Papers in Press

“Papers in Press” includes peer-reviewed, accepted manuscripts of research articles, reviews, and short notes to be published in Paleontological Research. They have not yet been copy edited and/or formatted in the publication style of Paleontological Research. As soon as they are printed, they will be removed from this website. Please note they can be cited using the year of online publication and the DOI, as follows:

Timing of bellerophontoid (Gastropoda) demise in the Early Triassic of South Primorye, Russian Far East

YASUNARI SHIGETA¹, TARO KUMAGAE², YURI D. ZAKHAROV³ and ALEXANDER M. POPOV³

¹Department of Geology and Paleontology, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan (e-mail: shigeta@kahaku.go.jp)

²Business Development Department, Asia and Oceania Project Division, Japan Petroleum Exploration Co., Ltd. 1-7-12 Marunouchi, Chiyoda-ku, Tokyo 100-0005, Japan

³Far Eastern Geological Institute, Russian Academy of Sciences, Far Eastern Branch, Stoletija Prospect 159, Vladivostok 690022, Russia
Abstract. The stratigraphic distribution and modes of occurrence of Early Triassic Bellerophontoidea (Gastropoda) are studied at seven sections in South Primorye, Russian Far East, where depositional environments ranging from nonmarine, via shoreface, to distal basin plain settings are recorded. Warthia zakharovi and Dicellonema abreakensis are abundant in Induan (Griesbachian and Dienerian) fine- to medium-grained, hummocky cross-stratified (HCS) sandstone beds occasionally intercalated with wavy-mudstone layers, whereas they are absent in coarser-grained cross-stratified succession. This observation suggests that bellerophontoids inhabited a lower shoreface environment above the storm wave base and possibly an inner shelf environment as well during this particular stage. Olenekian (Smithian and Spathian) bellerophontoids have not been found in the storm-induced sandstone beds, but W. zakharovi does occur in the lower Smithian sandstone beds of distal turbidites intercalated in the laminated mudstone. This mode of occurrence strongly suggests that W. zakharovi inhabited a deeper environment than lower shoreface, most probably an inner shelf environment, and after death, its shells were transported from their habitat to the basin-floor by sediment gravity flow. Bellerophontoids have not been found in
middle Smithian and younger strata in South Primorye, and the timing of this
disappearance is synchronous with other areas of the world. Bellerophontoids were
distributed over wide-ranging areas from the equator to the high latitudes during Induan
time, but they disappeared from the lower latitude areas and the shallower marine
environment of middle latitude South Primorye during the early Smithian, before
eventually becoming extinct during middle Smithian time. Such a step by step demise
strongly implies that the severe global warming and related harmful events that occurred
during the Smithian may have had a serious effect on bellerophontoids. This suggests
that because the Bellerophontoidea went extinct before the beginning of the late
Smithian, the group may have been more sensitive to global warming and related
harmful events than other organisms.

Key words: Bellerophontoidea, demise, Gastropoda, Smithian, South Primorye, Triassic

**Introduction**

The Bellerophontoidea, an extinct group of gastropods, is characterized by a
coiled bilaterally symmetrical shell with a median slit. It experienced high diversity and
abundance in the Paleozoic seas and even though it survived the end-Permian extinction, its diversity was severely diminished leading to its eventual extinction later in the Early Triassic. Bellerophontoidea is considered to be a typical example of a “Dead Clade Walking” phenomenon of survival without recovery (Jablonski, 2001, 2002; Nützel, 2005; Kaim and Nützel, 2011).

Early Triassic bellerophontoids have been reported from North America (Wyoming), Greenland, Spitsbergen, Europe (Italy, Hungary, Montenegro), Tibet, South China, Russia (South Primorye, Kolyma, Verkhoyansk), Pakistan (Salt Range), India (Kashmir), Oman, Japan and Australia (Queensland); the following three genera are recognized within the group: *Dicellonema* Yü and Wang in Yü (1975), *Retispira* Knight, 1945, *Warthia* Waagen, 1880 (Kaim and Nützel, 2011). While most occurrences are of Induan age (Griesbachian and Dienerian), early Olenekian (Smithian) bellerophontoids are known from several regions in Asia and found also in Australia. The reported occurrence in Tibet, consisting only of a single specimen whose stratigraphic level is uncertain, was originally considered to be of Anisian age (Yü, 1975). However, as discussed by Kaim and Nützel (2011) it is most likely Smithian in age. Therefore, the fact that there are no confirmed records of bellerophontoids from Spathian and younger strata, suggests that the group became extinct in the Smithian.
According to Kaim and Nützel (2011), the Bellerophontoidea probably went extinct at the Smithian-Spathian boundary, but the precise timing of this extinction has not been fully examined based on a detailed study of its stratigraphic distribution. In order to better understand the extinction timing of the Bellerophontoidea, we made a thorough geological survey of the Lower Triassic in South Primorye, where continuous molluscan-rich sequences ranging from the upper Griesbachian to the Spathian are widely distributed (Burij and Zharnikova, 1978; Markevich and Zakharov, 2004; Maeda et al., 2009; Shigeta et al., 2009b; Kaim, 2009). In this paper, we describe the detailed stratigraphic distribution and modes of occurrence of bellerophontoids in South Primorye and discuss the timing of their demise.

