***Devonohelicoceras hidaense*, a new torticonic oncocerid (Cephalopoda)
from the Lower Devonian of Central Japan**

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Abstract: Based on the four specimens from the Lower Devonian (Emsian?) D4 Member of the Fukuji Formation, and a specimen from an unknown locality, a new genus and species of the oncocerid cephalopod, *Devonohelicoceras hidaense*, is described as the second known oncocerid from Japan. The present genus is most similar to the Late Silurian genus *Foersteoceras*, but differs in its weakly depressed whorl section, submarginal siphuncle with positional shifting, and well-developed actinosiphonate deposits. It is likely that the actinosiphonate deposits functioned as a substratum of adhesive liquid which has a lower specific gravity than the sea water.

Key words: Actinosiphonate deposits; *Devonohelicoceras* gen. nov.; *D. hidaense* sp. nov.; Fukuji Formation; Lower Devonian; Oncocerida.

Introduction. With the exception of the most primitive and specialized forms, oncocerid cephalopods are characterized by possessing actinosiphonate deposits which consist of the endosiphuncular longitudinal lamellae in a radial arrangement. This bizarre structure was first recognized in the mid-19th century by Barrande (1855),¹⁾ and was further studied regarding its taxonomic implications,²⁾⁻⁵⁾ function,^{6),7)} ontogenetic development,⁸⁾ and ultrastructure.⁹⁾ The authors had an opportunity of detecting the five oncocerid specimens, whose well-preserved siphuncles provide new insights into the actinosiphonate deposits. Based on this material, the new taxon *Devonohelicoceras hidaense* gen. et sp. nov. is described herein as the second record of this order in Japan, succeeding to the first one by Niko and Nishida (2002).¹⁰⁾ Except for a paratype, HMM 04300, whose label lacks proper locality information, the specimens were collected from the fallen blocks in talus on the northern flank (locality FH-6, latitude 36°12'55" N and longitude 137°31'20" E) of the Kanashirozako Valley in the Fukuji area, Gifu Prefecture, Central Japan. The lithofacies surrounding all the examined specimens, including HMM 04300, is black argillaceous limestone of bioclastic wackestone, which indicates a

shallow-marine environment. It is, thus, suggested that *Devonohelicoceras hidaense* was derived from the Lower Devonian (Emsian?) D4 Member¹¹⁾ (= the Upper shaly and Upper carbonate members in Kuwano, 1987¹²⁾) of the Fukuji Formation.

Institutional abbreviations used for repository numbers are: HMM, Hikaru Memorial Museum, Takayama; NSM, National Science Museum, Tokyo; UMUT, University Museum of the University of Tokyo.

Systematic paleontology

Order Oncocerida Flower in Flower and Kummel,
1950¹³⁾

?Family Naedyceratidae Shimanskiy and Zhuravleva in
Shimanskiy, 1956¹⁴⁾

Genus *Devonohelicoceras* gen. nov.

Type species. *Devonohelicoceras hidaense* sp.
nov., by monotypy.

Diagnosis. High-spined (approximately 40° in apical angle) torticones composed of loosely coiled whorls with weakly depressed oval section; siphuncular position submarginal, shifts from near apical internal whorl seam to near middle of external exposed side of whorls with shell growth; septal necks loxochonitic to suborthochoanitic; connecting rings undifferentiated, relatively thin for the order; endosiphuncular deposits well developed, mainly differentiated into lining and multi-layered actinosiphonate deposits.

