

***Dignomia munsterii* (Brachiopoda, Lingulata) from the Ordovician of Bolivia, with redescription of the genus**

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ABSTRACT

Specimens of *Dignomia* have been recorded in the Anzaldo Formation (Upper Ordovician) in three localities in the Cochabamba area of the Cordillera Oriental, Bolivia. They had been attributed to *Lingula munsterii* d'Orbigny, 1842 found in company with *L. submarginata* d'Orbigny, 1850, both are indubitable *Dignomia*. These species were collected in the Cordillera Oriental in the Cochabamba region and in the Chuquisaca area, near Zudáñez the type locality and belong in fact to *Dignomia*. *Dignomia munsterii* is described and a new generic diagnosis is proposed. The emended diagnosis is based on characters of the shell and anatomic traits that permit its recognition as a discrete genus of the Lingulidae, the family to which it belongs. The type species is *Lingula alveata* Hall, 1863. *Dignomia* is found in strata ranging in age from Lower Silurian to Middle Devonian in North and South America. At least six previously described species can be referred to *Dignomia* but all are inadequately described without reference to the scars indicating the sites of attachment of the visceral organs.

KEY WORDS

Brachiopoda,
Lingulidae,
Dignomia,
Ordovician,
Bolivia.

RÉSUMÉ

Dignomia munsterii (Brachiopoda, Lingulata) de l'Ordovicien de Bolivie, et redescription du genre.

Des exemplaires de *Dignomia* ont été récoltés dans la Formation Anzaldo (Ordovicien supérieur) dans trois localités de la région de Cochabamba (Bolivie) dans la Cordillère Orientale des Andes. Ils ont été attribués à *Lingula munsterii* d'Orbigny, 1842 qui appartient sans conteste au genre *Dignomia*, de même que *L. submarginata* d'Orbigny, 1850 : ces deux espèces ont été décrites de la région de Cochabamba (Cordillère Orientale) et de celle de Chuquisaca (à Zudáñez qui est la localité type). Une redescription de *Dignomia munsterii* et une nouvelle diagnose générique sont proposées. Grâce à l'étude des caractères de la coquille et des caractéristiques anatomiques, le genre *Dignomia*, dont la diagnose a été amendée, a été reclassé dans la famille des Lingulidae et se distingue bien des autres genres de cette famille. L'espèce type est *Lingula alveata* Hall, 1863. L'extension géologique du genre va du Silurien inférieur au Dévonien moyen et la distribution géographique se situe en Amérique du Nord et du Sud. Au moins six espèces peuvent être rapportées au genre *Dignomia*, mais toutes ont été décrites de façon inadéquate car sans référence aux traces donnant la disposition des caractères anatomiques du corps.

MOTS CLÉS

Brachiopoda,
Lingulidae,
Dignomia,
Ordovicien,
Bolivie.

INTRODUCTION

Lingulids are the most common inarticulated brachiopods encountered in the Upper Ordovician of Bolivia. Alcide d'Orbigny (1842) was the first to describe them in his exceptional *Voyages en Amérique Méridionale*. Of the three new species of *Lingula* described by this author (1842: 25-27, pl. 2), *Lingula submarginata* d'Orbigny, 1850 (pro *Lingula marginata* d'Orbigny, 1842, not Phillips, 1836) and *L. munsterii*, collected from Zudáñez (= Tacopaya) in the Chuquisaca region and from Palta-cueva in the Cochabamba region belong with certainty to the genus *Dignomia* (by the way, the genus *Lingula* arose only in the Tertiary, or perhaps in the Late Cretaceous [Biernat & Emig 1993; Emig 2003]). The syntypes of *L. munsterii* are deposited in the d'Orbigny collection in the Muséum national d'Histoire naturelle in Paris. D'Orbigny never fixed a holotype. No specimen referred to *L. submarginata* (or to *L. marginata*) could be found in d'Orbigny's collection.

In the last century several French and German expeditions worked in Bolivia, including the important investigations of Dereims (1906) and of Steinmann & Hoek (1912). Their collections included *L. munsterii* and three new forms: *Lingula lineata*, *L. ellipsiformis* and *L. boliviana*. More recently, Gagnier *et al.* (1986, 1996) recorded *Dignomia* from three localities in the vicinity of Cochabamba. Emig *in* Gagnier *et al.* (1996) described them briefly and referred them to a new species of *Dignomia*. Recently, Aceñolaza *et al.* (2003) reviewed the Ordovician lingulid shell beds in South America.

MATERIAL

The fossil specimens were collected in Bolivia in the Cochabamba region from the Anzaldo Formation (*sensu* Rodrigo de Walker & Toro 1987) at the following localities (Figs 1; 2): Cerro San Pedro in eastern suburb of Cochabamba Ciudad; Cerro Chakeri in the north of the pueblo of Sacabambilla,

