THE BELEMNITE GENERA DICOELITES BOEHM AND PRODICOELITES STOLLEY

by G. R. STEVENS

ABSTRACT. Dicoelites Boehm (type species Belemnites dicoelus Rothpletz) contains two separate groups of belemnites which have in common only the possession of a dorsal as well as a ventral groove. B. dicoelus, with a slender elongate cylindrical guard, belongs to one group and Dicoelites keeuwensis Boehm, with a short robust conical guard, to the other. In this paper the name Dicoelites is restricted to belemnites of the dicoelus group, to which Stolley has given the name Prodicoelites, and a new genus, Conodicoelites, is proposed for those of the keeuwensis group, with D. keeuwensis as type species. Both genera and their main species are described. Dicoelites species are known from the Middle and Upper Jurassic of Indonesia, South America, and the Himalayas and Conodicoelites from the Middle and Upper Jurassic of Indonesia, New Zealand, the Himalayas, Swiss Alps, and Polish Carpathians.

THE generic name *Dicoelites* was first published by Boehm (1906, p. 389) and has been in constant use ever since. Species have been described from the Middle and Upper Jurassic of the Swiss Alps, the Carpathians, Crimea, the Caucasus, Siberia, the Himalayas, Indonesia, and New Zealand.

In his review of Indonesian faunas Boehm (1906, p. 389) cited two species as belonging to *Dicoelites*:

- (a) Belemnites dicoelus Rothpletz from Rotti, Indonesia (Rothpletz 1892, p. 105, pl. 13, figs. 9, 14–15);
- (b) Belemnites sulcacutus Suess (nomen nudum) from the Himalaya (Diener 1895, pp. 583-6);

and also the *Belemnites* sp. described by Dacqué (1905, p. 153, pl. 15, figs. 11–12) from Somaliland, and the belemnites from Wai Miha, Sula Islands (Indonesia), later described by Boehm (1912).

No type species was designated by Boehm in his 1906 paper, but *Belemnites dicoelus* Rothpletz is the type species by monotypy as at that time *B. sulcacutus* Suess was a *nomen nudum* (see p. 616).

In a discussion of Neumayr's (1889) group of belemnites, the 'Absoluti', Boehm (1909, pp. 565–6) discussed *Dicoelites*, referred to *B. dicoelus* Rothpletz and the Wai Miha belemnites, and also included in the genus the species *B. meyrati* Ooster (Swiss Alps), *B. waageni* Neumayr (Carpathians), and *Belemnites* sp. indet. described by Gottsche (1878, p. 8, pl. 4, fig. 2) from the Argentinian Cordillera.

Dicoelites was fully discussed by Boehm in 1912 and the belemnites from Wai Miha were described as D. keeuwensis Boehm, D. cf. keeuwensis and Dicoelites sp. In the same paper B. bisulcatus Stoliczka and B. avena Dumortier were included in Dicoelites and Boehm also discussed the possibility of B. budhaicus Stoliczka being a Dicoelites.

B. dicoelus is based on two fragments (Rothpletz 1892, pl. 13, figs. 9, 14–15) each 30–35 mm. long; one an apical fragment (fig. 9) and the other a stem fragment, and this poor preservation probably prompted the recognition by later workers of B. meyrati [Palaeontology, Vol. 7, Part 4, 1964, pp. 606–20, pl. 94.]

Ooster as the type species for *Dicoelites* (see Bülow-Trummer 1920, p. 133; Naef 1922, p. 254; Lissajous 1925, p. 40). This designation of *meyrati* as type species is invalid as it was not one of the species originally mentioned by Boehm (1906).

Stolley (1927, p. 122; 1929, pp. 116, 196) recognized that *Dicoelites* Boehm contained two separate groups of belemnites, which have in common only the possession of a dorsal as well as a ventral groove. *B. dicoelus* Rothpletz belongs to one group and *Dicoelites keeuwensis* Boehm to the other. Stolley restricted the name *Dicoelites* to belemnites similar to *D. keeuwensis* and *B. meyrati*, and included *B. dicoelus* in a new genus, *Prodicoelites*, but this placing of *B. dicoelus* was correctly rejected by Spath (1927–33, p. 663; 1935, p. 222).