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Fig. 1. *Devonohelicoceras hidaense* gen. et sp. nov. **1, 2.** Paratype, HMM 04342; **1**, axial (slightly oblique in basal shell) polished section of shell, $\times 1$; **2**, partial enlargement of Fig. 1.1 to show cross sections of whorls and apical siphuncular positions, $\times 3$. **3-7.** Holotype, HMM 04332; **3**, longitudinal (= perpendicular section to axis of shell) polished section of whorl, $\times 2$; **4**, partial enlargement of Fig. 1.3 to show siphuncular structure, $\times 5$; **5**, cross (= axial section of shell) thin section of siphuncle, apical side up, torticone axis side right, $\times 10$; **6**, partial enlargement of Fig. 1.5 to show shape of actinosiphonate deposits, $\times 50$; **7**, cross polished section of adoral whorls, arrow indicates siphuncle, torticone axis side on right, $\times 2$. **8, 9.** Paratype, UMUT PM 28069, longitudinal thin sections of whorl; **8**, details of septal neck on shell wall side (slightly oblique), $\times 25$. **9**, details of septal neck on anti-shell wall side, $\times 25$. Abbreviations: AES = apical external whorl seam; AIS = apical internal whorl seam; BES = basal external whorl seam; BIS = basal internal whorl seam.

Fig. 2. *Devonohelicoceras hidaense* gen. et sp. nov. **1**. Holotype, HMM 04332, partial enlargement of Fig. 1.5 to show details of siphuncular structure, $\times 100$. **2-4**. Paratype, HMM 04300; **2**, axial polished section of shell, $\times 1$; **3**, shell surface and internal mold, $\times 2$; **4**, partial enlargement of Fig. 2.2 to show cross sections of whorls, arrow indicates siphuncle, $\times 2$. Abbreviations: CR = connecting ring; LD: lining deposits; CP: central plate; CC: central core; AL: amorphous layer; AM: arenaceous material.

Discussion. The assignment to the family Naedyceratidae is tentative. *Devonohelicoceras* gen. nov. is superficially similar in its gross morphology to *Foersteoceras* (Ruedemann, 1925),¹⁵⁾ which has been assigned by Zhuravleva (1962)¹⁶⁾ to the Naedyceratidae, by Sweet (1964)⁵⁾ to the Brevioceratidae, and by Dzik (1984)¹⁷⁾ to the Westonoceratidae. Although the present knowledge about the siphuncular structure of *Foersteoceras* is insufficient for the systematic assignment, this new genus is referable to the first family rather than to the latter two, because it has a torticonic shell, undifferentiated connecting rings, and actinosiphonate deposits.

Etymology. The generic name is a combination of the Devonian, in which the type specimens of this genus occurs, and the Greek *ἐλικτός*, which means spiral, in reference to the shell shape.

Devonohelicoceras hidaense sp. nov.

Figs. 1, 2

Diagnosis. Same as for the genus.

Description. Dextral, high-spined torticones, with apical angle of about 40° and deep umbilicus, composed of loosely coiled 5+ whorls; the largest whorl diameter of the holotype at least 89 mm (imperfect); whorl section weakly depressed approximately along the torticone axis, oval with rounded internal and external exposed sides, weakly concave apical contact zone as contact groove, and weakly convex basal (shell bottom side) contact zone; dimensions of whorl section in the holotype are 27.6+ mm in width and 22.4 mm in height near the last septum; width/height ratios of whorl in phragmocone range from 1.2 to 1.4; positions of whorl seams on both internal and external shell surfaces are deeply concave.

