Original article

New specimens of *Lingulocystis* Thoral, 1935 (Eocrinoidea, Blastozoa) from the Arenig (Lower Ordovician) of Montagne noire (southern France): Intraspecific morphological variability, stratigraphic, and palaeoecological implications

Nouveaux spécimens de *Lingulocystis* Thoral, 1935 (Eocrinoidea, Blastozoa) de l’Arénig (Ordovicien inférieur) de Montagne noire (France) : variabilité intraspécifique et implications paléoécologiques et stratigraphiques

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Abstract

The genus *Lingulocystis* Thoral, 1935 is a preponderant component of the echinoderm fauna of the Lower Ordovician of Montagne noire (France), as suggested by its abundant remains. Its morphology is characterized by a flattened theca, composed of a frame enclosing numerous small polygonal central plates. The new specimens have been determined partly as *Lingulocystis elongata* Thoral, 1935 and partly as *Lingulocystis aff. deani* Ubaghs, 1994. This study is the first report of *Lingulocystis* in the Foulon Formation. New stratigraphic ranges have been defined for both species: *L. elongata* from the early Tremadoc (Saint-Chinian Formation) to the middle Arenig (lower part of the Landeyran Formation), *L. aff. deani* from the early Arenig (Cluse de l’Orb Formation and Foulon Formation), and *L. deani* from the middle Arenig (upper part of the Landeyran Formation). The new specimens of *L. elongata* highlight its intraspecific variability, mainly concerning the size and arrangement of the central plates, the size of the theca, and the type of stem columnal articulations. Sedimentological studies in Montagne noire currently use the presence...
of *Lingulocystis* remains as taphonomic and palaeoecological indicators. The presence of two types of columnal articulations enhances the palaeoecological use. The development of the synostosial articulation seems to be correlated with a proximal platform palaeoenvironment, whereas development of the symplexial type seems to be related to a deeper palaeoenvironment or relatively high hydrodynamic conditions.

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Résumé


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**Keywords:** Echinodermata; Systematics; Palaeoecology; Lower Ordovician; France

**Mots clés :** Echinodermata ; Systématique ; Paléoécologie ; Ordovicien inférieur ; France

1. Introduction

Flattened eocrinoids are generally considered as a polyphyletic assemblage of widely divergent forms (Sumrall et al., 2001). All share thecal flattening, but the main differences concern the number of ambulacra, the thecal plating, and the shape of the stem. The thecal plating of *Lingulocystis* Thoral, 1935 is characterized by the presence of a frame composed of elongate marginal plates enclosing numerous polygonal central plates. The adoral edge is overlain by two lateral ambulacra, and the columnal-bearing stem is inserted into four basals. Because of these distinctive characteristics, Paul (1988), and Dean and Smith (1998) considered *Lingulocystis* as the immediate outgroup of flattened eocrinoids, based on phylogenetic analyses.

Thoral (1935) initially attributed *Lingulocystis* to the carpoids and described two varieties: *Lingulocystis elongata typica* and *Lingulocystis elongata lata* based on two specimens found in the Lower Ordovician (*La Maurerie* Formation), north of Saint-Chinian (Hérault, France; Fig. 1). Later, Chauvel (1941) considered the genus as an eocrinoid rather than as a carpoid. After re-evaluation, Ubaghs (1960) rejected the distinction of two subspecies of *L. elongata* and confirmed the assignment of *Lingulocystis* to the eocrinoids. He used ten additional specimens
of \textit{L. elongata}, collected in the north of Assignan (Col des Châtaigniers, Fig. 1) and from the surroundings of Roquebrun (Fig. 1). These specimens were collected in various stratigraphic levels, comprised between \textit{La Maurerie} Formation and the Foulon Formation (early Arenig; Fig. 2).

Three species have been defined so far in the genus \textit{Lingulocystis}: (1) \textit{L. elongata} Thoral, 1935 from the late Tremadoc to the early Arenig of southern Montagne noire (France; Thoral, 1935; Ubaghs, 1960) and \textit{L. cf. elongata} from the middle Arenig (San Bernardo Formation) of the Salta Province (Argentina, Gutiérrez-Marco and Aceñolaza, 1999; Aceñolaza and Gutiérrez-Marco,
The genus *Lingulocystis* is a predominant component of the echinoderm fauna in the Lower Ordovician of the Montagne noire, as suggested by its particularly abundant remains. The skeleton of *Lingulocystis* is weakly articulated and therefore highly sensitive to the relative rate of burial, bottom-water oxygenation, and turbulence (Type 1 echinoderms, defined by Brett et al., 1997). The presence of *Lingulocystis* is often associated with shallow water and proximal platform environment (Courtessole et al., 1983; Vizcaíno et al., 2001). Numerous remains (fragments or complete thecae) are frequently collected, but rarely described, as they are often employed as palaeobiologic and taphonomic indicators because of their abundance and degree of preservation. *Lingulocystis* remains are generally used to confirm or invalidate sedimentological interpretations of the Montagne noire (Vizcaíno et al., 2001).