The group of *B. dicoelus* consists of belemnites with an elongate and cylindrical guard, a prominent ventral groove, and a dorsal groove, normally less prominent. The dorsal groove is extremely variable and may extend the length of the guard, making the dorsal and ventral surfaces almost identical, e.g. *D. stefaninii* Spath (Spath 1935, pl. 25, fig. 3); but more commonly the dorsal groove is short and weakly developed, e.g. *D. mihanus* Boehm (Boehm 1912, pl. 32, fig. 10). The species that may be included in the group typified by *B. dicoelus* are as follows: *D. mihanus* Boehm; *B. bisulcatus* Stoliczka (Stoliczka 1866, pl. 8, figs. 1 and 4, *not* figs. 2 and 3); *D. stefaninii* Spath, and the *Prodicoelites* species recognized by Stolley (1929, 1935). The *Dicoelites* described by Krimholz (1932, pp. 37–38, pl. 2, figs. 18–32; 1953, p. 54, pl. 4, figs. 5a–b), *D. fogdti* (Callovian of Crimea), and *D. exiguus* (U. Bajocian–L. Bathonian of the Caucasus) are species of doubtful affinity, but may prove to be members of the *dicoelus* group.

The group of *D. keeuwensis* consists of belemnites with a short robust guard, conical in outline and profile, possessing a well-developed ventral groove extending almost to the apex and a similarly well-developed but slightly shorter dorsal groove. Other species, later included by Boehm (1912, pp. 136–8) in *Dicoelites*, which may be included in this group are: *D.* cf. *keeuwensis* Boehm (Boehm 1912, pl. 32, fig. 8), *B. meyrati* Ooster, and B. *waageni* Neumayr. *B. sulcacutus* Suess, cited in Boehm's original generic designation (1906, p. 389), was a *nomen nudum*, but it has since been validated by Stolley (see p. 616) and is a member of the *D. keeuwensis* group.

A number of species have been incorrectly assigned to *Dicoelites* by various authors. *B. avena* Mayer was included in *Dicoelites* by Boehm (1912, p. 137) and Bülow-Trummer (1920, p. 133), but as Naef has observed (1922, p. 254) this species is probably a member of the Duvaliinae. Bülow-Trummer (1920, p. 134) also included *B. budhaicus* Stoliczka in *Dicoelites*, but as pointed out by Stolley (1929, p. 213) this species is a *Hibolithes*.

Lissajous (1915, p. 27; 1925, pp. 41, 101) included two French species: *B. jacquoti* Terquem and Jourdy (Upper Bajocian) and *B. pellati* de Loriol (Portlandian) in *Dicoelites*, but this generic placing is not confirmed and Bülow-Trummer (1920, pp. 145, 200) has placed them in *Hibolithes* and *Cylindroteuthis* respectively.

Stolley (1929, p. 196) recognized the belemnite identified and figured by Boehm (1912, p. 138, pl. 32, fig. 9) as *Dicoelites sp.* as *D. impar* Stolley (no. G678.1905, Mineralogical-Geological Institute, Utrecht; not found by the writer, 1958, and by Dr. C. W. Drooger, 1962), but it is thought to be a *Belemnopsis* variant with an impersistent dorsal groove.

Saks (1961a, b) has described D. bidgievi Saks and D. sibiricus Saks from Siberia, which he grouped with forms such as the *Prodicoelites* species rather than with conical forms such as D. meyrati. However, his figured specimens appear to be either Hibolithes

(D. bidgievi) or Belemnopsis (D. sibiricus) guards badly affected by corrosion, this giving them an entirely spurious shape.

The heterogeneity of *Dicoelites* Boehm as presently recognized makes subdivision imperative, but not with the nomenclature proposed by Stolley. Instead, the writer restricts *Dicoelites* Boehm to the belemnites allied to *B. dicoelus* and proposes a new genus, *Conodicoelites*, for the belemnites allied to *B. meyrati* and *D. keeuwensis*.

Genus DICOELITES Boehm

partim Stevens 1964 (non partim Stolley 1927)

1906 Dicoelites Boehm, p. 389 (partim, non Belemnites sulcacutus Suess and belemnites from Wai Miha, Sula Islands later recognized (Boehm 1912) as D. keeuwensis Boehm and Dicoelites sp.)

1927 Prodicoelites Stolley (partim); Stolley, p. 122 (B. dicoelus Rothpletz and D. mihanus Boehm only).

Type species. Belemnites dicoelus Rothpletz. Upper Jurassic, Rotti, Indonesia. Rothpletz 1892, p. 105, pl. 13, figs. 9, 14–15. Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich.

