Early Jurassic belemnites from the Gondwana margin of the Southern Hemisphere—Sinemurian record from South Tibet

Yasuhiro Iba a,⁎, Shin-ichi Sano b, Xin Rao c, Dirk Fuchs a, Tingen Chen c, Robert Weis d, Jingeng Sha c

a Department of Natural History Sciences, Hokkaido University, N10W8, Kitaku, Sapporo, Hokkaido 060-0810, Japan
b Fukui Prefectural Dinosaur Museum, Fukui 911-8601, Japan
c State Key Laboratory of Palaeoecology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China
d Musée National D’Histoire Naturelle, 25 Rue Münster, 2169 Luxembourg, Luxembourg

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ABSTRACT

Belemnites (Order Belemnitida), a very successful group of Mesozoic coleoid cephalopods, dominated fossil coleoid assemblages throughout the Jurassic and Cretaceous. According to the current view, the phylogenetically earliest known belemnites have been reported from the lowermost Jurassic (Hettangian) of northern Europe. The earliest belemnites are characterized by low diversity and small-sized rostra. Their distribution has until recently been assumed to be restricted to northern Europe until the Pliensbachian. Early belemnites (the Sinobelemnitidae and the Belemnitina) are now also known from the Late Triassic of China and the Hettangian–Sinemurian of Japan, and therefore from the eastern Tethys and western Paleo-Pacific oceans. It has been suggested that the distribution of belemnites became more widespread and expanded to the Southern Hemisphere for the first time in the Toarcian. Here we re-describe a Sinemurian belemnite from South Tibet, which was located at the Gondwana margin at that time. The specimen is characterized by a long rostrum with one deep and long alveolar groove with a splitting surface, whose position cannot be determined as being either dorsal or ventral. This morphological feature allows an assignment of the re-described rostrum to either the Sinobelemnitidae or the Pachybelemnopseina. The Sinemurian belemnite from Tibet represents the earliest firm record of the Belemnitida from the Southern Hemisphere, suggesting that the wide distribution and diversification of this order was established much earlier than previously thought.

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1. Introduction

Belemnites (Order Belemnitida) are an extinct group of coleoid cephalopods, which had significant biomass and occur abundantly and worldwide in the Late Mesozoic. Belemnites therefore likely played an important role in Jurassic–Cretaceous marine environments as both predators and prey (e.g., Doyle and Macdonald, 1993; Rexfort and Mutterlose, 2006). The understanding of the rise, radiation and fall of belemnites is therefore crucial for unraveling the evolution of the Mesozoic marine ecosystems. Distribution and diversity patterns of belemnites in Middle Jurassic to Cretaceous times have been well recognized (e.g., Doyle, 1987; Mutterlose, 1998; Christensen, 2002; Kořťák, 2004; Iba et al., 2011). Their evolutionary history in the Early Jurassic is, however, not fully understood (e.g., Doyle, 1994; Doyle et al., 1997; Sanders et al., in press). Previously, it was thought that belemnites originated during the earliest Jurassic (Hettangian) and their distribution was restricted to Europe until the Pliensbachian. The causes for this paleogeographically limited distribution remains open (Doyle, 1993, 1994; Doyle et al., 1994; Weis and Delsate, 2006). In order to solve this enigma, the swimming ability of early belemnites, which certainly controls their biogeographic patterns, has been discussed recently (e.g., Weis et al., 2012). Hettangian records from Japan recently reported by Iba et al. (2012) shed new light on the neglected existence of early Jurassic belemnites outside Europe (Yokoyama, 1904). The observations by Iba et al. (2012) moreover re-opened the discussion on the presence of Late Triassic (Carnian) belemnites in South China (Zhu and Bian, 1984). Considering these East Asian belemnites were attributed to the Sinobelemnitidae. Iba et al. (2012) argued that the earliest belemnites originated in the eastern Tethys and western Paleo-Pacific rather than in Europe. Consequently, the early evolutionary history of the Belemnitida now needs a complete revision that requests a new focus on records outside of Europe.

