Notes on the early devonian brachiopod Leptaena uralensis de Verneuil, 1845

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Abstract
On the basis of the type material, an attempt is made to review the widely reported brachiopod Leptaena uralensis de Verneuil, 1845, much more commonly known as Megastrophia uralensis (de Verneuil, 1845). Assignment of this species to Megastrophia is still tentative, and many reports of the species, especially those based on crack-out material, must remain doubtful. The species has an established narrow geographic and stratigraphic range to the upper Emsian (upper Lower Devonian) of mostly Siberia, Mongolia and China.

Keywords
Megastrophia uralensis, uralensis, brachiopod, stropheodontid, biogeography, Emsian, Devonian, Siberia, China, GeoQuest

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THE ORIGINAL type material of *Leptaena ouralensis* de Verneuil, 1845 (p. 220, pl. XIV, fig. 1a-b-c-d) was collected from Isvioska, near Nizhnij Turinsk, on the east side of the Ural Mountains of Russia by the expedition of Roderick Impey Murchison, Édouard de Verneuil and Le Comte Alexandre Keyserling in 1841 (see Collie & Diemer 2004).

De Verneuil (1845) stated that the first fragmental material of the species was collected on the banks of the Serebrianka River, a tributary of the Tchusovaya River, and more material was collected on the Isvioska River.

During a brief visit to the palaeontological museum of the Université Claude Bernard Lyon 1 in Villeurbanne, France, in September 2011, I found four de Verneuil specimens (2052, 2070 and 2077; on the board with this last number were two ventral valves) in addition to the four I had previously borrowed and photographed (2066, 2067, 2068, 2069). These four digit numbers are those cited in the priceless original de Verneuil fossil catalogue held by the museum; these eight rock specimens have now been renumbered and catalogued.

*Megastrophia* Caster, 1939

Remarks. This stropheodontid genus was discussed by Williams (1953) who recognised the nominotypical subgenus and *Megastrophia (Protomegastrophia)* Caster, 1939. Harper & Boucot (1978a, b) also discussed the genus, erecting the new subgenus *M. (Megastrophiella)* and recognising *Protomegastrophia* as a subgenus of *Brachyprion*. As the latter authors differentiated the genera on the basis of features of the cardinal process lobes, the present type material does not permit confident subgeneric assignment.

*Megastrophia* (*Megastrophia?) uralensis (de Verneuil, 1845) (Figs 1-2)

1845 *Leptaena ouralensis* de Verneuil, p. 220-222, pl. 14, figs 1a-d.
1887 *Strophomena uralensis* Verneuil; Chernyshev, p. 108.
1930 *Stropheodonta uralense* Verneuil; Nalivkin, p. 69, pl. 1, figs 1a-c, 12a-c, 15a-b.
1947 *Stropheodonta uralensis* Verneuil, 1845; Nalivkin, pl. 14, figs 3-4.
1955 *Stropheodonta uralensis* (Verneuil); Rzhonsnitskaya, p. 244, pl. 54, fig. 3a-b.
1961 *Megastrophia uralensis* (Verneuil, 1845); Kul’kov in Gratsianova et al., p. 437, table D-67, fig. 3.

SYSTEMATICS

All this de Verneuil type material is held in the palaeontology museum at the Université Claude Bernard Lyon 1 at Villeurbanne, France; the prefix EM pertains to this collection.
Figure 1. Type material of *Megastrophia uralensis* (de Verneuil, 1845). A, view of two specimens EM 25053A-B, x1.5. B-C, lectotype dorsal valve EM 25053A in dorsal and posterior views respectively, showing thin median ridge, small subcircular muscle field, a linear arrangement of nodes anteriorly and parvicostellate sculpture, x 1.5. D, exterior of ventral valve 25053 B showing nervostrophid sculpture, x 2.25. E, EM 25050, shell broken largely along concave external surface of dorsal valve, but showing interarea of ventral valve, x 1.4. F, EM 25052, shell broken largely along convex internal surface of dorsal valve showing median ridge and interarea of ventral valve, x 1.8. G, lateral view of deformed ventral valve EM 25051, x 0.9.
1962 *Megastrophia uralensis* (Verneuil); Tyazheva, p. 41, pl. 9, fig. 6-7.

1962 *Megastrophia uralensis sibirica* subsp. nov.; Krilova, p. 47, pl. 2, fig. 8, pl. 3, figs 4-5.