Diagnosis. Guard slender and elongate, hastate. Length about eight or nine times maximum transverse diameter. Outline symmetrical, hastate. Position of maximum transverse diameter placed posteriorly, sides of guard gradually converging anteriorly to form a long almost parallel-sided stem region. Sides of guard converging posterior to position of maximum transverse inflation to form a sharply pointed apical region (apical angle c. 10°). Profile symmetrical and similar to outline. Cross-sections of guard usually circular or compressed. Median ventral groove narrow and deep, extending from the alveolar region, where it is deepest, to the posterior extremity of the apex. Dorsal groove narrow and shallow, in most species not extending very far backwards from the alveolar region. Lateral lines usually present. Alveolus not penetrating deeply into the guard. Apical line excentric, ventrally placed.

Stratigraphic distribution. Dicoelites appears to range in age from the Callovian to Oxfordian, but may extend into the Lower Kimeridgian (see p. 617).

Described species. Stolley (1929, 1935) described a number of new species of *Prodicoelites* (i.e. *Dicoelites* Boehm s.str. Stevens) from Indonesia but their validity has been questioned by Spath (1927–33, pp. 662–3; 1935, p. 223). In view of this criticism the writer proposes to review and consolidate the previous work on the *B. dicoelus* group of belemnites, based on an examination of the material available in the collections of the Technical University, Delft (Boehm, Jonker, Molengraaff, Verbeek Collections); Utrecht University (van Nouhuys Collection); Bonn University (Wanner Collection); Göttingen University (Tornquist Collection); and the Natural History Museum, Basel (Weber Collection). Spath doubted the taxonomic value of dorsal grooves in belemnites and stated that the belemnites grouped by Stolley under *Prodicoelites* are '...a heterogeneous assemblage of individual variations of different groups of *Belemnopsis*...' (Spath 1927–33, p. 663). The writer agrees with Spath that Stolley included some *Belemnopsis* variants in *Prodicoelites*. The specimens figured by Spath (1927–33, pl. 124, figs. 6, 8) are regarded as *Belemnopsis* variants. Also the belemnite identified as *B. tanganensis* (Futterer) by Spath (1927–33, p. 10) and included in *Prodicoelites* by Stolley

is a *Belemnopsis* with a slight dorsal groove. Similar specimens from the Bajocian of Western Australia (cuttings at Geraldton and Bringo: see Whitehouse 1924) have been examined by the writer; like Spath's specimens, these are indistinguishable from *Belemnopsis*, except that a dorsal groove of variable nature is present in some individuals (cf. Stolley 1927, p. 122, footnote). Spath (1927–33, p. 10; see also Stolley 1927, p. 122, and 1929, p. 178, footnote 2) noted the presence of a shallow dorsal alveolar groove on Waagen's specimen of *B. gerardi* Oppel (Waagen 1873–5, p. 13, pl. 2, fig. 3) and a similar groove has been noted by the writer on two specimens of a new *Belemnopsis* from the Bajocian of New Zealand.

The majority of the *Belemnopsis* variants referred to above have weakly developed dorsal grooves; but in the Somaliland species, *D. stefaninii* Spath, the dorsal groove is almost as well developed as the ventral groove, and as Spath (1935, p. 222) remarked, '... in some apical halves it is impossible to distinguish the two sides'. However, as Spath (1935, p. 223) pointed out, except for the presence of the dorsal groove, the guard of *D. stefaninii* is identical with that of *B. tanganensis* (Futt.): cf. Spath 1935, pl. 25, figs. 2, 3. Spath's specimen of *B. tanganensis* came from the top of the Gahodleh Shales, whereas the specimen of *D. stefaninii* came from the base of the Daghani Shales (Spath 1935, pp. 206–8; Arkell 1956, pp. 308–9), being separated by the Wanderer Limestone (103 metres). Thus *D. stefaninii* may represent a late development of *B. tanganensis*. Spath (1935, p. 223) stated that some of his specimens of *B. tanganensis* showed a slight dorsal groove. It appears that the dorsal groove may have become extended in later forms.

Dicoelites littlei Stefanini (1925) has a narrower ventral groove than D. stefaninii and B. tanganensis, and is perhaps comparable to the specimen from Kachh figured by Spath (1927–33, pl. 124, fig. 8). Like D. stefaninii, D. littlei appears to be a variant of Belemnopsis.