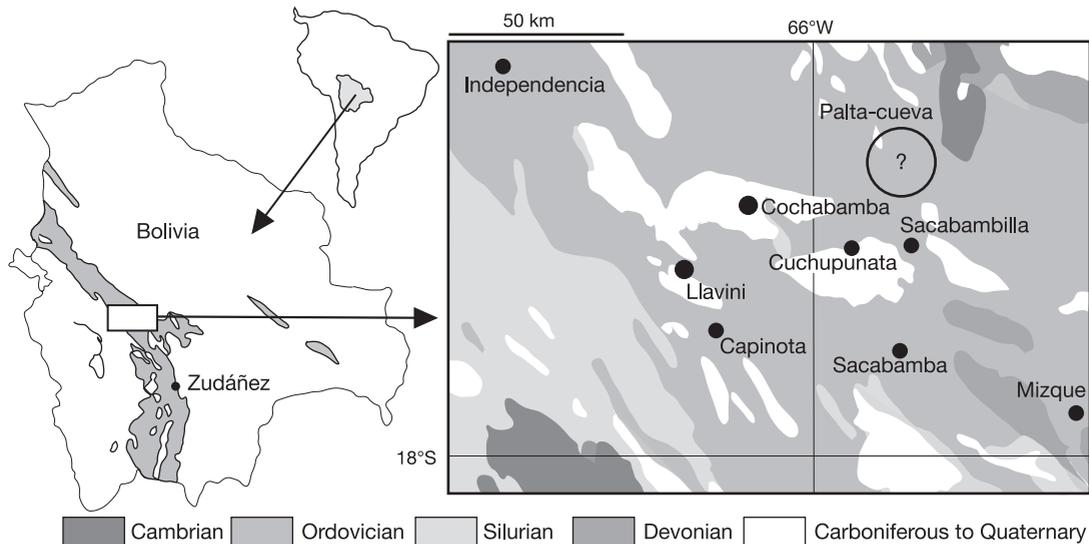


FIG. 1. — Maps of Bolivia showing the distribution of the Ordovician (from Pareja & Ballon 1978).

about 50 km east of Cochabamba; Sacabamba in the Rio Challaque, about 60 km south of the town of Cochabamba. Thirty more or less complete valves of lingulides from these localities were studied (Figs 1; 3).

The specimens described in this paper are housed in the “Typhothèque des Invertébrés fossiles du Muséum national d’Histoire naturelle”: MNHN R06654 – the syntypes of *Lingula munsterii* (a dorsal and a ventral valve) from Zudáñez (= Tacopaya), Chuquisaca region; MNHN A24313 – Cerro San Pedro in Cochabamba (17°23’45”S, 66°07’40”W); MNHN A24314 – Cerro Chakeri, Puntata Province, north of Sacabambilla (17°30’00”S, 66°47’58”W). A large collection from Cerro San Pedro in Cochabamba Ciudad is also housed in the Museo de la Universidad de Zaragoza.

GEOLOGICAL SETTING AND AGE

In Bolivia, the most nearly complete sequence of the Ordovician is in the Cordillera Oriental (Martínez *et al.* 1971; Gagnier *et al.* 1996). Outcrops extend from the Peruvian border in the northeast to Argentina in the South (Fig. 1). The three locali-

ties where *Dignomia* has been recorded are in the Anzaldo Formation (also called the Cuchupunata Formation by many Bolivian geologists) which may attain a thickness of 2000 m (Fig. 2). In the Cochabamba area, Steinmann & Hoek (1912) differentiated three units based mainly on fauna, from bottom to top (Fig. 2): “Bilobites Sandstein”, “*Lingula* Sandstein”, and “oberer Quarzit”. The latter has been named the San Benito Formation, while the two lower levels have been combined as the Anzaldo Formation. Ordovician rocks in this region form the Cochabamba Group (Fig. 2) comprised of the Independencia Formation, the Capinota Formation, the Anzaldo Formation and the San Benito Formation. The Independencia Formation is dated Arenigian, the Capinota and the lower part of the Anzaldo Formation are Llanvirnian-Llandeilian, and upper portion of the Anzaldo Formation and the San Benito Formation are of Caradocian age. The precise age of the upper portion of the Anzaldo Formation remains under debate. Suárez-Soruco (1976) considers the *Dignomia* localities to be Caradocian, but Rodrigo de Walker & M. Toro (pers. comm.) argue for a Llanvirnian-Llandeilian age based on trilobites. Gagnier *et al.* (1996) report that vertebrates from these localities are similar to

Divisions of Steinmann & Hoek (1912)	SYSTEM		Centre of Eastern Cordillera			
			Cochabamba Sucre		Chapare	
Upper Quartzite	upper	Ashgill	Cochabamba Group	?	?	?
Sandstone		Caradoc		Mizque	?	San Benito
with Lingula	middle			Llandeilo	Anzaldo	Anzaldo
Sandstone with Bilobites		Llandvirn		Capinota	Capinota	
Level with geodes	lower	Arenig	Independencia	Limbo Group	Avispas	
		Tremadoc			Putintiri	

FIG. 2. — Stratigraphical sequence of the Ordovician of the central Cordillera Oriental with the position of the studied *Dignomia* beds indicated in deep grey.

early Llanvirnian forms from Australia (Ritchie & Gilbert-Tomlinson 1977), and therefore the two localities must be contemporaneous. The latest palaeontological data (Gagnier *et al.* 1996) regarding the Anzaldo Formation suggest a Caradocian age (or perhaps older) because the underlying Capinota Formation is of Llanvirnian-Llandeilian age and the overlying San Benito Formation is also Caradocian in age (Fig. 2).

Lingulid specimens from Rio Challaque (Sacabamba) were collected in the basal part of the stratigraphic section composed of 300 m of lutite, well bedded yellowish sandstone with limonitic alterations and grey to greenish grey and yellow sandstone. Rodrigo de Walker & Toro (1987) correlated this Sacabamba section (Anzaldo Formation) with Cerro Chakeri (Sacabambilla). No correlation has yet been made with the Cerro San Pedro locality (Cochabamba), but the *Dignomia* occur within the “lingulid sandstone” (*sensu* Steinmann & Hoek 1912).

