

# UPPER JURASSIC BELEMNITES FROM THE ORVILLE COAST, WESTERN ANTARCTICA, AND THEIR PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

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**ABSTRACT.** Specimens of three belemnite genera (*Belemnopsis* Bayle, *Hibolites* Montfort and *Prodwalia* Riegraf) are described from the Upper Jurassic Latady Formation of the Orville Coast, southernmost Antarctic Peninsula region. The species indicate a Kimmeridgian–Tithonian age. The belemnite assemblages, which are known from New Zealand and Indonesia as the *uhligi*-complex, also show a Mediterranean influence. It is possible to distinguish two stratigraphically separate immigration horizons. In the Kimmeridgian and Early Tithonian there existed faunal links with New Zealand, whereas, in the Late Tithonian, the fauna shows more Mediterranean affinities.

## INTRODUCTION

Throughout the Mesozoic, most of Antarctica was influenced by continental conditions and marine rocks have been described from the Antarctic Peninsula only. The central part of the Antarctic Peninsula is largely composed of calc-alkaline igneous rocks of Mesozoic–Cenozoic age (Andean Intrusive Suite and Antarctic Peninsula Volcanic Group). Within the fore- and back-arc basins, situated west and east of the volcanic arc, marine sediments accumulated (Rowley and others, 1983; Thomson, 1982; Thomson and others, 1983).

Rocks of the fore-arc include the fossiliferous Fossil Bluff Formation (Kimmeridgian–Albian) from which Willey (1972, 1973) described five belemnite genera: *Dimitobelus* Whitehouse, *Peratobelus* Whitehouse (family Dimitobelidae), *Belemnopsis* Bayle, *Hibolites* Montfort and *Neohibolites* Stolley (family Belemnopseidae). In the south-eastern part of the back arc-basin an alternation of dark sandstones, siltstones, clay and shales was deposited in the Late Jurassic. These rocks comprise the Lataday Formation and crop out along the Lassiter and Orville coasts (fig. 1). The greatest thickness of the Lataday Formation was estimated by Laudon and others (1983) to be several kilometres. None of the sections from the Orville Coast described by Laudon and others (1983) exposes the base or the top of the formation.

Apart from the material discussed by Willey (1972, 1973), belemnites have been found only at few localities. Stevens (1967) described *Conodicoelites* sp. from the Upper Jurassic (? Lower Kimmeridgian) of Lyon Nunataks, eastern Ellsworth Land; Laudon and others (1969) mentioned *Belemnopsis* sp. from sediments of similar age in the Behrendt Mountains and Weather Guesser Nunataks, eastern Ellsworth Land. Marine sediments of Byers Peninsula, Livingstone Island, South Shetland Islands, have yielded a Tithonian–Berriasian fauna including *Belemnites* (*Hibolites*) aff. *jaculum* (Phillips) (Tavera, 1970).

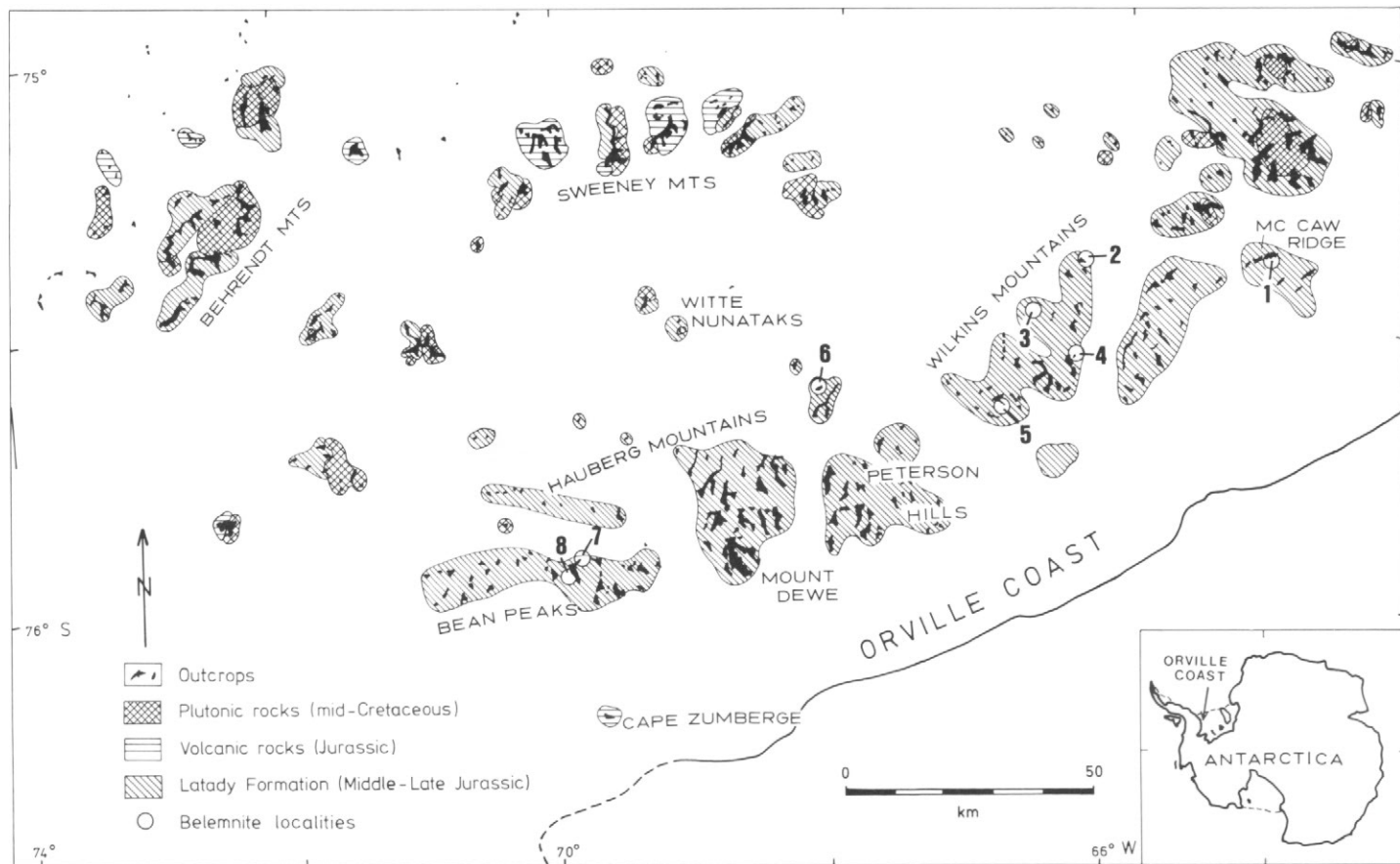


Fig. 1. Schematic outcrop map of the Orville Coast area, showing the belemnite-bearing localities mentioned in the text. Adapted from Thomson (1983).

## MATERIAL AND LOCALITIES

The belemnite guards described here are from the Upper Jurassic Lataday Formation of Orville Coast, Antarctica. They are most common in the Wilkins and the Hauberg mountains, and rarer in the Sweeney and Behrendt mountains. All the specimens referred to have come from the area between Bean Peaks, McCaw Ridge, Behrendt Mountains and Sweeney Mountains (Fig. 1). The material was collected in 1977-78 by a US Geological Survey party, led by Dr P. D. Rowley, and funded by National Science Foundation grant DPP 76-12557. Dr M. R. A. Thomson of British Antarctic Survey joined the party as palaeontologist and all fossils collected, including those described here, are housed in the collections of the British Antarctic Survey in Cambridge.

## MEASUREMENT OF BELEMNITE GUARD

The system of measurement commonly used by many authors (e.g. Stevens, 1965; Willey, 1973; Challinor, 1975*b*) has been adopted here, but the terms for the measurements differ (Fig. 2).

Preservation is poor. None of the guards is well preserved or complete, and the measurements that characterize the form of the guard could not be taken from exactly defined places. The anterior part of the guard is defined as the area near the alveolus, whereas the posterior part is that near the apical region.

In order to characterize the cross-section of various parts of the guard numerically, the ratio of the lateral and the corresponding dorso-ventral diameter has been calculated ( $Q = B : D$ ).