The purpose of this paper is to describe new specimens of *Lingulocystis* from the Arenig of the Montagne noire, to discuss intraspecific variability in *L. elongata* Thoral, 1935, and the palaeoecologic adaptations of the genus *Lingulocystis*. The new specimens presented below come from eight different sites, one near Caunes-Minervois (Aude, France), four from south of Roquebrun...
and three from the Landeyran Valley (Hérault, France; Fig. 1). They were collected from five of the six formations mentioned below (Fig. 2).

The material referred in this paper is preserved in the following collections: collection Griffe, Musée du Biterrois (MBB-GG); collection Vizcaíno, Carcassonne (VOMN); collection Courtessele-Vizcaíno, Carcassonne (O); collections géologiques, Muséum national d’histoire naturelle, Paris (Gg); collections paléontologiques, université de Montpellier-2 (UM and USTM-ACI); collections paléontologiques, université de Lyon-1 (FSL).

2. Geographical and stratigraphic locations

The study area stretches from Lugné to Saint-Nazaire-de-Ladarez (Fig. 1) in the southern Montagne noire (France). The sedimentary rocks in this area have been dated from the early to the middle Arenig (Lower Ordovician), and are usually divided into seven levels or faunal zones corresponding to six formations (Fig. 2) (Courtessole et al., 1985; Vizcaíno et al., 2001; Vizcaíno and Álvaro, 2003). The Saint-Chinian Formation consists of monotonous, dark-grey claystones and siltstones, bearing fine- to medium-grained sandstone intercalations, and siliceous concretions. The Formation called La Maurerie crops out in the southwest of Roquebrun (Fig. 1). It can be defined as a succession of sandstones, alternating with shales bearing centimetric siliceous concretions. This formation is characterized by the active progradation of inner-platform facies (shallow water and high energetic environment; Vizcaíno et al., 2001). The Setso Member (faunal zone i, up to 30 m), is composed of homogeneous black to grey shales (occurring in the Setso stream; Fig. 1). The overlying Cluse de l’Orb Formation (faunal zone j; 150–220 m thick) consists of layers of white quartzites, alternating with grey sandstones, and sandy shales bearing some siliceous fossiliferous concretions and glauconitic remains (Dabard and Chauvel, 1991). The sedimentary features of the Setso Member reflect a deepening to storm-dominated open-sea platform (Cluse de l’Orb Formation; Eschard in Courtessole et al., 1985). The Foulon Formation (faunal zone k; 60–100 m thick) corresponds to an alternation of fine-grained sandstones with shales bearing siliceous concretions and glauconitic remains. Regressive and proximal conditions have been displayed in this formation (Dabard and Chauvel, 1991). Finally, the Landeyran Formation (200–400 m) is composed of brown, grey, and green homogeneous shales, bearing siliceous nodules. This latter formation is divided into two faunal zones (l and m) corresponding to two zones of trilobites (Fig. 2). The lower part of the Landeyran Formation shows a deepening trend with offshore deposits whereas its upper part reflects a gradual progradation and shallowing pattern (Vizcaíno et al., 2001). Vizcaíno and Álvaro (2003) summarized the palaeoenvironmental interpretations based on sedimentology and on trilobite faunas. They recognized two distinct Arenigian regressive progradational trends associated with coarse-grained siliciclastic sediments (the upper part of the Cluse de l’Orb Formation and the Foulon Formation) bounded by a shale-dominated, transgressive depositional system (Setso Member and Landeyran Formation).

3. Systematic descriptions

Phylum BLASTOZOA Sprinkle, 1973
Class EOCRINOIDEA Jaekel, 1918
Family LINGULOCYSTIDAE Ubaghs, 1960
Genus Lingulocystis Thoral, 1935
3.1. Type species

*L. elongata* Thoral, 1935; Lower Ordovician, Montagne noire (France).

