyrochitina* sp. figured by Cramer (1969). These figured specimens are here placed with species found in the present study. Dimensions are given for each species and follow the scheme of Paris (1981) where L = total length; Dp = chamber diameter; Lp = chamber length; Dc = neck diameter; Ln = neck length. Dimensions are given in micrometres (μm) and no correction factors allowing for compression are used. Where three numbers are given for a dimension these correspond to the minimum value (arithmetic mean) and maximum values. The number of specimens measured is given. Occasionally not all measurements could be obtained from all specimens owing to damage, though in all cases specimens retained sufficient diagnostic features to facilitate identification. Where this is the case, the number measured corresponds to the highest number of measurements for any one dimension (e.g. up to 5 specimens measured, where some dimensions will have five measurements, others less than five owing to loss of features, such as neck flanges, in some specimens). Species occurrences are given as locality code characters for brevity (see Askew and Wellman (2018) for explanation). Previous records are taken from consultation of the John Williams Index of Paleopalynology (for details see Riding et al. (2012)) and are summarized for taxa with worldwide or near-worldwide distributions. Materials (rock samples, residues and slides) are housed in the collections of the Centre for Palynology, Department of Animal and Plant Sciences, University of Sheffield, UK. Figured specimens are located using an England Finder.

Genus **Alpenachitina** Dunn and Miller, 1964

Type species: Alpenachitina eisenacki Dunn and Miller, 1964

Alpenachitina eisenacki Dunn and Miller, 1964

Plate I, 1

Description: Chamber ovoid to cylindrical with a flat to slightly convex base. The neck occupies ~20% of the total length. The flexure is conspicuous and the aperture flares, gaining ~40% extra width at the aperture versus its narrowest point. Granulate ornament seen near aperture. Flanks bear large processes with up to fourth order dichotomous branching arranged in rings on the margin and shoulder, up to 4 μm wide and up to 20 μm long.

Dimensions: L = 118–132; Dp = 79–80; Lp = 91–99; Dc = 30–41; Ln = 27–32 (up to 2 specimens measured).

Remarks: Alp. eisenacki as originally described has a proportionately longer, non–flaring neck bearing an additional ring of processes. If the synonymy of this species with *Alp. ontariensis* Legault, 1973, as proposed by Almeida-Burjack and Paris (1989), is accepted then the flaring neck without true oral processes of the specimens seen here falls within the diagnosis of *Alp. eisenacki*, despite the poor preservation of the present material. This is despite the generic diagnosis of *Alpenachitina* describing three distinct "crowns" of processes on the margin, shoulder and neck.

Occurrence: Sites 3, 16.

Previous records: Considered characteristic of the Middle Devonian, though with a much larger reported range. Known from late Pragian to Frasnian strata and with an almost worldwide distribution, being absent from Europe, Asia and Australia.

Genus: **Ancyrochitina** Eisenack, 1955a

Type species: *Ancyrochitina ancyrea* (Eisenack, 1931)

Ancyrochitina ancyrea (Eisenack, 1931)?

Plate I, 2

Description: Chamber conical with a flat to slightly convex base. The neck may occupy ~50% of the total length, though damage makes this unclear. The flexure is conspicuous and the aperture flares, though damage precludes measurement of its magnitude. Possible microgranulate ornament observed on surface. Processes seen on margin with up to fifth order dichotomous branching, up to 24 μm long.

Dimensions: L = 106; Dp = 90–92; Lp = 67; Dc = 32 – [unknown]; Ln = 51 (up to 2 specimens measured).

Remarks: The specimens recovered here are damaged, precluding a more confident identification. Those characteristics which are preserved, namely the small surface ornament and ramified processes, match previously described specimens of *Anc. ancyrea*, a well-known species.

Occurrence: Sites 14, G.

Previous records: *Anc. ancyrea* is reported from Middle Ordovician to middle Frasnian strata and with an almost worldwide distribution, being absent from Australia.

Ancyrochitina cf. *flexuosa* Burjack, 1996

Plate I, 3

Description: Chamber lenticular to conical with a flat to slightly convex base. The neck occupies ~46% of the total length. The flexure is conspicuous and the aperture may flare, gaining ~17% extra width at the aperture versus its narrowest point when it does so. Processes seen with up to fourth order dichotomous branching arranged in a ring on the basal margin and irregularly arranged on the neck towards the aperture, up to 8 μm wide and up to 46 μm long, smaller on the neck.

Dimensions: L = 117 (138) 167; Dp = 74 (96) 115; Lp = 55 (77) 97; Dc = 31 (37) 45–36 (44) 50; Ln = 41 (64) 98 (up to 17 specimens measured).

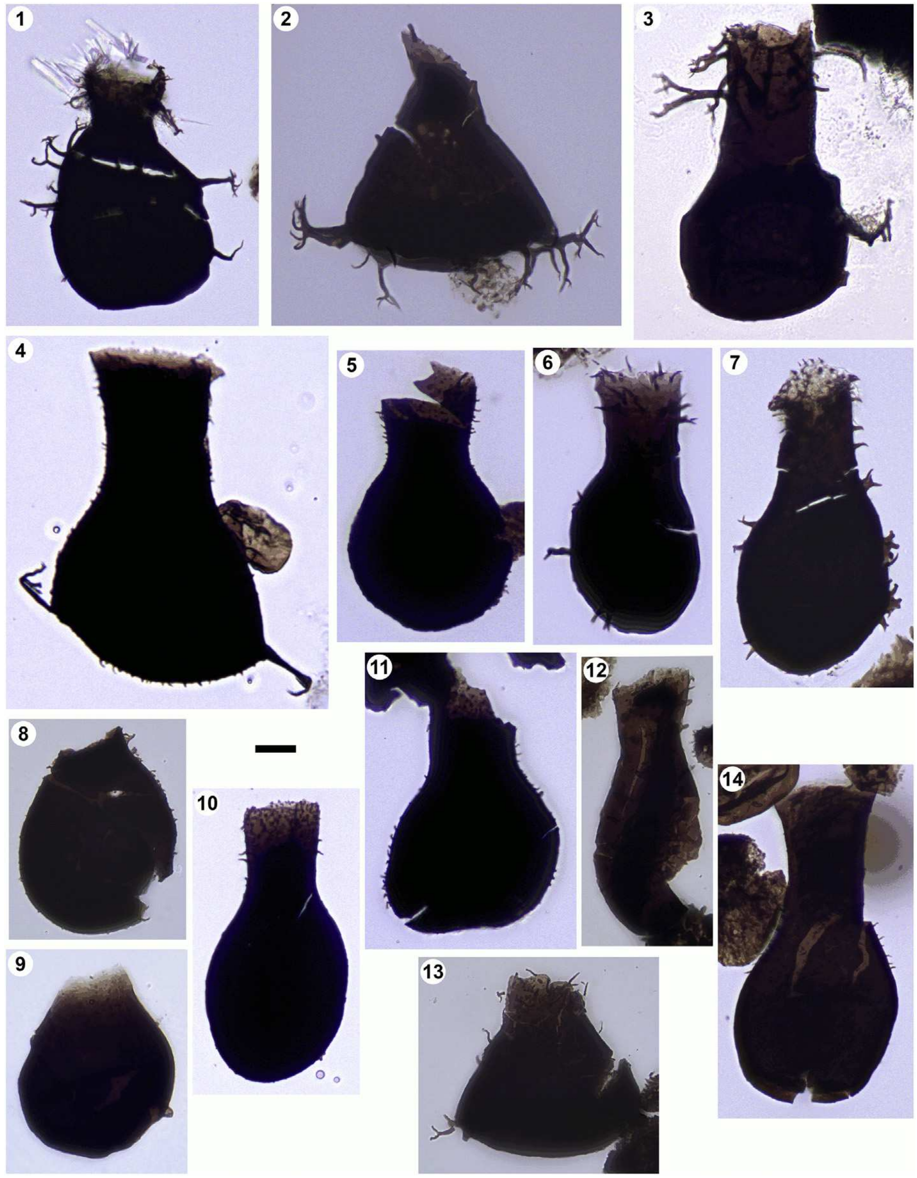

Plate I. Scale bar = 20 μm and is the same for all images. 1) *Alpenachitina eisenacki*; AJA2-3C-O2; T39. 2) *Ancyrochitina ancyrea*?; AJA2-GI-O1; H52/4. 3) *Anc.* cf. *flexuosa*; AJA2-GB-O1; N48. 4) *Anc. taouratinensis*; AJA11A-O1; Y33/1. 5) *Angochitina capillata*; AJA10B-O1; S30/3. 6) *Ang. devonica*; AJA2-3T-O1; N35. 7) *Ang. milanensis*; AJA10B-O2; K29. 8) *Ang.* sp. C; AJA10B-O2; X29/1. 9) *Ang.* sp. E; AJA3A-O1; W44/1. 10) *Ang.* sp. D; AJA10B-O1; S40/4. 11) *Ang. mourai*; AJA11A-O1; O45/3. 12) *Ang.* sp. B; AJA2-GY-O1; U43/2. 13) *Ancyrochitina* cf. *tomentosa*; AJA2-7L-O1; V43/3. 14) *Angochitina.* sp. A; AJA2-7E-O1; H35.