In the light of this, it is necessary to reassess observations made by Chen (1982), who described belemnites from the Sinemurian (Early Jurassic) to Cretaceous of South Tibet. Chen (1982) reported on the occurrence of three Sinemurian belemnite taxa, Salpingoteuthis sp., Belemnopsis sp. and Passaloteuthinae gen. et sp. indet. Doyle et al. (1997) reviewed all published records of Early Jurassic belemnites in the world, and concluded that true belemnites did not expand into the Southern Hemisphere in pre-Toarcian time. Doyle et al. (1997)
rejected therefore the affinity of the Tibetan material to the Belemninitida and included the material under discussion in the Order Aulacocerida, another coleoid group that was common in the Triassic but declined in the Early Jurassic. To overcome these inconsistencies in taxonomy and to find new evidence for Early Jurassic non-European belemnites, we re-studied the “Salpingoteuthis” specimen of Chen (1982) from the Sinemurian of South Tibet. The rostrum represents the earliest belemnite record in the Southern Hemisphere at that time. Its paleobiogeographical and evolutionary significance is discussed in the present study.

2. Material

The material of Chen (1982), which is stored in the collection of the Nanjing Institute of Geology and Palaeontology (NIGP), has been studied. The single specimen described and figured as Salpingoteuthis sp. in Chen (1982) comes from Guomachong, Ridang, Lhunze County, South Tibet (Fig. 1) and consists of an incomplete belemnite rostrum (NIGP no. 58844). Two other Sinemurian belemnites listed by Chen (1982), Belemnopsis sp. and Passaloteuthinae gen. et sp. indet., were not found in the collections in Nanjing.

3. Geological setting

Salpingoteuthis sp. of Chen (1982) co-occurred with ammonites Euagassiceras sp. and Gleviceras sp. in the Ridang Formation in Guomachong, Ridang, Lhunze County, South Tibet (Fig. 1) (Chen, 1982). Both Euagassiceras and Gleviceras indicate the Sinemurian age, and show wide distribution: Euagassiceras occurs from Europe, Mexico, Argentina, Ecuador, Colombia, and Gleviceras from Europe, Morocco, Canada, Alaska, Mexico, and Peru (Howarth, 2013). Wang and He (1981) also reported these two Sinemurian ammonites from the same formation and area. The co-occurrence of ammonites suggests that the belemnite specimen described here can be assigned to the Sinemurian.

The area where the specimen has been found is located in the south of the Yarlung Zangbo Suture Zone, and thus belongs to the northern Himalaya region (Fig. 1). Since the Yarlung Zangbo Suture Zone represents the collisional tectonic boundary between the Eurasian Plate and the Indian Plate, the Northern Himalaya represents a part of northern Indian Plate. This area was therefore located in the Southern Hemisphere, namely the Gondwana margin, in Jurassic times.

4. Systematic paleontology

Subclass Coleoidea Bather, 1888
Order Belemninitida Zittel, 1895

4.1. Description

The medium-sized, slender conical rostrum exhibits both a symmetrical outline and profile (Fig. 2a–e). The apex and alveolar region are missing. Most of the rostrum is still covered with sediments (Fig. 2b). Its external shape, especially that in the apical region (Fig. 2a, and b6–8), does not represent its original morphology (Fig. 2a, b). The total length of the preserved rostrum is 66.3 mm. The maximum dorso-ventral diameter and lateral diameter, which is located at the anterior end is 7.3 mm and 7.8 mm, respectively (Fig. 2b1). The transverse section is dorso-ventrally depressed in the stem region (Fig. 2b1–5) and circular in the apical region (Fig. 2b6–8). The ratio of the dorso-ventral diameter/lateral diameter is ranges from 1.0 (Fig. 2b8) to 1.2 (Fig. 2b1). A single alveolar groove is visible on the external surface of the rostrum, which was shown in Chen (1982, plate 20-16). Unfortunately, this part of the rostrum was cut longitudinally in subsequent scientific works and half of the rostrum of the alveolar part was lost. The transverse sections (Fig. 2b) suggest that the alveolar groove extends up to the apical part (Fig. 2a, b7), but it does not reach the apex (Fig. 2a, b8). The groove is deep and V-shaped in the anterior part, it cuts the growth lines, accompanied by a well-developed splitting surface (Fig. 2a, b1–3, f, g). Posteriorly, the groove becomes gradually shallower until it peters out in the apical region (Fig. 2b4–6). Unfortunately, it cannot be determined whether the alveolar groove is situated on the ventral or dorsal side, because the phragmocone is missing. Also, there is no evidence of either an apical groove or striae.