3.2. Remarks

*Lingulocystis* differs from other eocrinoid genera in having a flattened theca, composed of differentiated elongate marginals and tiny polygonal central plates. The attachment appendage is a columnal-bearing stem. Several biserial brachiololes are mounted on two lateral ambulacra, representing the shared BC and DE ambulacra. The A ambulacra seems to be reduced to one plate, bearing one brachiolo in the middle part of the adoral edge of the antanal face. The location of the anal pyramid at the edge of the central area indicates an anteroposterior flattening (sensu Sumrall, 1997).

The three species can be distinguished by the number of marginal plates, the variability in size of the central plates, the location of the anal pyramid, and the number of brachiolar insertions. *L. elongata* is notably characterized by great variability in the size of its central plates, and by the presence of one rib of larger plates in the central area (Thoral, 1935; Ubaghs, 1960; Gutiérrez-Marco and Aceñolaza, 1999). The main features of *L. boliviensis* are a small number of adoral plates, a curved adoral edge, and polygonal columnals (Sprinkle, 1973). *L. deani* is identified by the presence of a brachiolar facet on each adoral plate, and the location of its anal pyramid at the top of the theca (Ubaghs, 1994).

3.3. *L. elongata* Thoral, 1935

3.3.1. Material

Numerous isolated columnals and seven articulated specimens. VOMN 929a and b and O1053 were collected in the Cluse de l’Orb Formation (*Taihungshania shui landeyranensis* zone) at “La Borie de Berlan” (Fig. 1). USTM-ACI 610a and b and Gg2001/3403 were respectively found near Lugné and along the road from Roquebrun to Vieussan (Cluse de l’Orb Formation; *Colpocoryphe maynardensis* zone). VOMN 2352a and b and MBB-GG45 were collected in strata of the lower part of the Landeyran Formation (*Apatocephalus incisus* zone) along the road of Les Bénédèdes. FSL 168 699 and MBB-GG46 come from the Lower Ordovician of Caunes-Minervois (Fig. 1).

3.3.2. Description

All specimens are preserved as mould impressions of one or both sides in concretions or compact sandstones. They are mostly complete with well-exposed thecae and attached stems. Some articulated brachiolar plates are present when the adoral part of the theca is preserved. The thecal length varies from 24.8 to more than 35.5 mm, and the width from 10.8 to more than 24.5 mm (Table 1).

The theca is flattened, elongate and paddle-shaped. The adoral edge is straight in the middle part and slightly rounded at each extremity (Pl. 1, Figs. 3, 4). The marginal frame is composed of six to nine elongate rounded D-shaped plates. In some specimens, the number of these lateral marginals is different from one side to another. In MBB-GG46, on the left side of the anal face, eight marginals are exposed, whereas the right side is composed of seven elements (Pl. 2, Figs. 5, 6). In MBB-GG45, both sides have eight lateral marginals. The basal marginals are paired. The adoral edge is composed of eight to ten relatively short plates supporting the ambulacral system.
Table 1
Table of measurements of maximal length (L), width (W), and thickness (thick) of the theca
Tableau 1
Tableau des mesures de la longueur (L), de la largeur (W) et de l’épaisseur (thick) de la thèque

<table>
<thead>
<tr>
<th>L. elongate</th>
<th>Published range</th>
<th>VOMN 2352</th>
<th>VOMN 929</th>
<th>O1053</th>
<th>MBB-GG 45</th>
<th>MBB-GG 46</th>
<th>USTM -ACI 610</th>
<th>L. deani Holotype</th>
<th>L. aff. deani Holotype</th>
<th>L. boliviensis Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (mm)</td>
<td>28.5–32</td>
<td>&gt;35.5</td>
<td>&gt;25.5</td>
<td>&gt;26.2</td>
<td>25.8</td>
<td>24.8</td>
<td>31.7</td>
<td>21.1</td>
<td>23.2</td>
<td>35.5</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>11–17</td>
<td>&gt;24.5</td>
<td>18.5</td>
<td>&gt;12.8</td>
<td>10.8</td>
<td>12.9</td>
<td>16.7</td>
<td>12.8</td>
<td>11.7</td>
<td>20.1</td>
</tr>
<tr>
<td>L/W (mm)</td>
<td>2.1–2.5</td>
<td></td>
<td>2.4</td>
<td>1.9</td>
<td>1.9</td>
<td>1.6</td>
<td>2.0</td>
<td>1.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thick (mm)</td>
<td>3</td>
<td>2.1</td>
<td>2.3</td>
<td>1.8</td>
<td>1.7</td>
<td>2.2</td>
<td>1.5</td>
<td>1.5</td>
<td>1.5</td>
<td></td>
</tr>
</tbody>
</table>

$L/W$ represents the length over width ratio. The measurements of UM 309 and FSL 168 699 (specimens iii and iv of Ubaghs, 1960) are not given here because of their incomplete preservation, and those of L. cf. elongata (in Gutiérrez-Marco and Aceñolaza, 1999) are not reported here because either width or thickness measurements (or both) are absent. The characteristics of L. boliviensis come from the description of Sprinkle (1973).