Apl	apical length, distance from protoconch to apex
Bp	lateral (transverse) diameter at the protoconch
Dp	dorso-ventral (sagittal) diameter at the protoconch
Bap	lateral diameter of the anterior part, between protoconch and B max
Dap	dorso-ventral diameter of the anterior part, between protoconch and D max
B max	maximum lateral diameter
D max	lateral diameter of the posterior part, between B max and apex
Dpp	dorso-ventral diameter of the posterior part, between D max and apex

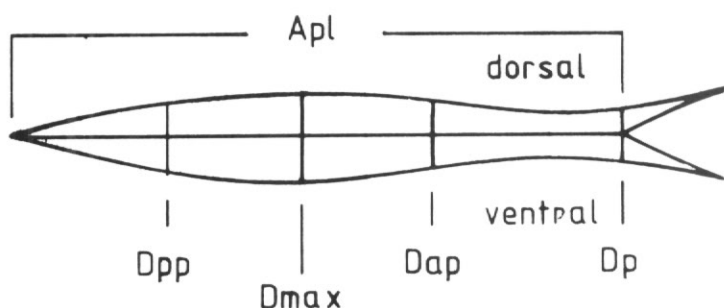
## SYSTEMATICS

The order Belemnitida is interpreted here in the sense of Jeletzky (1966). Three suborders may be recognized: (1) Belemnitina, characterized by one or more apical furrows; (2) the Belemnopseina, having alveolar grooves; (3) the Diplobelina, a group of small forms with much reduced guards.

- Class CEPHALOPODA Cuvier 1797
- Subclass COLEOIDEA Bather 1888
- Order BELEMNITIDA Naef 1912
- Suborder BELEMNOPSEINA Jeletzky 1965
- Family BELEMNOPSEIDAE Naef 1922
- Genus: *Hibolithes* Montfort 1808

Type species: *Hibolithes hastatus* Montfort 1808

profile (lateral view)



apical region | stem region | alveolar region

outline (ventral view)

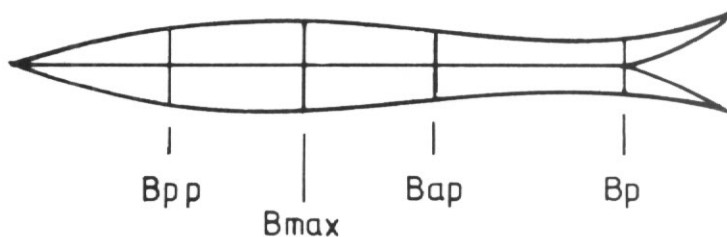


Fig. 2. Diagrammatic illustration of the profile and outline of a belemnite guard, indicating the symbols used in measurement. D, dorso-ventral diameter; B, lateral diameter; Apl, apical length.

*Diagnosis:* Guard elongate and slender, normally club shaped. A median ventral groove, often confined to the alveolar region, occasionally extends onto the stem region. The apical line is ortholineate.

*Comparison:* The guards of *Mesohibolites* are more stout and conical in shape, with a long median ventral groove. *Neohibolites* differs by having a short groove and a less-elongated guard.

*Remarks:* The genus *Hibolites* includes a wide range of forms ranging from elongate-cylindrical to stout, strongly hastate in shape. The length of the central groove varies as well. Another problem is the fact that *Hibolites* occurs in the Indo-Pacific and Tethyan realms as well as in the Boreal one. Isolation of *Hibolites* in these regions may have resulted in the evolution of endemic forms and it is possible that morphologically similar forms may have developed independently at any time within the three regions.

	1.	2.	3.	
<i>H. marwicki marwicki</i> Stevens				v d
<i>H. ex. gr. lagoicus</i> Boehm				v d
<i>H. compressus</i> Stolley (iuv. form)				v d
<i>H. joleaudi</i> Besairie				v d
<i>H. aff. marwicki marwicki</i> Stevens				v d
<i>H. brouweri</i> Kruizinga				v d
<i>H. verbeeki</i> Kruizinga				v d
<i>H. sp.</i>				v d

Fig. 3. Diagrammatic cross-sections of various species of *Hibolithes*. v, ventral; d, dorsal; 1, cross-section of the alveolar region; cross-section of the stem region; 3, cross-section of the apical region.

*Distribution:* *Hibolithes* ranges from the Middle Jurassic (Bajocian) up into the Lower Aptian. Its known geographical distribution is as follows: Middle Jurassic of central and southern Europe and New Zealand; Upper Jurassic of central and southern Europe, India, Madagascar, South America, New Zealand and Indonesia; Lower Cretaceous of central and southern Europe, northern Europe, North America, Madagascar, Australia and Indonesia.

*Hibolithes* aff. *marwicki marwicki* Stevens 1965 Fig. 4a, b  
aff. 1965 *Hibolithes marwicki marwicki* Stevens; p. 104, pl. 18, figs. 15-17.

*Material:* One specimen (V.106.1/b) from Bean Peaks, Orville Coast; locality 8 (Fig. 1).

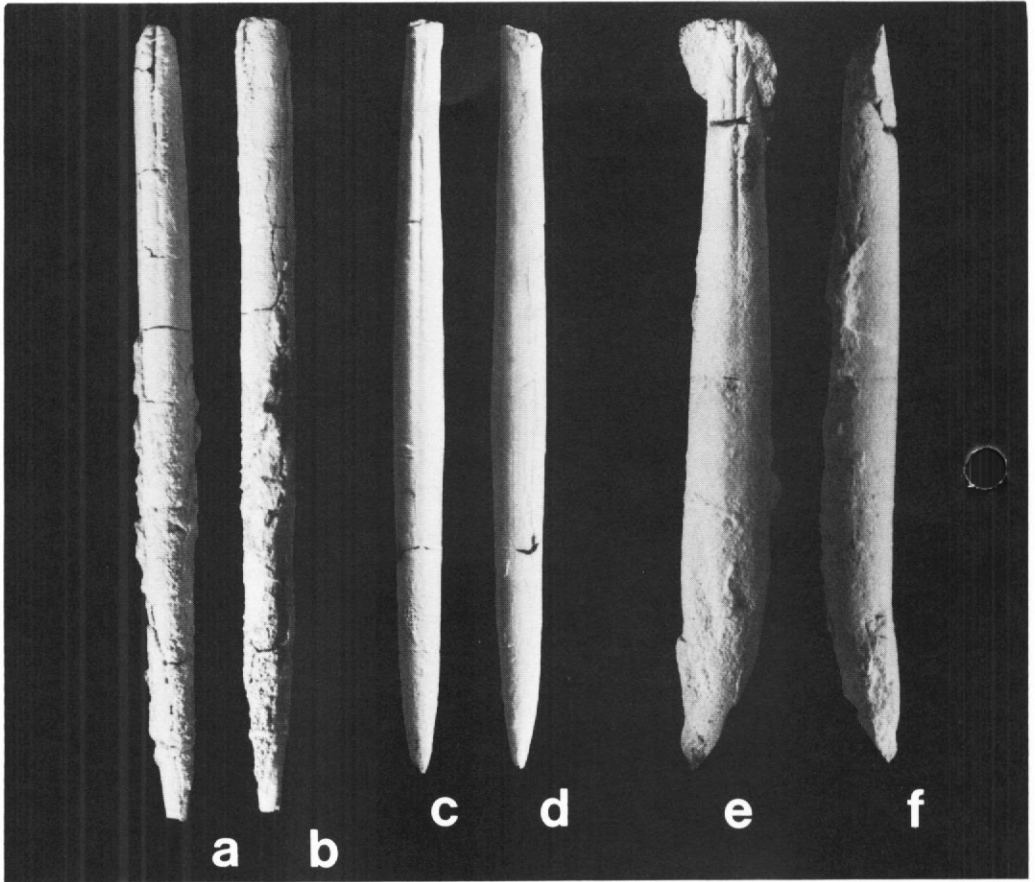


Fig. 4. a. *Hibolithes* aff. *marwicki marwicki* Stevens; ventral aspects of a guard; Orville Coast, Bean Peaks,  $\times 1$ , coated (V.106.1/b).  
 b. Right lateral aspects of the same specimen.  
 c. *Hibolithes marwicki marwicki* Stevens; ventral aspect of a cast; Te Puti Point, Kawhia Harbour, New Zealand; figured by Techmann (1923, p. 261, pl. 16),  $\times 1$ , coated (C. 29630, British Museum (Natural History)).  
 d. Right lateral aspect of the same specimen.  
 e. *Hibolithes* aff. *verbeeki* Kruizinga; ventral aspect of a guard; Orville Coast, Bean Peaks, coated (V.106.1/d).  
 f. Right lateral aspects of the same specimen.