Shell surface smooth, without distinct ornamentation. Body chamber at least 25 mm (imperfect) in length; mature constriction of shell not recognized in preserved parts of the examined specimens; aperture not preserved. Sutures transverse, without clearly defined sutural elements. Camerae empty, short, with the maximum width/length ratios 9–14; septal curvature relatively deep for the family. Siphuncle submarginal, situated near the apical internal whorl seam in relatively early growth stages (Fig. 1.2), then its position shifts toward the middle of the external exposed side in the most adoral phragmocone (Fig. 1.7) nearly through the apical external whorl seam (Fig. 2.4); profile of siphuncle is depressed, with 4.8 mm in width and 4.1 mm in height at the whorl width of approximately 23 mm, and 6.4 mm in width nearly at the last septum in the holotype; septal necks retrochoanitic, shift from loxochanitic nearly on the side of shell wall (Fig. 1.8) to suborthochoanitic on the anti-shell wall side (Fig. 1.9), long, attaining 0.96 mm in the well-preserved suborthochoanitic septal neck at approximately 16 mm in whorl height of the paratype (UMUT PM 28069); connecting rings weakly inflated with approximately 2.4 in the form ratio (maximum width/length), undifferentiated, and relatively thin (about 0.06 mm) for the oncocerids. Endosiphuncular deposits well developed, differentiated mainly into lining deposits and actinosiphonate deposits, latter of which form radially arranged longitudinal lamellae with columnar to clavate cross sections (Figs. 1.6, 2.1); lining deposits thickened on the connecting rings, and may be differentiated in two (outer and inner) layers; thickness of lining deposits ranges from 0.10 to 0.17 mm; number of longitudinal lamellae is around 25 in each siphuncular segment; length of lamellae in cross section longer on the apical side than on the bottom side of the shell, attaining 1.7 mm; microstructure of the longitudinal lamellae is differentiated into central core and overlapping dark, amorphous layer which also partly covers the lining deposits and frequently contains foreign particles (probably arenaceous material); lining deposits and central core are continuous; microgranular intercalations with triangular profiles are usually recognized in the lining deposits at the base of longitudinal lamellae; each microgranular intercalation is divided by central plate.

Discussion. In the Oncocerida, the characteristic shell shape of high-spined torticones is the exceptional morphology of *Foersteoceras* (the solely known type species, *Trochoceras turbinata* [sic] Hall, 1852, pl. 77, fig. 1¹⁸⁾) from the Upper Silurian of Laurentia and the present *Devonohelicoceras hidaense* from Fukuji.

Despite the small number of available specimens (Ruedemann, 1925, text-fig. 40, pl. 19, fig. 1, pl. 20, figs. 1, 2, pl. 21, figs. 1, 2¹⁵⁾), we think that the following diagnoses of this Fukuji species are sufficient to establish the new genus *Devonohelicoceras*: (1) the weakly depressed whorl sections across the torticone axis at successive positions, *versus* laterally compressed ones in *Foersteoceras*, (2) the position of the submarginal siphuncle, shifting from near the apical internal whorl seam to near the middle of the external exposed side of the whorls, *versus* the marginal position near the basal external whorl seam in *Foersteoceras*, whose siphuncular position is clearly shown on the weathered external whorl surface of the holotype as indicated by Ruedemann (1925, pl. 19, fig. 1, pl. 20, fig. 1¹⁵⁾), and (3) the well-developed actinosiphonate deposits, *versus* the vestigial or rudimentary deposits in *Foersteoceras*.

Dextral torticonic forms are also recognized in some Middle Palaeozoic oncocerids, such as *Guixianoceras* (Lai and Zhang, 1988¹⁹⁾ (type species, *G. subtriangulatum* Lai and Zhang, 1988 (pl. 3, figs. 1a–c¹⁹⁾), *Mitroceras* (Hyatt, 1894²⁰⁾ (type species, *Trochoceras gebhardii* [sic] Hall, 1852 (pl. 77, fig. 2, pl. 77A, figs. 1a–d¹⁸⁾), *Naedyceras* (Hyatt, 1884²¹⁾ (type species, *Trochoceras eugenium* Hall, 1861 (p. 108, 109²²⁾; Hall, 1879, p. 396, 397, pl. 58, figs. 3, 4, pl. 59, figs. 10, 11²³⁾), and *Oxygonioceras* (Foerste, 1925²⁴⁾ (type species, *Trochoceras oxynotum* Barrande, 1865, pl. 14, figs. 1–11²⁵⁾). Besides their low-spined (more than 100° in the apical angle) shells, differences from *Devonohelicoceras hidaense* gen. et sp. nov. are as follows: *Guixianoceras* has the transverse lateral ribs, *Mitroceras* has the subquadrate whorl sections in the adoral phragmocone, *Naedyceras* has a weakly constricted body chamber and the cyrtconic septal necks, and *Oxygonioceras* exhibits an angular to subangular venter and the definite lateral lobes in its sutures.