At both Cerro San Pedro and Cerro Chakeri (Sacabambilla), the specimens of *Dignomia* are preserved as several beds of numerous flat lying valves, some shells are *in situ*. A 3 to 20 cm band

of argillaceous sandstone separates each fossiliferous sandstone level. In Cerro Chakeri, *Dignomia* occurs in thin beds (0.5-1 cm thick) of fine to coarse sandstones, consisting exclusively of flat-lying valve fragments. In addition, some complete, rather well preserved, large, solitary valves were collected in a layer of coarse sandstone. Below and above the lingulid beds, there occur many of the vertical cylindrical burrows which may be interpreted as traces of lingulid burrows. The three localities studied include several phosphorite levels, composed principally of crushed *Dignomia* valves, but containing some small vertebrate fragments. These large concentrations of lingulid valves have been referred (see Suárez-Soruco 1976) to *Lingula ellipsiformis* Hoek, 1912, *L. munsterii*, *Bistramia elegans* Hoek, 1912; other invertebrates have been identified, among them the trilobite *Huemacaspis bistrami* (Hoek, 1912) and the vertebrate *Sacabambaspis janvieri* Gagnier, 1987 (see Gagnier *et al.* 1986; Toro *et al.* 1994).

The invertebrate fauna represents a marine, intertidal or subtidal benthic assemblage. In light of recent ecological investigations of living *Lingula* Bruguière, 1797 (cf. Emig 1986, 1997), fossilization of flat-lying valves may occur preferentially when the environment changes drastically, e.g., a large decrease in salinity, the effects of storms and subaqueous slumps both of which produce thick deposits of coarse or fine sediment. The absence of fossil lingulid shells in other sandstone beds does not preclude the presence in them of an original population of *Dignomia* because in normal environments the shell of the lingulides is not preserved (Emig 1990). Because of the elongate oval outline of their shell, often called linguliform, *Dignomia* are believed to have constructed vertical burrows like those of the extant lingulides. That presumption is corroborated by the occurrences of burrow traces below and above the lingulid-shell beds. Furthermore, the sediment in which the *Dignomia* valves were fossilized appears to have been close to the substrate in which they lived (Emig 1983, 1997; Toro *et al.* 1994). Various interpretations of the means by which *Dignomia* fossilization occurred may be proposed: 1) as a consequence of storms the sediment containing the lingulid valves is eroded and dispersed, the lingulid valves are crushed,

washed and accumulated at the shore line. This mechanism would also account for the phosphorite levels (Aceñolaza *et al.* 2003); and 2) low salinity (less than 15 psu over at least 2-3 days), due to exceptional heavy rain and/or river flooding, that causes the ultra-rapid deposition of both fine and coarse sediment which favors fossilization of lingulid valves. In general, this occurs in the intertidal and subtidal zones near an estuary or delta.

REDESCRIPTION OF THE GENUS *DIGNOMIA* HALL, 1871

Phylum BRACHIOPODA
Subphylum LINGULIFORMEA Williams,
Carlson, Brunton, Holmer & Popov, 1996
Class LINGULATA Gorjansky & Popov, 1985
Order LINGULIDA Waagen, 1885
Superfamily LINGULOIDEA Menke, 1828
Family LINGULIDAE Menke, 1828

Genus *Dignomia* Hall, 1871

TYPE SPECIES. — *Lingula alveata* Hall, 1863.

TYPE LEVEL. — *Dignomia* ranges from Middle Ordovician to the Middle Devonian.

GEOGRAPHICAL DISTRIBUTION. — North and South America.

EMENDED DIAGNOSIS (FIGS 3-5). — Shell thin, elongate oval in shape; externally, two diverging medio-lateral grooves (internally ridges) extend from the umbonal region to the anterior margin, and a narrow median groove (a septum internally) extends from the umbonal region to the anterior margin of the dorsal valve but in the ventral valve only over the anterior half of the shell. Asymmetrical muscle system with three internal oblique muscles; unpaired posterior adductor muscle; no *vascula media* observed. (Note: these three characters are prerequisite to a diagnosis of the family Lingulidae – see Emig 2003).

REMARKS

Hall (1863), in the original description of *Lingula alveata* (only two valves were described), indicates that the valves “have a somewhat elevated or thickened border extending from the beak, within which is a distinct groove nearly parallel with the margin

and reaching half of the length of the shell”, that is concurrent with our observation and could describe a ventral valve. The other valve (a cast) “preserves the mark of a thin septum, which extends from just beneath the beak three-fourths the length of the shell”: this valve is dorsal, and is probably the dorsal valve represented by Rowell (1965). The specimens mentioned were found in the shales of the Hamilton Group (Ludlowville, Cayuga county, New York) and in sandstone near Fultonham (Schoharie county, New York), both dated Middle Devonian. Hall (1871) created the genus *Dignomia* but gave no diagnosis; only the cast (see above) was figured on plate 13, figure 3. The genus has been recorded “in the Lower Silurian and Devonian, and probably in the Middle Silurian” (Hall 1863; Cleland 1903). The description of two dorsal valves of *Dignomia alveata* by Hoare & Steller (1969) agrees with the genus characteristics; their specimens came from the Silica Formation (Middle Devonian; Ohio and Michigan).