**Lower Triassic in South Primorye**

**Geological setting**

Strata of the Lower Triassic Series, consisting mainly of siliciclastic rocks formed by various depositional environments, are widely distributed in South Primorye (Markevich and Zakharov, 2004) and are divided lithologically into the Lazurnaya Bay and Zhitkov formations in ascending order (Zakharov, 1996, 1997). The Lazurnaya Bay
Formation unconformably overlies pre-Triassic basement rocks, and consists mainly of conglomerates and sandstones of various coastal environments influenced by waves and storms. The overlying Zhitkov Formation is dominated by mudstones of an offshore setting as well as sandstones derived from sediment gravity flows (see Maeda et al., 2009). Taken as a whole these sediments represent a fining upward and deepening transgressive succession. Furthermore, shallow-marine facies of the Lazurnaya Bay Formation are prevalent in the western part (Russky Island, Atlassov Cape), while offshore facies of the Zhitkov Formation are predominant in the northeastern and eastern parts (Artyom, Abrek Bay). As indicated by Zakharov (1968, 1997) and Shigeta and Maeda (2009), an eastward-deepening setting is inferred.

Both formations yield numerous well-preserved marine invertebrate fossils such as cephalopods, bivalves, gastropods and brachiopods from various horizons (e.g. Markevich and Zakharov, 2004). Based on ammonoid and conodont biostratigraphy, the Lower Triassic ranges in age from early Induan (Griesbachian) to the end of late Olenekian (Spathian) (Zakharov, 1968; Markevich and Zakharov, 2004).

**Paleogeography**

It is a widely accepted fact that the collision and amalgamation of continental or
microcontinental blocks was one of the major tectonic processes responsible for the formation of East Asia during the Permian and Triassic periods. The age distribution pattern of detrital monazites in the sandstones of the Lower Triassic in South Primorye is very similar to that of the Khanka Block, which was part of a continent attached to the Northeast China Block (Khanchuk, 2001; Yokoyama et al., 2009a, b). This evidence suggests that South Primorye was probably located along the eastern continental margin of the Khanka Block in the middle northern latitudes on the western side of the Panthalassa (Shigeta et al., 2009a).

**Studied sections in South Primorye**

In order to better understand the precise stratigraphic distribution and the habitat of bellerophontoids in South Primorye, we conducted a thorough geological survey of Lower Triassic rocks at seven sections (Figures 1, 2): Abrek Bay, Artyom, Seryj Cape, Tri Kamnya Cape, northeastern coasts of the Russky Island, southeastern coasts of the Russky Island, and Atlassov Cape sections. Although bellerophontoids were not found in all of these sections, we describe the lithology, sedimentary structures and modes of fossil occurrence for all sections to estimate the habitat by comparing sedimentary
Sections where bellerophontoids were found

*Abrek Bay section.*—The Abrek Bay section, located about 48 km southeast of the center of Vladivostok in a quarry on the northeastern coast of Abrek Bay, consists of a well exposed, approximately 165 m thick, continuous succession of the Lazurnaya Bay and Zhitkov formations (1 in Figures 1, 2; Maeda *et al.*, 2009). These strata unconformably overlie the Permian Abrek Formation and strike N40–70°E and dip 15–50° westward. The 85 m thick Lazurnaya Bay Formation consists of basal conglomerate, medium-grained bedded sandstone, and fine-grained sandstone intercalated with wavy-mudstone layers, while the overlying approximately 80 m thick Zhitkov Formation is comprised of dark gray, laminated mudstone with intercalations of fine-grained sandstone beds (Figure 2).