A similar impersistent dorsal groove apparently also occurs in some *Hibolithes*. Stolley (1927, p. 122; 1929, p. 184) noted such a groove in specimens of *H. wuerttembergicus* (Oppel) from north-west and southern Germany, but the writer has not seen such a feature in the *Hibolithes* he has examined. These specimens noted by Stolley (and included by him in *Prodicoelites*) are regarded as *Hibolithes* variants (see Naef 1922, pp. 249, 254).

Nevertheless, some forms originally included in *Prodicoelites* by Stolley differ from *Belemnopsis* (and *Hibolithes*) in other respects than in possessing a dorsal groove, and these are particularly typified by the *Prodicoelites* described from Indonesia by Stolley (1929). These *Prodicoelites* differ from *Belemnopsis* in that their guards are very elongate and cylindrical and are often markedly compressed, with flattened sides, and the ventral groove is of a different type: narrow and deep, becoming slit-like in the alveolar region.

Most of Stolley's *Prodicoelites* material from Indonesia is fragmentary, though some of the Jamdena localities have yielded some reasonably complete specimens (Weber Collection, Basel.) The fragmentary nature of the material is probably a result of the extreme attenuation of the guard, rendering it susceptible to fracturing, and also due to the friable nature of the enclosing rock, usually siltstone. Thus many of Stolley's *Prodicoelites* species were based on fragments.

Stolley recognized eight Indonesian species of *Prodicoelites* in his 1929 and 1935 papers and after a re-examination of the original material the writer is able to recognize

four of these species. Two of these species have been recognized in collections from South America and the Himalayas as well as from Indonesia.

All the species are cylindrical and attenuate, with a sharply pointed apical region. The apical line is excentric, ventrally placed (*not* dorsally placed; see Stolley 1929, p. 187). The species vary chiefly in the nature of their dorsal and ventral grooves and the cross-sections of the guard. The species are as follows:

Dicoelites dicoelus (Rothpletz)

Plate 94, figs. 17-20

- 1892 Belemnites dicoelus Rothpletz, p. 105, p. 13, figs. 9, 14-15.
- 1906 Dicoelites dicoelus (Rothpletz); Boehm, p. 389.
- 1915 Dicoelites dicoelus (Rothpletz); Lissajous, p. 27.
- 1920 Dicoelites dicoelus (Rothpletz); Bülow-Trummer, p. 134.
- 1922 Dicoelites dicoelus (Rothpletz); Naef, p. 254.
- 1925 Dicoelites dicoelus (Rothpletz); Lissajous, p. 40 (footnote), 41.
- 1927 Dicoelites dicoelus (Rothpletz); Stolley, p. 122.
- 1929 Prodicoelites applanatus Stolley, pp. 186-8, pl. 6, figs. 8-22.
- 1952 Dicoelites dicoelus (Rothpletz); Roger in Piveteau, p. 716.
- cf. 1865 Belemnites sulcatus Miller; Salter and Blanford, p. 76, pl. 10, figs. 1-8.
- cf. 1904 Belemnites sulcatus Miller; Crick, pp. 63-64.
- ? cf. 1929 Prodicoelites cf. dicoelus (Rothpletz); Stolley, pp. 185-6, pl. 6, fig. 44.
- non 1823 Belemnites sulcatus Miller, p. 59, pl. 8, figs. 3-5.

Diagnostic features. Characterized by a markedly compressed cross-section throughout the length of the guard. Prominent lateral flattened areas developed. Very deep slit-like ventral groove, deepening towards alveolus. Dorsal groove extremely faint and shallow, confined to alveolar region.

Lectotype. Rothpletz in his original description (1892, p. 105, pl. 13, figs. 9, 14–15) figured three specimens, one (fig. 15) being a juvenile. The originals of figs. 9 and 15 were not located in the collections of the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, by the writer

EXPLANATION OF PLATE 94

All figures natural size.