In South America, d’Orbigny (1842) described from the Cochabamba and Chuquisaca regions of Bolivia two species: *Lingula submarginata* and *L. munsterii*, both of which are assigned here to the genus *Dignomia*. In his diagnosis of *L. submarginata*, d’Orbigny states: “Marquée en long de très légères stries, plus prononcées en approchant du bord. On remarque à partir du sommet, vers le bord, deux sillons assez prononcés, qui laissent entr’eux une surface bombée, formant feston sur le bord”. The shell length is 20 mm and the width 10 mm. The second species, *L. munsterii*, has a similar description: “Ornée en long de stries fines” and “sur le milieu de la longueur, on remarque trois sillons qui partent du sommet et vont en s’écartant vers le bord; l’un est au milieu, les deux autres sont aux côtés d’une partie légèrement saillante”. The shell length is 18 mm and the width 8 mm. According to d’Orbigny (1842), the specimens of both species were collected together in the same locality, that is “au sommet de la côte de Tacopaya [now: Zudáñez], entre Valle Grande et Chuquisaca [other name: Sucre]” (Fig. 1). The syntypes of *L. munsterii* have been studied: they belong with no doubt to *Dignomia*. D’Orbigny (1842) also recorded *L. munsterii* east of Cochabamba, “près de Palta-cueva, au sommet

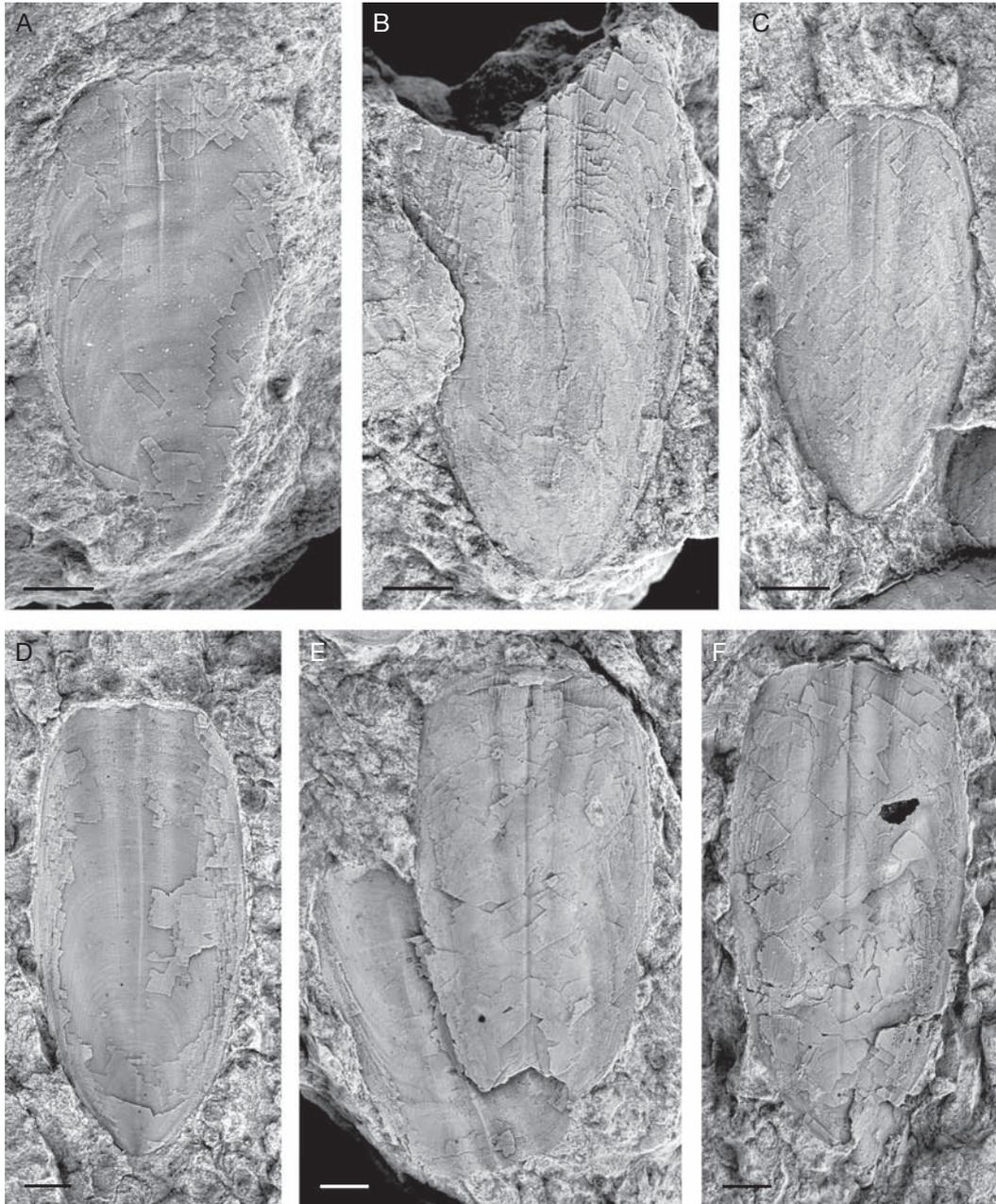


FIG. 3. — *Dignomia munsterii*: **A, B**, ventral valves; **A**, internal face; **B, C**, external faces; **D-F**, dorsal valves; **D**, internal face; **E, F**, external faces. Scale bars: 2 mm.

de la Cordillère de Cochabamba, sur le chemin de Yuracares (Bolivia), à la hauteur absolue de près de 5000 mètres” (Fig. 1).

Kayser (1897) described a broad *Dignomia*, that he named *D. subalveata* with generic characteristics like those of the diagnosis above (Fig. 4). The specimens

were collected in the “*Lingula*-Schichten” (*Lingula*-layers) from Jachal (Argentina). Branisa (1965) stated that *Lingula munsterii* is clearly identified by the large size of the shell and by its ornamentation, i.e. a central groove and two lateral ones as shown in the figure 4 of his plate 2: the three specimens represented are similar to our specimens (see Fig. 4). Branisa’s description of *Lingula lepta* Clarke, 1912 (= *Dignomia subalveata* (Kayser, 1897)) was confirmed by Castellaro (1966), collected in San Juan (Bolivia; Lower Devonian). Recently, Toro *et al.* (1994) reported *Lingula* sp. cf. *munsterii* with *Dignomia*-like characteristics in the area of Llavini (Cochabamba, Bolivia) in the Anzaldo Formation (Ordovician) (Fig. 1).

