Revision of Early Spathian (Late Olenekian, Early Triassic) Ammonoids from the Osawa Formation at Akaushi in the Motoyoshi Area, South Kitakami Belt, Northeast Japan

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Revision of early Spathian (late Olenekian, Early Triassic) ammonoids from the Osawa Formation at Akaushi in the Motoyoshi area, South Kitakami Belt, Northeast Japan

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Abstract. A taxonomic revision of the ammonoid assemblage previously reported from the Osawa Formation at Akaushi in the Motoyoshi area, i.e., *Columbites parisianus*, *Subcolumbites perrinismithi* and *Eophyllites* cf. *dieneri*, leads to the conclusion that the fauna should be attributed to *Hellenites tchernyschewiensis*, *H. inopinatus*, *Neocolumbites grammi*, *N. insignis*, *Procolumbites ussuriensis* and *P. subquadratus*. In addition, this fauna also includes *Deweveria kovalenkoi*. Because these ammonoids are characteristic of the *N. insignis* Zone of South Primorye, Russian Far East, the lowest part of the Osawa Formation clearly correlates with the upper part of the lower Spathian (upper Olenekian, Lower Triassic), and the faunal similarity suggests that the South Kitakami Belt may have been located near South Primorye on the western side of the Panthalassa.

Keywords: ammonoid, Osawa Formation, South Kitakami Belt, Spathian, Triassic

Introduction

The 250–300 m thick marine Osawa Formation, comprising the second formation of the Lower–Middle Triassic Inai Group (*ca*. 3000 m, maximum thickness; Ichikawa, 1951; Onuki and Bando, 1959), is widely distributed in the South Kitakami Belt, Northeast Japan, which is regarded as a fragment of continental origin (= South Kitakami Terrane; Kobayashi, 1999). Consisting mainly of dark gray, laminated mudstone intercalated with turbiditic fine sandstone beds, the formation contains a wide range of Spathian (late Olenekian) fossil groups, i.e., ammonoids (Bando, 1964, 1970; Bando and Shimoyama, 1974; Ehiro, 1993, 2016, 2022; Ehiro *et al*., 2016), a nautiloid (Niko *et al*., 2016), coleoids (Niko and Ehiro, 2018, 2022), pelecypods (Murata, 1973, 1978), brachiopods (Murata, 1973), thylacocephalans (Ehiro *et al*., 2015, 2019), primitive ichthyopterygians (Shikama *et al*., 1978; Takahashi *et al*., 2014), bony fishes (Nakajima *et al*., 2017; Nakajima and Komura, 2020), cartilaginous fish (Kato *et al*., 1995), coprolites (Nakajima and Izumi, 2014) and plants (Kon'no, 1973). This fossil assemblage documents an additional record of a fairly rapid recovery of a complex Spathian marine ecosystem following the Permian/Triassic boundary (PTB) mass extinction event, similar to the earliest Spathian Paris Biota discovered in southeastern Idaho, USA, which includes more than 20 distinct metazoan orders (Brayard *et al*., 2017).

The biostratigraphy of the Osawa Formation has been updated by recent works focused on the ammonoid faunas from the middle and uppermost parts (Ehiro *et al*., 2016; Ehiro, 2022). However, ammonoids from the lowest part have not been studied since Bando and Shimoyama (1974). In order to update the biostratigraphy of the Osawa Formation, the taxonomy of the ammonoid specimens described by Bando and Shimoyama (1974) from Akaushi in the Motoyoshi area (see Figure 1 in Bando and Shimoyama, 1974) is herein revised, a newly collected ammonoid specimen from Akaushi is also examined, and the age of the lowest part of the Osawa Formation is discussed. Additionally, implications of this revision for paleobiogeography and the Early Triassic biotic recovery are also explored.

Material and methods

Material

Most of the specimens described by Bando and Shimoyama (1974) with the prefix OS and GLKU are now stored at the Tohoku University Museum, Sendai