* Only the measurements of specimens considered as adults were reported from Ubaghs (1960).
Plate 1. *L. elongata* Thoral, 1935; all the photographs of the latex casts are with their interpretative camera lucida drawings. 1, 2, VOMN 2352a and 3, 4, VOMN 2352b: aboral part of the theca and proximal part of the stem. The arrow on Fig. 2 shows the important thickness of the theca and the shape in D of the marginal plates. 5, 6, MBB-GG45: anal face of the theca and proximal part of the stem. 9, 10, MBB-GG46: anal face of the theca, showing three ribs of larger central plates (see the arrow), articulated with the longest preserved stem. *L. aff. deani* Ubaghs, 1994.

7, 8, VOMN 3434: photograph and interpretative drawing of the adoral part of the antanal face of the theca; the small arrows indicate the brachiolar facets on the adoral marginal plates. Scale bar represents 5 mm.

This number is consistent with the previously published observations on *L. elongata* (Ubaghs, 1960). The summit is composed of a double row of alternate plates. The central area is plated by numerous tiny irregular polygonal plates, interpreted as a flexible tegument. The central plates show great variability in size and shape both within and between specimens. For example, the
Plate 2. *L. aff. deani* Ubaghs, 1994; 1, 2, VOMN 111: photograph and interpretative drawing of the theca bearing brachioles and stem. The arrow indicates the oral plates surrounding and overlying the mouth. 11, 12, VOMN 537: photograph and interpretative drawing of the adoral part of the anal face with eight articulated brachioles (see the arrow). *L. elongata* Thoral, 1935; 3, USTM-ACI 610a: photograph of the latex cast of the anal face. 4, USTM-ACI 610b: photograph of the latex cast of the antanal face. 5–8, VOMN 929a and b: photographs and interpretative drawings of the latex casts of both faces of the theca. 9, 10, O1053: photograph and interpretative drawing of the latex cast of the antanal face and the articulated stem. Scale bar represents 5 mm.

Planché 2. *L. aff. deani* Ubaghs, 1994; 1, 2, VOMN 111: photographie et dessin interprétatif de la tige avec des sutures droites, de la thèque montrant des insertions brachiolaires. Les flèches indiquent les plaques qui surmontent la bouche. 11, 12, VOMN 537 : photographie et dessin interprétatif de la partie adorale de la face anale portant 8 brachioles articulés (voir la flèche). *L. elongata* Thoral, 1935; 3, USTM-ACI 610a et 4 USTM-ACI 610b : photographies de la face anale et de la face antanale, respectivement. 5–8, VOMN 929a et b : photographies et dessins interprétatifs des deux faces de la thèque, respectivement de la face anale et de la face antanale. 9, 10, O1053 : photographie et dessin interprétatif de la partie aborale de la face antanale de la thèque articulé à la tige. Les barres d’échelle représentent 5 mm.
central plates range from less than 0.5 to 3.5 mm in size; most are around 1.9 mm, in VOMN 2352 (Pl. 2, Figs. 1–4). The average size of the centrals varies from 0.8 to 2.2 mm in all the specimens. The general pattern of the central plating is the same on both sides of the theca, even if the exact organization of the plates is quite different. The larger plates occur mostly in the middle part of the central area. The most elongate plates are commonly arranged in one or more lengthwise ribs (e.g., one rib in USTM-ACI 610a and b, two in VOMN 2352a and b, and three in MBB-GG45 and in MBB-GG46; Pl. 1, Figs. 3, 4 and Pl. 2, Figs. 1, 2, 9, 10). In published specimens of \( L. \) elongata, only one rib was described (Thoral, 1935; Ubaghs, 1960; Gutiérrez-Marco and Aceñolaza, 1999). Thecal plates have a smooth interior side and a smooth to finely granulated exterior side: no ornamentation in FSL 168 699 and USTM-ACI 610a and b (Pl. 1, Figs. 3, 4) versus fine granulations in VOMN 929a and b, O1053, MBB-GG45, MBB-GG46, and VOMN 2352a and b (Fig. 3(2)). The previously described specimens of \( L. \) elongata from Montagne noire have only smooth exterior sides (Thoral, 1935; Ubaghs, 1960). Fine granulations have been mentioned in the description of the Argentinean specimens of \( L. \) cf. elongata (in Gutiérrez-Marco and Aceñolaza, 1999).