4.2. Comparison with selected belemnite genera of the Early–Middle Jurassic

The present specimen (NIGP no. 58844; Salpingoteuthis sp. of Chen (1982)) is definitely not congeneric with Salpingoteuthis (Doyle, 1992), because of the lack of diagnostic characters such as multiple, elongated ventral and dorsal grooves along the rostrum. It is even doubtful to include the specimen in the Suborder Belemnitina due to the presence of an alveolar groove and the absence of an apical groove.

With respect to the existence of an alveolar groove, the Family Sinobelemnitidae (suborder uncertain) and the Suborder Pachybelemnopaenia (Belemnova) must be taken into consideration. The rostra of both taxa can be distinguished by the position

Fig. 1. Map showing the locality of the Sinemurian belemnite in South Tibet. Geological map is modified from the Bureau of Geology and Mineral Resources of Xizang Autonomous Region (1993). Abbreviations: Ca: Cambrian, Tr: Triassic, Ju: Jurassic, Cr: Cretaceous, Eo: Eocene, Ce: Cenozoic.
of the groove, which is dorsal in the Sinobelemnitidae and, with the exception of the Duvaliidae, Dicoelitidae, Pseudodicoelitidae, ventral in the Pachybelemnopseina (Iba et al., 2012) (Table 1). Since it is difficult to determine whether the alveolar groove in our present specimen is located dorsally or ventrally, the assignment to either the Sinobelemnitidae or the Pachybelemnopseina is difficult to assess.

The Sinobelemnitidae, which has a dorsal alveolar groove with a distinct splitting surface, include only two genera, Sinobelemnites (Carnian) and Sichuanobelus (Carnian–Sinemurian) (Zhu and Bian, 1984; Iba et al., 2012; Iba, in press). The rostrum of Sinobelemnites is characterized by laterally compressed rostra with well-developed multiple lateral lines. Since these morphological characters are absent in our Tibetan specimen, it can be clearly differentiated from Sinobelemnites. The Sichuanobelus rostrum is characterized as a laterally compressed rostrum without lateral lines (Table 1). There is a minor difference between rostrum shape of Sichuanobelus and Tibetan specimen (i.e., laterally compressed or dorso-ventrally depressed rostrum) (Table 1).

The Duvaliidae, which occurs worldwide from Bathonian–Aptian has no splitting surface along its dorsal alveolar groove (Doyle and Mariotti, 1991 and our own observations). The lack of splitting surface in the Duvaliidae shows large morphological differences with the Tibetan specimen (Table 1). The dicoelitid belemnites, such as Dicoelites can be considered as early members of the Pachybelemnopseina, whose earliest records were recognized in the Toarcian of Arctic Canada and South Tibet (Jeletzky, 1980; Wu, 1982). Dicoelites rostra have both a ventral and a dorsal alveolar groove (Stevens, 1964; Jeletzky, 1980). These morphological characters are absent in the Tibetan specimen (Table 1).

Weis et al. (2012) considered the Holcobelidae (Early Aalenian to Early Bajocian) to be the earliest representative of the Pachybelemnopseina. Calabribelus has an alveolar groove, which is U-shaped in transverse section. In contrast, Holcobelus has an intermediate groove with a rudimentary developed splitting surface (Weis et al., 2012). These morphological characters of the Holcobelidae are not developed in the specimen from Tibet (Table 1).

Other stratigraphically early genera of the Pachybelemnopseina such as Hibolithes and Pachybelemnopsis (Bajocian to Early Cretaceous for both genera) possess a ventral alveolar groove with well-developed splitting surface (e.g., Weis et al., 2012). The former genus differs significantly from the Tibetan belemnite by the hastate shape of the rostrum, and by its alveolar groove that is usually restricted to
The rostrum of *Pachybelemnopsis* is similar to that of the Tibetan specimen in having a comparatively long alveolar groove, and by a generally dorso-ventrally depressed rostrum (Riegraf, 1980; Mariotti et al., 2007; Weis et al., 2012). The Tibetan specimen, however, shows minor differences, such as circular shape in transverse section in the apical region.

Though the morphology of the specimen NIGP no. 58844 closely resembles that of *Sichuanobelus* (*Sinohelminitidae*) or *Pachybelemnopsis* (*Pachybelemnopsisena*), studied belemnite, cannot properly be assigned to either of these two families, because of the unknown position of the alveolar groove. The specimen is, therefore, tentatively determined as Belemninitida gen. et sp. indet. in this paper. A more refined taxonomic assignment of the material from Tibet should be discussed in future studies based on additional material.