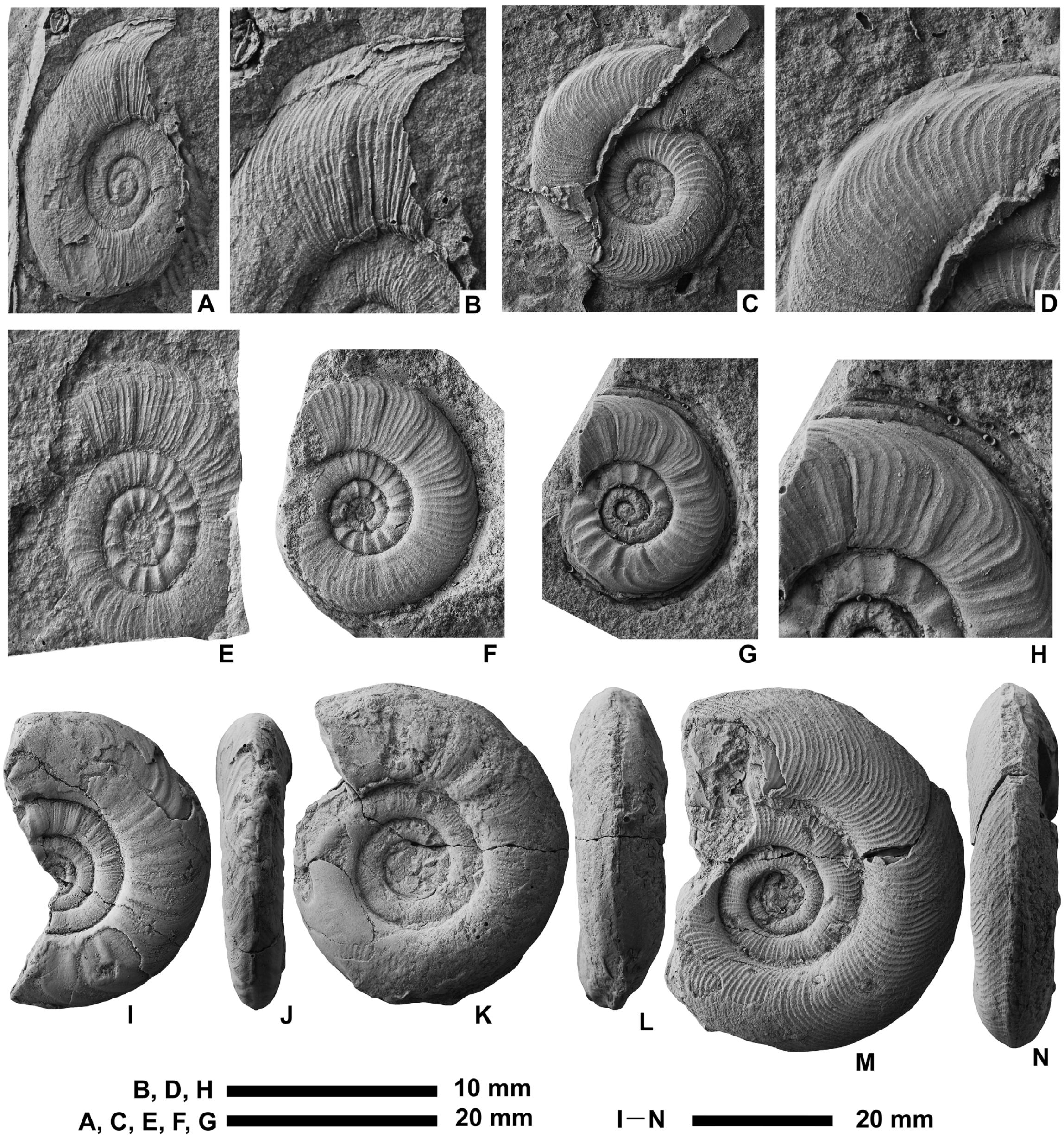

Figure 1. Early Spathian ammonoids from the lowest part of the Osawa Formation at Akaushi in the Motoyoshi area, Northeast Japan, the *Neocolumbites insignis* Zone in South Primorye, Russia, and middle Spathian ammonoids from Albania. **A–D, I, J,** *Hellenites tchernyschewiensis* Zakharov, 1968; A, B, NMNS PM35865, silicon rubber cast of the outer mold of IGPS coll. cat. no. OS-1002-2 from Akaushi, left lateral view; C, D, NMNS PM35876, silicon rubber cast of the outer mold from Zhitkov Cape on Russky Island, South Primorye, left lateral view; I, J, NMNS PM35877, plaster model of the holotype DVGI 484/801 (= Zakharov, 1968, pl. 30, fig. 1) from Tchernyshev Bay on Russky Island, right lateral (I) and ventral (J) views; **E–H,** *Hellenites inopinatus* Kiparisova, 1961; E, NMNS PM35866, silicon rubber cast of the outer mold of IGPS coll. cat. no. OS-1002-1 from Akaushi, right lateral view; F, NMNS PM35878, plaster model of DVGI 486/801 (= Zakharov, 1968, pl. 29, fig. 7) from Zhitkov Cape, right lateral view; G, H, NMNS PM35881, plaster model of the holotype CGM 185/5504 (= Kiparisova, 1961, pl. 33, fig. 4) from Zhitkov Cape, right lateral view; **K– N,** *Subcolumbites perrinismith* (Arthaber, 1908) from Albania; K, L, NMNS PM35882, plaster model of the holotype IPUW 1911-4-63 (= Arthaber, 1908, pl. 11, fig. 1), right lateral (K) and ventral (L) views; M, N, NMNS PM35883, plaster model of IPUW 1911-4-64 (= Arthaber, 1911, pl. 23, fig. 20), right lateral (M) and ventral (N) views.

and are registered as the IGPS (Institute of Geology and Paleontology, Tohoku University) collection. When the fossil locality record reported by Bando and Shimoyama (1974) contrasts with the original specimen label, this paper gives priority to that on the original label as follows.

IGPS coll. cat. no. OS-1101-9 was described as *Eophyllites* cf. *dieneri* (Arthaber, 1908) from Osawa by Bando and Shimoyama (1974, pl. 40, fig. 1), but the locality Akaushi is written on the original specimen label.

IGPS coll. cat. nos. OS-1101-4, 1101-11, 1000, 1108-8 and 1002-1 were described as *Columbites parisianus* Hyatt and Smith, 1905 from Osawa by Bando and Shimoyama (1974, pl. 40, figs. 2, 4, 6, 8; pl. 41, fig. 10, respectively), but the locality Akaushi is written on the original specimen label.

IGPS coll. cat. no. OS-1002-2 was described as *Subcolumbites perrinismithi* (Arthaber, 1908) from Akaushi by Bando and Shimoyama (1974, pl. 41, fig. 9), and this locality agrees with that on the original specimen label.

IGPS coll. cat. no. OS-1101-7 was described as *Columbites parisianus* from Akaushi by Bando and Shimoyama (1974, pl. 42, figs. 1, 3), and this locality agrees with that on the original specimen label. The specimen number was written as OS-1101 and the outer mold as OS-1101-8 in Bando and Shimoyama (1974), but both are currently registered as OS-1101-7.

In addition to the specimens of Bando and Shimoyama (1974), a newly collected ammonoid specimen from Akaushi was examined. For the taxonomic study of these specimens, the Early Triassic ammonoid collections described by Arthaber (1908, 1911), Diener (1913), Kiparisova (1961), Zakharov (1968), Tozer (1994) and Smyshlyaeva and Zakharov (2015) were examined. Also examined were plaster cast models of Hyatt and Smith's (1905) collection, which were donated by the California Academy of Sciences (San Francisco) to the National Museum of Nature and Science, Tsukuba.

Methods

For specimens with an outer mold (IGPS coll. cat. nos. OS-1101-4, 1101-11, 1108-8, 1002-1, 1002-2), rubber casts were made from silicon. For specimens without an outer mold (IGPS coll. cat. nos. OS-1101-9, 1000), replicas were made from plaster. For specimen IGPS coll. cat. no. 1101-7, both plaster model and silicon rubber cast of the outer mold were made. The silicon rubber casts and plaster models were painted black, whitened with ammonium chloride, and photographed.

Paleontological description

Systematic descriptions basically follow the classification established by Shevyrev (1986) and Tozer (1981). Morphological terms are those used in Arkell (1957).

Institution abbreviations.—CGM, Central Scientific Research Geological Prospecting Museum (TsNIGR Museum), St. Petersburg; DVGI, Far Eastern Geological Institute, Vladivostok; IGPS, Institute of Geology and Paleontology, Tohoku University, Sendai; IPUW, Department of Palaeontology, University of Vienna, Vienna; NMNS, National Museum of Nature and Science, Tsukuba; USNM, United States National Museum of Natural History, Washington, D.C.

Order Ceratitida Hyatt, 1884
Superfamily Dinaritoidea Mojsisovics, 1882
Family Columbitidae Spath, 1934
Genus ***Hellenites*** Renz and Renz, 1948

Type species.—*Tropiceltites paraematurus* Arthaber, 1911.

Hellenites tchernyschewiensis Zakharov, 1968

Figure 1A–D, I, J

Hellenites tchernyschewiensis Zakharov, 1968, p. 150, pl. 30, fig. 1, text-fig. 35b, c; Zakharov, 1997, pl. 3, figs. 3, 4.
Subcolumbites perrinismithi (Arthaber). Bando and Shimoyama, 1974, p. 302, pl. 41, fig. 9; Ehiro *et al*., 2015, fig. 3.1.
Columbites parisianus Hyatt and Smith. Ehiro *et al*., 2015, fig. 3.2.

Holotype.—DVGI 484/801, figured by Zakharov (1968, p. 150, pl. 30, fig. 1), from the *Neocolumbites insignis* Zone (upper lower Spathian) in Tchernyshev Bay on Russky Island, South Primorye, Russia (Figure 1I, J).

Material examined.—One specimen, IGPS coll. cat. no. OS-1002-2, of Bando and Shimoyama (1974, pl. 41, fig. 9); holotype, DVGI 484/801; one specimen, NMNS PM35876, from the *Neocolumbites insignis* Zone of Zhitkov Cape on Russky Island.

Descriptive remarks.—Specimen (IGPS coll. cat. no. OS-1002-2; Figure 1A, B) is characterized by very evolute shell with a fairly wide umbilicus and a distinct ventral keel. Ornamentation consists of fine, dense, rectiradiate ribs, which strongly project forward on ventrolateral shoulder. Although the specimen is slightly deformed laterally due to compaction, its distinctive ornamentation and distinct ventral keel support its attribution with reasonable confidence to *Hellenites tchernyschewiensis* (Figure 1C, D, I, J). Although the holotype, which is 42.9 mm in shell diameter, has many radial folds on the shell surface of the outer whorls, the inner whorls are ornamented by only fine, dense ribs, which support this assignment (Figure 1I, J).

Discussion.—Specimen IGPS coll. cat. no. OS-1002-2 (Figure 1A, B) was assigned to *Subcolumbites perrinismithi* by Bando and Shimoyama (1974), but this identification is not adopted because of the absence of an easily recognized reticulate sculpture formed by concave ribs and weak strigations, which is one of the diagnostic features of *Subcolumbites* Spath, 1930 (Figure 1K–N).

Specimens illustrated as *Subcolumbites perrinismithi* and *Columbites parisianus* by Ehiro *et al*. (2015, figs. 3.1, 3.2) have a keel and fine, dense, rectiradiate ribs strongly projecting forward on the ventrolateral shoulder, which are features that match those of *Hellenites tchernyschewiensis*.

Occurrence.—*Hellenites tchernyschewiensis* is known from the *Neocolumbites insignis* Zone (upper lower Spathian) of South Primorye, Russia and the lowest part of the Osawa Formation.