1974 *Megastrophia uralensis* (Verneuil); Wang et al., pl. 11, figs 13-25.

1975 *Megastrophia uralensis* (Verneuil, 1845); Gratsianova, p. 26-27, pl. 4, figs 1-8.

1977 *Megastrophia uralensis* (Verneuil, 1845); Gratsianova & Schischkina, pl. 21, figs 1-5; pl. 22, figs 104; pl. 23, figs 1-7.

1977 *Leptaena uralensis*; Nalivkin, p. 266.

1977 *Megastrophia semispheroides* Hou & Xian; Yang et al., p. 316.

1978 *Megastrophia uralensis* (Verneuil); Gratsianova, p. 53, fig. 15; pl. 54, figs 9-10; pl. 56, fig. 16; pl. 57, fig. 1.

1979 *Megastrophia uralensis* (Verneuil, 1845); Wang & Zhu, p. 18, pl. 1, figs 18-20; pl. 20, figs 13-17; pl. 34, fig. 5.

1981 *Megastrophia uralensis* (Verneui); Sapelnikov & Mizens, p. 13, pl. 2, fig. 12.

1981 *Megastrophia uralensis* (Verneui); Sapelnikov et al., pp. 8, 37.

1991 *Megastrophia uralensis* (Verneuil, 1845); Menakova in Dshalilov, p. 182, pl. 92, fig. 1.

1996 *Megastrophia uralensis* (Verneuil); Alekseeva et al., p. 31, pl. 1, figs 5-7.

2001 *Megastrophia uralensis* (de Verneuil); Talent et al., p. 38, 40, 55-56, 71, 77, 110, 143.

2003 *Megastrophia uralensis* (Verneuil, 1845); Afanasjeva et al., p. 91, pl. 33, figs 1-2.

2007 *Megastrophia uralensis* (Verneuil, 1845); Kim et al., p. 255, pl. 85, figs 28-32.

2011 *Megastrophia uralensis* (Verneuil, 1845); Kim, pl. 3, figs 28-29.

2012 *Megastrophia uralensis*; Talent et al., fig. 2, p. 824.

**Type material.** EM 25053A (de Verneuil number 2069) is here selected as lectotype from the type series of de Verneuil; it is a dorsal valve (Fig. 1A-C) broken largely along the external surface, but retaining some vestiges of internal structures. The rock bearing this specimen also bears a ventral valve, now numbered EM 25053B.

The type series has been renumbered as follows: 2052 = EM 25056; 2066 = EM 25050A, 2067 = EM 25052; 2068 = EM 25051; 2069 = EM 25053A-B (one dorsal valve and one ventral valve, not of the same shell); 2070 = EM 25050B; 2077A = EM 25054; 2077B = EM 25055.

Specimens illustrated by de Verneuil appear to be: EM 25056 (his fig. 1a-b, a large ventral valve with some remaining pieces of the dorsal valve of the same shell), perhaps with additions from EM 25055; EM 25050A (his fig. 1c; 2066, counterpart of 2070; this specimen bears inked lines accentuating radial sculpture); and EM 25054 (his fig. 1d). The illustrations of de Verneuil appear to be diagrammatic, so confident identification of actual specimens from his illustrations (no catalogue numbers being cited in the caption) is not possible. It seems possible that figures incorporate features from more than one specimen; further, some damage or preparation over the years may have substantially altered the appearance of specimens.

The four specimens photographed by me are: the lectotype dorsal valve EM 25053A, but also showing the ventral valve interarea; EM 25051 (a large, deformed ventral valve); EM 25053B (a ventral valve broken along the external surface and showing well preserved sculpture with nervate tendencies). EM 25052, the fourth specimen (not illustrated by de Verneuil), is a dorsal valve broken so as to show some external sculpture and a slender median ridge internally. Specimens photographed by Dr Abel Priere are EM 25054 (ventral valve), EM 25055 (ventral valve) and EM 25056 (large ventral valve).

**Description.** Strongly concavo-convex, thin, rather alate shells up to about 75 mm wide and 40 mm long. Sculpture on both valves parvicostellate with 4-6 fine costellae between the major ribs, which tend to be discontinuous on one specimen (i.e. the nervate condition shown by EM 25053B, see Fig. 1D). Apsacline ventral interarea several mm high, weakly curved, and strongly denticulate and striated; pseudodeltidium apparently simple. No information on ventral valve interior. Dorsal valve with a slender median ridge which extends to about 70% of valve length and a small subcircular adductor field with low rounded bounding ridges located well posterior of midlength. An irregular oblique row of nodes, flanking the median ridge, arises posterior of midlength and extends to at least 70% of dorsal valve length. Cardinal process lobes not seen, but apparently small (cf. Gratsianova 1978, pl. 56, fig. 16). Marginally, dorsal valve has low, linear, rounded ribs internally, as illustrated by Alekseeva et al. (1996, pl. 1, fig. 5). Pseudopunctae abundant.