Rowell (1965) diagnosed *Dignomia* as follows: “Relatively large, wide, thin-shelled forms, long conspicuous median ridge in both valves, with 2 low, broadly diverging ridges that extend anterolaterally from beak”. This description is confirmed by our present observations, but Rowell’s figure 158:4 does not represent the interior of a ventral valve, but an external view of a dorsal valve. Nevertheless, Holmer & Popov (2000) in the second edition of the *Treatise* have curiously simplified this original diagnosis to: “Shell subtriangular to suboval; ventral interior with two widely divergent ridges posteriorly (may be impression of pedicle nerve); dorsal interior with long median ridge. All other characters inadequately known”; the figure 37:5a used by Holmer & Popov to illustrate *Dignomia* is that in Rowell (1965) with the identical caption, but the valve represented on figure 37:5b to illustrate *Dignomia* is not *Dignomia* but probably a *Barroisella* (compare it with fig. 9:1b in Holmer & Popov 2000). After an examination by A. Balinski and C. C. Emig during a recent visit in Warsaw (Poland) the two fragments referred to *Dignomia* sp. by Balinski (1995) are assigned to *Barroisella* Hall & Clarke, 1892.

Finally, the genus *Dignomia* appears to have been well recognized and defined by many authors. The characteristics of the shell defined in the emended diagnosis are sufficiently well described to permit the recognition with all certainty that *Dignomia* belongs to the order Lingulida. Furthermore, this genus has three characteristics defined in the di-

agnosis of the family Lingulidae (see Emig 2003): an asymmetrical muscle system with three internal oblique muscles, an unpaired posterior adductor muscle and the absence of *vascula media* (Fig. 5). On this basis we consider that *Dignomia* belongs to the family Lingulidae as did Rowell (1965). However, this genus was classed as *incertae sedis* in the family “Uncertain” by Holmer & Popov (2000) in the second edition of the *Treatise of Invertebrate Paleontology*.

Dignomia munsterii (d’Orbigny, 1842)

Lingula submarginata d’Orbigny, 1850 (pro *Lingula marginata* d’Orbigny, 1842: 28, pl. 2 fig. 5; non Phillips, 1836): 14.

Lingula lineata Hoek in Steinman & Hoek, 1912: 232.

Dignomia boliviana Emig in Gagnier *et al.*, 1996: 338, fig. 6.

MATERIAL EXAMINED. — See Chapter Material.

DIAGNOSIS (FIGS 3-5). — The outline of the shell is an elongate oval. Two large medio-lateral grooves, longitudinally striated, extend from the umbonal region to the anterior margin of the valves; a median groove is narrow. On the outer surface of the dorsal valve is a median groove that occupies its whole length. On the ventral valve, the groove extends from the anterior margin to about the half to two-thirds of the length.

Anterior margin straight, without indentation at the level of the grooves. Lateral margins subparallel; width of the shell largest at or above the middle; surface smooth with numerous weak, occasionally well marked, growth lines. Umbonal region rounded on dorsal valve, pointed on ventral valve. Small propleura slightly curved with a weak pedicle groove, continuous with internal valve side. The ventral lophophoral cavity occupies approximately 36% of the length of the valve. Mantle canals curved. A pair of narrow subparallel, V-shaped, grooves extend from the anterior adductor scars to the unpaired posterior adductor scars; three long oblique internal muscles; a V-shaped perimial line.

No internal observation of dorsal valve.

DESCRIPTION

Our specimens were cited under *Dignomia boliviana* nov. sp. by Emig in Gagnier *et al.* (1996) but never described completely. The d’Orbigny (1842)

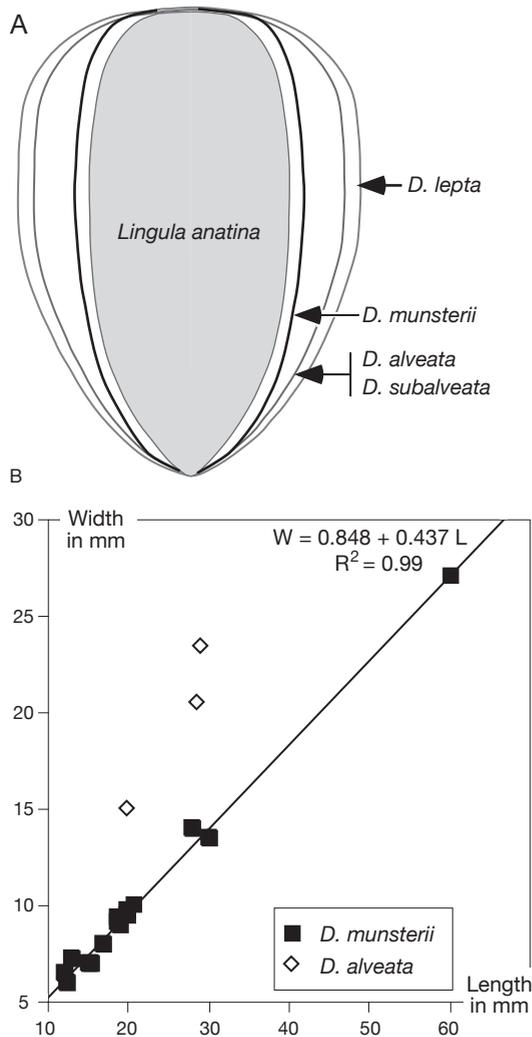


FIG. 4. — **A**, the shell shape of *Dignomia munsterii* compared to those of *D. alveata*, *D. subalveata* and *D. leptae*, and to *Lingula anatina*; **B**, regression curve of *Dignomia munsterii* which is similar to the populations of *Lingula anatina* from New Caledonia: $W = -0.229 + 0.435L$ ($R^2 = 0.98$; $n = 165$).

description of two species, *Lingula submarginata* (see also below) and *L. munsterii*, both of which are obviously *Dignomia* (see above) and are similar in aspect to our specimens collected in the same area. That was corroborated by the study of the syntypes of *L. munsterii*. Therefore we consider our specimens should be named *Dignomia munsterii*, the better-described of d'Orbigny's two species. However, as

the name *marginata* was preoccupied by *Lingula marginata* Phillips, 1836 a species from the Carboniferous of England, d'Orbigny (1850) proposed its replacement by *Lingula submarginata*.