Hellenites inopinatus Kiparisova, 1961

Figure 1E–H

Hellenites? *inopinatus* Kiparisova, 1958, pl. 13, fig. 9; Kiparisova, 1961, p. 169, pl. 33, fig. 4.
Hellenites inopinatus Kiparisova. Zakharov, 1968, p. 149, pl. 29, figs. 8–11, text-fig. 35d; Zakharov, 1997, pl. 3, fig. 2.
Columbites parisianus Hyatt and Smith. Bando and Shimoyama, 1974, p. 301, pl. 41, fig. 10.

Holotype.—CGM 185/5504, figured by Kiparisova (1958, pl. 13, fig. 9; 1961, p. 169, pl. 33, fig. 4), from the *Neocolumbites insignis* Zone (upper lower Spathian) of Zhitkov Cape on Russky Island, South Primorye, Russia (Figure 1G, H).

Material examined.—One specimen, IGPS coll. cat. no. OS-1002-1, of Bando and Shimoyama (1974, pl. 41, fig. 10); holotype, CGM 185/5504; three paratypes, DVGI 486/801, 489/801, 485/801, figured by Zakharov (1968, pl. 29, figs. 7, 9, 10).

Descriptive remarks.—Specimen (IGPS coll. cat. no. OS-1002-1; Figure 1E) is characterized by very evolute coiling and a fairly wide umbilicus. The ornamentation consists of distant, strong, slightly rursiradiate and rectiradiate ribs on earlier whorls, which become denser and finer on the later whorls. Ribs strongly project forward on ventrolateral shoulder. Although the specimen is slightly deformed laterally due to compaction and the ventral part is poorly preserved, its distinctive ornamentation permits its identification with reasonable confidence as *Hellenites inopinatus* (Figure 1F–H).

Discussion.—Specimen IGPS coll. cat. no. OS-1002-1 (Figure 1E) was assigned to *Columbites parisianus* by Bando and Shimoyama (1974), but the rib features are significantly different from comparable-sized *C. parisianus* specimens, which usually have strong, prorsiradiate ribs associated with ventrolateral tuberculation (Figures 2N–R, 3I–L). As Kummel (1969) and Guex *et al*. (2010) stated, *C. parisianus* exhibits a wide range of the intraspecific variation, including relatively compressed spineless forms with rounded to ovoid whorl sections and ribs varying from barely discernable to moderately strong on outer whorls (Figure 2N, O), and forms with sharp ribs and a cadicone to quadrastic whorl section with strong ventrolateral spination (Figure 2P–R). However, their inner whorls are characterized by coronate whorls and strong prorsiradiate ribs associated with distinctive ventrolateral tuberculation (Figure 3I–L).

Comparison.—*Hellenites inopinatus* differs from *H. tchernyschewiensis* by its distant, strong ribs on earlier whorls.

Occurrence.—*Hellenites inopinatus* is known from the *Neocolumbites insignis* Zone (upper lower Spathian) of South Primorye, Russia and the lowest part of the Osawa Formation.

Genus ***Neocolumbites*** Zakharov, 1968

Type species.—*Neocolumbites grammi* Zakharov, 1968.

Neocolumbites grammi Zakharov, 1968

Figure 2A–E

Neocolumbites grammi Zakharov, 1968, p. 111, pl. 21, figs. 6–9, text-fig. 28g.
Eophyllites cf. *dieneri* (Arthaber). Bando and Shimoyama, 1974, p. 306, pl. 40, fig. 1.
Columbites parisianus Hyatt and Smith. Bando and Shimoyama, 1974, p. 301, pl. 40, fig. 2.

Holotype.—DVGI 469/801, figured by Zakharov (1968, p. 111, pl. 21, fig. 6), from the *Neocolumbites insignis* Zone (upper lower Spathian) in Tchernyshev Bay on Russky Island, South Primorye, Russia.

Material examined.—Two specimens, IGPS coll. cat. nos. OS-1101-9 and OS-1101-4, of Bando and Shimoyama (1974, pl. 40, figs. 1, 2); paratype, DVGI 470/801, figured by Zakharov (1968, pl. 21, fig. 7).

Descriptive remarks.—Specimens (IGPS coll. cat. nos. OS-1101-9 and OS-1101-4; Figure 2A, B) are characterized by a moderately evolute shell with a moderately wide umbilicus. The ornamentation consists of weak radial folds and fine growth lines, which are rursiradiate and concave on umbilical wall and shoulder, straight and prorsiradiate on the flank, and forward projected on ventrolateral shoulder. The specimens are strongly deformed laterally due to compaction and the ventral parts are poorly preserved, but their distinctive ornamentation supports their identification with reasonable confidence as *Neocolumbites grammi* (Figure 2C–E).

Discussion.—Specimen IGPS coll. cat. no. OS-1101-9 (Figure 2B) was assigned to *Eophyllites* cf. *dieneri* (Arthaber, 1908) by Bando and Shimoyama (1974), but the growth line features are different from *Eophyllites dieneri*, which has more or less straight, rectiradiate lines on the flanks that continue straight across the venter (Figure 2K–M; Spath, 1934; Kummel, 1969). Although Bando