*Description:* The outline of the elongate and slender guard is symmetrical and slightly hastate. The sides diverge in the anterior part of the stem region towards the apex and reach the maximum lateral diameter (B max) about mid way along the rostrum, after which they converge gradually ending in an elongate apical region. The profile is asymmetrical because the ventral surface is almost straight, except where it curves towards the apex. Although the dorsal surface remains straight in the anterior part, it converges rapidly towards the apex in the posterior part. Cross sections of the anterior part of the guard are oval and laterally compressed but they become circular posteriorly. The median ventral groove attains a length of 3.5 cm. It is deepest near the anterior end and shallows towards the apex. Lateral lines are not apparent.

*Comparison:* The specimen described here from the Orville Coast is similar to *H. marwicki marwicki* Stevens (1965) (Fig. 4c, d) from New Zealand, but differs in being less hastate and having a shorter median ventral groove.

Other species that are rather similar to the Orville Coast specimen are: (1) the group of *Hibolithes lagoicus* (Boehm); (2) *Hibolithes compressus* Stolley; (3) *Hibolithes joleaudi* Besairie.

Boehm (1907a) described three belemnite species from the Upper Jurassic of Taliabu (Indonesia): *Belemnites lagoicus*, *B. cf. lagoicus* (= *H. windhouweri* Stolley 1929), and *B. aff. lagoicus* (= *H. boehmi* Stolley 1929). The present *H. aff. marwicki marwicki* differs from this group by having a more slender and elongate guard and by the lateral compression of its anterior part; specimens of the *lagoicus*-group differ in having circular sections.

*H. compressus*, described by Stolley (1935) from the Upper Oxfordian (redated as Lower Tithonian by Stevens (1965)) of Misol, Indonesia, can be subdivided into two types: a strongly club-shaped stout variety (Stolley, 1935, pl. IV, figs. 1–3) and a very elongate slender variety (Stolley, 1935, pl. IV, fig. 5). Without stating reasons, Stolley interpreted the elongate form as a juvenile, and the club-shaped form as an adult specimen of the same species. The 'juvenile' form of *H. compressus*, which probably is a different species, seems to resemble *H. marwicki marwicki*, although the latter differs, by the circular cross-section of its posterior stem and apical region.

Finally, there are similarities to *H. joleaudi* first mentioned by Besairie (1936) from the Tithonian and Berriasian of Madagascar. Besairie (1936, pl. XXIII, figs. 5, 6 and 7, 8) figured two types; *H. aff. marwicki marwicki* resembles the elongate slender type (pl. XXIII, figs. 5, 6) but differs by the form of the cross-section of the alveolar region. The cross-section of *H. aff. marwicki marwicki* is markedly compressed while *H. joleaudi* is only slightly compressed or nearly circular. The second form figured by Besairie (1936, pl. XXIII, figs. 7, 8) is strongly compressed in the alveolar and stem region (Fig. 3).

*Affinities:* The four belemnite associations discussed above (*H. marwicki marwicki*, *H. lagoicus*, *H. joleaudi*, *H. aff. marwicki marwicki*) are probably equivalent forms of similar age, which are restricted to different faunal provinces or subprovinces. However, the sparse material that is available from Antarctica is not sufficient to solve this problem. Because only one incomplete specimen is known from Antarctica, the erection of a new species has been avoided.

*Distribution:* Species resembling the present *H. aff. marwicki marwicki* show a stratigraphical range that includes the Lower Tithonian (*H. compressus*), Upper Jurassic (*H. lagoicus*), Lower Tithonian (*H. marwicki marwicki*) and the Tithonian-Berriasian (*H. joleaudi*). *H. compressus* is known from Misol (Indonesia), Madagascar (?), and Antarctica (?), *H. lagoicus* from Taliabu (Indonesia), *H. joleaudi* from Madagascar and *H. marwicki marwicki* from New Zealand. As *H. aff. marwicki marwicki* is closest to the species from New Zealand and Indonesia it is considered to be Lower Tithonian.

*Hibolites aff. verbeeki* Kruizinga 1921

Fig. 4e, f

- aff. 1921 *Hibolites verbeeki* Kruizinga; p. 179, pl. 6, fig. 1
- ? 1927 *Hibolites flemingi* Spath; p. 13, pl. 1, fig. 2
- ? 1932 *Hibolites flemingi* Spath; Besairie, p. 8, pl. 4, fig. 3
- ? 1936 *Hibolites flemingi* Spath; Besairie, p. 146, pl. 22, figs. 19, 20

*Material:* One specimen (V.106.1/d) from Bean Peaks, Orville Coast; locality 8 (Fig. 1).

*Description:* Moderately well-preserved, elongate, slender guard; the apex is missing and the alveolus has been eroded. The symmetrical outline is hastate. The sides diverge from the alveolus then change to a parallel course after 4 cm. After a further 2 cm they converge gradually towards the apex. The profile is symmetrical but less hastate. The ventral and dorsal surfaces diverge gradually in the anterior part for about 4 cm, then continue straight and converge in the posterior part.

Although the cross-section of the anterior part of the stem region and the alveolar region is circular, it is depressed in the posterior stem and apical regions. The alveolar region is characterized by a moderately deep median ventral groove, which shallows markedly towards the posterior and fails to reach the area of largest lateral diameter (B max).

*Comparison:* *H. brouweri* Kruizinga, *H. hastatus* (Blainville) and *H. girardoti* (Loric) have some characters in common with the present *H. aff. verbeeki*. However, their ventral grooves all extend much farther posteriorly. *H. aff. verbeeki* differs from *H. verbeeki* by its more elongate and slender guard and less inflated profile. *H. aff. verbeeki* seems to resemble *H. flemingi*, first briefly described and figured by Spath (1927) and later by Besairie (1936); the more slender forms figured by Besairie are particularly close to *H. aff. verbeeki*.

*Distribution:* *H. flemingi* appears in the Middle Kimmeridgian and ranges up into the Tithonian; *H. verbeeki* occurs in the Kimmeridgian and Tithonian, to judge by the associated belemnites (*Belemnopsis uhligi* Stevens, *B. alfurica* (Boehm), *B. sularum* (Boehm)). *H. flemingi* and *H. verbeeki* are restricted to the Indo-Pacific provinces: Pakistan, Somaliland and Madagascar (*H. flemingi*) and the Sula Islands (Taliabu Indonesia (*H. verbeeki*)).

*Hibolithes aff. arkelli* Stevens 1965

Fig. 5a, b, g, h, i, j

aff. 1965 *Hibolithes arkelli* Stevens; p. 99, pl. 15, figs. 1–10

aff. 1975b *Hibolithes arkelli arkelli* Stevens; Challinor, p. 803, figs. 40–43, 46–47

*Material:* Ten fragments (V.158.9, Th. 42.48, V.106.2/c, V.106.6, Th. 42.45, Ke.117.4, Th. 48.20, V.158.4) from Bean Peaks and Wilkins Mountains, Orville Coasts, localities 2, 4, 7, 8, (Fig. 1).

*Description:* All the fragments are poorly preserved and lack both alveolus and apex. The symmetrical outline is slightly hastate. The sides diverge gradually towards the apex and the largest lateral diameter (B max) lies near the apex. The profile is also symmetrical, the divergence of the dorsal and ventral surfaces is, however, less than that of the sides of the outline. The median ventral groove is moderately deep and rather narrow (about 1.7 mm). It extends far onto the stem region but shallows before reaching the area of the largest lateral diameter.

Strong lateral compression results in an oval cross-section throughout the whole guard. The lateral diameters (B) are always smaller than the dorso-ventral ones (D). Specimen V.158.9 has a ratio of  $Q_{ap} = 0.84$  (B<sub>ap</sub>:D<sub>ap</sub>) in the anterior and of  $Q_{max} = 0.88$  (B max:D max) in the central part. Instead of lateral lines, which are not visible, a shallow lateral depression is apparent in some specimens.