Shell and internal features

The length of the shell of our specimens ranges from 12 to 30 mm (mean 19.1 ± 5.5 mm; $n = 12$), and the width from 5.9 to 14 mm (mean 9.3 ± 2.4 mm; $n = 12$). The W/L ratio lies between 0.45 and 0.55 (mean 0.49 ± 0.02) (Fig. 4B). D'Orbigny (1842) measured two specimens. The W/L ratio is $10/20 = 0.5$ for the specimen referred to *Lingula submarginata*, and for *L. munsterii* the W/L ratio is $8/18 = 0.44$. The general shape of the shell of *Dignomia* appears similar to those of the species of *Lingula* with an elongate oval shell (W/L = 0.38–0.53; mean 0.43 ± 0.3 – 0.48 ± 0.3 mm derived from the geographic populations; $n = 155$) (Fig. 4).

The two medio-lateral grooves are visible on the inner faces of both valves as ridges (or septa), sometimes well developed especially near the anterior margin, at the site where the central exhalant pseudosiphon and the two lateral inhalant ones separate (Figs 3; 5). The anterior margin of the valves is straight and flat. These ridges may have a morpho-functional role related to the disposition of the lophophore in the lophophoral cavity. On the outer side, longitudinal ribs exist in the grooves and commonly extend laterally (Figs 3; 5).

Ventral valve. The internal umbonal region differs from that of the lingulides in the presence of small propleas and the absence of a true pedicle groove (Fig. 5). The existence of a pair of V-shaped grooves – the impressions of the pedicle nerves (Biernat & Emig 1993) – on the inner side of the ventral valve in *Dignomia* (Fig. 5) can be considered as general in the superfamily Linguloidea since Cambrian times (Biernat & Emig 1993; Emig 2002, 2003). These grooves extend from the anterior adductor muscles until the level of the posterior adductor muscle where they join.

The disposition of the mantle canals in *Dignomia* could be seen in only one ventral valve (Fig. 5). The distance from the distal tips of the mantle canal to the anterior margin of the valve represents 17%

of the total length of the valve. The length of the lophophoral cavity, i.e. the distance between the distal limits of the anterior adductor muscle scars to the anterior margin of the valve is 36% of the total length of the valve. Both measurements are congruent with those seen in *Lingula*, respectively 17-22% (mean $20 \pm 1.7\%$; $n = 44$) and 35-46% (mean $41 \pm 4.5\%$) (Biernat & Emig 1993; Emig & Bitner 2005a). No *vascula media* could be found (Fig. 5).

The disposition of the body muscles on the ventral side is similar to that in the family Lingulidae (see Emig 1982, 2003; Emig & Bitner 2005a, b): the oblique muscles have a V-shaped arrangement and a perimial line, the trace of the attachment of the body wall to the valves (a line surrounding the body muscles); the internal oblique muscles are represented by long scars (Fig. 5). Such a disposition is similar to that described by Egorov & Popov (1990) in the lingulide *Semilingula*. The trace of the posterior adductor muscle could not be followed completely in *Dignomia* but it seems to be unpaired (Fig. 5) and similar in shape to that of *Lingularia*.

Dorsal valve. Muscle arrangement and disposition of the mantle canal could not be observed on dorsal valve.

DISCUSSION

At least six species can be referred to *Dignomia* but all have been poorly described without reference to the scars indicating the sites of attachment of the visceral organs: *D. alveata*, *D. subalveata*, *D. lepta*, *Lingula munsterii*, *L. submarginata* and *L. lineata*.

Of these, *D. alveata* (Hall, 1863) is the type species, briefly redescribed by Hoare & Steller (1969). *D. subalveata* was named by Kayser (1897). *Dignomia lepta* (Clarke, 1912) according to Castellaro (1966) is a junior synonym of *Dignomia subalveata*. All these species have broad valves. The length of the shell ranges from 20 to 38.1 mm (mean 28.8 ± 6.4 mm; $n = 5$) and the width from 15 to 23.4 mm (mean 19.6 ± 4.2 mm; $n = 3$). The W/L ratio lies between 0.72 and 0.81 ($n = 2$). All these authors focused on the distinctive characteristics of *Dignomia* among the inarticulated brachiopods

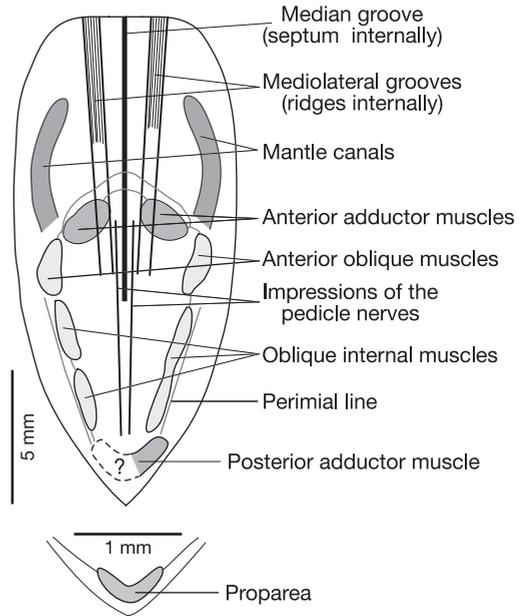


FIG. 5. — Arrangement of the musculature and disposition of the two main anterior mantle canals on the ventral face of *Dignomia munsterii*; the pair of V-shaped narrow grooves extending posteriorly from the anterior adductor scars correspond to the impression of the pedicle nerves. Umbonal region of the internal side of a ventral valve.