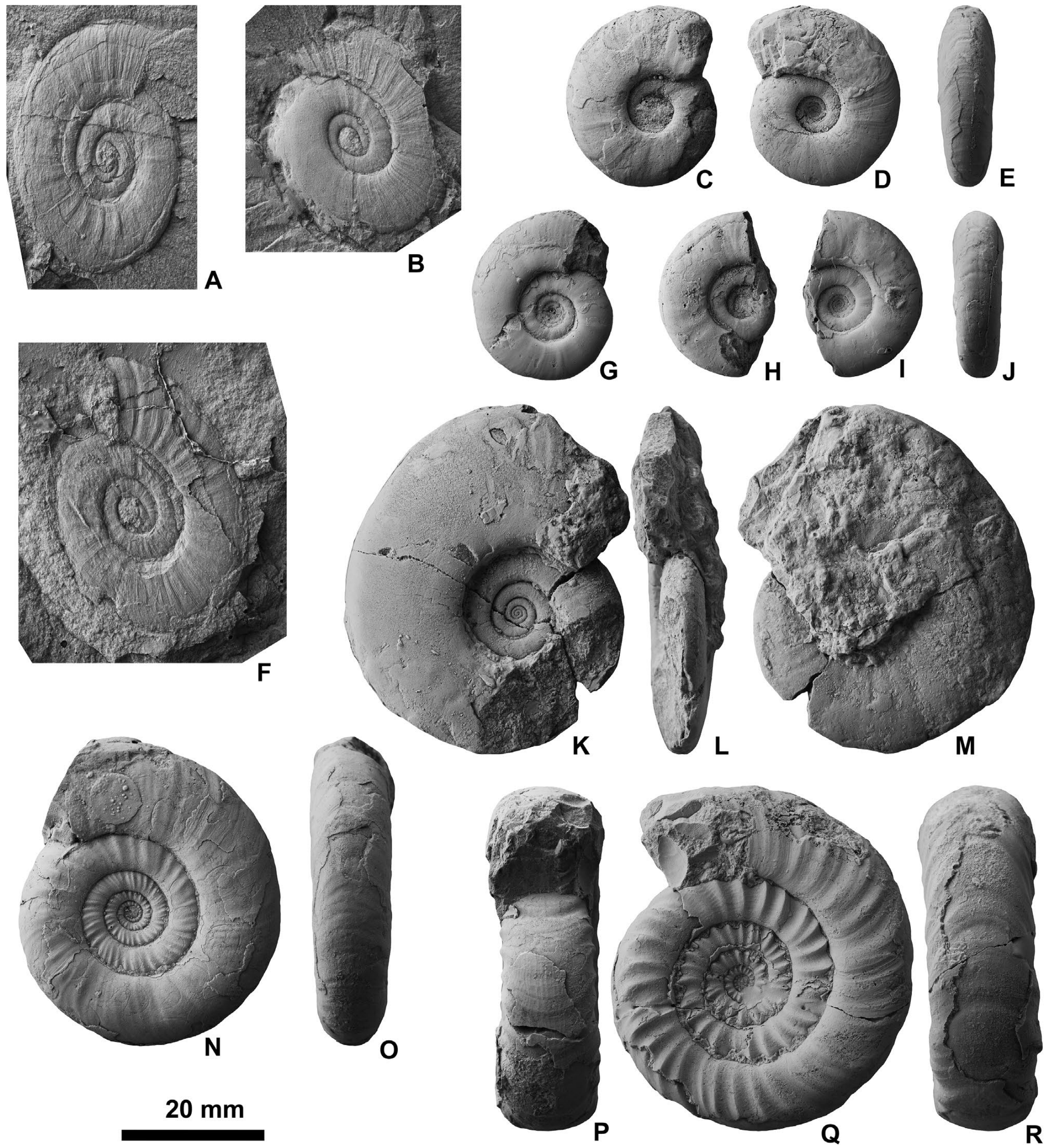

Figure 2. Early Spathian ammonoids from the lowest part of the Osawa Formation at Akaushi in the Motoyoshi area, Northeast Japan, the *Neocolumbites insignis* Zone in Tchernyshev Bay on Russky Island, South Primorye, Russia and the *Columbites parisianus* Zone in Idaho, western USA, and middle Spathian ammonoids from Albania. **A–E,** *Neocolumbites grammi* Zakharov, 1968; A, NMNS PM35869, silicon rubber cast of the outer mold of IGPS coll. cat. no. OS-1101-4 from Akaushi, left lateral view; B, NMNS PM35870, plaster model of IGPS coll. cat. no. OS-1101-9 from Akaushi, right lateral view; C–E, NMNS PM35884, plaster model of the paratype DVGI 470/801 (= Zakharov, 1968, pl. 21, fig. 7) from Tchernyshev Bay, left lateral (C), right lateral (D) and ventral (E) views; **F–J,** *Neocolumbites insignis* Zakharov, 1968; F, NMNS PM35869, silicon rubber cast of the outer mold of IGPS coll. cat. no. OS-1101-4 from Akaushi, left lateral view; G, NMNS PM35885, plaster model of the paratype DVGI 480/801 (= Zakharov, 1968, pl. 21, fig. 11) from Tchernyshev Bay, left lateral view; H–J, NMNS PM35886, plaster model of the holotype DVGI 478/801 (= Zakharov, 1968, pl. 21, fig. 9) from Tchernyshev Bay, left lateral (H), right lateral (I) and ventral (J) views; **K–M,** *Eophyllites dieneri* (Arthaber, 1908), NMNS PM35887, plaster model of the paralectotype IPUW 1911-4-26 (=Arthaber, 1908, pl. 13, fig. 4), from Albania, left lateral (K), apertural (L) and right lateral (M) views; **N–R,** *Columbites parisianus* Hyatt and Smith, 1905 from Idaho; N, O, NMNS PM35888, plaster model of the holotype USNM 75246a (= Hyatt and Smith, 1905, pl. 1, figs. 9, 10) from Paris Canyon, right lateral (N) and ventral (O) views; P–R, NMNS PM35889, from Bear Lake Hot Springs, apertural (P), right lateral (Q) and ventral (R) views.