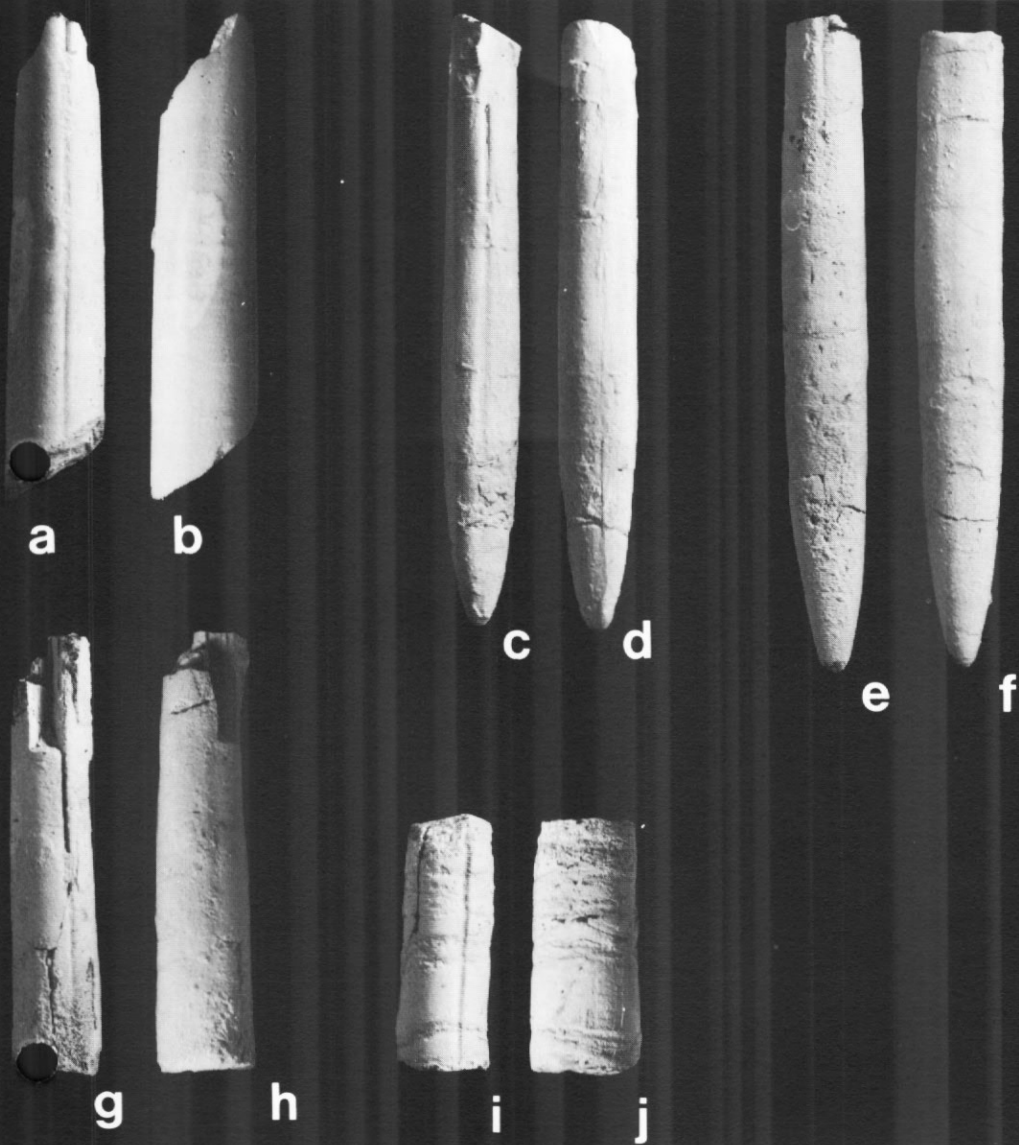


Fig. 5. a. *Hibolithes* aff. *arkelli* Stevens; ventral aspect of a guard; Orville Coast, Wilkins Mountains;  $\times 1$ , coated (V.158.9).  
 b. Right lateral aspect of the same specimen.  
 c. *Hibolithes arkelli* Stevens; ventral aspect of a cast; Te Puti Point, Kawhai Harbour, New Zealand; figured by Trechmann (1923, p. 260, pl. 16, fig. 12),  $\times 1$ , coated (C. 29631, British Museum (Natural History)).  
 d. Right lateral aspect of the same specimen.  
 e. *Hibolithes* sp.; ventral aspect of a guard; Orville Coast, Bean Peaks,  $\times 1$ , coated (V.106.2/a).  
 f. Left lateral aspect of the same specimen.  
 g. *Hibolithes* aff. *arkelli* Stevens; ventral aspect of a guard; Orville Coast, Wilkins Mountains,  $\times 1$ , coated (Th. 42.48).  
 h. Right lateral aspect of the same specimen.  
 i. *Hibolithes* aff. *arkelli* Stevens; ventral aspect of a guard; Orville Coast, Bean Peaks,  $\times 1$ , coated (Ke. 117.4).  
 j. Right lateral aspect of the same specimen.

*Comparison:* *H. aff. arkelli* is similar to belemnites described by Stolley (1935) from the Middle Kimmeridgian and the Lower Tithonian of Misol (Indonesia): *H. longiscissus* (pl. 3, figs. 8, 9) and *H. compressus* (pl. 4, figs. 1-3, non 4, 5). The specimens from the Orville Coast differ from *H. longiscissus* and *H. aff. longiscissus* by possessing a greater lateral compression and a shorter median ventral groove, and from *H. compressus* by the less club-shaped form of the guard.

Challinor (1975a) subdivided *H. arkelli* Stevens into two subspecies: *H. arkelli arkelli* and *H. arkelli grantmackiei*. *H. arkelli grantmackiei* had a less extensive median ventral groove and smaller dorso-ventral and lateral diameters. Measurements taken from Orville Coast specimens show affinities to the subspecies *H. arkelli arkelli*, although the short groove is similar to that of *H. arkelli grantmackiei*.

*Distribution:* *H. arkelli grantmackiei* Challinor is known from the upper Kinohaku Siltstone and the lower Waiharakeke Conglomerate (both units are of upper Middle Kimmeridgian age), *H. arkelli arkelli* Stevens from the upper Waiharakeke Conglomerate and the Puti Siltstone (both Lower Tithonian) of New Zealand.

*Hibolithes* sp.

Fig. 5e, f

*Material:* Two specimens (V.106.2/a. V.106.6) from Bean Peaks, Orville Coast, locality 8.

*Description:* The outline of the elongate and slender guard is symmetrical. The sides diverge posteriorly towards the area of the largest lateral diameter about half way along the guard, and then converge gradually towards the apex. The slightly asymmetrical profile shows an almost straight dorsal surface except where it converges abruptly towards the apex. The ventral surface is slightly more inflated, it diverges posteriorly from the dorsum in a convex curvature then ends in an elongated apical region.

Due to the lateral compression, the lateral diameter is smaller than the dorso-ventral one throughout the whole guard. The cross-section of the anterior part is nearly triangular for the ventral surface is narrow and ridge-like. A shallow, rather short, indistinct median ventral groove extends for about 2 cm towards the apex and the lateral lines form a shallow depression. The apical region is elongate.

*Comparison:* *H. joleaudi* Besairie, *H. argentinus* Feruglio, *H. cf. lagoicus* (Boehmer) (= *H. windhouweri* Stolley), *H. marwicki marwicki* Stevens, *H. subfusiformis* (Raspail), *H. arkelli* Stevens and *H. compressus* Stolley seem to resemble the present *Hibolithes* sp. However, *H. joleaudi* and *H. argentinus* differ by their dorso-ventral depression of the stem region. Cross-sections of *H. marwicki marwicki* and *H. windhouweri* are circular in the stem region and furthermore *H. marwicki marwicki* is characterized by a very long median ventral groove. The median ventral groove of *H. compressus* extends further to the apex, and the guard is more club shaped ('adult' form, compare p. 7) than in *Hibolithes* sp. *Hibolithes* sp. differs from *H. arkelli* by the short median ventral groove, the triangular cross-section and by being less compressed. *Hibolithes* sp. seems to resemble in some aspects *H. arkelli grantmackiei* Challinor (1975a).

*Distribution:* *H. arkelli grantmackiei* occurs in the Middle Kimmeridgian, whereas *H. arkelli arkelli*, *H. compressus*, *H. windhouweri* and *H. marwicki* have been described from the Lower Tithonian, *H. subfusiformis* from the Tithonian-Neocomian and

*H. argentinus* from the (?) Tithonian. Apart from *H. subfusiformis*, which has been reported from Europe, Madagascar and India, all other species are restricted to the Indo-Pacific region: *H. arkelli* – New Zealand, *H. compressus* – Indonesia, Madagascar, *H. windhouwri* – Indonesia, *H. joleaudi* – Madagascar and *H. marwicki marwicki* – New Zealand.

Genus: *Belemnopsis* Bayle & Zeiller 1878

Type species: *Belemnites bessinus* d'Orbigny 1842

*Diagnosis*: Guard elongate, cylindrical, occasionally hastate or subhastate. A prominent broad and deep median ventral groove extends from the alveolar region almost to the apex. The apical line is ventrally placed.