5. Discussion and conclusions

5.1. Paleobiogeographical significance

The current hypothesis about the distribution of early belemnites is briefly summarized below. The earliest known belemnites are *Sinohelminitidae*, which were discovered in sediments of Late Triassic age (Carnian) in the Sichuan Province, South China (Zhu and Bian, 1984; Iba et al., 2012; Iba, in press). A possible Permian record also from South China (Chen and Sun, 1982) still needs to be re-investigated. Apart from the South Tibetan record described here, Early Jurassic (Hettangian–Pliensbachian) belemnites have been described only from Europe and Japan (e.g., Doyle, 1994; Iba et al., 2012, 2014, in press). Both areas were located at the northern Tethys margin at that time. Small forms of the *Belemninita* occur in Europe. On the other hand, large endemic forms of the *Belemninita*, and also *Sinohelminitidae* were recovered from Japan (Fig. 3).

Doyle et al. (1997) presumed that all belemnite records in the Southern Hemisphere from pre-Toarcian Jurassic sediments are members of the *Aulacocerida*. Following this, *Aulacocerids* were common components of the coleoid faunas of the Southern Hemisphere at that time. Doyle et al. (1997) concluded that a global turnover from *Aulacocerids* to belemnites occurred in the Toarcian. It has been considered that the distribution of belemnites became more widespread and expanded to the Southern Hemisphere for the first time in the Toarcian (e.g., Doyle et al., 1997). The oldest (Toarcian) specimens confirming this hypothesis are 1) *Brevibelus* and *Cylindroteuthis* from Chile, New Caledonia and New Zealand, 2) *Acrocoelites*-related forms from Argentina and possibly Antarctica, which show clear affinity to European taxa, and 3) *Dicoelites* from South Tibet. *Dicoelites* specimens of Toarcian age are unknown from Europe, but present in Arctic Canada (Jeletzky, 1980). In the present paper, however, the occurrence of a Sinemurian belemnite from South Tibet has been confirmed. This region was located at the Gondwana margin at that time, and thus the Tibetan Sinemurian belemnite represents the earliest firm record of belemnites from the Southern Hemisphere. This finding suggests that the worldwide distribution of the *Belemninita* was established much earlier than previously thought (Fig. 3). The paleobiogeography of early belemnites needs a complete revision considering their worldwide distribution since the Sinemurian at the latest. It is therefore suggested that records of putative belemnite in the Early Jurassic and even Triassic times, especially from the Southern Hemisphere and eastern Tethys, need to be re-investigated in order to reassess the coleoid paleobiogeography and turnover in Triassic–Early Jurassic times.

5.2. Evolutionary significance and importance of the Tibetan belemnite records

The Tibetan Sinemurian rostrum (NIGP no. 58844) is characterized by the presence of a single alveolar groove and the absence of apical grooves. These morphological characters have never been observed in
Early Jurassic belemnites (the Belemnitina) from Europe. Two belemnite groups, the Sinobelemnitidae and the Pachybelemnopsinae, have developed an alveolar groove similar to the Tibetan specimen, either dorsally or ventrally. As already discussed above, the systematic assignment either to the Sinobelemnitidae or the Pachybelemnopsinae is still uncertain. In both cases, however, the evolutionary history of belemnites with alveolar grooves needs revisions, and thus will briefly be discussed here.

The sinobelemnitids have been described from the Carnian of China and the Hettangian–Sinemurian of Japan (Iba et al., 2012; Iba, in press). These stratigraphic ranges are concordant with those of the Tibetan specimen. The sinobelemnitids are, so far, known only from the eastern Tethys or the western Paleo-Pacific, thus they are considered endemic to this region. If the Tibetan Sinemurian specimen belongs to the Sinobelemnitidae, the paleobiogeographic distribution of this belemnite family is much wider than previously thought, perhaps even global.

The early evolutionary history of the Pachybelemnopsinae is still uncertain, though its earliest records have been considered to be of Toarcian–Aalenian age. The Sinemurian age of the Tibetan specimen is remarkably older than these records. If the Tibetan Sinemurian specimen belongs to the Pachybelemnopsinae, the origin of this suborder must be dated back by at least 15 m.y. into the Sinemurian.