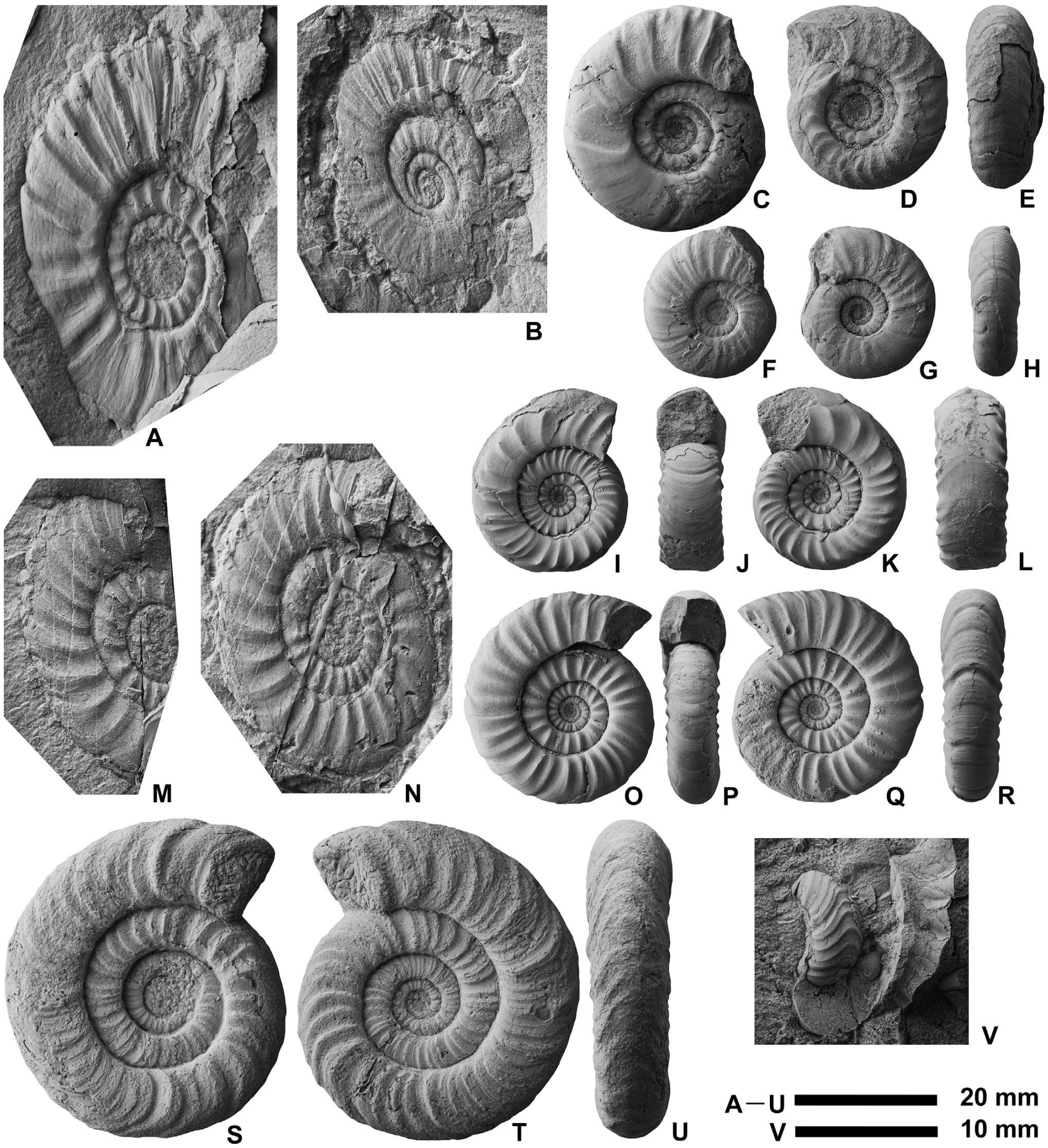

Figure 3. Early Spathian ammonoids from the lowest part of the Osawa Formation at Akaushi in the Motoyoshi area, Northeast Japan, the *Neocolumbites insignis* Zone in Tchernyshev Bay on Russky Island, South Primorye, Russia and the *Columbites parisianus* Zone in Idaho, western USA. **A–H,** *Procolumbites ussuriensis* (Zakharov, 1968); A, NMNS PM35868, silicon rubber cast of the outer mold of IGPS coll. cat. no. OS-1101-11 from Akaushi, left lateral view; B, NMNS PM35867, plaster model of IGPS coll. cat. no. OS-1000 from Akaushi, left lateral view; C, NMNS PM35891, plaster model of the paratype DVGI 464/801 (= Zakharov, 1968, pl. 20, fig. 7) from Tchernyshev Bay, left lateral view; D, E, NMNS PM35892, plaster model of the paratype DVGI 466/801 (= Zakharov, 1968, pl. 20, fig. 8) from Tchernyshev Bay, right lateral (D) and ventral (E) views; F–H, NMNS PM35893, plaster model of the paratype DVGI 468/801 (= Zakharov, 1968, pl. 20, fig. 9) from Tchernyshev Bay, left lateral (F), right lateral (G) and ventral (H) views; **I–L,** *Columbites parisianus* Hyatt and Smith, 1905, NMNS PM35890, from the *Columbites parisianus* Zone at Bear Lake Hot Springs, Idaho, western USA, left lateral (I), apertural (J), right lateral (K) and ventral (L) views; **M, N, S–V,** *Procolumbites subquadratus* Zakharov, 1968; M, NMNS PM35872, silicon rubber cast of the outer mold of IGPS coll. cat. no. OS-1101-7 from Akaushi, left lateral view; N, NMNS PM35873, plaster model of IGPS coll. cat. no. OS-1101-7, left lateral view; S–V; NMNS PM35895, from Tchernyshev Bay; left lateral (S), right lateral (T) ventral (U) views and close up of the inner whorls (V); **O–R,** *Procolumbites karataucicus* Astachova, 1960, NMNS PM35894, from the *Procolumbites* Zone north of Georgetown, Idaho, western USA (coll. Jim Jenks), left lateral (O), apertural (P), right lateral (Q) and ventral (R) views.

and Shimoyama (1974, p. 306) reported that the ratio of umbilical diameter (*U*) to shell diameter (*D*) was 0.48, this measurement appears to have been taken at a point where the ventral part was broken. The *U*/*D* is about 0.36 where the venter is well preserved (27 mm in shell diameter). This value is greater than that for the type specimens of *Eophyllites dieneri* (*U*/*D* = 0.30) but is about the same as the holotype of *Neocolumbites grammi* (*U*/*D* = 0.35).

Specimen IGPS coll. cat. no. OS-1101-4 (Figure 2A) was assigned to *Columbites parisianus* by Bando and Shimoyama (1974), but the rib features are significantly different from comparable-sized *C. parisianus* specimens, which have strong, prorsiradiate ribs associated with ventrolateral tuberculation (Figure 3I–L).

Occurrence.—*Neocolumbites grammi* is known from the *N. insignis* Zone (upper lower Spathian) of South Primorye, Russia and the lowest part of the Osawa Formation.

Neocolumbites insignis Zakharov, 1968

Figure 2F–J

Neocolumbites insignis Zakharov, 1968, p. 112, pl. 21, figs. 9a, b–11, text-fig. 28h.
Columbites parisianus Hyatt and Smith. Bando and Shimoyama, 1974, p. 301, pl. 40, fig. 6.

Holotype.—DVGI 478/801, figured by Zakharov (1968, p. 112, pl. 21, fig. 9a, b), from the *Neocolumbites insignis* Zone (upper lower Spathian) in Tchernyshev Bay on Russky Island, South Primorye, Russia (Figure 2H–J).

Material examined.—One specimen, IGPS coll. cat. no. OS-1108-8, of Bando and Shimoyama (1974, pl. 40, fig. 8); holotype, DVGI 478/801; paratype, DVGI 480/801, figured by Zakharov (1968, pl. 21, fig. 11).

Descriptive remarks.—Specimen (GPS coll. cat. no. OS-1108-8; Figure 2F) is characterized by a fairly evolute shell with a fairly wide umbilicus. The ornamentation consists of weak radial folds and weak ribs as well as fine growth lines which are slightly concave. Although the specimen is strongly deformed laterally due to compaction and the ventral parts are poorly preserved, its distinctive ornamentation supports its identification with reasonable confidence as *Neocolumbites insignis* (Figure 2G–J).

Discussion.—Specimen IGPS coll. cat. no. OS-1108-8 (Figure 2F) was assigned to *Columbites parisianus* by Bando and Shimoyama (1974), but the rib features are significantly different from comparable-sized *C. parisianus* specimens, which have strong, prorsiradiate ribs associated with ventrolateral tuberculation (Figure 3I–L).

Comparison.—*Neocolumbites insignis* differs from *N. grammi* by its wider umbilicus.

Occurrence.—*Neocolumbites insignis* is known from the *N. insignis* Zone (upper lower Spathian) of South Primorye, Russia and the lowest part of the Osawa Formation.

Genus ***Procolumbites*** Astachova, 1960

Type species.—*Procolumbites karataucicus* Astachova, 1960.

Procolumbites ussuriensis (Zakharov, 1968)

Figure 3A–H

Columbites sp. Kiparisova, 1961, p. 119, pl. 26, fig. 8, text-fig. 81.
Columbites ussuriensis Zakharov, 1968, p. 107, pl. 20, figs. 6–9, text-fig. 28b; Zakharov and Rybalka, 1987, pl. 3, fig. 15; Zakharov, 1997, pl. 2, figs. 3, 4; Smyshlyaeva and Zakharov, 2015, pl. 1, figs. 7–10.
Columbites parisianus Hyatt and Smith. Bando and Shimoyama, 1974, p. 301, pl. 40, figs. 4, 6.

Holotype.—CGM 23/8701, figured by Zakharov (1968, p. 107, pl. 20, fig. 6), from the *Neocolumbites insignis* Zone (upper lower Spathian) on Golyj (Kom-Pikho-Sakho) Cape, on the eastern coast of Ussuri Gulf, South Primorye, Russia.

Material examined.—Two specimens, IGPS coll. cat. nos. OS-1000 and OS-1101-11, of Bando and Shimoyama (1974, Pl. 40, figs. 4, 6); three paratypes, DVGI 464/801, 466/801, 468/801, figured by Zakharov (1968, pl. 20, figs. 7, 8, 9).

Descriptive remarks.—Specimens (IGPS coll. cat. nos. OS-1000, OS-1101-11; Figure 3A, B) are characterized by a moderately evolute shell with a moderately wide umbilicus. The ornamentation consists of constrictions and strong, major ribs, which are rursiradiate and concave on umbilical wall and shoulder, and straight and prorsiradiate on the flank, as well as growth lines and fine ribs between major ribs. Both specimens exhibit ribbing on the inner whorls, but that on the specimen in Figure 3A is especially strong. Although the specimens are strongly deformed laterally due to compaction and the ventral part is poorly preserved, their distinctive ornamentation supports their attribution with reasonable confidence to *Procolumbites ussuriensis*.

Discussion.—Specimens IGPS coll. cat. nos. OS-1000 and OS-1101-11 (Figure 3A, B) were assigned to *Columbites parisianus* by Bando and Shimoyama (1974), but the rib features are significantly different from similar-sized *C. parisianus* specimens, which have strong, prorsiradiate ribs associated with ventrolateral tuberculation (Figures 2N–R, 3I–L).

The type specimens were originally described as *Columbites* by Zakharov (1968), but their ribs together with an absence of tuberculation suggests an assignment to *Procolumbites*. For diagnoses of both genera, see Guex *et al*. (2010, p. 30, 36).

Occurrence.—*Procolumbites ussuriensis* is known from the *Neocolumbites insignis* Zone (upper lower Spathian) of South Primorye, Russia and the lowest part of the Osawa Formation.

Procolumbites subquadratus Zakharov, 1968

Figure 3M, N, S–V

Procolumbites subquadratus Zakharov, 1968, p. 110, pl. 21, figs. 4, 5, text-fig. 28f.
Columbites parisianus Hyatt and Smith. Bando and Shimoyama, 1974, p. 301, pl. 42, figs. 1, 3.

Holotype.—CGM 27/8701, described by Zakharov (1968, p. 110), from the *Neocolumbites insignis* Zone (upper lower Spathian) in Tchernyshev Bay on Russky Island, South Primorye, Russia.

Material examined.—One specimen, IGPS coll. cat. no. OS-1101-7, of Bando and Shimoyama (1974, pl. 42, figs. 1, 3); paratype, DVGI 460/801, figured by Zakharov (1968, pl. 21, fig. 4); one specimen, NMNS PM35895, from the *Neocolumbites insignis* Zone in Tchernyshev Bay on Russky Island.