Remarks: *Anc. flexuosa* as originally described has a flaring neck and a discrete ring of oral processes, in contrast to the occasional flare and irregular arrangement of the neck processes seen in these specimens, hence their uncertain identification. The neck processes on the specimens seen here are rather more disorganized. The shape of these specimens is somewhat variable, particularly the neck, however this was also seen by Burjack (1996) and allowed for in the original description. Many of the specimens seen here resemble *Anc. postdesmea* Grahn, 2002, since synonymized with *Anc. flexuosa* (Grahn, 2011).

Occurrence: Sites 3, 7, 13, 14, G.

Previous records: *Anc. flexuosa* is reported from the Lochkovian to Givetian of Brazil (Lange, 1967; Burjack, 1996; Grahn, 2002; Grahn and de Melo, 2004, 2005; Grahn et al., 2006, 2008) the early Givetian of Paraguay (Grahn et al., 2002) and Canada (Legault, 1973) and the early to middle Givetian of Bolivia (Grahn, 2002).

Ancyrochitina taouratinensis Boumendjel, 1985
Plate I, 3

Description: Chamber conical to slightly lenticular with a flat to slightly convex base. The neck occupies ~37% of the total length. The flexure is conspicuous and the aperture flares, gaining ~27% extra width at the aperture versus its narrowest point. Granulate and small spinose ornament observed on surface. Processes seen on margin with up to fourth order dichotomous branching, 3–8 μm wide and 7–23 μm long.

Dimensions: L = 106 (116) 128; Dp = 55 (76) 83; Lp = 66 (76) 89; Dc = 28 (34) 40–37 (43) 58; Ln = 28 (43) 58 (up to 7 specimens measured).

Remarks: Specimens included in this taxon exhibit various degrees of damage resulting in loss of processes, though some remnant remains in all cases. The species is distinguished from *Anc. ancyrea* by its granulate surface ornament.

Occurrence: Sites 3, 7, 11, 14, G.

Previous records: Reported from the early Givetian of Algeria (Boumendjel, 1985; Boumendjel et al., 1988), the early to middle Givetian of Morocco (Rahmani-Antari and Lachkar, 2001), Bolivia

(Grahn, 2002) and Brazil (Burjack, 1996; Grahn and de Melo, 2004, 2005; Grahn et al., 2006) and the middle to late Givetian of Paraguay (Grahn et al., 2002).

Ancyrochitina cf. *tomentosa* Taugourdeau and de Jekhowsky, 1960

Plate I, 13

Description: Chamber conical with a flat to slightly convex base. The neck occupies ~40% of the total length. The flexure is conspicuous and the aperture does not flare. Micrograngulate and spinose or elongated filamentous ornament seen on neck up to 6 μm high. Processes seen on margin with dichotomous branching, up to 11 μm long.

Dimensions: L = 130; Dp = 78–83; Lp = 53–78; Dc = 34–43; Ln = 52 (up to 2 specimens measured).

Remarks: The thin, filamentous neck ornament of this species serves to distinguish it from other members of the genus. The specimens seen here are damaged, as seen in the figured specimen, rendering their identification uncertain. Characteristics described here are not necessarily seen on all specimens owing to damage, though their distinctive neck ornament is sufficient to refer them to this taxon. Their squat shape resembles *Anc. t. compactus* Taugourdeau, 1965.

Occurrence: Sites 3, 7.

Previous records: *Anc. tomentosa* is reported from middle Llandovery to Frasnian strata and with an almost worldwide distribution, being absent from Australia.

Genus: **Angochitina** Eisenack, 1931

Type species: *Angochitina echinata* Eisenack, 1931

Angochitina capillata Eisenack, 1937

Plate I, 5

Description: Chamber spherical to ovoid in shape. The neck occupies ~39% of the total length. The flexure is conspicuous and the aperture may flare, gaining ~15% extra width at the aperture versus its narrowest point when it does so. Microgranulate, granulate and spinose ornament up to 5 μm high evenly distributed across surface.

Dimensions: L = 106 (127) 153; Dp = 57 (74) 101; Lp = 71 (80) 86; Dc = 29 (35) 45–39 (41) 42; Ln = 37 (50) 67 (up to 6 specimens measured).

Remarks: The species was originally described as having an ovoid chamber, though Jenkins (1969) describes and figures specimens with a more variable chamber shape, including more spherical ones very similar to those seen here. Some previously recorded specimens appear to have thicker spines than those seen here, thought his measurement is never specified in the original description.

Occurrence: Sites 3, 10, G.

Previous records: Reported from Middle Ordovician to Famennian strata and with a worldwide distribution.

Angochitina devonica Eisenack, 1955b

Plate I, 6; Plate III, 1

? 1969a *Ancyrochitina* sp.; Cramer, pl. IV, fig. 46

? 1969a *Ancyrochitina* sp.; Cramer, pl. IV, fig. 47.

Description: Chamber spherical to ovoid in shape. The neck occupies ~40% of the total length. The flexure is conspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Spinose ornament seen on surface with rare branching spines and larger branching processes, up to 6 μm wide and up to 22 μm long. Simple ornament more common on the neck, branching spines and processes are largely limited to the chamber.

Dimensions: L = 131 (158) 195; Dp = 65 (79) 87; Lp = 84 (98) 118; Dc = 30 (34) 38–36 (43) 48; Ln = 47 (59) 77 (up to 4 specimens measured).

Remarks: These specimens seem to have a proportionately shorter neck than the species as originally described, however they are well distinguished from *Ang. milanensis* by possessing fewer wide–based spines and granulae. This is seen in both the transmitted light and SEM images given in the plates; no more than three wide-based structures are seen in *Ang. devonica* specimens here, while they are common in *Ang. milanensis*.

Occurrence: Sites 3, 16, G.

Previous records: Reported from Middle Ordovician to Famennian strata and with an almost worldwide distribution, being absent from Australia.

Angochitina milanensis Collinson and Scott, 1958

Plate I, 7; Plate III, 2–3

Description: Chamber ovoid. The neck occupies ~33% of the total length. The flexure is conspicuous and the aperture often flares, gaining ~28% extra width at the aperture versus its narrowest point when it does so. Ornament of spines, simple or with up to third order dichotomous branching and up to 27 μm long, with wide–based, branching granulae mostly limited to the chamber, up to 23 μm wide and up to 15 μm long.

Dimensions: L = 95 (117) 156; Dp = 58 (71) 91; Lp = 65 (80) 104; Dc = 15 (32) 44–35 (41) 53; Ln = 27 (39) 57 (up to 27 specimens measured).

Remarks: This species is distinguished in this assemblage by its wide–based elements. *Ang. devonica* can exhibit the same ornament type but it is usually smaller and the overall shape is more elongate.

Occurrence: Sites 3, 10, G.

Previous records: Reported from the Late Silurian to Pragian of Egypt (El Shamma et al., 2012) the Pragian to Famennian of North Africa (Taugourdeau et al., 1967), the Pragian to Middle Devonian of Algeria (Taugourdeau and de Jekhowsky, 1960; Taugourdeau, 1962; Jardiné and Yapaudjan, 1968; Boumendjel et al., 1988), the Eifelian of North America (Taugourdeau et al., 1967), the Middle Devonian of Canada (Boneham, 1967; Legault, 1973) and Australia (Jansonius, 1969), the Givetian of the USA (Collinson and Scott, 1958; Dunn, 1959; Wicander and Wood, 1997) and Libya (Paris et al., 1985) and the Late Devonian of Morocco (Grignani and Mantovani, 1964).

Angochitina mourai Lange, 1952

Plate I, 11

Description: Chamber spherical or nearly so. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~10% extra width at the aperture versus its narrowest point. Granulate and spinose ornament up to 3 μm high seen across whole surface.

Dimensions: L = 42 (86) 115; Dp = 29 (57) 76; Lp = 29 (61) 78; Dc = 17 (29) 37–20 (32) 40; Ln = 13 (27) 42 (3 specimens measured).

Remarks: Distinguished from *Ang. capillata* by its more often spherical chamber. The specimens seen here strongly resemble the specimen figured as pl. II, 1 of Grahn and de Melo (2002).

Occurrence: Sites 3, 7, 13, G.

Previous records: Reported from Early Silurian to early Famennian strata and with an almost worldwide distribution, being absent from Asia.