*Comparison*: The genus *Hibolithes*, which resembles *Belemnopsis* in some aspects, differs by its markedly hastate guard and the shorter ventral groove, which is often restricted to the alveolar region.

*Belemnopsis* aff. *keari* Stevens 1965

Fig. 6a–d

- pars 1965 *Belemnopsis keari* Stevens; p. 74, pl. 3, figs. 1–3, 7–9; pl. 4, figs. 1–3; non pl. 2, figs. 6–17; pl. 3, figs. 10–12; pl. 4, figs. 4, 8–12; pl. 5, figs. 1–9, ? 13–15
- pars 1965 *Belemnopsis alfurica* (Boehm); Stevens, p. 78, pl. 4, figs. 5–7; ? pl. 5, figs. 16–18; non pl. 5, figs. 10–12
- non 1979a *Belemnopsis keari* Stevens; Challinor, p. 115, figs. 43–50; p. 116, figs. 51–58.

*Material*: Three fragments (V.106.1/e, Th.45.9) from Bean Peaks, Orville Coast, locality 8 (Fig. 1).

*Description*: The symmetrical outline of the slender, elongate guard is slightly hastate. The sides diverge from the alveolus continuously for about 3 cm where the greatest lateral diameter ( $B_{max}$ ) measures 1.255 cm, and from there they converge posteriorly, slightly at first and then more strongly towards the apex.

Profile asymmetrical, showing no hastation. The ventral surface is almost straight, while the dorsal surface is slightly inflated and curved convexly. The greatest dorso-ventral diameter ( $D_{max} = 1.075$  cm) lies about 2–3 cm behind the anterior end. A median ventral groove, which is relatively broad and moderately deep extends throughout the whole guard. The groove is very narrow in the anterior part but widens towards the apex; its depth is constant throughout the stem region but it shallows gradually posteriorly. The groove is 1.5 mm deep and 2.9 mm wide where the lateral diameter measures 1.13 cm. Cross-sections of stem and apical region are markedly depressed, although it is only slightly depressed ( $Q_{ap} = 1.02$ ) in the anterior part of the stem region. The degree of depression becomes greater posteriorly and reaches its maximum in the area which is most club shaped ( $Q = 1.18$ ). The cross-section of the alveolus appears to be equidimensional or slightly compressed.

*Remarks*: Several *Belemnopsis* species, which seem to resemble the specimens from the Orville Coast, have been described from the Upper Jurassic of Indonesia, New

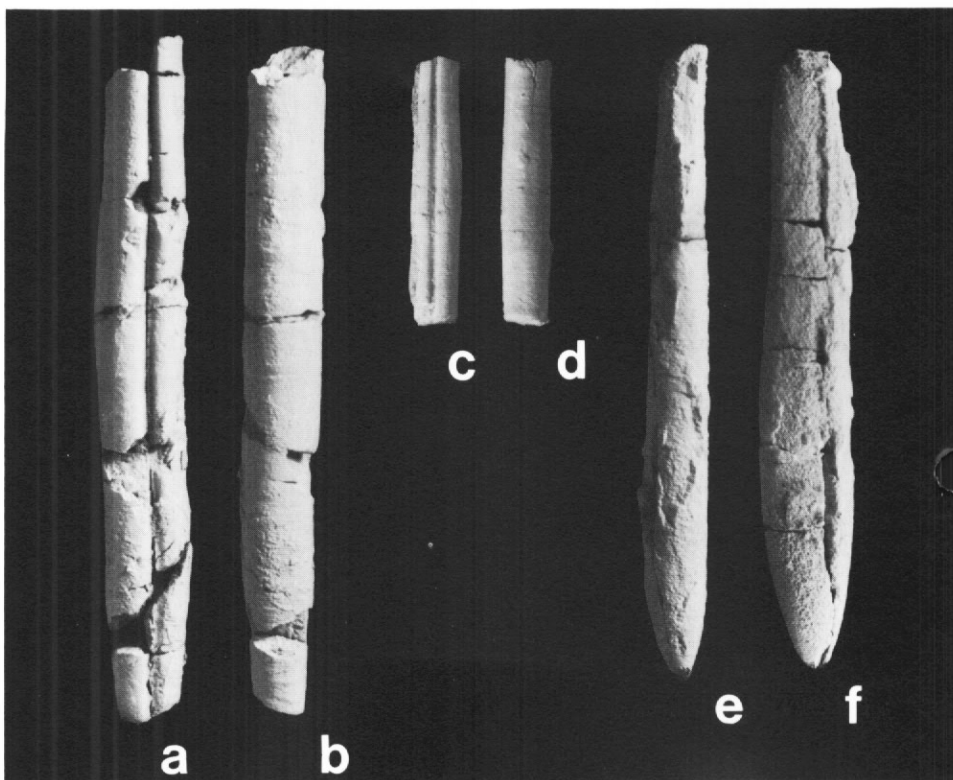


Fig. 6. a. *Belemnopsis* aff. *keari* Stevens; ventral aspect of a guard; Orville Coast, Bean Peaks,  $\times 1$ , coated (V.106.1/c).  
 b. Right lateral aspect of the same specimen.  
 c. *Belemnopsis* aff. *keari* Stevens; ventral aspect of a guard; Orville Coast, Bean Peaks,  $\times 1$ , coated (By. 19.19).  
 d. Right lateral aspect of the same specimen.  
 e. *Produvalia* aff. *neyrivensis* Favre; dorsal aspect of a guard; Orville Coast, McCaw Ridge,  $\times 1$ , coated (Th. 51.15/a).  
 f. Lateral aspect of the same specimen, ventral surface left.

Zealand, Madagascar and Tanganyika. Some of the species of Indonesia, which are sometimes only based on only one or two specimens, may prove to be invalid in future. Furthermore, there are discrepancies between text and figures in some references and occasionally a species has been described in a different way by subsequent authors. For example, Boehm (1907b, p. 73) described *Belemnopsis moluccana* as being stout with a circular cross-section, while his figure (pl. 11, fig. 12) shows that it is depressed. According to Stolley (1929), *B. moluccana* (Boehm) is slightly hastate and has depressed stem and apical regions (Stolley, 1929, pl. 2, figs. 9–12; pl. 3, figs. 1–6). Challinor and Skwarko (1982, p. 25) shared this opinion.

*Comparison:* *B. moluccana* (Boehm) *sensu* Stolley, *B. talibutica* (Boehm), *B. keari* Stevens, *B. aucklandica* (Hochstetter) and *B. tanganensis* (Futterer) are all similar to the Antarctic material. *B. aff. keari* differs from *B. aucklandica* and *B. moluccana* by its more elongate guard and less prominent groove; the guard of *B. taliabutica* is stouter. *B. keari* is characterized by a more hastate guard and a deep groove.

*B. tangansensis* seems to resemble the present *B. aff. keari*. The latter differs, however, by a deeper groove, an elongate apical region, and the position of the largest lateral diameter ( $B_{\max}$ ), which is about half the length of the guard. The specimen described here from the Orville Coast is similar to *B. keari* Stevens (1965), but differs in being less hastate in both profile and outline and the groove is less prominent than *B. keari*.

*Distribution*: *B. tangansensis* ranges from the ? Upper Oxfordian to Middle Kimmeridgian, *B. keari* sensu Stevens from the Lower to Middle Kimmeridgian. *B. tangansensis* is restricted to East Africa and South Arabia, *B. keari* to New Zealand.

Family DUVALIIDAE Pavlow 1914

Genus *Produvalia* Riegraf 1981

Type species: *Belemnites monsalvensis* Gillieron 1873

*Remarks*: The genus *Duvalia* Bayle and Zeiller 1878 includes species that are strongly compressed while the dorso-ventral diameter is large. Riegraf (1981, p. 106) established a new genus *Produvalia* for stout, fairly elongate guards that have a more or less inflated ventral surface while the cross-section is either circular or more compressed. *Produvalia* differs from *Duvalia* by its less inflated ventral surface and it is restricted to the Upper Jurassic, whereas *Duvalia* occurs in the uppermost Jurassic and in the Lower Cretaceous. The new genus *Produvalia* is subdivided in two subgenera (*Produvalia* and *Pachyduvalia*). The guards of *Pachyduvalia* are less compressed than those of *Produvalia*, and are very similar to the duvaliid genus *Conobelus*, whereas the compressed guards of *Produvalia* resemble some ventrally less inflated species of *Duvalia*, particularly *D. dilatata dilatata*, a highly variable species ranging from Valanginian–Hauterivian.