Descriptive remarks.—Specimen IGPS coll. cat. no. OS-1101-7 (Figure 3M, N) is characterized by a very evolute shell with a wide umbilicus. The ornamentation consists of distinct, prorsiradiate ribs, which bend gently forward on ventrolateral shoulders. Although the specimen is strongly deformed laterally due to compaction and the ventral part is poorly preserved, its distinctive ornamentation supports its attribution with reasonable confidence to *Procolumbites subquadratus* (Figure 3S–V).

Discussion.—Specimen IGPS coll. cat. no. OS-1101-7 (Figure 3M, N) was assigned to *Columbites parisianus* by Bando and Shimoyama (1974), but the rib features are significantly different from comparable-sized specimens of *C. parisianus*, which have strong, prorsiradiate ribs associated with ventrolateral tuberculation (Figures 2N–R, 3I–L).

Procolumbites subquadratus described by Zakharov (1968, p. 110), was based on three specimens from the *Neocolumbites insignis* Zone (upper lower Spathian) in Tchernyshev Bay on Russky Island, South Primorye. The holotype (CGM 27/8701) has never been illustrated, and of the two paratypes, one was a small specimen with a diameter of 14.2 mm (Zakharov, 1968, pl. 21, fig. 4), and the other was a fragment of the ventral part with a diameter of about 20 mm (Zakharov, 1968, pl. 21, fig. 5). Specimen NMNS PM35895 (Figure 3S–V) from Tchernyshev Bay is probably an adult shell because its inner whorls exhibit features similar to the paratypes such as distinct, prorsiradiate ribs, which bend gently forward on ventrolateral shoulders before crossing the slightly raised venter in a convex arch. Specimen IGPS coll. cat. no. OS-1101-7 is very similar to NMNS PM35895 with its very evolute shell and slightly concave, strong ribs, which suggest that it should be attributed to *P. subquadratus*.

Occurrence.—*Procolumbites subquadratus* is known from the *Neocolumbites insignis* Zone (upper lower Spathian) of South Primorye, Russia and the lowest part of the Osawa Formation.

Family Hemilecanitidae Guex *et al*., 2010
Genus ***Deweveria*** Guex *et al*., 2005a

Type species.—*Deweveria dudresnayi* Guex *et al*., 2005a.

Deweveria kovalenkoi Smyshlyaeva and Zakharov, 2015

Figure 4A–D

Glyptophiceras cf. *gracile* (Spath). Bando, 1970, p. 343, pl. 37, fig. 1, text-fig. 5.
Deweveria kovalenkoi Smyshlyaeva and Zakharov, 2015, p. 114, pl. 1, fig. 5, text-fig. 3e.

Holotype.—DVGI 100/840, figured by Smyshlyaeva and Zakharov (2015, p. 114, pl. 1, fig. 5), from the *Neocolumbites insignis* Zone (upper lower Spathian) on Russky Island, South Primorye, Russia.

Material examined.—One specimen, NMNS PM35874, extracted from laminated mudstone of the lowest part of the Osawa Formation at Akaushi Port (38°47′45.29″N, 141°32′14.03″E); one specimen, IGPS coll. cat. no. GLKU-C402, of Bando (1970, pl. 37, fig. 1); holotype, DVGI 100/840.

Descriptive remarks.—Specimens (NMNS PM35874, Figure 4A; IGPS coll. cat. no. GLKU-C402, Figure 4B) are characterized by a fairly evolute, compressed shell with indistinct ventral shoulder, narrowly rounded venter, and slightly flattened flank. The umbilicus is moderately wide with low, vertical wall and rounded shoulder. The ornamentation consists of fine, sinuous growth lines as well as low, fold-type ribs disappearing on later whorls. The specimens are strongly deformed laterally due to compaction and the ventral portions are poorly preserved, but their distinctive ornamentation supports their identification with reasonable confidence as *Deweveria kovalenkoi* (Figure 4C, D).

Discussion.—Specimen IGPS coll. cat. no. GLKU-C402 (Figure 4B), collected from a float siltstone block that undoubtedly came from the lower part of the Osawa Formation at Monzen in the Motoyoshi area (Ehiro, 2002), was originally identified as the Griesbachian ammonoid *Glyptophiceras* cf. *gracile* Spath, 1930 by Bando