Etymology. The specific name is derived from Hida, which is a historic provincial name for the type locality.

Material examined. The holotype, HMM 04332, is an imperfect phragmocone with an apical body chamber. The following three paratypes are assigned: HMM 04300, incomplete phragmocone attaining approximately 71 mm in whorl diameter; HMM 04242, incomplete phragmocone attaining approximately 60 mm in whorl diameter; and UMUT PM 16243, fragmentary whorls of phragmocone. In addition, a fragmentary specimen, NSM PM 16243, is also referred to this species.

Function of the actinosiphonate deposits.

Foreign particles in the actinosiphonate deposits are composed of fragments of quartz each of which as a single crystal, calcite, or of an agglutinate grain with two subrounded quartz fragments in an argillaceous matrix, diameters of these particles in thin sections range from 0.04 to 0.27 mm, with a mean of 0.12 mm ($n = 13$). Adherence of foreign particles on an amorphous layer may be followed by additions of new biotic deposits. Thus, they seem to have been trapped in a mucilaginous amorphous layer (Fig. 2.1). In addition, no apparent silicification is recognized in the shell of any *Devonohelicoceras* specimen examined. Shape and mode of occurrence of the particles probably deny the possibility that they are derived from post-mortem alteration and metamorphism. The presence of the arenaceous material indicates the direct entrance of sea water into the siphuncle. This suggests that oncocerids had a more complicated siphuncular cord with a "sac" through the sides of the mantle or the prolonged part of the mantle cavity, compared to living *Nautilus*, whose siphuncular cord is composed of only an outer siphuncular epithelium and an inner blood circulatory region. The large siphuncles of oncocerids, including a siphuncular diameter for *Archiacoceras subventricosus* (Archiac and Verneuil, 1842, pl. 30, fig. 1, 1A²⁶) of up to 21.5 mm, support this presumption.

As summarized by Crick and Teichert (1979),⁹⁾ there were three major hypotheses concerning the function of the actinosiphonate deposits: (1) they increase the surface area of the endosiphuncle to allow more efficient gas removal from the chambers, (2) they serve as a counterweight to reduce buoyancy, and (3) they are gerontic calcifications of the vascular tissues of the siphuncular cord. Based on the present new knowledge derived from the siphuncular structure of *Devonohelicoceras hidaense*, the present authors propose herein the fourth hypothesis, that the actinosiphonate deposits act on a substratum of adhesive liquid, which has a relatively lower specific gravity than the sea water. The main components of this adhesive liquid is inferred to be ammonium chloride, which is a buoyancy regulator in some living squids, such as chiroteuthids and octopoteuthids.²⁷⁾ The refilling rate of cameral liquid in *Nautilus macromphalus* is very slow at only 0.02–0.1 ml/h (Ward and Greenwald, 1981²⁸⁾). It is difficult to expect that the refilling system of oncocerids has a drastically higher degree of efficiency than *Nautilus*. In other words, the rapid subsidence to the sea bottom by expelling this "light" liquid may have been an effective

way to avoid predator attacks for oncocerids which probably had a shallow-marine habitat.