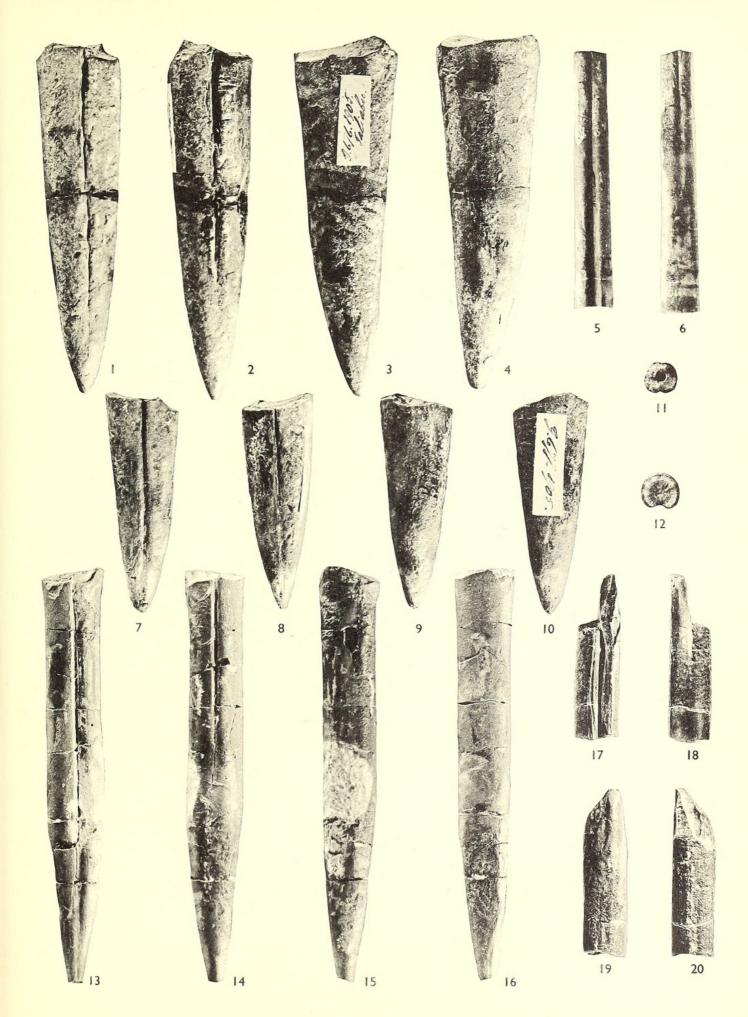
Figs. 1–4. Conodicoelites keeuwensis (Boehm). Lectotype. Keeuw, Wai Miha, Taliabu, Sula Islands, Indonesia. G676.1905, van Nouhuys Collection, Mineralogisch-Geologisch Instituut, Utrecht. (Figured Boehm 1912, pl. 32, figs. 6, 7a, b.) 1, Ventral. 2, Dorsal. 3, Left lateral (i.e. ventral groove to left). 4, Right lateral.

Figs. 5, 6, 11, 12. *Dicoelites mihanus* Boehm. Lectotype. Keeuw, Wai Miha, Taliabu, Sula Islands, Indonesia. G679.1905, van Nouhuys Collection, Mineralogisch-Geologisch Instituut, Utrecht. (Figured Boehm 1912, pl. 32, figs. 10*a*–*d*.) 5, Ventral. 6, Dorsal. 11, Anterior cross-section. 12, Posterior cross-section.

Figs. 7–10. Conodicoelites keeuwensis (Boehm). Betino, Wai Miha, Taliabu. G677.1905, van Nouhuys Collection, Mineralogisch-Geologisch Instituut, Utrecht. (Figured Boehm, 1912, pl. 32, figs. 8*a–c.*) 7, ? Ventral. 8, ? Dorsal. 9, ? Left lateral. 10, ? right lateral.

Figs. 13–16. Conodicoelites waageni (Neumayr). Lectotype. Balin, Polish Carpathians. Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. (Figured Neumayr, 1871, pl. 9, fig. 1.) 13, Ventral. 14, Dorsal. 15, Left lateral. 16, Right lateral.

Figs. 17–20. *Dicoelites dicoelus* (Rothpletz). Lectotype. Rotti, Indonesia. Wichmann Collection, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. (Figured Rothpletz, 1892, pl. 13, fig. 14*a*, b.) 17, Ventral. 18, Dorsal. 19, Left lateral. 20, Right lateral.



STEVENS, Dicoelites and Prodicoelites



in May 1960 and by Dr. K. Werner Barthel in July 1962. The original of fig. 14 was found, however, and is illustrated as Plate 94, figs. 17–20, from photographs kindly supplied by Dr. Barthel. This specimen is hereby designated lectotype for *Dicoelites dicoelus* (Rothpletz). Rothpletz's three specimens were collected by A. Wichmann in 1888–9 from Rotti Island, Indonesia.