Aside from the lowermost part of the Lazurnaya Bay Formation, the remaining Lower Triassic strata are very fossiliferous, and ammonoids, nautiloids, gastropods, bivalves, brachiopods, conodonts and shark fossils are abundant throughout the sequence. Shigeta *et al.* (2009b) and Igo (2009) recognized nine ammonoid zones and three conodont zones ranging from the upper Induan (Griesbachian) to middle lower
Olenekian (middle Smithian), and placed the Induan-Olenekian (I/O) boundary at a horizon between AB1019 and AB1021 in the middle part of the Zhitkov Formation (Maeda et al., 2009, figs. 9, 17) based on the first occurrence of the conodont \textit{Novispathodus ex gr. waageni} (Sweet, 1970). However, we recently confirmed the occurrence of \textit{N. ex gr. waageni} at AB1014 in the lower part of the formation (Maeda et al., 2009, fig. 8). Thus, since the First Appearance Datum (FAD) of \textit{N. ex gr. waageni} has been basically accepted as the primary marker for the definition of the I/O boundary (Tong et al., 2003; Krystyn et al., 2007; Zhao et al., 2007), the I/O boundary should be placed at a horizon just below AB1014.

Specimens assignable to the Bellerophontoidea are found in various horizons of the Lazurnaya and Zhitkov formations. Kaim (2009) described two bellerophontoids from the Abrek Bay section, \textit{Warthia zakharovi} Kaim, 2009 and \textit{Bellerophon abrekenis} Kaim, but the latter species was later reassigned to genus \textit{Dicellonema} by Kaim and Nützel (2011). According to Kaim (2009), \textit{W. zakharovi} occurs in the lower part of the Lazurnaya Formation (AB1004, 1008; Griesbachian) and lower and middle parts of the Zhitkov Formation (AB1016, 1021; lower Smithian; see Figures 3E, F, 4I–L, T–W). In addition to these horizons, we confirmed the occurrence at AB1015 in the lower part of the formation (Figure 2). Occurrences of \textit{D. abrekenis} were documented in AB1010
(Figure 4A–D) and AB1012 of the middle and upper parts of the Lazurnaya Bay Formation (upper Griesbachian and Dienerian) and in AB1013 of the lowest part of the Zhitkov Formation (probably Dienerian). The upper part of the Zhitkov Formation is correlated with the middle Smithian. This part includes several fossiliferous beds (Maeda et al., 2009), but we were unable to find specimens assignable to the Bellerophontoidea.

_Seryj Cape section._—Located about 17 km northeast of the center of Vladivostok, the Lazurnaya Bay Formation approximately 120 m thick is well exposed along the shore southwest of Seryj Cape on the western coast of the Ussuri Gulf (3 in Figures 1, 2; Markevich and Zakharov, 2004). The strata generally strike NE–SW and dip 30–45° southward. Medium- to coarse-grained sandstone and conglomerate comprise the lowest part, while the remainder of the formation consists of fine- to medium-grained, hummocky cross-stratified (HCS) sandstone.

Shell fragments of ammonoids, gastropods, bivalves and brachiopods are occasionally abundant on the 1st- and 2nd-order erosional surfaces of the HCS sandstone beds, and the lower part of formation yields Griesbachian ammonoids, such as *Tompophiceras ussurense* (Zakharov in Zakharov and Rybalka, 1987) and
Lytophiceras eusakuntaka Zakharov in Zakharov and Rybalka, 1987 as well as bellerophontoids. Warthia zakharovi and Dicellonema abrekenosis occur together at SE-Bel-1 (43°10′30.9″N, 132°5′50.7″E; see Figure 4E–H, M-P) and B. abrekenosis specimens occur on erosional surfaces of HCS sandstone beds at SE-Bel-2 (43°10′26.5″N, 132°5′45.2″E; see Figure 3A–D).

Tri Kamnya Cape section.—The Tri Kamnya Cape section, located about 16 km east-northeast of the center of Vladivostok along the shore northeast of Tri Kamnya Cape on the western coast of the Ussuri Gulf, consists of a well exposed approximately 80 m thick succession of the Lazurnaya Bay and Zhitkov formations in ascending order (4 in Figures 1, 2; Shigeta and Kumagae, 2015). These strata generally strike NE–SW and dip 30–45° southward.

The Lazurnaya Bay Formation attains more than 60 m thick and consists of fine-to medium-grained, HCS sandstone in the lower part of the formation and low-angle cross-stratified, relatively thin-bedded muddy sandstone with intercalated sandy mudstone beds in the upper part. In contrast, the overlying 20 m thick Zhitkov Formation is comprised of dark grey laminated mudstone intercalated with fine-grained sandstone.
Ammonoids, gastropods, bivalves and brachiopods are abundant in the Zhitkov Formation, which yields typical upper lower Smithian ammonoids such as *Palaeokazakhstanites ussuriensis*, *Shamaraites schamaraensis* (Zakharov, 1968) and *Euflemingites prynadai* (Kiparisova, 1947). In addition, a single specimen assignable to *Warthia zakharovi* was found at Tr-Bel-1 (43°9’34.7”N, 132°4’20.6”E; see Figure 4Q–S).