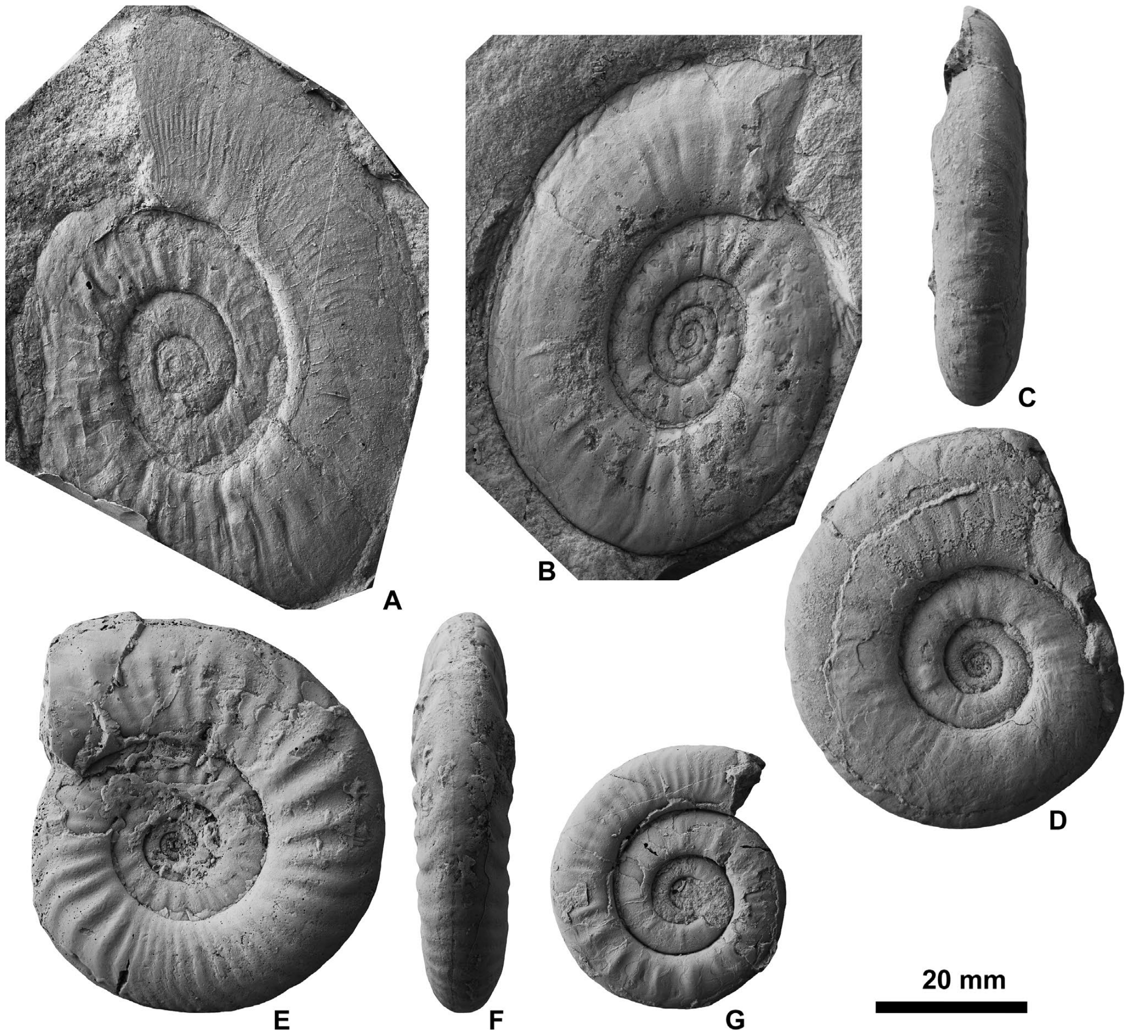

Figure 4. Early Spathian ammonoids from the Osawa Formation in the Motoyoshi area, Northeast Japan and Early Triassic ammonoids from Russia, Kashimir and Arctic Canada. **A–D,** *Deweveria kovalenkoi* Smyshlyaeva and Zakharov, 2015; A, NMNS PM35874, silicon rubber cast of the outer mold from Akaushi, in the Motoyoshi area, right lateral view; B, NMNS PM35875, plaster model of IGPS coll. cat. no. GLKU-C402 originally studied by Bando (1970) from a float siltstone block at Monzen in the Motoyoshi area, left lateral view; C, D, NMNS PM35897, plaster model of the holotype DVGI 100/840 from the *Neocolumbites insignis* Zone on Russky Island, South Primorye, Russia, ventral (C) and left lateral (D) views; **E, F,** *Glyptophiceras aequicostatus* (Diener, 1913), NMNS PM35898, plaster model of the holotype GSI 11270 (= Diener, 1913, pl. 2, fig. 10) from the upper Smithian in Kashimir, right lateral (E) and ventral (F) views; **G,** *Hypophiceras gracile* (Spath, 1930), NMNS PM35899, plaster model of GSC 28030 (= Tozer, 1994, pl. 2, fig. 3) from the lower Griesbachian *Otoceras boreale* Zone on Ellesmere Island, Arctic Canada, left lateral view.

(1970). Nakazawa *et al*. (1994, p. 88) pointed out that the specimen is more similar to the late Smithian taxon *G. aequicostatus* (Diener, 1913), and Shigeta and Nakajima (2017) attributed it to the early Spathian ammonoid *Neocolumbites*. *Glyptophiceras gracile*, which was assigned to *Hypophiceras* Trümpy, 1969 by Tozer (1994), differs from the specimen by its very evolute shell with very wide umbilicus (Figure 4G). *Glyptophiceras aequicostatus* also differs by its strong, rounded ribs that strongly project forward on the outer flank (Figure 4E, F). As described above, *Neocolumbites* differs by its smooth shell with weak radial folds.

Smyshlyaeva and Zakharov (2015) stated that the folds on the outer whorls of the holotype of *Deweveria kovalenko* are barely noticeable, but the reason for this observation is because the shell material on the venter and outer flank of the last quarter of the outer whorl is missing, hence the folds and growth lines appear weaker on the inner mold.

There is a slight difference in the ratio of the first lateral

			Western USA Guex *et al.* (2010) Jenks *et al.* (2013)		Chaohu Tong *et al.* (2004) Ji *et al.* (2015)	South Primorye Zakharov (1997) Shigeta and Kumagae (2016) Zakharov *et al.* (2021)	South Kitakami This study
upper Olenekian	SPATHIAN	upper	*Haugi*	*Subrobustus*		*Ussuriphyllites amurensis*	Osawa Formation
				Haugi		*Prohungarites* sp.-*Paranorellona parisi*	
		middle	*Subcolumbites*	*Silberlingera*	*Subcolumbites*	*Subfengshanites multiformis*	
				Fengshanites / *Prohungarites*			
		lower	*Columbites*	*Procolumbites*	*Procolumbites*	*Neocolumbite insignis*	★ Akaushi
				Columbites parisianus	*Tirolites* - *Columbites*	*Tirolites subcassianus*	Hiraiso Fm.
				"*Tirolites harti* beds"			
				"*Bajarunia confusionensis* beds"			

Figure 5. Correlation of ammonoid zones of the lowest part of the Osawa Formation (South Kitakami) at Akaushi (indicated by star) with other important Spathian (upper Olenekian, Lower Triassic) ammonoid localities. Zakharov and Mousavi (2013) correlated the *Ussuriphyllites amurensis* Zone with the lower Anisian of South Primorye, but Shigeta and Kumagae (2016) dispute this stratigraphic assignment and regard it as upper Spathian. Recently, Popov *et al*. (2019) reported the occurrence of the *Prohungarites* sp.-*Paranorellin parisi* Beds between the *Subfengshanites multiformis* Zone and *Ussuriphyllites amurensis* Zone and correlated it with the upper Spathian. The stratigraphic correlation of the *Ussuriphyllites amurensis* Zone (upper Spathian or lower Anisian) is still a matter of debate.

saddle and second lateral saddle and the denticulations at base of the lobes between IGPS coll. cat. no. GLKU-C402 and the holotype of *D. kovalenko*, but these differences in suture lines fall within the range of interspecific variation as shown by Kummel (1969) for many other Spathian ammonoids.

Occurrence.—*Deweveria kovalenkoi* is known from the *Neocolumbites insignis* Zone (upper lower Spathian) of South Primorye, Russia and the lowest part of the Osawa Formation.

Discussion

Age of the lowest part of the Osawa Formation

The Lower Triassic ammonoid fauna in the South Kitakami Belt has been considered as "*Columbites*" and "*Subcolumbites*" assemblages for a long time (Ichikawa, 1967). Except true *Subcolumbites* (e.g. Bando, 1964, pl. 3, figs. 18, 19; pl. 4, fig. 3; Ehiro *et al*., 2019, fig. 5), however, the present study revealed that the considerable material from the Osawa Formation should be distinguished from *Columbites* or *Subcolumbites* as described above. The taxonomic reassignment brings further results.

Ammonoids from the lowest part of the Osawa Formation at Akaushi, previously assigned to the *Columbites parisianus* Subzone of the *Subcolumbites* Zone by Bando and Shimoyama (1974), were later correlated with the middle lower Spathian *C. parisianus* Subzone of the western USA (Ehiro *et al*., 2019). The present taxonomic revision of this fauna leads to the conclusion that these specimens should be attributed to *Hellenites tchernyschewiensis*, *H. inopinatus*, *Neocolumbites grammi*, *N. insignis*, *Procolumbites ussuriensis* and *P. subquadratus* instead of their previous designations as *Columbites parisianus*, *Subcolumbites perrinismithi* and *Eophyllites* cf. *dieneri*. Because these ammonoids are characteristic of the *N. insignis* Zone (= upper lower Spathian) in South Primorye (Zakharov, 1968, 1997), their occurrences in the lowest part of the Osawa Formation clearly constrain the age of this particular horizon (Figure 5; Jenks *et al*., 2015; Shigeta and Kumagae, 2016; Shigeta and Nakajima, 2017). Furthermore, *Procolumbites*, which is of late early Spathian age, suggests that the horizon also correlates with the *Procolumbites* Zone of the western USA and South China (Figure 5; Tong *et al*., 2004; Galfetti *et al*., 2007; Guex *et al*., 2010; Jenks *et al*., 2013; Ji *et al*., 2015).

Shigeta and Nakajima (2017) reported the occurrence of *Tirolites* cf. *ussuriensis* Zharnikova (in Buryi and Zharnikova, 1981) from the lower part of the Hiraiso Formation, which is conformably overlain by the Osawa Formation, and correlated it with the lower–middle lower Spathian *Tirolites*-*Amphistephanites* Zone (= *Tirolites* *subcassianus* Zone of Zakharov *et al*., 2021). Ehiro *et al*. (2019, fig. 5) illustrated a middle Spathian *Subcolumbites perrinismithi* specimen from the lower part of the main portion of the Osawa Formation. These studies thus corroborate the conclusion of this work that the lowest part of the Osawa Formation correlates with the upper lower Spathian.