The anal pyramid is located at the edge of the central area, at a distance of 1/4–1/3 down to the adoral edge. The periproct is covered by 10–16 straight needle-like plates (e.g., MBB-GG45; Pl. 2, Figs. 5, 6). This structure has a rounded outline averaging 1.2 mm in diameter. No other pores through to the interior of the theca were observed.

The exposed adoral edges show two lateral ambulacra. They are separated by two or three elongate adoral marginals surrounding the mouth. The mouth and the ambulacral food grooves are covered by numerous alternate small plates. Each ambulacrum is composed of three or four plates per side, each plate bearing one brachiolar facet. The left ambulacrum seems in general to be more well-developed than the right one. The total number of brachi­oles was probably 13–15, that is, about the same number as for \( L. \) elongata and \( L. \) boliviensis (Ubaghs, 1960; Sprinkle, 1973, respectively), but lower than expected for \( L. \) deani (Ubaghs, 1994).

The stems attached to the thecae are incompletely preserved. MBB-GG45 possesses the longest stem, about 38.8 mm in length with a constant diameter of about 1.1 mm (Pl. 2, Figs. 9, 10). In the largest specimen, the stem diameter is 3.4 mm. The stem is composed of numerous rounded columnals, showing an alternation between thin and thick plates in the proximal part. The suture between the columnals is straight or irregular in USTM-ACI 610a and b and in the proximal part of the stem of O1053 (Fig. 3(5)). Sutures are crenulated in VOMN 2352a and b, MBB-GG45, MBB-GG46, and in the distal part of the preserved stem of O1053 (Fig. 3(1, 3, 5)). Ubaghs (1960) described straight and irregular sutures, indicating a synostosial articulation. These new specimens suggest the occurrence of a second type of articulation (i.e., symplexy).

### 3.3.3. Remarks

The new specimens from Montagne noire differ from \( L. \) boliviensis in having a straighter adoral edge, elongate ribs composed of larger plates in the central area, and above all, a round cross section of the columnals. They differ from \( L. \) deani in having a paddle-shaped theca, fewer brachi­oles, and in particular, strongly pronounced ribs composed of larger plates in the central area. They exhibit most of the major features of \( L. \) elongata (e.g., paddle-shaped theca, rib of larger plates, two lateral ambulacra, rounded columnals), but in addition, show two types of columnal articulations.
Fig. 3. 1, 2. *L. elongata* Thoral, 1935; VOMN 2352a. 1. Detail of the proximal part of the stem; 2. detail of the granulated ornamentation of the central thecal plates. 3. *L. elongata* Thoral, 1935; MBB-GG46; enlargement of crenulated sutures between stem columnals. 4. *L. aff. deani* Ubaghs, 1994; VOMN 537; detail of the pustule ornamentation on the thecal plates and of the aboral frame, bearing two brachiolar facets. 5. *L. elongata* Thoral, 1935; O1053; stem showing straight sutures in its proximal part and crenulated sutures in its most distal part. Arrows indicate the ornamentation of the thecal plates or the crenulated sutures between the columnals. The white circlet indicates the brachiolar facet. Scale bar represents 1 mm.

3.3.4. Occurrence

Cluse de l’Orb Formation (*Taihungshania shui landeyranensis* zone; *Colpocoryphe maynardensis* zone) and the lower part of the Landeyran Formation (*Apatokephalus incisus* zone).

3.4. *L. aff. deani* Ubaghs, 1994

3.4.1. Material

One complete specimen (VOMN 111) comes from the southern side of l’Embouriel (Foulon Formation, *Neseuretus (N.) arenosus* zone). Two half thecae with articulated brachiolae (VOMN
537, VOMN 3434) were collected in southern hillside of La Vernède, and “La Borie de Berlan”, respectively. Both are dated from the lower part of the Cluse de l’Orb Formation (*Taihungshania shui landeyranensis* zone).