Sections where bellerophontoids were not found

*Artyom section.*—The Artyom section consists of a 138 m thick continuous succession of the Zhitkov Formation in a quarry about 8 km south of Artyom City, located approximately 30 km northeast of the center of Vladivostok (2 in Figures 1, 2; Shigeta and Kumagae, 2015, 2016). Strata generally strike E–W and dip 25–40° southward. The 11 m thick lowest part was previously included in the Lazurnaya Bay Formation, but its alternating beds of sandstone and sandy mudstone suggest that this part should be included in the Zhitkov Formation. The overlying 127 m thick portion is composed of dark grey to black laminated mudstone with intercalations of fine-grained sandstone in the lower part and weakly bioturbated, dark grey to black mudstone in the middle and upper parts (Shigeta and Kumagae, 2015, 2016).
Ammonoids, gastropods, bivalves, brachiopods and conodonts are abundant in the fine-grained sandstone beds in the lower part of the Zhitkov Formation. The lower Smithian ammonoid *Palaeokazakhstanites ussuriensis* (Zakharov, 1968) is found in the lower part of this interval, the middle Smithian index ammonoid *Owenites* Hyatt and Smith, 1905, occurs in the middle part, and the upper Smithian index ammonoid *Anasibirites* Mojsisovics, 1896 is found in the uppermost part. The middle and upper parts of the Zhitkov Formation are generally unfossiliferous, but rare occurrences of Spathian ammonoids in sandstone beds have been reported (Shigeta and Kumagae, 2016). Although many beds in the lower part of the formation are fossiliferous, we were unable to find specimens assignable to Bellerophontoida in the Artyom section.

**Northeastern coast of the Russky Island section.**—A 235 m thick succession of the Lower Triassic is well exposed along the northeastern coast of Russky Island from Margaritov Cape to Zhitkov Cape. (5 in Figures 1, 2; Markevich and Zakharov, 2004).

Structurally, the section is complex, beds generally strike NE–SW to NW–SE and dip 5–30° southward, while at south end of Zhitkov Cape, the dip is much steeper (30–60°).

The basal part of the Lazurnaya Bay Formation, consists of boulder conglomerate, which unconformably overlies pre-Triassic igneous rock at Margaritov Cape, while the
main part of the formation consists of fine- to medium-grained, HCS sandstone.

Bioturbated mudstones with intercalations of fine-grained sandstone beds characterize the overlying 82 m thick Zhitkov Formation, which is well displayed at the south end of Zhitkov Cape.

Fossils have not been found in the conglomerate of the basal part of the Lazurnaya Bay Formation, but bivalves and ammonoids are abundant in the main part. The middle Smithian index ammonoid Owenites is found in the middle part. The Zhitkov Formation yields the upper lower Spathian ammonoid Neocolumbites insignis Zakharov, 1968 from the lower part and the middle Spathian ammonoid Subfengshanites multiformis (Kiparisova, 1947) from the upper part. Although this section contains many fossiliferous beds, specimens assignable to the Bellerophontoidea have not been found in the middle Smithian to Spathian interval.

Southeastern coast of the Russky Island section.—Located about 18 km south of the center of Vladivostok, a thick succession of Lower Triassic strata more than 170 m thick is well exposed along the southeastern coast of Russky Island from Tobizin Cape to Tchernyshev Cape (6 in Figures 1, 2; Markevich and Zakharov, 2004). Strata generally strike NE–SW and dip 5–15° southward. The Lazurnaya Bay Formation, more
than 106 m thick, consists of fine- to medium-grained, HCS sandstone, while the
overlying, approximately 64 m thick, Zhitkov Formation is comprised of bioturbated
mudstone intercalated with fine-grained sandstone beds.

Bivalves, ammonoids, nautiloids and brachiopods are abundant in the Lazurnaya
Bay Formation. In particular, the middle part contains the lower Spathian ammonoid
*Tirolites ussuriensis* Zharnikova in Burij and Zharnikova (1981). The middle part of the
Zhitkov Formation yields the upper lower Spathian ammonoid *Neocolumbites insignis*
Zakharov, 1968 and the upper part contains the middle Spathian ammonoid
*Subfengshanites multiformis* (Kiparisova, 1947). As with the section on the NE coast of
Russky Island, this section also contains many intercalated fossiliferous beds probable
middle Smithian to Spathian age, but no specimens assignable to Bellerophontoidea
have been found.