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References

- 1) Barrande, J. (1855) Bull. Soc. Géol. France 2 **12**, 441-489, pls. A-C.
- 2) Hyatt, A. (1900) *In* Text-book of Palaeontology (ed. Zittel, K. A. von). Vol. 1, 1st ed., Macmillan and Co., Limited, London-New York, pp. 502-592.
- 3) Foerste, A. F. (1926) Denison Univ. Bull. J. Sci. Lab. **21**, 285-384, pls. 32-53.
- 4) Flower, R. H. (1943) Bull. Amer. Paleont. **28**, 30-67, pls. 2-5.
- 5) Sweet, W. C. (1964) *In* Treatise on Invertebrate Paleontology (ed. Moore, R. C.). Geological Society of America, Univ. of Kansas Press, New York-Lawrence, pp. K277-K319.
- 6) Strand, T. (1934) Norsk Geol. Tidsskr. **14**, 1-117, pls. 1-13.
- 7) Flower, R. H. (1938) Palaeont. Amer. **2**, 1-84, pls. 1-4.
- 8) Mutvei, H. (1964) Ark. Zool. **16**, 375-424, pls. 1-29.
- 9) Crick, R. E., and Teichert, C. (1979) Paleontology **22**, 747-766.
- 10) Niko, S., and Nishida, T. (2002) Proc. Japan Acad. **79B**, 105-107.
- 11) Niikawa, I. (1980) J. Geol. Soc. Japan **86**, 25-36 (in Japanese with English abstract).
- 12) Kuwano, Y. (1987) Bull. Natn. Sci. Mus. Tokyo C **13**, 77-105.
- 13) Flower, R. H., and Kummel, B. (1950) J. Paleont. **24**, 604-616.
- 14) Shimanskiy, V. N. (1956) Problemy i zadachi paleontologicheskikh issledovaniy. Kohspekt lektsii (Problems and Tasks of Paleontological Research. Summary of Lecture). Akad. Nauk SSSR, Moskva (in Russian).
- 15) Ruedemann, R. (1925) New York State Mus. Bull., no. 265, pp. 1-134.
- 16) Zhuravleva, F. A. (1962) *In* Osnovy Paleontologii (Fundamentals of Paleontology) (ed. Ruzhentsev, V. E.). Izdatel'stvo Akad. Nauk SSSR, Moskva, pp. 101(137)-115(159) (translated from Russian in Jerusalem, 1974).
- 17) Dzik, J. (1984) Palaeont. Polonica, no. 45, pp. 1-219, pls. 1-47.
- 18) Hall, J. (1852) Palaeontology of New-York. Vol. 2. Containing Descriptions of the Organic Remains of the Lower Middle Division of the New-York System (Equivalent in Part to the Middle Silurian Rocks of Europe.). C. Van Benthuyssen, Albany.
- 19) Lai, C., and Zhang, Z. (1988) Prof. Pap. Strat. Palaeont., no. 21, pp. 29-47, pls. 1-4 (in Chinese with English abstract).
- 20) Hyatt, A. (1894) Proc. Amer. Phil. Soc. **32**, 349-647, pls. 1-14.

- 21) Hyatt, A. (1883-1884) *Proc. Boston Soc. Nat. Hist.* **22**, 253-272 [1883], 273-338 [1884].
- 22) Hall, J. (1861) *Contributions to Palaeontology. Being Some of the Results of Investigations Made During the Years 1859 and 1860. Fourteenth Annual Report of the Regents of the University of the State of New York on the Condition of the State Cabinet of Natural History and the Historical and Antiquarian Collection Annexed Thereto.* C. Van Benthuysen, Albany.
- 23) Hall, J. (1879) *Palaeontology: Vol. 5. Part 2. Containing Descriptions of the Gastropoda, Pteropoda and Cephalopoda of the Upper Helderberg, Hamilton, Portage and Chemung Groups.* C. Van Benthuysen and Sons, Albany.
- 24) Foerste, A. F. (1925) *Denison Univ. Bull. J. Sci. Lab.* **21**, 1-69, pls. 1-24.
- 25) Barrande, J. (1865) *Système silurien du centre de la Bohême, Première Partie: Recherches paléontologiques.* Vol. 2, Classe des Mollusques, Ordre des Céphalopodes, part 6. Praha.
- 26) Archiac, A. d', and Verneuil, E. de (1842) *Trans. Geol. Soc. London* **2** **6**, 303-410, pls. 25-38.
- 27) Clarke, M. R., Denton, E. J., and Gilpin-Brown, J. B. (1979) *J. Mar. Biol. Ass. United Kingdom* **59**, 256-276.
- 28) Ward, P. D., and Greenwald, L. (1981) *J. Mar. Biol. Ass. United Kingdom* **62**, 469-475.