**Selection of lectotype.** In response to my questions about this species, the late Dr Rimma Gratsianova sent me in 1981 *inter alia* copies of two plates and some text that appeared to be from a publication by Breivel & Breivel (1978) sent to her by the authors. In this text, Breivel & Breivel selected a neotype for *M. uralensis*; this was presumably deemed necessary as Nalivkin (1977) had reported that he was unable to identify the original type material (see below for translation of parts of the Nalivkin paper). However, Dr Larissa Mizens (personal communication, June 2010) has informed me that the 1978 publication never appeared. A lectotype is selected here (see above) from the de Verneuil type series, even though the specimen is less than ideally preserved and shows little distinctive morphology.

Nalivkin (1977, p. 263) commented on the original (figured?) de Verneuil material as follows: “Unfortunately, a part of Verneuil's materials [have been] sometimes taken out of cabinets, some examples appear to be lost, although there is a hope of finding them in other parts of the same store or even in other museums. The originals on the plates were not selected by Verneuil” [and] “Leptaena uralensis. Many (examples), typical, but I could not detect originals. Locality ’Izviostka’.” (kindly translated by Dr Larissa Mizens, Yekaterinburg).

**Species name.** The original spelling of the species name (*ouralensis*) has, as far as I am aware, been used only by the original author. The specific name *uralensis* has been used exclusively ever since and is retained here. The original spelling could be retained here in accordance with ICZN Article 32. However, according to ICZN Article 33.2.3.1, the subsequent usage is treated as a justified emendation and the specific name *uralensis* is accepted here by me.

**Generic assignment.** Assignment of *uralensis* to *Megastrophia* or (more recently) *Megastrophia* (*Megastrophia*) has been accepted without question for at least 50 years, being first suggested by Gratsianova et al. (1961). *Megastrophia* was
extensively discussed by Harper & Boucot (1978b) and it seems possible that uralensis belongs to the nominotypical subgenus in being large and (see below) in having cardinal process lobes joined basally. As no critical internal details are preserved (although preparation of some type material of uralensis might expose these) this must await resolution by further study. The slight nervate tendency in sculpture does not really resemble any of the nervostrophiids illustrated by Harper & Boucot (1978a) and much more information is needed on this aspect of the morphology of uralensis.

Remarks. It is clear that de Verneuil (1845, p. 222) erred in identifying the specimens illustrated in his plate 14, figs 1a-b and d as dorsal valves, and his plate 14, fig. 1c as a ventral valve. His fig. 1c clearly shows the ventral interarea with delthyrium, but most of the specimen shows the (concave) exterior of the dorsal valve. His fig. 1d clearly shows the parvicostellate sculpture; he remarked on the fine costellae between the major ribs.

If the material illustrated by Gratsianova (1975), Gratsianova & Shischkina (1977 and Alekseeva et al. (1996) all belongs to uralensis, further characters of uralensis include a short, flabellate ventral muscle field with a prominent median ridge and the distinctive structure of the cardinal process lobes (see below). Material illustrated by Alekseeva et al. (1996, pl. 33, fig. 5) from the NE part of the USSR includes a ventral valve with internal ribbing similar to that of the uralensis types, but confident comparison of the type uralensis with the illustrated dorsal valve (Alekseeva et al. 1996, fig. 6) with a subcircular muscle field is inconclusive due to the poor preservation of the lectotype of uralensis; their illustrated specimen does, however, show cardinal process lobes joined basally, suggesting assignment to M. (Megastrophia).

Discussion. It is appropriate to place here a cautionary note about the above synonymy. Much crack-out material assigned to this species for more than 130 years (excluding the original description) is probably indeterminate to both species and genus, showing neither external sculpture nor internal features. The status of the Russian subspecies M. uralensis siberica and the Chinese species M. semispheroidea.
are yet to be determined.