*Atlassov Cape section.*—The Atlassov Cape section, situated about 18 km
northwest of the center of Vladivostok, is located about 1 km north of Atlassov Cape on
the western coast of the Amur Gulf. This well-exposed succession consists only of the
uppermost part of the Lazurnaya Bay Formation of 9 m thick and the overlying Zhitkov
Formation of 43 m thick (7 in Figures 1, 2; Zakharov et al., 2006). These strata
generally strike N60–65° E and dip 30–40° southward. The Lazurnaya Bay Formation consists of fine- to medium-grained, HCS sandstone and the overlying Zhitkov Formation is comprised of alternating beds of sandstone and bioturbated mudstone.

Ammonoids, bivalves and gastropods are abundant in the Zhitkov Formation; the middle Spathian ammonoid *Subfengshanites multiformis* (Kiparisova, 1947) is found in the lower part and the upper Spathian ammonoid *Ussuriphyllites amurenensis* (Kiparisova, 1961) occurs in the upper part. No specimens assignable to Bellerophontoidea have been found in this section.

**Discussion**

**Modes of bellerophontoid occurrence and habitat**

The Induan bellerophontoids *Warthia zakharovi* and *Dicellonema abrekensis* occur abundantly in the fine- to medium-grained, amalgamated HCS sandstone (without associated mudstone) of the Lazurnaya Bay Formation at the Seryj Cape section together with shell-fragments of ammonoids, bivalves, gastropods and brachiopods. Accumulations of these fossils are often seen on the erosional surfaces of HCS sandstone bottoms (Figure 3A–D). Sandstone characterized by HCS are interpreted as
representing deposition above storm wave base (SWB) in the lower shoreface and inner shelf environments; furthermore, HCS sandstone beds without associated mudstone beds represent coastal deposits below fair-weather wave base (Dott and Bourgeois, 1982; Cheel and Leckie, 1993).

At the Abrek Bay section bellerophontoids occur in fine-grained sandstone intercalated with wavy-mudstone layers in the Lazurnaya Bay Formation. Neither the sandstone nor the mudstone beds exhibit obvious sedimentary structures, but this facies gradually changes upward into mudstone with slump-folded and brecciated intercalations of the Zhitkov Formation, which implies a deposition in a slope. This evidence suggests that the sandstone in which the bellerophontoids occur was probably deposited in a lower shoreface–inner shelf environment. However, it is unclear whether the bellerophontoids actually inhabited the inner shelf environment, because after death their shells were transported from their habitat to the inner shelf by current and sediment gravity flow.

In contrast to sandstones deposited in lower shoreface and inner shelf environments, bellerophontoids are not found in the medium- to coarse-grained sandstones with large-scale, high-angle cross-stratification that are typically observed in the lowest part of the Lazurnaya Bay Formation in the Abrek Bay and Seryj Cape.
sections; these sandstones were probably deposited in an upper shoreface. This suggests that bellerophontoids inhabited a lower shoreface environment influenced by storms below the fair-weather wave base and possibly an inner shelf environment during the Induan (Figure 5).

The early Smithian bellerophontoid *Warthia zakharovi* is abundant in sandstone beds sporadically intercalated in the laminated mudstone deposited under an extensive anoxic environment (Maeda et al., 2009). Specimens occasionally preserved as accumulations in the bed exhibit a monospecific assemblage (Figure 3E, F). These beds consist of fine- to medium-grained, well to moderately sorted sandstone exhibiting a fining upward graded-bedding, and the basal part, characterized by erosional surfaces, contains rip-up clasts of laminated mudstones (Maeda et al., 2009). These features are typical characteristics of Ta flow regime of the Bouma sequence (Bouma, 1962; Lowe, 1982; Mulder and Alexander, 2001). Because these strata were obviously deposited in an anoxia which was free from benthic activities, the bellerophontoid shells were most likely transported from their habitat to the basin-floor by sediment gravity flow. Olenekian (Smithian and Spathian) bellerophontoids have not been found in the fossiliferous HCS sandstone beds. This evidence suggests that bellerophontoids inhabited a deeper environment than lower shoreface, most likely an inner shelf
environment (Figure 5). Such fossiliferous sandstone beds are also observed in the middle Smithian to Spathian parts of the Zhitkov Formation, but bellerophontoids have not been found in this interval in South Primorye.