### 3.4.2. Description

The specimens are preserved as mould impressions in concretions or compact shales. The complete theca (VOMN 111) is 23.2 mm in length and 12.8 mm in width (Table 1). The two other specimens are 14.7 and 20.1 mm in width (VOMN 537 and VOMN 3434, respectively).

The theca is strongly flattened and trigonal in shape with a straight adoral edge. The lateral frame of VOMN 111 is composed of seven plates on the right side and eight on the left. VOMN 111 and VOMN 537 have nine plates per side forming the adoral frame (Pl. 1, Figs. 1, 2). VOMN 3434 shows a more developed adoral edge with 14 plates per side.

The central area is made of numerous polygonal plates, which are relatively variable in size (ranging from 0.5 to 2.5 mm). The few larger plates occur preferentially in the middle part of the theca and they could be slightly oriented in a possible column. This organization is quite different from the first description of *L. deani*, in which no rib of larger plates was distinguished in the central area (Ubaghs, 1994). The external sides of the thecal plates are ornamented with small pustules in VOMN 111 and VOMN 537 (Fig. 3(2)) whereas they are smooth in VOMN 3434 (Pl. 2, Figs. 7, 8), and in the single published specimen of *L. deani* (Ubaghs, 1994).

The badly preserved anal pyramid is probably located laterally to the second lateral marginal in the central area (VOMN 537). The periproct seems to be covered by numerous needle-like plates. No other openings were observed.

A double row of alternate plates forms the adoral edge. Two extended ambulacra are each composed of five to seven plates per side and are separated only by one or two plates overlying the mouth. Each ambulacral plate bears a brachiolar facet. The mouth seems to be covered by relatively large, straight plates. They seem to be slightly raised above the plate surface, showing a synarthrial facet of articulation (Fig. 3(4)).

The preserved parts of brachioles indicate that the brachioles are relatively thin and elongate. They are composed of tiny biserial plates (VOMN 537). Cover plates are small and convex. The estimated total number of brachioles is 18–22, which agrees with the estimated number of the holotype (Ubaghs, 1994).

The single preserved stem measures 10.1 mm in length and 1.3 mm in diameter. The proximal part corresponds to an alternation of thin and thick rounded columnals. The stem is inserted in four paired basal plates. The sutures between columnals are straight, indicating a synostosial articulation (Pl. 2, Figs. 1, 2).

### 3.4.3. Remarks

These three specimens show few differences with the holotype of *L. deani* described by Ubaghs (1994): (1) slight variations in size and in the organization of central plates and (2) the ornamentation on the thecal plates (e.g., pustules). All features correspond to the primary description of *L. deani*. These three new specimens are attributed to *L. aff. deani*. They clearly differ from *L. elongata* and from *L. boliviensis* because of the presence of a brachiolar facet on each marginal adoral plate, and of a pronounced, straight adoral edge.

### 3.4.4. Occurrence

Base of the Cluse de l’Orb Formation (*Taihungshania shui landeyranensis* zone) and the Foulon Formation (*Neseuretus (N.) arenosus* zone).
4. Discussion

4.1. Additional morphological details

These additional specimens supply some new morphological details and highlight the differences or the similarities between the three described species of *Lingulocystis* Thoral, 1935. The new morphological details concern: (1) the presence of ornamentation; (2) the type of stem articulation; (3) the organization of the central plates; and (4) the shape of the adoral plates.

The organization of the central plates in *L. elongata* (Thoral, 1935) is clearly defined as strengthening elongate ribs of larger plates, whereas the new specimens of *L. aff. deani* Ubaghs, 1994 show a slight variation in size and a possible succession of relatively large plates in the central area. These observations seem to reduce the difference concerning the plating between these two species. However, they seem to emphasize the distinction between the latter and *L. boliviensis* Sprinkle, 1973, with all central plates of equal size.

The ornamentation corresponds to granulations in *L. elongata* (and *L. cf. elongata* in Gutiérrez-Marcos and Aceñolaza, 1999) and to pustules in *L. aff. deani* (Fig. 3(4, 5)). The presence of ornamentation seems to confirm the distinction between these two species and *L. boliviensis*, even if *L. boliviensis* is defined on a single specimen.

The adoral edge of VOMN 111 and VOMN 537 (*L. aff. deani*) is clearly straight (Pl. 1, Figs. 1, 10). MBB-GG45, MBB-GG46, and USTM-ACI 610a and b (*L. elongata*) show a relatively straight central aboral edge with slightly curved extremities (Pl. 1, Figs. 2, 3 and Pl. 2, Figs. 5, 6, 9, 10). *L. boliviensis* has a curved adoral edge and a smaller number of adoral plates (Sprinkle, 1973). These observations seem to support the differences between the three species.