— shape and internal ridges — but none recognized that these same features were the bases for the establishment of a genus.

Two other species, from South America, classically identified (see Suárez-Soruco 1976) as *Lingula munsterii* d'Orbigny, 1842, and *L. lineata* Steinman & Hoek, 1912, are similar in appearance to our specimens (previously named *Dignomia boliviana* in Gagnier *et al.* 1996). *Lingula marginata* d'Orbigny, 1842 (= *L. submarginata* d'Orbigny, 1850), was omitted in the listings of previous authors. From plate 8 (figs 1, 6-8) of Steinman & Hoek (1912) there is no doubt that the first two species of *Lingula* share the three characteristic grooves of *Dignomia*: on the original figures the W/L ratio ranges between 0.40 and 0.45. On figure 4, plate 2 of Branisa (1965), *Lingula munsterii* has a ratio of about 0.45-0.47; but the specimens referred to *L. lineata* seem to be different from *Dignomia*. Branisa (1965) collected the specimens in Cuchupunata (Upper

Ordovician) (Fig. 1). Toro *et al.* (1994) cited *Lingula* sp. cf. *munsterii* with a W/L ratio of 0.45 in the basal part of the Anzaldo Formation in Llaviní (Cochabamba region) (Fig. 1). *Lingula munsterii* was reported by Gagnier *et al.* (1986) in the fauna of the Anzaldo Formation (Upper Ordovician) at Sacabamba (Fig. 1). This fauna is characteristic of a marine, probably near shore littoral, well oxygenated environment. Lingulides occur also in shell concentrations in nearshore littoral sandstones with *Cruziana* and *Skolithos* (Anzaldo Formation) from the latest Darriwilian-early Upper Ordovician (Steinmann & Hoek 1912; Gagnier 1987; Gagnier *et al.* 1996; Aceñolaza *et al.* 2003).

The species of *Dignomia* described in these occurrences cannot be identified by taxonomic character because the specimens were described inadequately: the only differences available are in the outlines of the shell (Figs 3; 4A): subelliptical with curved sides in *D. alveata*, *D. subalveata* and *D. lepta* (see Hall 1863, 1871; Hoare & Steller 1969) and linguliform in *L. munsterii* (see d'Orbigny 1842; Branisa 1965; Toro *et al.* 1994), *L. submarginata* (see d'Orbigny 1842, 1850) and *D. lineata* (see Steinmann & Hoek 1912). In the present study the collected specimens are classed as *Dignomia munsterii* although it is obvious that further investigation is needed.

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REFERENCES

- ACEÑOLAZA G. F., EMIG C. C. & GUTIÉRREZ-MARCO J. C. 2003. — Lingulid shell beds from the Ordovician of Argentina, with notes on other peri-Gondwanan occurrences. *Serie de Correlación Geológica* 17: 237-244.
- BALINSKI A. 1995. — Brachiopods and conodont biostratigraphy of the Famennian from the Debnik Anticline, Southern Poland. *Palaeontologia Polonica* 54: 3-88.
- BIERNAT G. & EMIG C. C. 1993. — Anatomical distinction of Mesozoic lingulide brachiopods. *Acta Paleontologica Polonica* 38 (1/2): 1-20.
- BRANISA L. 1965. — Los fósiles guías de Bolivia. I. Paleozoico. *Boletín del Servicio Geológico de Bolivia*, La Paz 6: 1-282.
- CASTELLARO H. A. 1966. — Brachiopoda, in *Guía paleontológica Argentina*. Part. I: Paleozoico, Sección 4. Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires: 86-87.
- CLELAND H. F. 1903. — A study of the fauna of the Hamilton Formation of the Cayuga lake section in Central New York. *U.S. Geological Survey Bulletin* 206: 1-112, 4 pls.
- DEREIMS A. 1906. — *Excursiones científicas 1901-1904*. Anexos y Memorias de Gobierno y Fomento, La Paz, 81 p.
- D'ORBIGNY A. 1842. — *Voyage dans l'Amérique Méridionale*. Part IV, *Paléontologie*. Paris, Pitois-Levrault.
- D'ORBIGNY A. 1850. — *Prodrome de paléontologie stratigraphique universelle des animaux mollusques & rayonnés: faisant suite au cours élémentaire de paléontologie et de géologie stratigraphiques*. Vol. 1: 14, n° 225. Masson, Paris, 394 p.
- EGOROV A. N. & POPOV L. E. 1990. — [A new genus of lingulid from the Early Permian layers of the Siberian platform]. *Paleontologicheskii Zhurnal* 1990 (4): 111-115 (in Russian).
- EMIG C. C. 1982. — Taxonomie du genre *Lingula* (Brachiopodes, Inarticulés). *Bulletin du Muséum national d'Histoire naturelle de Paris* sér. 4, sect. A, 4 (3/4): 337-367.
- EMIG C. C. 1983. — Comportement expérimental de *Lingula anatina* (Brachiopode, Inarticulé) dans divers substrats meubles (Baie de Mutsu, Japon). *Marine Biology* 75: 207-213.
- EMIG C. C. 1986. — Conditions de fossilisation du genre *Lingula* (Brachiopoda) et implications paléocologiques. *Palaeogeography Palaeoclimatology Palaeoecology* 53: 245-253.
- EMIG C. C. 1990. — Examples of post-mortality alteration in Recent brachiopod shells and (paleo)ecological consequences. *Marine Biology* 104: 233-238.
- EMIG C. C. 1997. — Ecology of the inarticulated brachiopods, in KAESLER R. L. (ed.), *Treatise on Invertebrate Paleontology*, Part H: *Brachiopoda Revised*. Geological Society of America, Boulder; University of Kansas Press, Lawrence, vol. 1: 473-495.
- EMIG C. C. 2002. — Tools for linguloid taxonomy: the genus *Obolus* (Brachiopoda) as an example. *Carnets de Géologie/Notebooks on Geology* Article 2002/01