**Timing of bellerophontoid demise**

Smithian (early Olenekian) bellerophontoids are known from Tibet, the Salt Range, Verkhoyansk, South Primorye and Australia. We herein report the occurrence of *Warthia zakhari* from the lower Smithian of South Primorye. In the Salt Range, Waagen (1895) referred to the Bellerophontoidea-bearing beds as *Stachella* (or *Bellerophon*) beds and reported their stratigraphic position to be between the *Flemingites flemingianus* beds and the Lower sandstone beds in the Ceratite Sandstone, which is correlated with the upper lower Smithian (Brühwiler et al., 2012). Kaim et al. (2013) revealed that *W. hisakatsui* Murata, 1981 occurs in the *F. nanus* beds of the middle lower Smithian to the *F. flemingianus* beds of the uppermost lower Smithian. In Verkhoyansk, Dagys et al. (1979) reported the occurrence of *W. borealis* (Spath, 1930) in the *Hedenstroemia hedenstroemi* Zone of the lower Smithian (Tozer, 1994) or possibly uppermost Induan (Zakharov and Moussavi, 2013). In Australia, *Warthia* sp, which was originally illustrated as *Stachella* sp. (Runnegar, 1969, pl. 103, figs. 1, 2,
8–10), occurs in the Flemingites-bearing beds of the lower Smithian. Although the occurrence in Tibet was originally considered to be of Anisian age (Yü, 1975), it is now believed to be of probable Smithian age as discussed by Kaim and Nützel (2011). Aside from the questionable occurrence in Tibet, it is certain that the Bellerophontoidea disappeared throughout the world during the middle Smithian.

Kaim and Nützel (2011) has revealed that bellerophontoids were widely distributed from the equator to high latitudes in the many areas of world during Induan time (Figure 6A). Retispira occurred mostly in the low latitude areas of Panthalassa, whereas Dicellonema and Warthia exhibited a worldwide distribution. Bellerophontoids disappeared from the lower latitude areas during the early Smithian; Retispira became extinct and Dicellonema occurs only rarely in Tibet, while Warthia was widely distributed in middle to high latitude areas (Figure 6B). Our study reveals that Warthia disappeared from the shallower marine (lower shoreface) environment in South Primorye during the early Smithian, but continued to inhabit a deeper environment, most likely a shelf environment before eventually going extinct during the middle Smithian.

During the Induan, the gradient of functional diversity of marine ecosystems between the equator and northern latitudes was low (Foster and Twitchett, 2014), which
may reflect the cosmopolitan nature of Induan benthic faunas (Benton and Twitchett, 2003). Foster and Twitchett (2014) suggested that this low gradient implies relatively greater ecological impact in the tropics, which may be a consequence of climatic warming as well as the loss of reef ecosystems. According to Foster et al. (2015, 2018), nearshore environments recorded in western Palaeotethys during the Induan and Smithian are characterized by taxonomically homogenous fossil assemblages of low diversity and low evenness, but shoal and mid-ramp environments further offshore contain high diversity faunas with a greater functional complexity. The nearshore, wave-aerated habitats may have been stressful environments such as high temperatures, large salinity fluctuations, high turbidity, and/or eutrophication (Nützel and Schulbert, 2005; Algeo and Twitchett, 2010; Song et al., 2014; Schobben et al., 2015; Foster et al., 2015, 2018).

The global warming event that began in the early Smithian became more severe as time progressed and by middle Smithian time, temperatures of the upper water column in the equatorial areas approached 38°C, or possibly even 40°C (Sun et al., 2012; Zhang et al., 2019). It is generally agreed that these high temperatures drove the drastic change of marine and terrestrial ecosystems and probably were a major cause of a deep-cutting extinction at the beginning of the late Smithian (Zhang et al., 2019). Our
study reveals the step by step demise of the Bellerophontoidea during early to middle Smithian time, which occurred earlier within low latitude areas and shallower waters. This evidence suggests that global warming and related harmful events very likely had a serious effect on the Bellerophontoidea. Because it became extinct before the beginning of the late Smithian, this group may had been more sensitive to global warming and related harmful events than other organisms.

Conclusions

We conclude that the Belleropphontoidea in South Primorye flourished in a lower shoreface environment influenced by storms and even possibly an inner shelf environment during the Induan, then disappeared from the lower shoreface environment and inhabited a probable inner shelf environment during the early Smithian before finally becoming extinct during middle Smithian time.

Bellerophontoids were geographically widely distributed ranging from the equator to high latitudes during Induan time, but they disappeared from the lower latitudes and the shallower marine environment of middle-latitude South Primorye during the early Smithian. This step by step demise strongly implies that the global
warming and related harmful events that became more severe during Smithian time most likely had a serious effect on the Bellerophontoidea. This fact that it went extinct before the beginning of the late Smithian, suggests that the group may have been more sensitive to global warming than other organisms.

Acknowledgements

We thank Andrzej Kaim (Instytut Paleobiologii PAN, Warszawa), an anonymous reviewer and associate editor Haruyoshi Maeda (Kyushu University Museum, Fukuoka) for valuable comments on the first draft. Thanks are extended to Jim Jenks (West Jordan, Utah) for his helpful suggestions and improvement of the English text. This study was financially supported by JSPS KAKENHI Grant Number JP16K05598 for Y. S. and by part of the grant RFBR 18-05-00023 for Y. Z.