*L. elongata* and *L. deani* have the same number of adoral plates, but they differ in shape. The adoral plates are relatively elongate in the central part of the adoral edge and narrow in its lateral part in *L. elongata*, whereas most adoral plates are relatively narrow in *L. aff. deani*. The shape of adoral plates seems to be closely related to the presence of brachioles.

4.2. Intraspecific variation within *L. elongata* Thoral, 1935

Ten specimens of *L. elongata* and three of *L. cf. elongata* were described by Ubaghs (1960) and by Gutiérrez-Marcos and Aceñolaza (1999), respectively. The current study reports seven additional specimens attributed to *L. elongata*. These 19 specimens, now available, allow the intraspecific variability within *L. elongata* to be appreciated in more detail. It was already appreciated by Thoral (1935) and Ubaghs (1960) when they described two varieties in *L. elongata*. Ubaghs (1960, 1967, 1994) recognized only one species, based on the points of similarity in the morphology of the two varieties (*L. elongata* var. *lata* Thoral, 1935 and *L. elongata* var. *typical* Thoral, 1935) and the absence of major points of dissimilarity (e.g., difference in size, in plating). The new specimens bring additional details, increasing the intraspecific variability, even if no new subspecies need to be defined.

For the comparison of the sizes of the thecae, only published and complete specimens with supposed adult morphology are considered here. The new specimens from Montagne noire show no clues to indicate their ontogenetic stage. Immature stages were defined with a length (*L*) less than 23 mm and a ratio *L/W* around 1.7 by Ubaghs (1960). The ranges of measurements of the new specimens from Montagne noire seem to indicate that these specimens present relatively mature morphologies (Table 1); all measurements being superior to those given for immature specimens by Ubaghs (1960). Moreover, *L. elongata* seems to show great variation in thecal size:
(1) \( L/W \) varying from 1.9 to 2.5, and (2) thickness ranging from 1.7 to 3 mm. The thickness of the thecae seems to fluctuate independently to length (Table 1). \( L. \) elongata and \( L. \) boliviensis seem to have a greater thecal size than \( L. \) deani, because the measurements of probable juvenile specimens of \( L. \) elongata are similar to those of adult specimens of \( L. \) deani. However, the size of the specimens could not be an additional diagnostic point, notably because no gonopore is known in \textit{Lingulocystis} and \( L. \) deani is known only by one specimen.

The major feature of \( L. \) elongata is to have differentiated plates in the central area. The size of central plates fluctuates from one specimen to another one: central plates are less wide than 0.8 mm on average in USTM-ACI 610a and b whereas they average 1.9 mm in VOMN 2352 (Pl. 1, Figs. 3, 4 and Pl. 2, Figs. 1–4). The organization of central plates varies from one to three ribs composed of larger plates. It was previously described only one rib of larger plates in \( L. \) elongata (Thoral, 1935; Ubaghs, 1960; Gutiérrez-Marco and Aceñolaza, 1999). Specimens FSL 168 699, USTM-ACI 610a and b, O1053, VOMN 929a and b, and UM 305 (holotype of \( L. \) elongata; Thoral, 1935; Ubaghs, 1960), showing one central rib, occur in the faunal zones h, i, and j. Specimens VOMN 2352 and MBB-GG46 showing two and three ribs, respectively, occur in the faunal zone l. The modification of the number of central ribs is surprisingly concordant with the stratigraphic position of the specimens. Moreover no ornamentation is present in specimens of \( L. \) elongata from the faunal zones h–j (e.g., USTM-ACI 610, VOMN 929), and abundant granulations are observed in specimens from the faunal zone l (VOMN 2352). The intraspecific variability based on the ornamentation and the complexity of the central area seems not to be correlated with the palaeoenvironmental conditions, notably because the different faunal zones showed various environmental changes from shallow, proximal conditions to open sea conditions (see the next paragraph; Vizcaíno et al., 2001). At this step of knowledge, the increase in complexity of the central area organization and the appearance of its ornamentation could be evolutionary trends in \( L. \) elongata. Pustules on thecal plates are also present in \( L. \) aff. \( L. \) deani (but not in \( L. \) deani) whatever the palaeoenvironmental conditions. It seems to confirm the possible evolutionary origin of this character.