- (CG2002_A01_CCE): 1-9, 3 figs, 2 tabl.
- EMIG C. C. 2003. — Proof that *Lingula* (Brachiopoda) is not a living-fossil, and emended diagnoses of the family Lingulidae. *Carnets de Géologie/Notebooks on Geology* Letter 2003/01 (CG2003_L01_CCE): 1-8, 7 figs, 1 tabl.
- EMIG C. C. & BITNER M. A. 2005a. — *Glottidia* (Brachiopoda: Lingulidae) from the Eocene La Meseta Formation, Seymour Island, Antarctica. *Palaentology* 48 (2): 423-431.
- EMIG C. C. & BITNER M. A. 2005b. — The brachiopod *Lingula* in the Middle Miocene of the Central Paratethys. *Acta Palaentologica Polonica* 50 (1): 181-184.
- GAGNIER P.-Y. 1987. — *Sacabambaspsis janvieri*, un heteróstraco del Ordovícico superior de Bolivia. *IV Congreso Latinoamericano de Paleontología (Santa Cruz de la Sierra, Bolivia, 1987), Memorias* 2: 665-677.
- GAGNIER P.-Y., BLIECK A. R. M. & RODRIGO G. 1986. — First Ordovician vertebrate from South America. *Geobios* 19: 629-634.
- GAGNIER P.-Y., BLIECK A., EMIG C. C., SEMPÈRE T., VACHARD D. & VANGUESTAINE M. 1996. — New paleontological and geological data on the Ordovician and Silurian of Bolivia. *Journal of South America Earth Sciences* 9 (5/6): 329-347.
- HALL J. 1863. — Description of a new species of Brachiopoda, from the Upper Helderberg, Hamilton, and Chemung groups. *Annual Report of the New York State Cabinet of Natural History* 16: 19-37.
- HALL J. 1871. — Notes on some new or imperfectly known forms among the Brachiopoda, etc. *Annual Report of the New York State Cabinet of Natural History* 23: 244-247, pl. 13.
- HOARE R. D. & STELLER D. L. 1969. — Inarticulate brachiopods of the Silica Formation (Devonian), Ohio and Michigan. *Contributions of the Museum of Paleontology, University of Michigan* 22 (20): 263-272.
- HOLMER L. E. & POPOV L. E. 2000. — Lingulida, in KAESLER R. L. (ed.), *Treatise on Invertebrate Paleontology*, Part H: *Brachiopoda Revised*. Geological Society of America, Boulder; University of Kansas Press, Lawrence, vol. 2: 32-95.
- KAYSER E. 1897. — Beiträge zur Kenntniss einiger paläozoischer Faunen Süd-Amerikas. *Zeitschrift der deutscher Geologische Gesellschaft* 1897: 274-317, 12 pls.
- MARTÍNEZ C., SÚAREZ R. & SUBIETA T. 1971. — La Cadena Hercínica en la parte septentrional de la Cordillera Oriental de los Andes Bolivianos. *Boletín del Servicio Geológico de Bolivia*, La Paz 15: 26-35.
- PEREIRA J. L. & BALLON R. A. (compil.) 1978. — *Mapa geológico de Bolivia 1:1 000 000*. Yacimientos petrolíferos fiscales bolivianos; Servicio geológico de Bolivia, La Paz, 1 map + 27 p.
- RITCHIE A. & GILBERT-TOMLINSON J. 1977. — First Ordovician vertebrates from the Southern Hemisphere. *Alcheringa* 1: 351-368.
- RODRIGO DE WALKER G. & TORO M. 1987. — Inofaciés de la Formación Anzaldo (Ordovícico) en las regiones de Santivanez, Cuchupunata, y Sacabamba, Departamento de Cochabamba. *Acta del IV Congreso Latinoamericano de Paleontología (Bolivia)* 2: 647-664.
- ROWELL A. J. 1965. — Inarticulata, in MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part H: *Brachiopoda*. Geological Society of America, Boulder; University of Kansas Press, Lawrence, vol. 1: 260-296.
- STEINMANN G. & HOEK H. 1912. — Das Silur und Kambrium des Hochlandes von Bolivia und ihre Fauna. *Neues Jahrbuch für Geologie, Mineralogie und Paläontologie* 34: 176-252.
- SÚAREZ-SORUCO R. 1976. — El sistema Ordovícico en Bolivia. *Revista técnica de Yacimientos Petrolíferos Fiscales Bolivianos* 5 (2): 111-223.
- TORO M., BIRHUET R. & OSINAGA D. 1994. — La fauna de la sección basal de la Formación Anzaldo-Llanvirniano en la región de Llavini, Departamento de Cochabamba. *Memorias del XI Congreso Geológico de Bolivia, Santa Cruz de la Sierra*: 293-298.

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