Ehiro *et al*. (2016) reported "*Columbites parisianus*" from an exposure of the middle part of the Osawa Formation about 900 m north of Cape Tatezaki in the Utatsu area, together with *Subcolumbites*. However, the rib features of these specimens are significantly different from *C. parisianus* in having numerous, fine ribs as well as prominent major ribs, which strongly project forward on the ventrolateral shoulder. Shallow constrictions are immediately followed by major ribs. Their ornamentation and lack of a keel on the venter are very similar to the middle Spathian ammonoid genus *Epiceltites* Arthaber, 1911. As discussed above, specimens illustrated as *Subcolumbites perrinismithi* and *C. parisianus* from the Osawa Formation at Yamaya in the Motoyoshi area by Ehiro *et al*. (2015, figs. 3.1, 3.2) are here assigned to *Hellenites tchernyschewiensis*. Bando and Shimoyama (1974, pl. 40, fig. 9, pl. 41, fig. 1) reported "*Columbites parisianus*" from the upper part of the Osawa Formation at Osawa, but the rib features are significantly different from comparable-sized *Columbites* specimens, which have strong, prorsiradiate ribs associated with ventrolateral tuberculation. Prior research has pointed to the abnormal co-occurrence of *Columbites* and *Subcolumbites* throughout almost all horizons of the Osawa Formation, except for the uppermost part (Ehiro *et al*., 2019), but such biostratigraphic contradiction would be dissolved after the taxonomic reassignment of previous "*Columbites*" by this study.

Implications for paleobiogeography

As described above, the ammonoid assemblage from the lowest part of the Osawa Formation is very similar to that of the *Neocolumbites insignis* Zone in South Primorye, Russian Far East (Zakharov, 1968, 1997), but it differs from faunas from other localities such as South China and the western USA (Chao, 1959; Guex *et al*., 2010). Furthermore, the faunal composition of the Hiraiso Formation also closely resembles that of the *Tirolites ussuriensis* beds in South Primorye (Bittner, 1899; Kiparisova, 1938; Zakharov, 1968, 1997; Kashiyama and Oji, 2004; Shigeta and Nakajima, 2017).

Ehiro *et al*. (2016) stated that the ammonoid fauna of the middle part of the Osawa Formation is very similar to that of the western USA, but as discussed above, the attribution to *Columbites parisianus* is misleading. In addition, several species reported by Ehiro *et al*. (2016) occur in various faunas including the middle lower Spathian *Columbites parisianus* Zone, the upper lower Spathian *Procolumbites* Zone and the middle Spathian *Fengshanites*/*Prohungarites* Zone in the western USA (Guex *et al*., 2010; Jenks *et al*., 2013): e.g. *Albanites sheldoni* (Kummel, 1969) and *Nordophiceratoides bartolinae* (Guex *et al*., 2010) from the *Columbites parisianus* Zone, *Hellenites elegans* Guex *et al*., 2005b from the *Procolumbites* Zone, and *Tardicolumbites tardicolumbus* Guex *et al*., 2005a from the *Fengshanites*/*Prohungarites* Zone. Because the specimens reported by Ehiro *et al*. (2016) are strongly deformed laterally due to compaction and their ventral portions and suture lines are poorly preserved, further taxonomic studies based on better preserved specimens are needed in order to better define any faunal similarities.

The mid-Paleozoic to Triassic strata of the South Kitakami Belt are generally considered to have been deposited not far from the eastern margin of the South China Block in the low northern latitudes on the western side of the Panthalassa (Ehiro, 2001; Nakajima and Schoch, 2011; Okawa *et al*., 2013; Ehiro *et al*., 2016). The age distribution pattern of detrital monazites suggests that South Primorye was probably located along the eastern continental margin of the Khanka Block (Khanchuk, 2001; Yokoyama *et al*., 2009a, b), which was part of a continent attached to the Northeast China Block, in the lower–middle northern latitudes on the western side of the Panthalassa (Brayard *et al*., 2006). Recently Isozaki *et al.* (2017) studied the age distribution pattern of detrital zircon samples from middle-upper Paleozoic sandstones in South Primorye, and determined that they more or less have the same age spectra as those in Northeast and Southwest Japan, which suggests that these areas shared the same tectonic-sedimentary history on the same continental block and/or the same active continental margin. Because recent zircon geochronology studies in Japan have demonstrated an intimate link to the South China Block rather than the North China Block (e.g. Isozaki *et al*., 2014, 2015; Aoki *et al*., 2015), Isozaki *et al.* (2014, 2017) modified the paleogeographic positions of South Kitakami and South Primorye, thus suggesting their new positioning at the northeastern tip of South China Block named "Greater South China". The paleogeographic positions of South Kitakami is still a matter of debate, but the similarity in ammonoid faunas suggests that South Kitakami may have been located near South Primorye on the western side of the Panthalassa.

Implications for the Early Triassic biotic recovery

The ichthyopterygians were the most successful Mesozoic secondary aquatic reptile group, and their fossil record extends from the Lower Triassic Spathian to the Upper Cretaceous Cenomanian (Bardet, 1992; McGowan and Motani, 2003; Tongtherm *et al*., 2020). *Thaisaurus*, from the lower part of the Chaiburi Formation in southern Thailand, which occurs in a horizon that correlates with the middle lower Spathian *Columbites parisianus* Subzone in the western USA, is the oldest known ichthyopterygian (Tongtherm *et al*., 2020). The second oldest is *Chaohusaurus* from the upper lower Spathian *Procolumbites* Zone in South China (Ji *et al*., 2015), and fragments of ichthyopterygian skeletons have also been reported from the upper lower Spathian *Neocolumbites insignis* Zone in South Primorye (Nakajima *et al*., 2022).

The Osawa Formation is famous for the occurrence of the primitive ichthyopterygian, *Utatsusaurus hataii* Shikama *et al*., 1978. It occurs in the middle and upper parts of the formation (= middle and upper Spathian), but has not yet been found in the lowest part (= upper lower Spathian). Because South Kitakami was probably located near South China or South Primorye (see above discussion), it is anticipated that lower Spathian ichthyopterygians may eventually be found in the underlying Hiraiso and the lowest part of the Osawa formations.

Middle Spathian-aged ichthyopterygians have been found at many localities, including South China, British Columbia, western USA and Svalbard, suggesting that ichthyopterygians extended their geographical distribution throughout the Panthalassa during this period (Brinkman *et al*., 1992; Maxwell and Kear, 2013; Ji *et al*., 2015; Kelley *et al*., 2016). These fossil assemblages, including various taxa in the Osawa Formation, indicate that a complex marine ecosystem had been established by at least middle and late Spathian time. The Paris Biota of southeastern Idaho, USA reveals that a functionally complex and tropically multi-levelled marine ecosystem first appeared even earlier, i.e., in the earliest Spathian (Brayard *et al*., 2017), but as seen in the radiation of the ichthyopterygians, which added a new trophic level of top predators to the marine ecosystem, the recovery of the ecosystem may have accelerated during the middle Spathian.

Conclusions and remarks

A taxonomic revision of the ammonoid assemblage previously reported from the Osawa Formation at Akaushi in the Motoyoshi area, South Kitakami Belt, Northeast Japan, i.e., *Columbites parisianus*, *Subcolumbites perrinismithi* and *Eophyllites* cf. *dieneri*, leads to the conclusion that the fauna should be attributed to *Hellenites tchernyschewiensis*, *H. inopinatus*, *Neocolumbites grammi*, *N. insignis*, *Procolumbites ussuriensis* and *P. subquadratus*. In addition, this fauna also includes *Deweveria kovalenkoi*. Because these ammonoids are characteristic of the *N. insignis* Zone of South Primorye, Russian Far East, the lowest part of the Osawa Formation clearly correlates with the upper part of the lower Spathian (upper Olenekian, Lower Triassic), and the faunal similarity suggests that South Kitakami may have been located near South Primorye on the western side of the Panthalassa.

A complex marine ecosystem first appeared during the Spathian after the PTB mass extinction event. The Osawa Formation, attaining 250–300 m in thickness and ranging from the upper lower to upper Spathian, contains primitive ichthyoptergians and rich ammonoid faunas as well as thylacocephalan faunas and coprolites in various horizons. Further biostratigraphical, paleontological and paleoenvironmental studies of the Osawa Formation may provide an important key for further understanding the dynamics of the biotic recovery following the PTB mass extinction event.

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