Angochitina sp. A

Plate I, 14

Description: Chamber ovoid. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~30% extra width at the aperture versus its narrowest point. Microgranulate ornament seen on the chamber and neck, with a spinose ornament clustered on the shoulder up to 5 μm high.

Dimensions: L = 140–155; Dp = 71–103; Lp = 97–118; Dc = 32–39 – 44–48; Ln = 37–46 (2 specimens measured).

Remarks: These specimens most closely resemble *Ang. capillata* in this assemblage, except for their more ovoid chamber and particularly the restricted distribution of these specimens' spinose ornament. No existing species could be found to which these specimens could be confidently assigned.

Occurrence: Sites 3, 7.

Angochitina sp. B

Plate I, 12

Description: Chamber ovoid. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~40% extra width at the aperture versus its narrowest point.

Microgranulate ornament seen along with large, pointed cones up to 7 μm high distributed sparsely across the surface.

Dimensions: L = 119; Dp = 47–76; Lp = 80–105; Dc = 25–34; Ln = 36 (up to 2 specimens measured).

Remarks: The distinctive ornament of large cone–like elements distinguishes these specimens, for which no analog could be found in the literature. The ornamental elements could represent the bases of eroded spines but their rounded tips and lack of obvious signs of breakage do not support this interpretation.

Occurrence: Sites 13, G.

Angochitina sp. C

Plate I, 8

Description: Chamber very slightly ovoid. The neck is unknown. Sparse granulate and spinose ornament up to 4 μm high, distributed across surface. A single multi–rooted spine is seen on the shoulder.

Dimensions: Dp = 80; Lp = 87; Dc = 39 (1 specimen measured).

Remarks: This single specimen is unique in this assemblage in possessing multi-rooted spine ornamentation. The specimen strongly resembles *Ang. communis*Jenkins, 1967, though it is too damaged to permit a confident identification.

Occurrence: Site 10.

Angochitina sp. D

Plate I, 10; Plate III, 4

Description: Chamber ovoid. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~10% extra width at the aperture versus its narrowest point. Granulate and spinose ornament seen, dense on neck and occasionally seen on chamber, up to 4 μm high. Those seen on the chamber may be broken spine bases.

Dimensions: L = 120 (134) 160; Dp = 63 (76) 88; Lp = 88 (94) 107; Dc = 30 (40) 52–34 (45) 57; Ln = 32 (42) 54 (up to 3 specimens measured).

Remarks: The specimens found here resemble *Ang. toyetae* Cramer, 1964 figured by Legault (1973) as pl. VI, fig. 10, though that specimen is acknowledged to be damaged. The same is probably true of the specimens seen here.

Occurrence: Sites 3, 7, 10.

Angochitina sp. E

Plate I, 9

Description: Chamber spherical. Neck absent or very short. Surface glabrous except for a very fine microgranulate ornament seen around the aperture and a possible process scar seen on one specimen (pl. I, 13).

Dimensions: L = 69 (77) 82; Dp = 67 (72) 80; Lp = 63 (71) 82; Dc = 20 (24) 28 (up to 5 specimens measured).

Remarks: These specimens present few diagnostic features, other than their unusual proportions. The overall shape of these specimens is very similar to the genus *Desmochitina* Eisenack, 1931, but they do not possess the correct surface texture.

Occurrence: Sites 3, 10, G.

Genus: **Fungochitina** Taugourdeau, 1966

Type species: *Fungochitina fungiformis* (Eisenack, 1931)

Fungochitina cf. *lata* (Taugourdeau and de Jekhowsky, 1960)

Plate II, 1

Description: Chamber conical with a more or less rounded margin and a flat to convex base. The neck occupies ~35% of the total length. The flexure is conspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Fine microgranulate ornament seen across surface with occasional larger elements up to 2 μm high.

Dimensions: L = 90 (117) 140; Dp = 70 (81) 92; Lp = 53 (77) 93; Dc = 16 (31) 43–29 (37) 43; Ln = 20 (40) 52 (up to 11 specimens measured).

Remarks: The specimens seen here have shorter necks than the species as originally described, though they are damaged. This is the source of these specimens' tentative identification, despite their overall shape and ornamentation being characteristic of *F. lata*.

Occurrence: Sites 3, 4, 7, 13, 14, 16, 598, 600, G.

Previous records: *F. lata* is reported from the Late Silurian to the Late Devonian of Algeria (Taugourdeau and de Jekhowsky, 1960; Magloire, 1967; Paris, 1996; Paris et al., 1997; Boumendjel et al., 1997a, 1997b; Alem, 1998; Khodjaoui, 2008), the Early to Middle Devonian of the English Channel (Lefort and Deunff, 1970), the Lochkovian of Bulgaria (Haydoutov and Yanev, 1997; Lakova, 1985, 1993, 1995a, 1995b, 1999, 2001a, 2001b), France (Paris, 1976) and Romania (Vaida and Verniers, 2005a, 2005b, 2006a, 2006b) and the late Lochkovian of the USA (Bevington et al., 2010)

Fungochitina pilosa (Collinson and Scott, 1958)

Plate II, 2

Description: Chamber lenticular to conical with a convex base. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Microgranulate and spinose ornament up to 2 μm high seen on surface.

Dimensions: L = 102 (123) 148; Dp = 76 (87) 103; Lp = 61 (85) 105; Dc = 26 (37) 42–39 (45) 51; Ln = 27 (41) 49 (up to 4 specimens measured).

Remarks: This species is distinguished from *F.* cf. *lata* in this assemblage principally by its shorter neck and more rounded, sometimes lenticular chamber.

Occurrence: Sites 3, 4, 598, G.

Previous records: Reported from Late Silurian to late Frasnian strata and with an almost worldwide distribution, being absent from Asia and Australia.

Fungochitina cf. *pistilliformis* (Eisenack, 1931)

Plate II, 3

Description: Chamber conical with a flat to slightly convex base. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture does not flare. Microgranulate, granulate and spinose or elongated filamentous ornament seen on neck up to 5 μm high.

Dimensions: L = 77 (98) 110; Dp = 58 (79) 101; Lp = 63 (68) 78; Dc = 20 (32) 38; Ln = 12 (32) 46 (up to 4 specimens measured).

Remarks: *Conochitina pistilliformis* as described by Eisenack (1931) has a proportionately much longer neck than the specimens seen here, though many of these specimens are damaged and missing part of the neck. They are distinguished from *F.* cf. *lata* primarily by their restricted covering of ornamental elements, seen only on the neck.

Occurrence: Sites 3, 7, 10, G.

Previous records: *F. pistilliformis* is reported from the Middle Ordovician to Přídolí of the Baltic (Eisenack, 1931; Nestor, 1992), the Middle Ordovician to Middle Devonian of France (Doubinger and Ruhland, 1963; Doubinger et al., 1966; Poncet and Doubinger, 1966; Lefort and Deunff, 1971), the Late Silurian of Germany (Eisenack, 1955a; Behr et al., 1965), the Wenlock of Ireland (Holland and Smith, 1979), the Wenlock to Early Devonian of China (Hou, 1978; Wang et al., 2006), the Ludlovian of England (Lister and Downie, 1967; Sutherland, 1994), the late Ludlovian to Early Devonian of Romania (Beju, 1967; Popescu, 1987; Olaru and Tabără, 2011) and Tunisia (Grignani, 1967), the Přídolí of Estonia (Nestor, 2011), the Devonian of the Sahara (Taugourdeau, 1979), the Lochkovian of Algeria (Magloire, 1967) and the Late Devonian of Morocco (Grignani and Mantovani, 1964).

Genus: **Hoegisphaera** Staplin, 1961 emend. Paris et al., 1999

Type species: *Hoegisphaera glabra* Staplin, 1961

Hoegisphaera cf. *glabra* Staplin, 1961

Plate II, 6–7

Description: Chamber spherical. Neck absent. Operculum obvious. This structure is frequently found detached from the chamber (pl. II, 7). Surface otherwise glabrous.

Dimensions: Overall diameter: 65 (92) 114 (14 specimens measured); annular ring diameter: 22 (37) 49 (33 specimens measured).