References


Foster, W. J., Danis, S. and Twitchett, R. J., 2017: A silicified Early Triassic marine


Knight, J. B., 1945: Some new genera of the Bellerophontacea. *Journal of Paleontology,*


Mojsisovics, E., 1896: Beiträge zur Kenntniss der obertriadischen Cephalopoden-Faunen des Himalaya. *Denkschriften der kaiserlichen Akademie*


Shigeta, Y. and Kumagae, T., 2015: *Churkites*, a trans-Panthalassic Early Triassic


Yokoyama, K., Shigeta, Y. and Tsutsumi, Y., 2009a: Age distribution of detrital


*Supplemento agli Annali dei Musei Civici di Revereto, Sezione: Archeologia, Storia e Scienze Naturali*, vol. 11, p. 133–156.


Zhang, Lei, Orchard, M. J., Brayard, A., Algeo, T. J., Zhao, L., Chen, Z-Q. and Lyu, Z.,


**Author contributions**

All authors carried out the geological survey, collected fossils and contributed to the writing of the paper.
Figure 1. Index map showing study sections (1 through 7) in South Promorye. 1, Abrek Bay section; 2, Artyom section; 3, Seryj Cape section; 4, Tri Kamnya Cape section; 5, northeastern coast of the Russky Island section; 6, southeastern coast of the Russky Island section; 7, Atlassov Cape section.

Figure 2. Stratigraphic occurrence of bellerophontoids in studied sections (1 through 7, see Figure 1). For details of localities in Abrek Bay section with prefix “AB” see Maeda et al. (2009). As, Anasibirites; Ly, Lytophiceras eusakuntaka; Nc, Neocolumbites insignis; Nw, Novispathodus ex gr. Waageni; Ow, Owenites; Pk, Palaeokazakhstanites ussuriensis; Sf, Subfengshanites multiformis; Tl, Tirolites longilobatus; To, Tompophiceras ussurense; Tu, Tirolites ussuriensis; Up, Ussuriphyllites amurensis.
Figure 3. Modes of occurrence of bellerophontoids. **A–D, Dicellonema abrekenis**

(Kaim, 2009) in Induan hummocky cross-stratified sandstone at Se-Bel-2 in the Seryj Cape section; A, vertical section including shell accumulation (arrow); B, shell accumulation on a weathered bedding plane; C, D, *Dicellonema*, bivalve and *Gyronites* shells on a bedding plane (C, NMNS PM35484; D, NMNS PM35485); E, F, shell accumulation of *Warthia zakharooi* Kaim, 2009 in lower Smithian sandstone bed intercalated in laminated mudstone at AB1016 in the Abrek Bay section; E, horizontal view (NMNS PM14752); F, vertical view of a sectioned piece (NMNS PM35486).

Figure 4. Early Triassic bellerophontoids from South Primorye, Russian Far East. **A–H, Dicellonema abrekenis** (Kaim, 2009); A–D, NMNS PM23331, holotype from AB1010 in the Abrek Bay section, Induan; E–H, NMNS PM35487, from Se-Bel-1 in the Seryj Cape section, Induan; **I–W, Warthia zakharooi** Kaim, 2009; I–L, NMNS PM23322, holotype from AB1016 in the Abrek Bay section, lower Smithian; M–P, NMNS PM35488, from Se-Bel-1 in the Seryj Cape section, Induan; Q–S, NMNS PM35489, from Tr-Bel-1 in the Tri Kamnya Cape section, lower Smithian; T–W, NMNS PM23330, from AB1021 in the Abrek Bay section, lower Smithian.
Smithian.

Figure 5. Habitats of Early Triassic bellerophontoids from South Primorye. Key: White circles, *Dicellonema abrekenis* (Kaim, 2009); black circles, *Warthia zakharovi* Kaim, 2009; hyphens, bellerophontoids not yet found in these facies; blank, outcrops of these facies not present.