As a modern revision of the whole Duvaliidae (including the Jurassic *Produvalia*) is not available, the compressed duvaliids described below from the Upper Jurassic of the Orville Coast are tentatively assigned to *Produvalia* (*Produvalia*).

Subgenus *Produvalia* (*Produvalia*) Riegraf 1981

Type species: *Belemnites monsalvensis* Gillieron 1873

*Diagnosis*: Markedly compressed, slightly hastate to rod like guards, with a more or less inflated ventral surface. A median dorsal groove is developed.

*Comparison*: Guards of the subgenus *Produvalia* (*Produvalia*) differ from *Produvalia* (*Pachyduvalia*) by their lateral compression, and from *Duvalia* by their less inflated ventral surface.

*Produvalia* aff. *neyrivensis* (Favre 1876)

Fig. 6e, f

aff. 1876 *Belemnites neyrivensis* Favre, p. 23, pl. 1, fig. 15

*Material*: Two incomplete specimens (Th.51.5/a) from McCaw Ridge, Orville Coast, locality 1 (Fig. 1).

*Description*: The symmetric dorsal outline of the elongate guard is slightly hastate. The sides diverge gradually from the alveolus towards the maximum lateral diameter located near the apex, and then converge rapidly.

The profile is asymmetric. The venter is inflated and diverges posteriorly from the dorsum in the anterior stem region, becoming convex at the position of maximum inflation (D max) in the posterior third. From this point venter and dorsum converge towards the apex. The whole guard shows an intensive lateral compression, which continues into the apical region. In the stem region the ratio of compression  $Q(B:D)$  varies between 0.81 and 0.59 (0.62 for B max:D max), and 0.71 in the apical region.

Lateral lines have not been observed, but a shorter shallow groove is present on the dorsal surface extending from the alveolus.

*Remarks:* The genera *Belemnopsis* and *Hibolithes* both possess a median ventral groove extending posteriorly from the alveolus, whereas genera of the family Duvaliidae are characterized by a median dorsal groove. The dorsal or ventral position of the median groove may only be determined from the relative position of ventrally placed siphuncle, usually seen in longitudinal dorso-ventral thin sections. However, because of the poor preservation of the material (absence of the alveolus and strong corrosion of the whole guard) this was not possible. Nevertheless, as the guard is strongly compressed and has an irregular shape, it is considered to belong to the genus *Produvalia* and the groove is therefore assumed to be dorsal.

*Comparison:* There are broad similarities between Antarctic specimens and a variety of species from the Oxfordian of Switzerland: *Belemnites monsalvensis* Gillieron (1873) (Lower Oxfordian; Switzerland; South Germany, western Alps), *B. voironensis* Favre (1875) (Lower Oxfordian; Switzerland), *B. neyrivensis* Favre (1876) (Oxfordian; Switzerland), *B. dionysii* Favre (1876) (Oxfordian; Switzerland), *B. cf. didyanus* d'Orbigny (Favre, 1876; Oxfordian; France, Switzerland, Spain). The specimens described above differ from *B. monsalvensis*, *B. dionysii* and *B. cf. dionysii* (= *Produvalia* (*Produvalia*)) by their shorter median dorsal groove, from *B. voironensis* by their more elongate guard. *B. aff. neyrivensis* resembles *B. neyrivensis* by the short median dorsal groove and the dorso-ventral tapering in the anterior part of the stem region. The compression ratio  $Q$  max (B max:D max) in the *Produvalia neyrivensis* is 0.59, and 0.62 in *P. aff. neyrivensis*. *P. aff. neyrivensis* differs from *B. neyrivensis* by the inflation of the dorsal surface and the position of the maximum diameter. In *P. aff. neyrivensis* than maximum diameter lies much closer to the apex than in *P. neyrivensis*.

*P. aff. neyrivensis* resembles forms from the Tithonian and Valanginian of Madagascar recorded by Besairie (1930, pl. 15, fig. 6; pl. 23, figs. 4, 5) as *Duvalia dilatata*. The latter differs by being less depressed dorso-ventrally. Apart from the genera *Colonbelus* and *Pseudobelus*, Favre (1880, pl. 1, fig. 14) figures *Belemnites ensifer* Oppel. This species is related to the Oxfordian assemblage (*Produvalia* (*P. monsalvensis*, *P. (P.) voironensis*)) and is here regarded to be a *Produvalia* (*Produvalia*). In *P. aff. neyrivensis* the dorso-ventral constriction of the anterior part is stronger and the median dorsal groove is shorter.

*Distribution:* Species of the subgenus *Produvalia* are known from the Oxfordian of central Europe (*P. (P.) voironensis*, *P. (P.) dumortieri*, *P. (P.) monsalvensis*, *P. (P.) neyrivensis*), from the Kimmeridgian ? and Tithonian of central Europe (*P. (P.) ensifer*, *P. (P.) argoviana*) and from the Kimmeridgian from Madagascar (*P. (P.) ensifer*). Further duvaliid species of the Indo-Pacific region are known: *Pseudobelus tithonica* Oppel from the Kimmeridgian, *Duvalia sakalava* Besairie and *Duvalia lemonei* (Besairie) from the Tithonian of Madagascar. Stolley (1929, p. 208) described *Duvalia timorensis* from the Tithonian of Indonesia and Zwierzycki (1914) *Duvalia elegantissima* from the Tithonian of Tanganyika.

The Orville Coast material is supposed to be of Late Tithonian age for two reasons:

(1) The ammonites found nearby (? *Virgatosphincts denseplicatus*) suggest an early late Tithonian age (M. R. A. Thomson, personal communication).

(2) The immigration of duvaliid forms from the Tethys into the Indo-Pacific region took place in the Upper Tithonian (Stevens 1969, p. 174).

#### BIOSTRATIGRAPHY

Although the determinations given for the belemnites from the Orville Coast (Antarctica) are uncertain at the species level, it seems more reasonable to date the sections from which they came as Lower–Middle Kimmeridgian to Tithonian. All the species described above have close affinities to the *uhligi*-complex and its temporary replacements, described from the Upper Jurassic of New Zealand and Indonesia by Stevens (1965, p. 205–207). The *uhligi*-complex, named after *Belemnopsis uhligi* Stevens, is a belemnite assemblage characterized by species of *Belemnopsis* with robust slightly hastate to non-hastate guards having a prominent median ventral groove. In Indonesia the *uhligi*-complex (Middle Kimmeridgian–Middle Tithonian) consists of the following species, which are linked by intermediate forms: *B. uhligi* Stevens, *B. moluccana* (Boehm), *B. sularum* (Boehm), *B. indica* (Kruizinga), *B. aucklandica* (Hochstetter), *B. jonkeri* Stolley and *B. suavis* Stolley. There are precursor forms, *B. keari* Stevens and *B. alfurica* (Boehm) (Lower and Middle Kimmeridgian), which are slightly older than the forms of the *uhligi*-complex.

In New Zealand, where the *uhligi*-complex is younger (Upper Kimmeridgian–Middle Tithonian), it is characterized by *B. aucklandica*. Beds with belemnites of the *uhligi*-complex are underlain by strata that contain *B. keari* (Lower–Middle Kimmeridgian) and *B. alfurica* (Middle Kimmeridgian). Challinor (1979a) reassigned some of the forms described by Stevens (1965) under *B. keari* to *B. annae*, and included in *B. keari* guards that were figured by Stevens partly as *B. alfurica* and partly as *B. keari*. If this is valid, *B. alfurica* (Boehm) *sensu* Stevens should be referred to *B. keari* Stevens. The phylogenetic early forms of *B. keari* are split between two species: *B. annae* and *B. macrawi*, which occur in the upper Oraka Sandstone and in the Okineruru-Formation, Lower Kimmeridgian (Challinor 1979a). The author prefers Jeletzky's (1983, p. 961) concept of a broadly interpreted *B. keari*, which ranges from the Lower to the Middle Kimmeridgian and includes *B. keari*, *B. alfurica sensu* Stevens, *B. annae* and *B. macrawi*.

The *uhligi*-complex and allied species (*B. keari s.l.*) is known from New Zealand, New Caledonia, Australia, New Guinea and Papua, Indonesia, North India, Tanganyika and the Falkland Plateau (Stevens 1965, p. 205; Jeletzky 1983). The *uhligi*-complex may be subdivided into an older and a younger part, separated by major immigration of *Hibolithes*. All three belemnite assemblages (lower *uhligi*-complex, *Hibolithes*-complex and upper *uhligi*-complex) contain stratigraphically and geographically different forms. The lower *uhligi*-complex of Indonesia includes *B. moluccana* and *B. sularum*, the *Hibolithes*-complex and the upper *uhligi*-complex *B. aff. moluccana*, *B. aucklandica*, *B. sularum* and *B. indica*. In New Zealand the *uhligi*-complex consists of morphologically similar species, which may be part of variants of the Indonesian forms.