Remarks: This species is often extremely numerous in this material, possibly because of the ease with which damaged specimens can be

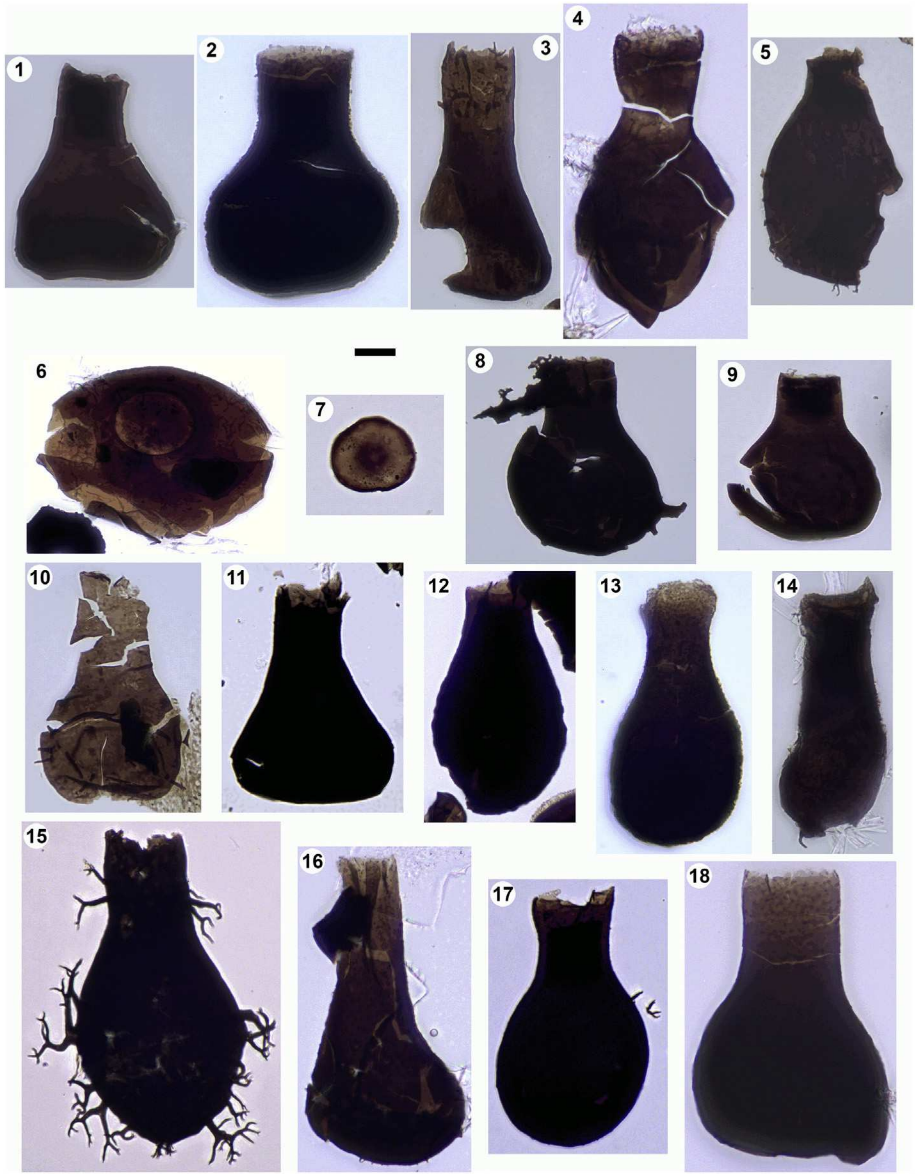

Plate II. Scale bar = 20 μm and is the same for all images. 1) *Fungochitina* cf. *lata*; AJA13B-O2; T43/4. 2) *F. pilosa*; AJA10B-O1; G45/2. 3) *F.* cf. *pistilliformis*; AJA2-7L-O1; V37/3. 4) *Lagenochitina* sp. A; AJA10B-O2; R44. 5) *Ramochitina* sp. A; AJA2-GQ-O1; F33. 6) *Hoegisphaera* cf. *glabra*; AJA120A-O2; T40. 7) *H.* cf. *glabra*; AJA2-GY-O1; X47 [Detached operculum]. 8) *Ramochitina corniculata*?; AJA3A-O1; L48. 9) *R. corniculata*?; AJA2-3B-O2; G37. 10) *R. derbyi*?; AJA2-GX-O1; T46/4. 11) *Saharochitina* sp. A; AJA2-PC-O1; O38/3. 12) *Sphaerochitina* cf. *compactilis*; AJA10B-O1; W34. 13) *Sph. cuvillieri*; AJA10B-O1; H37/2. 14) Chitinozoan type A; AJA2-3H-O2; T33. 15) *Ramochitina* cf. *magnifica*; AJA2-3C-O2; M46. 16) *Sphaerochitina ricardi*; AJA10B-O2; R45. 17) *Sph. sphaerocephala* sensu Díez and Cramer, 1978; AJA10B-O1; S45/1. 18) *Sph. sphaerocephala* sensu Díez and Cramer, 1978; AJA2-GG-O1; Q48.

identified by the prominent operculum. This may also be the reason for its seemingly large stratigraphical range elsewhere (see below).

Occurrence: Sites 3, 7, 120, 599, P.

Previous records: *H. glabra* is reported from Late Ordovician to Late Permian strata and with an almost worldwide distribution, being absent from Asia, though it is often considered characteristic of the Late Devonian (Paris et al., 2000). Reports of the species occurring more widely may be instances of homeomorphs.

Genus: **Lagenochitina** Eisenack, 1931 emend. Paris et al., 1999

Type species: *Lagenochitina baltica* Eisenack, 1931

Lagenochitina sp. A

Plate II, 4

Description: Chamber ovoid. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~30% extra width at the aperture versus its narrowest point. Surface glabrous.

Dimensions: L = 148; Dp = 79; Lp = 99; Dc = 34–44; Ln = 49 (1 specimen measured).

Remarks: This single specimen is placed in the genus *Lagenochitina* by its glabrous surface and ovoid chamber. The lack of SEM imagery of the specimen might render this identification doubtful, but no trace of ornament could be seen even under 100× magnification. No specific identification has been attempted owing to the specimen's damaged state.

Occurrence: Site 10.

Genus: **Ramochitina** Sommer and van Boekel, 1964 emend. Paris et al., 1999

Type species: Ramochitina ramosi Sommer and van Boekel, 1964

Ramochitina corniculata (Laufeld, 1974)?

Plate II, 8–9

Description: Chamber lenticular with a more or less convex base. The neck occupies ~35% of the total length. The flexure is conspicuous and the aperture may flare, gaining ~10% extra width at the aperture versus its narrowest point when it does so. Broken process bases seen on chamber, roughly arranged in longitudinal rows, up to 5 μm wide and up to 11 μm long. These bases may appear as isolated granules (Pl. II, 9) and may be disproportionately wide–based (Pl. II, 8).

Dimensions: L = 85 (91) 102; Dp = 66 (70) 75; Lp = 55 (59) 67; Dc = 24 (29) 31–29 (31) 33; Ln = 30 (32) 35 (3 specimens measured).

Remarks: These specimens are doubtfully assigned to the species on account of their relatively short necks and few spines, both attributed to damage. They do, however, bear a great similarity to the holotype of *R. corniculata* depicted in fig. 47B of Laufeld (1974) and the specimen figured here in Pl. II, 8 shows one process curved orally, characteristic of the species.

Occurrence: Sites 3, 7.

Previous records: *R. corniculata* is reported from the late Llandovery to middle Wenlock of Belgium (Verniers and Rickards, 1979; Verniers, 1999; Verniers, 1981; Verniers et al., 2002) and the Wenlock of Sweden (Laufeld, 1974; Jenkins and Legault, 1979) and Wales (Verniers, 1999).

Ramochitina derbyi Grahn and de Melo, 2002?

Plate II, 10

Description: Chamber a strongly rounded conical shape with a flat base. The neck occupies ~50% of the total length. The flexure is conspicuous and the aperture flares, gaining ~35% extra width at the aperture versus its narrowest point, though the neck is damaged. Spinose ornament observed arranged in rough longitudinal rows, up to 8 μm high and limited to the aboral end of the chamber around the margin.

Dimensions: L = 103; Dp = 62; Lp = 53; Dc = 26–35; Ln = 50 (1 specimen measured).

Remarks: This single specimen differs from the species as originally described by its lack of spines on the neck and fewer spines generally, though the latter may be due to damage. The general form and proportions of this specimen are comparable with *R. derbyi*.

Occurrence: Site G.

Previous records: *R. derbyi* is reported from the early Frasnian of Brazil (Grahn et al., 2002; Grahn and de Melo, 2002).

Ramochitina cf. *magnifica* Lange, 1967

Plate II, 15; Plate III, 5

? 1969a *Ancyrochitina* sp.; Cramer, pl. IV, fig. 45

Description: Chamber ovoid. The neck occupies ~35% of the total length. The flexure is conspicuous and the aperture does not flare. Ornament of processes with up to third order dichotomous and trichotomous branching, occasionally with wide bases. Processes 1–9 μm wide and 13–36 μm long. Processes arranged in longitudinal crests.