Recently, Weis et al. (2012) proposed a new hypothesis explaining the early evolution of the Pachybelemnopsinae. They suggest that this belemnite lineage started accordingly in the early Middle Jurassic with Holcobelus (intermediate groove with rudimentary splitting surface), evolved via Calabribelus (alveolar groove with rudimentary splitting surface), and finally reached Pachybelemnopsinae (alveolar groove with well-developed splitting surface). The center of origin was located in Europe and the Mediterranean region. The Tibetan Sinemurian record challenges this hypothesis since this specimen already has an alveolar groove with a well-developed splitting surface. Two different phylogenetic scenarios are possible: 1) the rostrum of the Sinemurian Tibetan belemnite independently developed the morphological character “alveolar groove with well-developed splitting surface” much earlier than the Holcobelus–Calabribelus–Pachybelemnopsinae lineage, or 2) this character is homologous and the Sinemurian Tibetan belemnite represents an earlier representative or even the root-stock of the Holcobelus–Calabribelus–Pachybelemnopsinae lineage.

Since the sinobelemnitids had acquired the character of a “single dorsal alveolar groove with well-developed splitting surface” already in the Late Triassic, much earlier than the Holcobelus–Calabribelus–Pachybelemnopsinae lineage that has a single ventral groove with rudimentary or well-developed splitting surface, the first explanation sounds possible. On the other hand, the occurrence of Calabribelus sp. in the Nieniexiongla Formation (Aalenian–Bajocian after Yin (2010)) in Zhada County, South Tibet, has been confirmed by our own observations. These Calabribelus specimens had been described by Chen (1982) as Hastites sp. (NIGP no. 58837) and Holcobelus cf. blainvilii (NIGP no. 58839). These specimens are characterized by a small-to-medium-sized rostrum, a cilindro-conical shape, a rounded lateral margin, the presence of a single, long (reaching to near apex) and deep (u-shaped in transverse section), ventral alveolar groove with rudimentary splitting surface, and the absence of an apical groove.

Although Calabribelus is usually considered to be endemic to Europe and the Mediterranean region (Weis et al., 2012), its coeval occurrence in South Tibet clearly indicates that this taxon is present at the Gondwana margin of the Southern Hemisphere. Thus, the evolutionary history of the Holocelididae, including the supposed Holcobelus–Calabribelus–Pachybelemnopsinae lineage, needs revision. These considerations need to account for records in the Southern Hemisphere and also the enigmatic records in northern Siberia and northeastern Russia (northern part of northwestern Paleo-Pacific) (Sachs and Nalnjaeva, 1975). The second hypothesis therefore also needs serious thought. The new observations discussed in this paper provide useful information for the future discussion of the early evolution of the Pachybelemnopsinae.

It should be noted that another early Pachybelemnopsinae related genus Diceloites was also recovered from the possibly Early Jurassic Pupuga Formation in Nyalam, western Tibet (Wu, 1982). However, the age of the Pupuga Formation is still debatable. Wu (1982) suggested a Toarcian age, based on the occurrence of several Early to Middle Jurassic ammonites. Later these ammonite records were completely revised, some of the specimens were re-assigned to an Early Cretaceous (Aptian) genus (Zhang, 1985). Other specimens are too poorly preserved to discern their systematic assignment. Some parts of the Pupuga Formation were, however, re-considered to be of Toarcian age based on the occurrences of new ammonite findings (Polyplectus disoides, Dumortieria sp. and Phymatoceras cf. crassicosta (Yin and Zhang, 1996; Yin, 2010)). The complex geological structure of this area, and the difficulty to date the Tibetan Diceloites precisely, allow no further interpretation at the moment. If a Toarcian age is confirmed, the Tibetan record represents one of the earliest records of the Dicoelitidae and possibly the earliest record of the Pachybelemnopsinae in the world along with the Arctic Canadian ones (Jeletzky, 1980; Doyle et al., 1997). The phylogenetic relationship between the Tibetan Sinemurian belemnite and the Toarcian Diceloites needs to be clarified, in order to better understand the early evolution of the Pachybelemnopsinae. Future studies should pay more attention to the Toarcian Diceloites, including a re-investigation of the Tibetan Diceloites specimen and its age assignment.

The early evolution of belemnites with an alveolar groove has not yet been fully understood. The presence of such belemnites in the Sinemurian of South Tibet indicates that belemnites had already diversified at this
time, much earlier than has been previously thought. Important belemnite records of the Early–early Middle Jurassic are still hidden in the Gondwana margin of the Southern Hemisphere. Further studies of the Early Jurassic belemnites from all over the world are necessary to reveal the early evolutionary history of belemnites on a global scale.

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