*B. spathi* Stevens and *B. aucklandica trechmanni* Stevens are common in the lower *uhligi*-complex, *H. marwicki mangaoraensis* Stevens, *H. marwicki marwicki* Stevens and *H. arkelli* Stevens in the *Hibolithes*-complex and *B. aucklandica aucklandica* (Hochstetter) in the upper *uhligi*-complex (Fig. 7). Sediments of Upper Tithonian and Lower Cretaceous (Valanginian–Berriasian) age are not represented in New Zealand, where the first known Cretaceous marine sediments are Aptian. Jeletzky (1983, p. 953)

International stages	INDONESIA		NEW ZEALAND		ANTARCTICA	MADAGASCAR	Belemnite assemblages of the Indo-Pacific region
	Belemnite succession of Misol after Stevens (1965)	Belemnite succession on the Sula Islands after Challinor & Skwarko (1982)	Local stages	Belemnite succession after Stevens (1965) and Challinor (1979,a,b)	Orville Coast Belemnite succession	Belemnite succession after Besairie (1936)	
TITHONIAN	U	<i>H. subfusiformis</i> <i>D. lata</i> <i>D. dilata</i>	no marine sediments		<i>Paff. neyrivensis</i>	<i>H. subfusiformis</i> <i>D. dilatata</i>	<i>Hibolites</i> - <i>Duvalia</i>
	M	<i>B. aff. moluccana</i> <i>B. aucklandica</i> <i>B. sularum</i> <i>B. uhligi</i>		<i>B. aucklandica auckland</i>		<i>H. astartinus</i> <i>H. joleaudi</i>	2. <i>uhligi</i> -complex
	L	<i>H. compressus</i> <i>H. aff. compressus</i>	<i>B. aucklandica similis</i>	PUAROAN	<i>H. marwicki mangolensis</i> <i>H. marwicki marwicki</i> <i>H. arkelli arkelli</i>	<i>H. aff. marwicki marwicki</i> <i>H. aff. arkelli</i>	<i>H. flemingi</i> <i>H. joleaudi</i> <i>H. compressus</i> <i>B. madagascariensis</i> <i>Ha. claviger</i> <i>R. sp.</i>
KIMMERIDGIAN	U			<i>B. aucklandica trechmanni</i> <i>B. spathi</i> <i>H. minor</i> <i>B. rarus</i> <i>B. stevensi</i> <i>D. kowhaiensis</i>			1. <i>uhligi</i> -complex
	M	<i>B. moluccana</i>	OHAUAN	← <i>B. keari</i> ← <i>B. maccrawi</i> <i>H. arkelli</i> ← <i>B. annae grantmackiei</i>	<i>B. aff. keari</i>	<i>H. flemingi</i> <i>H. savornini</i> <i>Ha. claviger</i> <i>R. sp.</i>	alfurica-keari complex
	L	<i>B. affurica</i> <i>B. cf. keari</i> <i>B. keari</i>	HETERIAN	<i>C. flemingi</i> <i>C. orakensis</i> <i>C. n. sp. STEVENS</i>	← <i>Conodicoelites</i> sp.	<i>B. casterae</i> <i>B. aff. gerardi</i>	
OXFORDIAN	<i>Di. longirostris</i> <i>Di. rotundus</i> <i>Di. bisulcatus</i>	<i>B. sp. B</i>		← <i>H. catlinensis</i>		<i>B. aff. gerardi</i> <i>H. weberi</i> <i>H. compressus</i> <i>B. calloviensis</i> <i>B. aff. calloviensis</i> <i>B. latesulcatus</i>	
CALLOVIAN		<i>Di. sp. B</i>				<i>B. calloviensis</i> <i>B. aff. orientalis</i>	
BATHONIAN		<i>B. sp. A</i> <i>C. kalepuensis</i>	UPPER TEMAIKAN	<i>H. sp.</i> <i>? Cy. sp.</i>		<i>B. aff. bessinus</i> <i>B. aff. orientalis</i> <i>B. calloviensis</i> <i>B. aff. bessinus</i>	
BAJOCIAN		<i>Di. A</i>	LOWER TEMAIKAN	<i>Br. sp.</i> <i>Cy. sp.</i>			

Fig. 7. Stratigraphic column for the Middle and Upper Jurassic of the Indo-Pacific region based on belemnites. B. = *Belemnopsis* Bayle; Br. = *Brachybelus* Naef; C. = *Conodicoelites* Stevens; Cy. = *Cylindroteuthis* Bayle; D. = *Duvalia* Bayle & Zeiller; Di. = *Dicoelites* Boehm; H. = *Hibolites* Mayer-Eymar; Ha. = 'Hastites' Mayer-Eymar; P. = *Produvalia* R. Naef; R. = *Rhopaloteuthis* Lissajous.



reported a similar hiatus (Upper Tithonian-Hauterivian) on the Falkland Plateau. In other areas (Indonesia) the upper *uhligi*-complex is, however, overlain by a lower *Hibolithes-Duvalia*-complex which extends from the Upper Tithonian into the 'Neocomian'. An equivalent *Hibolithes-Duvalia* complex has been recorded from the Upper Tithonian of Madagascar.

The specimens found in the Orville Coast area are related to the *uhligi*-complex and its precursors and descendants. A Lower-Middle Kimmeridgian age is probable for *B. aff. keari* even though these forms also resemble *B. tanganensis* (Futterer). *B. tanganensis* is presently known only from the ? Upper Oxfordian-Middle Kimmeridgian of East Africa and southern Arabia, and it may be that *B. tanganensis* is an equivalent species to *B. keari* s.l. that is restricted to the Ethiopian province.

Most of the belemnites assigned to *H. aff. marwicki marwicki*, *H. aff. verbeeki* and *H. aff. arkelli* are part of an assemblage equivalent to the first *Hibolithes*-complex, which subdivides the *uhligi*-complex. The specimens from Antarctica are very similar to the forms that are common in New Zealand, although the species are not exactly the same. There are also differences between the *Hibolithes*-complex from New Zealand and Indonesia at the species level. These differences may partly be due to the poor state of knowledge. According to these results, the Indo-Pacific province may possibly be subdivided into three subprovinces, each characterized by slightly different *Hibolithes* species.

*Produvalia aff. neyrivensis* confirms the presence of a second *Hibolithes-Duvalia*-complex (Upper Tithonian-Lower Cretaceous), which replaces the fauna of the upper *uhligi*-complex. These biostratigraphical results are confirmed by ammonites described by Thomson (1983; personal communication) from the same area as the belemnites. There are no well-preserved belemnites available from the Behrendt Mountains where the ammonites indicate Middle Bajocian and Oxfordian ages. All other sections (McCraw Ridge, Wilkins Mountains, Hauberg Mountains) from which specimens are described are of Tithonian age according to the ammonites. Thomson (1983, p. 318) suggested that the sequences exposed in the Bean Peaks-Hauberg Mountains-Peterson Hills area are early to earliest late Tithonian age, those of the Wilkins Mountains of early late Tithonian age, and that at Cape Zumberge of latest Tithonian age. Furthermore, the *Conodicoelites* sp., described by Stevens (1967, p. 348) from Ellsworth Land, is similar to species from New Zealand (*C. orakaensis* Stevens, *C. flemingi* Stevens) that are of Lower Kimmeridgian age.

#### PALAEOBIOGEOGRAPHY

Two distinct faunal realms, characterized by different belemnite assemblages, may be recognized in the Upper Jurassic:

(1) The boreal realm (including USSR, northern Europe, Greenland, North America), and

(2) The Tethyan (Mediterranean area and Indo-Pacific region). Both realms may be subdivided into provinces and subprovinces. A faunal realm is understood to be an area where new belemnite genera developed independently. Such genera do not occur in other realms or only at their borders. The term (faunal-) province is used if the fauna develops endemically, e.g. the genus *Belemnopsis* in the Indo-Pacific realm (compare discussion in Stevens, 1973, p. 267).