Dimensions: L = 155 (166) 185; Dp = 79 (89) 102; Lp = 97 (106) 123; Dc = 34 (45) 58; Ln = 36 (58) 81 (up to 4 specimens measured).

Remarks: The specimens found here are considerably smaller than the species as originally described but conform with it morphologically.

Occurrence: Sites 3, 120, P.

Previous records: *R. magnifica* is reported from the Early to Late Devonian of Argentina (Volkheimer et al., 1986; Noetinger and Di Pasquo, 2009), the late Lochkovian to Pragian of the Falkland Islands (Marshall, 2008), the late Lochkovian to Emsian of Canada (Achab et al., 1997), the Pragian of Paraguay (Grahn et al., 2000) and the Pragian to Emsian of Brazil (Lange, 1967; da Costa, 1971; Grahn, 1992, 1995; Grahn et al., 2000; Grahn et al., 2010a; Grahn et al., 2013) and Bolivia (Vavrdová et al., 1996; Grahn, 2002; Troth et al., 2011).

Ramochitina sp. A

Plate II, 5

Description: Chamber conical with a slightly convex base. The neck occupies ~20% of the total length. The flexure is conspicuous and the aperture does not flare. Microgranulate and longitudinal crest–like ornament seen on chamber, possibly made up of coalesced smaller elements. One small branching process also seen on margin.

Dimensions: L = 104; Dp = 61; Lp = 85; Dc = 25; Ln = 20 (1 specimen measured).

Remarks: This single specimen is reminiscent of *R. spinosa* (Eisenack, 1932), though it has a shorter neck and smaller ornament, possibly due to damage.

Occurrence: Site G.

Genus: **Saharochitina** Paris and Grahn *in* Paris et al., 1999

Type species: *Saharochitina jaglini* (Oulebsir and Paris, 1993)

Saharochitina sp. A Oulebsir and Paris, 1993

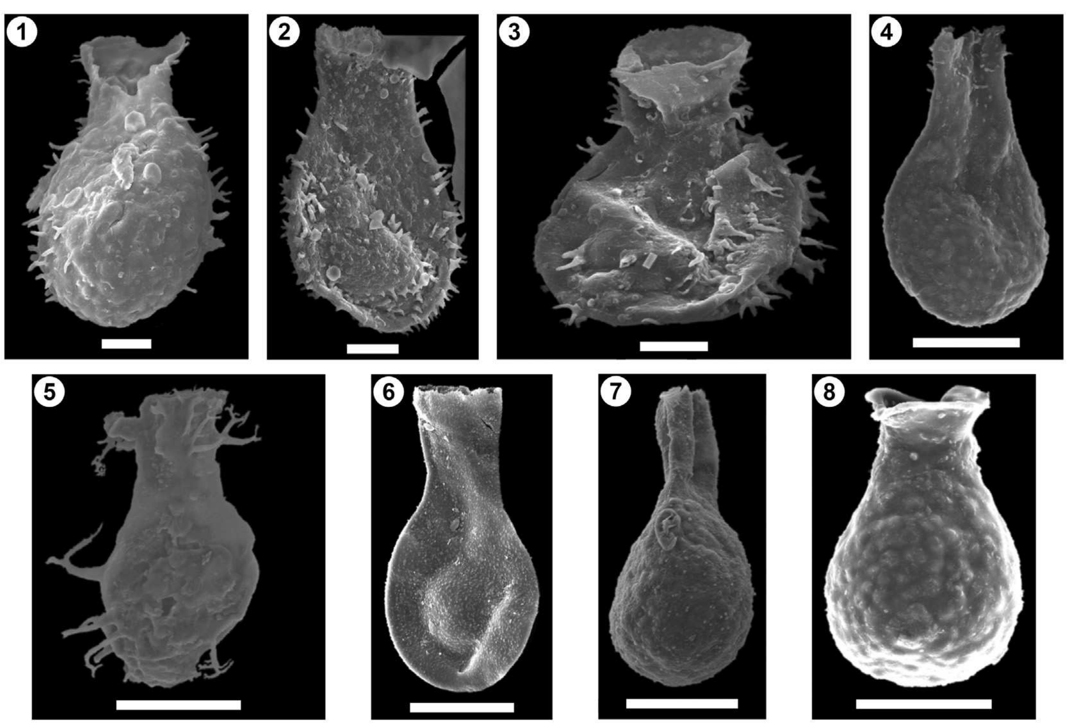

Plate III. SEM images taken at a variety of magnifications. Individual scale bars are given for each specimen. 1) *Angochitina devonica*; ER1C8; 832×; scale bar = 20 μm. 2) *Ang. milanensis*; ER2C5; 947×; scale bar = 20 μm. 3) *Ang. milanensis*; ER2C7; 916×; scale bar = 20 μm. 4) *Ang.* sp. D; ERP1C2; 548×; scale bar = 50 μm. 5) *Ramochitina* cf. *magnifica*; ER1C11; 674×; scale bar = 50 μm. 6) *Sphaerochitina cuvillieri*; ERP1C7; 723×; scale bar = 50 μm. 7) *Sph. ricardi*; ERP1C4; 609×; scale bar = 50 μm. 8) *Sph. sphaerocephala* sensu Díez and Cramer, 1978; ERP1C5; 675×; scale bar = 50 μm.

Plate II, 11

Description: Chamber conical with a very slightly convex base. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture does not flare. Surface glabrous.

Dimensions: L = 93; Dp = 69; Lp = 62; Dc = 28; Ln = 30 (1 specimen measured).

Remarks: This single specimen strongly resembles *Fungochitina*? sp. A of Oulebsir and Paris (1993), though with a slightly shorter neck. It is this short neck that distinguishes the form from *F.*? *jaglini*Oulebsir and Paris, 1993, since reassigned as the type species of *Saharochitina* by Paris et al. (1999) owing to its glabrous surface.

Occurrence: Site P.

Previous records: Oulebsir and Paris (1993) report their specimens from the Early and Middle Ordovician of Algeria.

Genus: **Sphaerochitina** (Eisenack, 1955a) emend. Paris et al., 1999

Type species: *Sphaerochitina sphaerocephala* (Eisenack, 1932)

Sphaerochitina cf. *compactilis* Jenkins, 1969

Plate II, 12

Description: Chamber ovoid to almost spherical. The neck occupies ~20% of the total length. The flexure is conspicuous and the aperture may flare slightly. Surface glabrous.

Dimensions: L = 97 (103) 109; Dp = 56 (68) 82; Lp = 73 (79) 85; Dc = 15 (28) 39–17 (18) 18; Ln = 12 (24) 30 (up to 5 specimens measured).

Remarks: *Sph. compactilis* as originally described has a conical to spherical chamber, however the figured specimens are better described as ovoid in the opinion of the present authors. The species is also described as having a neck occupying up to one-third of the total length, something that is not obvious in the figured specimens. Indeed, the specimens seen here bear a marked resemblance to the specimen figured in pl. 9, fig. 16 of Jenkins (1969).

Occurrence: Sites 3, 7, 16, G, P.

Previous records: *Sph. compactilis* is reported from the Middle Ordovician of Saudi Arabia (Al-Hajri, 1995) and Spain (Cramer-Díez et al., 1972) and the Late Ordovician of Canada (Martin, 1975, 1980, 1983; Jenkins, 1984) and the USA (Jenkins, 1969, 1970).

Sphaerochitina cuvillieri Taugourdeau, 1962.

Plate II, 13; Plate III, 6

Description: Chamber spherical to ovoid. The neck occupies ~ 37% of the total length. The flexure is conspicuous and the aperture flares, gaining ~17% extra width at the aperture versus its narrowest point. Micrograpulate or, occasionally, granulate ornament seen on surface.

Dimensions: L = 92 (116) 130; Dp = 50 (68) 89; Lp = 62 (76) 97; Dc = 25 (31) 39–31 (37) 49; Ln = 29 (43) 64 (up to 14 specimens measured).

Remarks: The specimens seen here do not show the tendency for their ornament to cluster that Taugourdeau (1962) described, though they match the type material in all other particulars including shape, proportions and ornament type.

Occurrence: Sites 3, 4, 7, 10, 598, G.

Previous records: Reported from the Early Silurian of Saudi Arabia (McClure, 1988), the Late Silurian of Tunisia (Grignani, 1967), the Frasnian (Taugourdeau, 1962) of Algeria, the Early to Middle Devonian of Brazil (van Boekel, 1966, 1968a, 1968b; da Costa, 1971), the early Emsian to early Eifelian of Spain (Díez and Cramer, 1978), the Frasnian of France (Moreau-Benoit, 1965) and the Late Devonian of Morocco (Grignani and Mantovani, 1964).