Figure 6. Paleogeographical distribution of bellerophontoids, *Dicellonema* (white circle), *Retispira* (white star) and *Warthia* (black circle), during Induan (A) and Smithian in early Olenekian (B) based on Kaim and Nützel (2011), Kaim et al. (2013) and Foster et al. (2017, 2019). Paleomaps modified after Péron et al. (2005), Brayard et al. (2006) and Shigeta et al. (2009a). NEC, Northeast China Block; 1, Wyoming; 2, Verkhoyansk; 3, Spitsbergen; 4, Greenland; 5, Kolyma; 6, Montenegro; 7, Hungary; 8, northern Italy; 9, Oman; 10, Kashmir; 11, Salt Range; 12, Tibet; 13, Spiti; 14, Queensland; 15, Guangxi; 16, Guizhou; 17, Chongqing; 18, Shikoku in Japan; 19, South Primorye.
Figure 1. Index map showing study sections (1 through 7) in South Promorye. 1, Abrek Bay section; 2, Artyom section; 3, Seryj Cape section; 4, Tri Kamnya Cape section; 5, northeastern coast of the Russky Island section; 6, southeastern coast of the Russky Island section; 7, Atlassov Cape section.

149x96mm (300 x 300 DPI)
Figure 2. Stratigraphic occurrence of bellerophontoids in studied sections (1 through 7, see Figure 1). For details of localities in Abrek Bay section with prefix “AB” see Maeda et al. (2009). As, Anasibirites; Ly, Lytophiceras eusakuntaka; Nc, Neocolumbites insignis; Nw, Novispathodus ex gr. Waageni; Ow, Owenites; Pk, Palaeokazakhstanites ussuriensis; Sf, Subfengshanites multiformis; Ti, Tirolites longilobatus; To, Tompophiceras ussurense; Tu, Tirolites ussuriensis; Up, Ussuriphyllites amurensis.
Figure 3. Modes of occurrence of bellerophontoids. A–D, Dicellonema abrekenensis (Kaim, 2009) in Induan hummocky cross-stratified sandstone at Se-Bel-2 in the Seryj Cape section; A, vertical section including shell accumulation (arrow); B, shell accumulation on a weathered bedding plane; C, D, Dicellonema, bivalve and Gyronites shells on a bedding plane (C, NMNS PM35484; D, NMNS PM35485); E, F, shell accumulation of Warthia zakharovi Kaim, 2009 in lower Smithian sandstone bed intercalated in laminated mudstone at AB1016 in the Abrek Bay section; E, horizontal view (NMNS PM14752); F, vertical view of a sectioned piece (NMNS PM35486).

214x279mm (300 x 300 DPI)
Figure 4. Early Triassic bellerophontoids from South Primorye, Russian Far East. A–H, Dicellonema abrekensis (Kaim, 2009); A–D, NMNS PM23331, holotype from AB1010 in the Abrek Bay section, Induan; E–H, NMNS PM35487, from Se-Bel-1 in the Seryj Cape section, Induan; I–W, Warthia zakharovi Kaim, 2009; I–L, NMNS PM23322, holotype from AB1016 in the Abrek Bay section, lower Smithian; M–P, NMNS PM35488, from Se-Bel-1 in the Seryj Cape section, Induan; Q–S, NMNS PM35489, from Tr-Bel-1 in the Tri Kamnya Cape section, lower Smithian; T–W, NMNS PM23330, from AB1021 in the Abrek Bay section, lower Smithian.

214x279mm (300 x 300 DPI)
Figure 5. Habitats of Early Triassic bellerophontoids from South Primorye. Key: White circles, Dicellonema abrekensis (Kaim, 2009); black circles, Warthia zakharovi Kaim, 2009; hyphens, bellerophontoids not yet found in these facies; blank, outcrops of these facies not present.

<table>
<thead>
<tr>
<th>Olenekian</th>
<th>upper shoreface</th>
<th>lower shoreface</th>
<th>inner shelf</th>
<th>slope to basin plain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spathian</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Smithian</td>
<td>late</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>middle</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>early</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Induan</td>
<td>—</td>
<td>○ ●</td>
<td>?〇〇</td>
<td>—</td>
</tr>
</tbody>
</table>

91x51mm (300 x 300 DPI)
Figure 6. Paleogeographical distribution of bellerophontoids, Dicellonema (white circle), Retispira (white star) and Warthia (black circle), during Induan (A) and Smithian in early Olenekian (B) based on Kaim and Nützel (2011), Kaim et al. (2013) and Foster et al. (2017, 2019). Paleomaps modified after Péron et al. (2005), Brayard et al. (2006) and Shigeta et al. (2009a). NEC, Northeast China Block; 1, Wyoming; 2, Verkhoyansk; 3, Spitsbergen; 4, Greenland; 5, Kolyma; 6, Montenegro; 7, Hungary; 8, northern Italy; 9, Oman; 10, Kashmir; 11, Salt Range; 12, Tibet; 13, Spiti; 14, Queensland; 15, Guangxi; 16, Guizhou; 17, Chongqing; 18, Shikoku in Japan; 19, South Primorye.

98x135mm (300 x 300 DPI)