The Upper Jurassic of the boreal realm is dominated by species of the genera *Cylindroteuthis* Bayle and Zeiller, *Pachyteuthis* Bayle and Zeiller and *Acroteuthis* Stolley (family Cylindroteuthididae) with a few *Hibolithes* in the Oxfordian. Different distributions of the subgenera and species enable a separation of the boreal realm into



Tithonian: ▲ *Belemnopsis* ■ *Hibolites* ◆ *Hastites* ● *Rhopaloteuthis* ⚡ *Duvalia* / *Produvalia*

Kimmeridgian: △ *Belemnopsis* □ *Hibolites* ◇ *Hastites* ○ *Rhopaloteuthis*  
 × *Dicoelites* \* *Conodicoelites*

Presumed belemnite migration routes:

⇒ Kimmeridgian, Lower Tithonian      → Upper Tithonian

Fig. 8. Palaeobiogeography of belemnites from the Upper Jurassic of the Indo-Pacific region. Plate tectonics after Smith and others (1981). Belemnite assemblages based on Besairie (1936), Challinor (1974, 1975a, b), Challinor and Skwarko (1982), Feruglio (1936), Jeletzky (1983), Spath (1927, 1934, 1939), Stevens (1965, 1967) Stolley (1929), Willey (1972, 1973). Hatched areas: continent; white areas: marine; 1–17; belemnite assemblages. 1, Orville Coast; 2, Alexander Island; 3, Patagonia; 4, South America; 5, Falkland Plateau; 6, Madagascar; 7, Tanganyika; 8, Somalia; 9, Arabia; 10, Iran; 11, Kutchh; 12, Spiti; 13, Australia; 14, Moluccas; 15, New Guinea; 16, New Caledonia; 17, New Zealand.

a Boreal-Atlantic province (Russian platform, North Europe, Greenland) and the Arctic province (Siberia, Canada). The Upper Jurassic of Tethys is, however, characterized by genera of the families Belemnopseidae (*Belemnopsis* Bayle, *Hibolithes* Montfort), Dioelitidae (*Dicoelites* Boehm, *Conodicoelites* Stevens) and Duvaliidae (*Produvalia* Riegraf, *Duvalia* Bayle and Zeiller, *Conobelus* Stolley, *Pseudobelus*

Blainville). The faunas of the Boreal and Tethyan realms overlap along their borders. In the Oxfordian, boreal species of the *Cylindroteuthididae* were able to migrate into France and southern Germany whereas the Tethyan genus *Hibolites* appeared in northern Germany and England.

Within Tethys two different belemnite provinces may be distinguished from the lower Upper Jurassic: (1) the Mediterranean province (southern Germany, Alps, France, Spain, Morocco, Sicily, Crimea, Bulgaria), and (2) the Indo-Pacific province (East Africa, India, Australia, Indonesia, New Zealand, South America, Antarctica). The following genera appear in the Mediterranean province: *Belemnopsis* (very rare), *Hibolites* (abundant), *Produvalia*, *Duvalia*, *Conobelus* and *Conodicoelites*. *Belemnopsis* is already replaced by *Hibolites* in the Late Callovian.

*Belemnopsis*, *Hibolites*, *Duvalia*, *Dicoelites* and *Conodicoelites*, which appear in the Indo-Pacific region, evolved from Mediterranean ancestors. However, the evolutionary culmination of these genera in the Indo-Pacific province is later, whereas some had already died out in the Mediterranean province. During the Early Oxfordian the faunas of both provinces are still similar in the Late Oxfordian a separation is obvious and distinct Indo-Pacific fauna developed. Apart from rare specimens of *Hibolites* and 'Hastites' (East Africa, Madagascar, India), the faunal pattern is dominated by the *orientalis-gerardi* group (Madagascar, India, Somaliland) of the genus *Belemnopsis*.

According to Stevens (1965; p. 171; 1973; p. 266), this *in situ* evolution of the belemnite faunas continued in the Kimmeridgian and Tithonian. In the Early Kimmeridgian three different provinces existed, due to a faunal separation in the Indo-Pacific province: (1) the Mediterranean province; (2) the Ethiopian province (Madagascar, East Africa, Ethiopia, Somaliland, Kutch), and (3) the Indo-Pacific province s.s. (Indonesia, New Zealand, Australia, Antarctica).

The fauna of the Lower Kimmeridgian of the Ethiopian province is characterized by the *B. orientalis-gerardi* group and *B. tanganensis* (Futterer). Both were replaced by the Middle Kimmeridgian by an *Hibolites*-'Hastites' assemblage which immigrated from Tethys and persisted into the Tithonian. In the Lower Kimmeridgian of the Indo-Pacific province, however, the *orientalis gerardi* group underwent a speciation: *B. keari* s.l. evolved and in the Middle Kimmeridgian species of the *uhligi*-complex appeared. The immigration of Tethyan derived forms (*H. minor* (Hauer)) has been proved (Stevens, 1965, p. 172), but it is of minor importance. The *in situ* evolution of the genus *Belemnopsis* was overshadowed in the Early Tithonian by a second immigration of Tethyan-derived *Hibolites*, which have been found in the Ethiopian and in the Indo-Pacific provinces. However, the belemnite faunas of both provinces differ at the species level. In the Ethiopian province *H. flemingi* Spath and *H. savornini* Nicolai occur, whereas in the Indo-Pacific province *H. arkelli* Stevens, *H. marwicki marwicki* Stevens and *H. marwicki mangaoraensis* Stevens are present. The genus *Belemnopsis* is rare there but it is dominant in the Middle Tithonian of the Indo-Pacific province. In this upper *uhligi*-complex, known from New Zealand, the Moluccas, Antarctica and the Falkland Plateau, *Hibolites* is replaced by species of *Belemnopsis* (*B. aucklandica trechmanni* Stevens). The upper *uhligi*-complex is, however, unknown from Madagascar and Tanganyika where *Hibolites* occurs.

In the Kimmeridgian and Tithonian of the Indo-Pacific region there are two different belemnite faunas: (1) *Belemnopsis*, (2) *Hibolites*, *Duvalia*, *Produvalia*; which show different migration-evolution patterns. The genera of both groups may be derived from Mediterranean ancestors. In the Bajocian *Belemnopsis* migrated from the Mediterranean into the Indo-Pacific region and, until the Callovian, the species of this group remained genetically closely related to the Mediterranean species. While

*Belemnopsis* became extinct in the Mediterranean during the Callovian and Oxfordian, new species evolved during the Upper Oxfordian–Tithonian of the Indo-Pacific region (*B. orientalis*, *B. gerardi*, *B. keari* s.l., *B. aucklandica aucklandica*, *B. moluccana*, *B. aucklandica trechmanni*). In contrast to *Belemnopsis*, which evolved independently, the Tethyan genera *Hibolithes*, *Duvalia*, *Produvalia* appeared in three separate migration waves in the Indo-Pacific region. These *Belemnopsis* assemblages underwent a speciation to form a new Indo-Pacific faunal realm that was independent of Europe but were, however, replaced repeatedly by new incursions.

The belemnopseids described from the Kimmeridgian and Lower Tithonian of the Orville Coast show Indo-Pacific affinities, whereas the duvaliid forms show Tethyan affinities. The *Conodicoelites* sp. described by Stevens (1967) closely resembles species in the belemnite faunas of New Zealand, as do *Belemnopsis* aff. *keari*, *Hibolithes* aff. *marwicki marwicki* and *H.* aff. *arkelli*. Stevens (1965, p. 171; 1967, p. 367) discussed comparable faunal links during the Early Tithonian between Mexico and South America on one hand and New Zealand on the other. The ammonite genera *Aulacosphinctes* and *Torquatisphinctes* and the belemnite genera *Belemnopsis* and *Hibolithes* of both areas are similar. Basically there are two possible routes along which these Indo-Pacific fossils of the Kimmeridgian and Lower Tithonian may have migrated into Antarctica: either along a trans-Gondwana route via Madagascar or via the Pacific margin of West Antarctica. The second explanation is more likely for a fauna that shows affinities to that of New Zealand but is missing from Madagascar and East Africa. This connection ended in the Middle and Upper Tithonian (Stevens, 1967, p. 367) and endemic forms such as *Belemnopsis patagonensis* (Favre) evolved in Patagonia.

If the upper Tithonian age for *Produvalia* is confirmed, it is possible that this form migrated from the Mediterranean area via Madagascar and East Africa using a shallow water route. This idea is supported by the presence of duvaliid belemnites in Madagascar (Besairie, 1930, 1936), which show close affinities to Mediterranean forms.

If this is true, a trans-Gondwana route between the South-American and African plate on one side and the Austral-Antarctic plate on the other must have already existed in the Tithonian. Thomson (1980, p. 271) mentioned Tithonian ammonites from the Orville Coast that closely resemble South American and Himalayan ammonite faunas.

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