Sphaerochitina ricardi Díez and Cramer, 1978

Plate II, 16; Plate III, 7

Description: Chamber spherical to lenticular in shape. The neck occupies ~60% of the total length. The flexure is conspicuous and the aperture does not flare. A sparse micrograpulate ornament is seen on the surface, with elements well separated from each other.

Dimensions: L = 153; Dp = 79; Lp = 68; Dc = 29; Ln = 85 (1 specimen measured).

Remarks: This single specimen strongly resembles *Sph. ricardi* in proportions and ornament, except it does not have the conical shape specified for the species. This is interpreted here as due to later distortion disguising the conical vesicle of this specimen, as it does resemble some of the specimens figured by Díez and Cramer (1978). The SEM image seen in Pl. III, 7 shows a specimen with an apparent ornament, however this is believed to be mineral growth.

Occurrence: Site 10.

Previous records: Reported from the Pragian of Australia (Winchester-Seeto and Carey, 2000) and the early Emsian to early Eifelian of Spain (Díez and Cramer, 1978).

Sphaerochitina sphaerocephala (Eisenack, 1932) sensu Díez and Cramer, 1978

Plate II, 17–18; Plate III, 8

Description: Chamber ovoid. The neck occupies ~35% of the total length. The flexure is conspicuous and the aperture may flare, gaining ~15% extra width at the aperture versus its narrowest point when it does so. A faint micrograpulate ornament is seen on the surface, with elements quite well separated from each other.

Dimensions: L = 103 (120) 133; Dp = 56 (80) 100; Lp = 73 (82) 98; Dc = 28 (36) 47–36 (40) 48; Ln = 23 (42) 65 (up to 7 specimens measured).

Remarks: One specimen (pl. II, 17) appears to have a single spine on the shoulder, though this may not be original; no other spines or spine bases are seen on this specimen. This species is distinguished from *Sph. cuvillieri* in this study by its much fainter, more widely spaced micrograpulate ornament. *Sph. sphaerocephala* as originally described has a much longer neck than the specimens seen here. Díez and Cramer (1978) figure shorter, more squat specimens, referencing Eisenack (1968) which included specimens of a similar shape. These show a marked similarity to those seen in the present study, though they may simply represent part of the considerable variation seen in *Sph. sphaerocephala*, rather than a distinct form. The SEM image seen in Pl. III, 8 shows a misshapen specimen, probably due to internal mineral growth.

Occurrence: Sites 3, 4, 7, 10, 11, 120, G.

Previous records: *Sph. sphaerocephala* is reported from Early Ordovician to Famennian strata and with an almost worldwide distribution, being absent from Australia. Díez and Cramer (1978) describe specimens similar to those found here from the early Emsian to early Eifelian of Spain and reference specimens found from the Ordovician to Silurian of the Baltic (Eisenack, 1968).

4.1. Other forms

Chitinozoan type A

Plate II, 14

Description: Chamber possibly claviform. The flexure is inconspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Micrograpulate and fine spinose ornament up to 6 μm high seen on surface.

Dimensions: L = 125–135; Dp = 52–69; Dc = 31–32 – 36–38 (2 specimens measured).

Remarks: *Clavachitina* Taugourdeau, 1966 is described by Paris et al. (1999) as being glabrous, precluding the spinose ornament of this species. This form may belong to *Belonechitina* Jansonius, 1964 but preservational deficiencies preclude a confident identification in either case.

Occurrence: Site 3.

5. Description of the chitinozoan assemblage

The chitinozoan assemblage consists of 29 taxa, including 20 named species identified confidently or uncertainly, assigned to nine named genera. The remaining nine taxa are left in open nomenclature, having no previously identified analog in the literature. Charts of the quantitative abundances of certain taxa are given as Figs. 3–5, with full charts available as supplementary information. Count data is available at Askew (2019). The assemblages recovered from each sampled site show no significant differences in their species compositions, therefore the community is considered here as a single regional assemblage.

No clear temporal changes are evident in the assemblage. Inceptions do occur through the sampled sections, but they show no evidence of being the result of assemblage composition changes through time. They do not appear in the same order, for instance, and no late-occurring species become important components of the assemblage. This may be connected to the short time period in which the formations were deposited (see Section 2), leaving no time for chitinozoan assemblages to change significantly. Out of the total assemblage only *Angochitina* sp. C, *Lagenochitina* sp. A, *Saharochitina* sp. A and *Sphaerochitina ricardi* are not seen in the sections. These are all extremely rare taxa, only occurring in one sample each in this study. That, combined with their lack of biostratigraphical importance, mean their absence in the stratigraphical sections is not considered significant.

Sphaerochitina is the most abundant genus herein, representing 28% of the assemblage when assessed quantitatively. *Hoegisphaera* (25%) and *Fungochitina* (25%) also occur in significant numbers. At the subfamily level, the Angochitininae are the most frequently encountered (33%), followed by the Lagenochitininae (28%), the Desmochitininae (25%) and the Ancyrochitininae (13%).

Reworking is not evident in the palynomorph assemblages previously described for the deposits (Askew and Wellman, 2018), and the chitinozoans show no obvious differences in preservation and thermal maturity, suggesting no noticeable reworking has occurred with them either. There is also no obvious, systematic reworking of older forms from the comparatively well-studied La Vid Group (Cramer, 1964; Cramer-Díez et al., 1972; Díez and Cramer, 1978) into the present assemblage.

6. Comparison with other chitinozoan assemblages

Chitinozoan regional assemblages that are contemporaneous with the present one are relatively well-known, however many reports contain very few species or are poorly age-constrained. Taxonomy can also be a confounding factor, as species concepts have been changed and taxa re-evaluated. Despite this, 28 assemblages (10 from Laurussia and 18 from Gondwana) containing sufficient taxa for a meaningful comparison with the present assemblage have been found.

Two measures of similarity have been used here. The coefficient of similarity (CS) (sensu Clark and Hatleberg (1983)) is expressed as CS $= 2|x|/(|a + b|)$ where a and b are the total number of species in assemblages a and b, respectively, and x is the number of species they share. Results below 0.2 indicate low similarity, while results between 0.2 and 0.55 are considered moderate to high (Clark and Hatleberg, 1983). Secondly, the Jaccard Index (JI) can be expressed as JI $= |x|/$

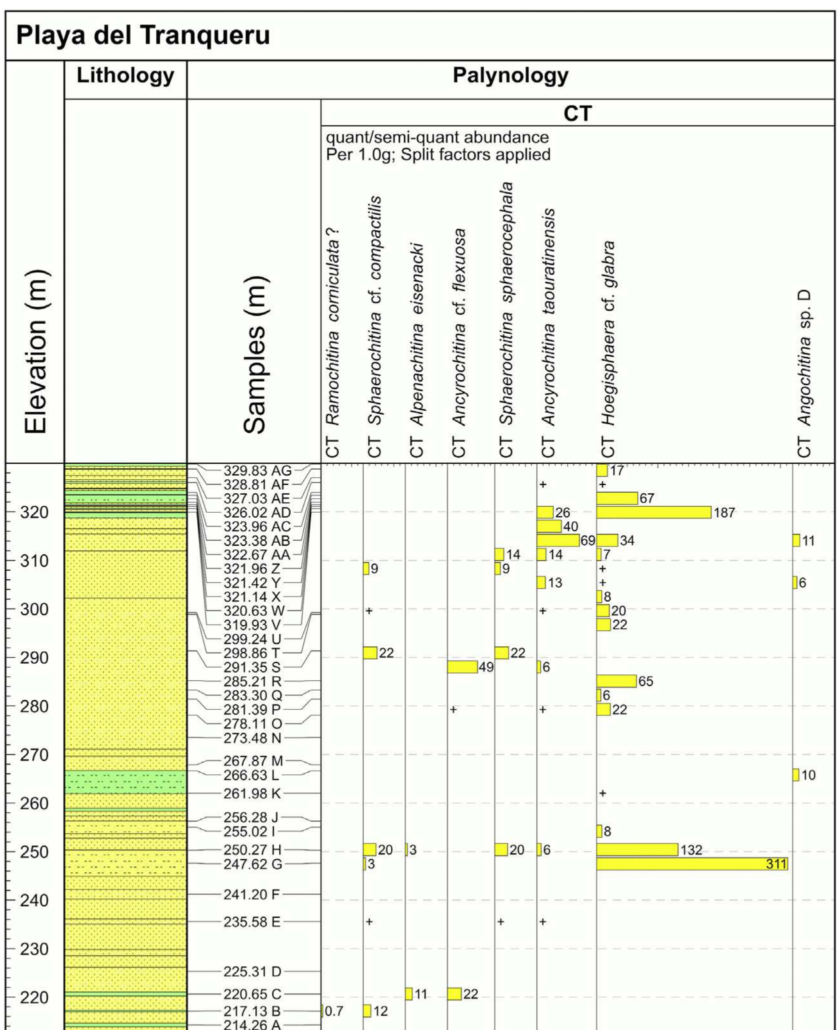

Fig. 3. Quantitative abundances of selected chitinozoan taxa at the Playa del Tranqueru site. Abundances expressed as numbers per gram of rock. Each horizontal tick represents 10 specimens per gram. The section's lithology is also shown. The "*Sphaerochitina sphaerocephala*" indicated here represents *Sph. sphaercephala* sensu Díez and Cramer, 1978 (see Section 4).