Notwithstanding the very limited information that can be gleaned from the type material, there is a lot of other material that has been identified as *Megastrophia uralensis*. Notable exceptions to this largely indeterminate crack-out material are the internals illustrated by Alekseeva et al. (1996, pl. 1, figs 5-7) and Gratsianova (1975, pl. 4, figs 1, 3-5: ventral valves only). Gratsianova & Schischkina (1977, pls 21-22) illustrated “M. (M.) uralensis (Vern.)” material with good parvicostellate sculpture and ventral internal moulds, and Gratsianova & Schischkina (1977, pl. 34) illustrated *M. (M.) bobilevi* Schischkina sp. nov. with internal moulds of both valves.

**Palaeogeographic distribution.** The invaluable compilation of Devonian brachiopod distribution by Talent et al. (2001) and followed up by Talent et al. (2012) has greatly clarified the geographic distribution of reports of *M. uralensis*; relevant references for the following comments are given by Talent et al. (2001). They reported the species from numerous regions, almost entirely from the late Emsian of Siberia, Mongolia and China, as follows:

1. Laurussia: Biya Gorizont and the Afonin Gorizont, west of the Urals;
2. Kazakhstania: East of the Urals, Karpinsk Gorizont and Tal’tiy Gorizont;
3. Siberia: Salair, Shanda Gorizont; Gorny Altai, Kuwash Beds;
4. South China;
5. Karakorum; and

According to Alekseeva (1992), the maximum palaeolatitude for the above continental plates was less than 45° N. Pedder & Oliver (1990, p. 267) concluded, with reference to the reconstruction of Scotese (2001) that “it is questionable that the original latitude of any large northern hemisphere Devonian coral fauna would have exceeded 45°”. Further comments on Devonian biogeography, based on fish, were made by Young (1990).

There are many important reports and illustrations of megastrophiid brachiopods from China. Hou (1981) recognised the *Zdimir* community with *Megastrophia uralensis* in what he considered Middle Devonian strata in his South China Province, but it is clear that such megastrophiid forms occur in Mongolia and, indeed across western Siberia, even occurring on the west side of the Urals (Chernyshev 1885). Hou & Wang (1996) considered that the Inner Mongolian Devonian fauna was close to that of North China but made no mention of *Megastrophia*. Limited material from South China was assigned to *uralensis* by Wang et al. (1974, pl. 9, fig. 12-15) and Wang & Zhu (1979, pl. 1, figs 18-20; pl. 20, figs 13-17; pl. 34, fig. 5); this material does not differ greatly in quality from much other inconclusive material. *Cymostrophia semisphaeroidea* Hou & Xian, 1975 has been assigned to *Megastrophia* (Yang et al. 1977, Wang & Rong 1986), and this parvicostellate species appears close to *uralensis*. Wang et al. (1987, p. 36, table 10) referred to “*Megastrophia*” in their *Hunanchonetes – Xenostrophia Community*; from the caption to their plate this refers to “*Megastrophia sphaeroidea* (Hou and Xian)”, apparently for *Cymostrophia semispaheroidea* Hou & Xian, 1975. Su (1976, 1980) described several species of *Megastrophia* from Inner Mongolia and NE China, including *Megastrophia manchurica* Hamada, 1971; all are strongly ribbed rather than parvicostellate, and assignment to *Megastrophia* seems questionable. Talent et al. (1987, pp. 230-231) reported *Megastrophia pseudointerstrialis* (Hou) from Nei Mongol. Harper & Boucot (1978b) referred *manchurica* to *?Strophodonta*. Xian (1988) described *M. ertaizensis* from the Longmenshan Mountains. Mendbajar (1994) described the new species *M. zhogtensis* from the Lower Devonian (Emsian) of eastern Mongolia (for details see Afanasjeva et al. 2003, p. 91-92). One interesting report is “*Megastrophia* ex. gr. *concava* (Hall)” from Vietnam (Nguyen et al. 1980, p. 108, pl. 41, figs 1, 3, 5), based on a ventral internal mould with a good muscle field; elsewhere in the same volume (p. 277), “*Megastrophia* (sic.) ex. gr. *dubrovensis* Rzhon.” is reported from the Miala Suite, to which a late Early to early Middle Devonian age is assigned.

Reports of *Megastrophia* from Australia are yet to be fully documented but the genus, along with the brachiopod *Zdimir* and a *serotinus* conodont fauna, has been reported from Mount Podge, Queensland (Talent & Yolkin 1987, Talent & Mawson 1994) and Mount Frome, New South Wales (Wright in Percival et al. 2010).

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