Intraspecific variation also concerns, in a less significant way, the number of marginal plates and the size of the columnals, which are all more well-developed in MBB-GG45 and MBB-GG46 than in the other specimens (as in \( L. \) aff. \( L. \) deani).

### 4.3. Stratigraphic and palaeoecological implications

The presence of \textit{Lingulocystis} in some strata in Montagne noire can be used as a bathymetric indicator. The abundance of \textit{Lingulocystis} remains is generally associated with shallow water and proximal conditions (Vizcaíno et al., 2001). The published presence of \textit{Lingulocystis} from the faunal zone i (\textit{Taihungshania shui landeyranensis} zone) to k (\textit{Neseuretus (N.) arenosus} zone) and its recovery in m (\textit{Hangshungolithus primitivus} zone) seemed to corroborate the expected shallow environments, based on the sedimentology and the trilobite fauna (Vizcaíno and Lefebvre, 1999; Vizcaíno et al., 2001). Faunal zone l (\textit{Apatokephalus incisus} zone), from which \textit{Lingulocystis} remains were thought to be absent, contains a bigger proportion of blind trilobites and corresponds to offshore deposits (Vizcaíno and Lefebvre, 1999).

This study is the first report of \textit{Lingulocystis} in faunal zone l (\textit{Apatokephalus incisus} zone) in Montagne noire. The new specimens of \( L. \) elongata confirm its occurrence from the \textit{La Maurerie} Formation (faunal zone g, \textit{Taihungshania miqueli} zone) to the Foulon Formation (faunal zone k, \textit{Neseuretus (N.) arenosus} zone), but they also extend its stratigraphic range from the upper boundary to the lower part of the Landeyran Formation (faunal zone l, \textit{Apatokephalus incisus} zone).
zone) (Fig. 2). The new specimens of *L. aff. deani* extend the stratigraphic range from the Cluse de l’Orb Formation (faunal zone i, *Taihungshania shui landeyranensis* zone) to the upper part of the Landeyran Formation (faunal zone m, *Hangshungolithus primitivus* zone).

The discovery of *Lingulocystis* in the lower part of the Landeyran Formation (faunal zone l, *Apatokephalus incisus* zone) seems to indicate that this genus could live in deeper conditions than those corresponding to the deposits of the Cluse de l’Orb Formation, the Foulon Formation, and the upper part of the Landeyran Formation (proximal inner-platform). However, specimens of *Lingulocystis* seem to be more abundant in shallower conditions (Ubaghs, 1960; Gutiérrez-Maro and Aceñolaza, 1999). Ubaghs (1960) indicated that *Lingulocystis* could live as a kite-strategist, with a light theca anchored to a soft substrate by a long stem with a distal grapnel, or with its distal end inserted into the substrate. Gutiérrez-Maro and Aceñolaza (1999) hypothesized that this genus can have an epipelagic mode of life, hanging with its long stem from floating algae. No additional clues for the mode of life interpretation have been discovered since the publication of these hypotheses.

The new specimens described above show two types of sutures for columnals, interpreted as two types of articulations. Specimens VOMN 2352a and b, MBB-GG45, and MBB-GG46 have crenulated sutures, which probably indicate symplexy. Specimens USTM-ACI 610a and b and VOMN 111 have straight sutures, interpreted as synostosis. One specimen O1053 shows irregular sutures in the proximal part of the stem and crenulated sutures in its distal part. These observations have been interpreted as a symplexy type of articulation. Stem flexibility is facilitated by symplexy rather than synostosis (Hess et al., 1999). Specimens showing crenulated sutures between columnals (symplexy articulation) occur only in the lower part of the Cluse de l’Orb Formation (faunal zone i, *Taihungshania shui landeyranensis* zone) and the lower part of the Landeyran Formation (faunal zone l, *Apatokephalus incisus* zone). The corresponding palaeoenvironmental interpretations reflect in both cases a deepening, respectively a storm-dominated open-sea platform and an outer platform (Vizcaíno et al., 2001). The specimens with straight sutures between the columnals (synostosial articulations) occur in the upper part of the Cluse de l’Orb Formation (faunal zone j, *Colpocoryphe maynardensis* zone) and in the Foulon Formation (faunal zone k, *Neseuretus (N.) arenosus* zone). The corresponding palaeoenvironmental conditions are interpreted as proximal inner-platform. The development of a symplexy articulation, which increases the flexibility of the stem, seems to be related to a life in a deeper palaeoenvironment or under relatively high hydrodynamic conditions.

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