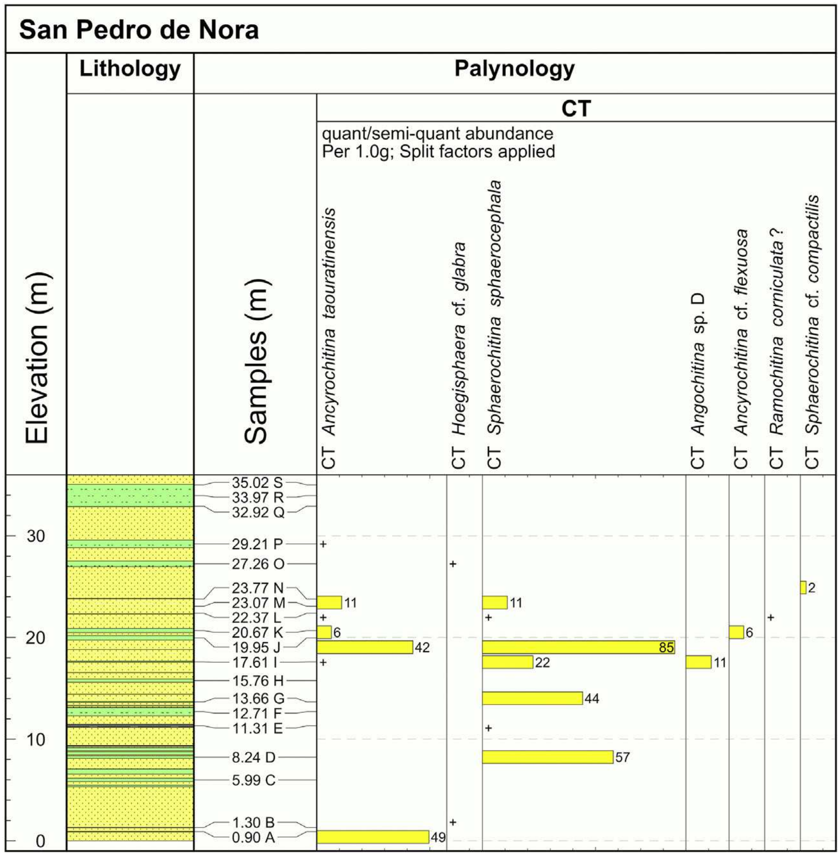

Fig. 4. Quantitative abundances of selected chitinozoan taxa at the San Pedro de Nora site. Abundances expressed as numbers per gram of rock. Each horizontal tick represents 10 specimens per gram. The section's lithology is also shown. The "*Sphaerochitina sphaerocephala*" indicated here represents *Sph. sphaercephala* sensu Díez and Cramer, 1978 (see Section 4).

($|a| + |b|$-$|x|$) where *a* and *b* are the total number of species in assemblages *a* and *b*, respectively, and *x* is the number of species they share. Completely dissimilar assemblages score 0 while identical ones score 1. These measures have been used previously in Paleozoic palynological applications (e.g. Le Hérissé et al., 1997; Wellman, 2018b; Wellman et al., 2013). In all cases, taxa with only a generic assignment and those designated "?" have been excluded from the calculations, while those designated "cf." have been treated as valid identifications where appropriate following individual assessment. All were assessed using modern taxonomic assignments.

Values for these metrics are given in Table 1. This assemblage is seen to not be particularly similar to contemporary ones from other parts of the world. It is most similar to that of Anan-Yorke (1974) from Ghana (CS: 0.480; JI:0.316), followed by those of Lange (1967) from Brazil (CS:0.370; JI:0.227) and Urban (1972) from the USA (CS:0.345; JI:0.208), showing no particular geographical bias. These three are fairly high similarity results, but most are moderate or low. At the continental scale, this assemblage is slightly more similar to Gondwana (CS:0.246; JI:0.140) than to Laurussia (CS:0.228; JI:0.129) but the difference is very small, and both continents show only a low to moderate degree of similarity.

Common Middle Devonian species such as *Alpenachitina eisenacki*, *Ancyrochitina ancyrea*, *Angochitina devonica*, *Ang. milanensis*, *Hoegisphaera glabra* and *Fungochitina pilosa* are represented here. Nevertheless, the Spanish material lacks some very widespread taxa, such as *Ancyrochitina cornigera*, *Anc. desmea*, *Anc. langei*, *Anc. morzadeci*, *Anc. spinosa* and *Ramochitina ramosi*. The absence of species belonging to *Urochitina* and *Eisenackitina* in this analysis is also notable, as both genera were common at the time (Paris et al., 1999). Indeed, only one species of desmochitinid, *Hoegisphaera* cf. *glabra*, was recovered here. This form is long ranging and possibly includes a number of homeomorphs.

Laurussia and Gondwana do not have particularly similar assemblages, with few species common on both continents. Despite this, the Spanish assemblage is not very similar to either of them. This may be connected to the isolated position of Spain during the Middle Devonian (see Section 1).

7. Biostratigraphical implications

Chitinozoan biostratigraphical schemes for the Middle Devonian are somewhat lacking owing to a paucity of comprehensive study of the period (Paris et al., 2000). Assemblages may differ significantly between regions (Miller, 1996), meaning regional schemes should be used with caution here, especially since no previous study of Spain has been performed and it has not been considered in previous schemes.

The formations in which this chitinozoan assemblage was found are well age-constrained by conodonts and dispersed spores (see Section 2) to the middle Eifelian to early Givetian stages, with the palynomorph-bearing material occurring in the early Givetian only. The depositional period of the formations is divided into three biozones in the global scheme of Paris et al. (2000). Lowermost is the *Alpenachitina eisenacki* Interval Range Biozone, also characterized by *Angochitina callawayensis* and *Eisenackitina turgifunda*. The next biozone, which straddles the Eifelian–Givetian boundary, is the *Eisenackitina aranea* Interval Range Biozone, which also includes *Ang. callawayensis* and *E. turgifunda* as well as *Linochitina santullanensis* and *Ancyrochitina langei*. Finally, the *Ancyrochitina cornigera* Interval Range Biozone occurs in the Givetian, also including *Alp. eisenacki*, *E. aranea*, *Fungochintina pilosa* and several species of *Ramochitina*.

Of these, only *Alp. eisenacki* and *F. pilosa* have been recorded in this Spanish assemblage. The presence of *F. pilosa* could indicate an age corresponding to the *Anc. cornigera* Interval Range Biozone which begins in

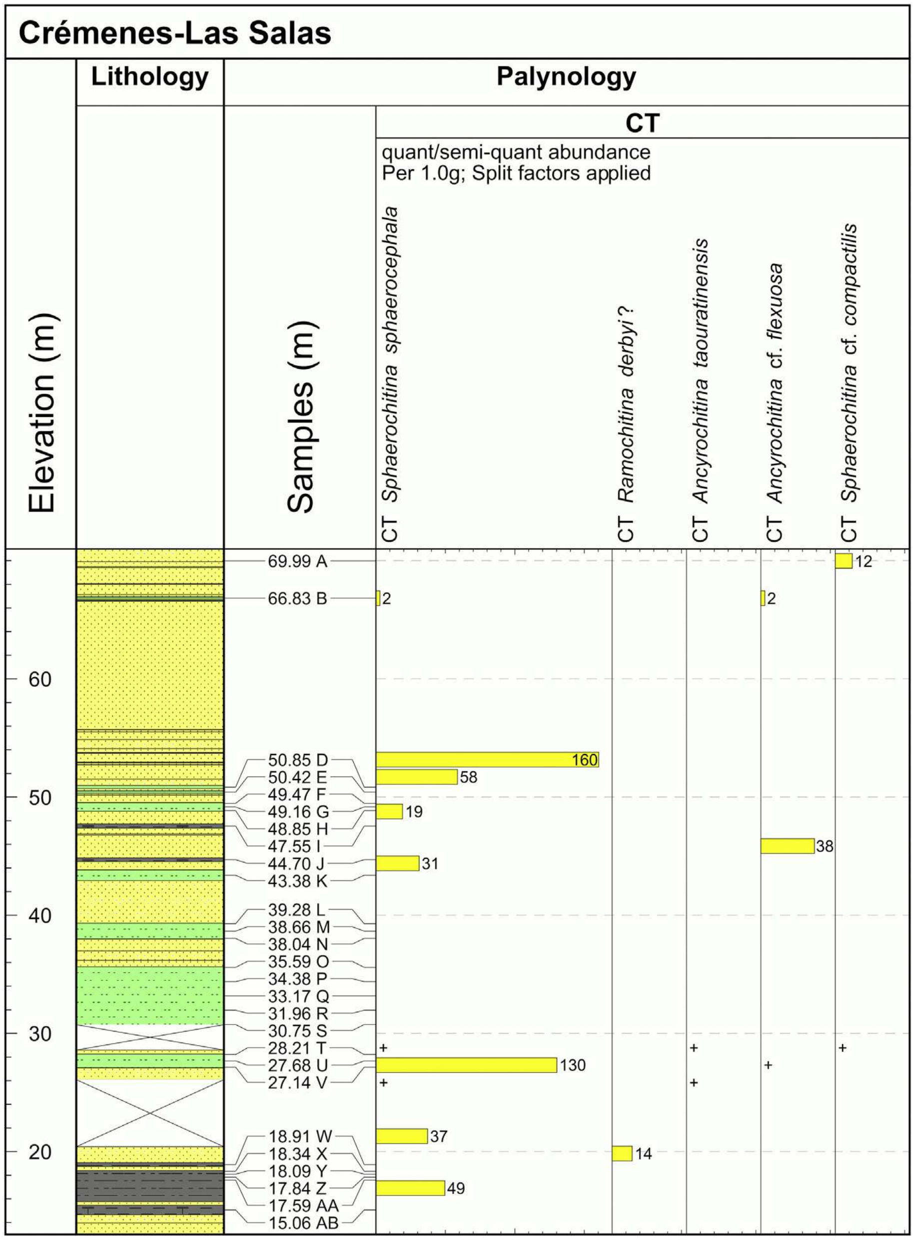

Fig. 5. Quantitative abundances of selected chitinozoan taxa at the Crémenes-Las Salas site. Abundances expressed as numbers per gram of rock. Each horizontal tick represents 10 specimens per gram. The section's lithology is also shown. The "*Sphaerochitina sphaerocephala*" indicated here represents *Sph. sphaercephala* sensu Díez and Cramer, 1978 (see Section 4).

the upper Middle *Polygnathus varcus* conodont zone (Paris et al., 2000), however this is younger than the top of the formation is known to be using conodont dating (see Section 2). The absence of other proxies prevents a trustworthy biostratigraphical conclusion.

The species identified here, both confidently and tentatively, are generally Middle Devonian species, though certain taxa are not previously recorded from this time period. *Ramochitina corniculata* is only known from the Silurian, while *R. derbyi* is known from the Frasnian, but both these species are only tentatively identified here owing to few, damaged specimens and may represent homeomorphs. *Saharochitina* sp. A Oulebsir and Paris, 1993 is recorded only from the Ordovician, though it is a very simple form with few distinguishing features and, again, may be a homeomorph. *Sphaerochitina compactilis* is another simple form, this time known from the Ordovician, with something of a disconnect between its description and the original figured specimens, also only identified tentatively here and possibly another homeomorph. *Sph. ricardi* is only reported up to the early Eifelian, though that report is from Spain. It is possible the present study represents a genuine expansion in this species' known temporal range. The specific form of *Sph. sphaerocephala* found here, *Sph. sphaerocephala* sensu Díez and Cramer (1978), is also only known from the early Eifelian of Spain, though the species sensu stricto ranges from the Ordovician to Famennian.

A somewhat varied biostratigraphical picture is presented by this data. Some "out of place" species may be homeomorphs or they may be valid extensions to the ranges of some species. The lack of previous study of this material lends support to the latter conclusion, but the limitations of primarily light microscopy studies such as this one largely preclude a definite say in this matter. None of these potentially discordant taxa are known to be particularly stratigraphically important in any case. Reworking is unlikely to account for these taxa; it is not evident in the rest of the assemblage and it cannot account for the supposedly

Table 1
Similarity measures calculated for various Middle Devonian chitinozoan assemblages compared with the Iberian one described here. The results for Laurussia and Gondwana are calculated using a composite assemblage based on the individual studies listed.

Assemblage	Coefficient of similarity	Jaccard Index
Laurussia	0.228	0.129
Legault, 1973 (Canada)	0.186	0.103
Pichler, 1971 (Germany)	0.174	0.095
Collinson and Scott, 1958 (USA)	0.286	0.167
Urban, 1972 (USA)	0.345	0.208
Urban and Kline, 1970 (USA)	0.000	0.000
Urban and Newport, 1973 (USA)	0.333	0.200
Wood, 1974 (USA)	0.162	0.088
Wood and Clendening, 1985 (USA)	0.182	0.100
Wright, 1976 (USA)	0.231	0.130
Wright, 1980 (USA)	0.231	0.130
Gondwana	0.246	0.140
Taugourdeau and de Jekhowsky, 1960 (Algeria)	0.250	0.143
Jardiné and Yapaudjan, 1968 (Algeria)	0.190	0.105
Boumendjel et al., 1988 (Algeria)	0.276	0.160
Ottone, 1996 (Argentina)	0.000	0.000
Noetinger, 2010 (Argentina)	0.240	0.136
Noetinger and Di Pasquo, 2011 (Argentina)	0.087	0.045
Noetinger et al., 2018 (Argentina)	0.000	0.000
di Pasquo et al., 2015 (Argentina; Bolivia)	0.000	0.000
Lange, 1967 (Brazil)	0.370	0.227
da Costa, 1971 (Brazil)	0.308	0.182
de Quadros, 1982 (Brazil)	0.296	0.174
Grahn and de Melo, 2004 (Brazil)	0.182	0.100
Gaugris and Grahn, 2006 (Brazil)	0.176	0.097
Grahn et al., 2008 (Brazil)	0.235	0.133
Grahn et al., 2010b (Brazil)	0.148	0.080
Bosetti et al., 2011 (Brazil)	0.083	0.043
Grahn et al., 2013 (Brazil)	0.074	0.038
Grahn et al., 2002 (Brazil; Paraguay)	0.286	0.167
Anan-Yorke, 1974 (Ghana)	0.480	0.316
Moreau-Benoit, 1984 (Libya)	0.091	0.048
Paris et al., 1985 (Libya)	0.273	0.158
Streel et al., 1988 (Libya)	0.333	0.200
Grahn, 2005 (western Gondwana)	0.258	0.148

younger species recorded here. These unexpected taxa add to the unusual chitinozoan assemblage recovered here from Middle Devonian Spain.

8. Conclusions

- A diverse assemblage of mostly well-preserved chitinozoans has been recovered from Middle Devonian deposits in northern Spain.
- The assemblage does not show strong similarity to contemporary assemblages from either Laurussia or Gondwana, reflecting the isolated position of Iberia during the Middle Devonian. Various taxa also appear to have occurred earlier in Spain than elsewhere, with others persisting for longer.
- The chitinozoan assemblage does not refute the Middle Devonian age of the formation determined by conodont and dispersed spore data.

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Appendix A. Alphabetic list of all chitinozoan taxa recovered in this study

Alpenachitina eisenacki Dunn and Miller, 1964
Ancyrochitina ancyrea (Eisenack, 1931)?
Ancyrochitina cf. *flexuosa* Burjack, 1996
Ancyrochitina taouratinensis Boumendjel, 1985
Ancyrochitina cf. *tomentosa* Taugourdeau and de Jekhowsky, 1960
Angochitina capillata Eisenack, 1937
Angochitina devonica Eisenack, 1955b
Angochitina milanensis Collinson and Scott, 1958
Angochitina mourai Lange, 1952
Angochitina sp. A
Angochitina sp. B
Angochitina sp. C
Angochitina sp. D
Angochitina sp. E
Fungochitina cf. *lata* (Taugourdeau and de Jekhowsky, 1960)
Fungochitina pilosa (Collinson and Scott, 1958)
Fungochitina cf. *pistilliformis* (Eisenack, 1931)
Hoegisphaera cf. *glabra* Staplin, 1961
Lagenochitina sp. A
Ramochitina corniculata (Laufeld, 1974)?
Ramochitina derbyi Grahn and de Melo, 2002?
Ramochitina cf. *magnifica* Lange, 1967
Ramochitina sp. A
Saharochitina sp. A Oulebsir and Paris, 1993
Sphaerochitina cf. *compactilis* Jenkins, 1969
Sphaerochitina cuvillieri Taugourdeau, 1962
Sphaerochitina ricardi Díez and Cramer, 1978
Sphaerochitina sphaerocephala (Eisenack, 1932) sensu Díez and Cramer, 1978
Chitinozoan type A

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2019.06.007.

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