Geographic and stratigraphic distribution. D. dicoelus has been recorded from the Landu and Renggou districts of Rotti (see Rothpletz 1892, p. 60) and from Timor and North Jamdena (as *Prodicoelites applanatus* Stolley). Stolley (1929, 1934) has dated the 'Prodicoelites Marls' of Indonesia as Callovian (Upper Dogger).

Dicoelites, many of them similar to Stolley's specimens of *P. applanatus*, have been identified by the writer in collections of the University of La Plata, Argentina (kindly made available by Dr. Rosendo Pascual), from Neuquen Province, Argentina and Puna, Chile.

Many of the Himalayan belemnites in the collections of the British Museum (Natural History) identified by previous workers as 'Belemnites sulcatus Miller' (e.g. Strachey Collection, see Salter and Blanford 1865, also Crick 1904) are very similar to, if not conspecific with, some of Stolley's specimens of *P. applanatus* from Indonesia but 'Belemnites sulcatus Miller' described and figured by Blanford (1863, p. 125, pl. 1, figs. 1, 2a-c) is a specimen of *B. uhligi* Stevens (Stevens 1963).

Dicoelites biscissus (Stolley)

1929 Prodicoelites biscissus Stolley, pp. 191-2, pl. 6, figs. 23-27.

Diagnostic features. Markedly compressed guard, as in *D. dicoelus*. Very deep slit-like ventral groove, deepening towards alveolus. Dorsal groove attains half depth of ventral groove and extends backwards into stem region.

Lectotype. Stolley's five figured specimens, from Rotti, Indonesia, are preserved in the Molengraaff Collection, Mineralogisch-Geologisch Museum, Technische Hogeschool, Delft, Nos. 14548 (Stolley, 1929, pl. 6, fig. 23), 14549 (fig. 24), 14550 (fig. 25), 14551 (fig. 26), 14552 (fig. 27). The originals of figs. 23–25 are fragments 15–25 mm. long and those of figs. 26 and 27 about 30 mm. long. The original of fig. 27 is the best illustrated of the specimens, being shown in Stolley's plate in four views (ventral, dorsal, lateral and cross-section) and is hereby designated lectotype of Dicoelites biscissus (Stolley). Geographic and stratigraphic distribution. D. biscissus has been recorded from the 'Prodicoelites Marls' of Rotti (Indonesia), of Callovian age according to Stolley (1929, 1934).

Dicoelites mihanus Boehm

Plate 94, figs. 5, 6, 11, 12

1878 Belemnites sp., Gottsche, p. 8, pl. 4, fig. 2.

1898-1901 Belemnites gottschei Tornquist, p. 162.

1912 Dicoelites mihanus Boehm, p. 139, pl. 32, figs. 10a-d.

1920 Dicoelites mihanus (Rothpletz); Bülow-Trummer, p. 134.

1921 Dicoelites cf. mihanus Boehm; Kruizinga, pp. 180-1, pl. 6, fig. 4.

1927 Dicoelites mihanus (Boehm); Stolley, p. 122.

- 1929 Prodicoelites mihanus (Boehm); Stolley, pp. 184, 188-9, 212, pl. 6, figs. 39-43.
- 1929 Prodicoelites rotundus Stolley, pp. 193-4, pl. 6, figs. 35-38.
- 1935 Prodicoelites rotundus Stolley, pp. 46-47, pl. 5, figs. 4, 5.
- cf. 1929 Prodicoelites cf. dicoelus Rothpletz; Stolley, pp. 185-6, pl. 6, fig. 44.
- cf. 1929 Prodicoelites cf. bisculcatus Stoliczka; Stolley, pp. 194–5, pl. 6, fig. 45.
- aff. 1935 Prodicoelites longirostris Stolley, pp. 42–44, pl. 2, fig. 1.

Diagnostic features. Cross-section roughly circular in apical and stem regions, compressed in alveolar region. Ventral groove deep and narrow, especially towards alveolus. Dorsal groove weakly developed and confined to alveolar region.

Lectotype (here designated). The original of Boehm 1912, pl. 32, figs. 10a–d. van Nouhuys Collection, Mineralogisch-Geologisch Instituut, Rijks-Universiteit, Utrecht. Accession no. 679.1905, Keeuw, Wai Miha, Taliabu, Sula Islands, Indonesia. Figured here as Plate 94, figs. 5, 6, 11, 12.

Geographic and stratigraphic distribution. Boehm's original specimens came from Keeuw, Wai Miha, Taliabu, Sula Islands and his age determination, Lower Callovian, has been accepted by later workers (e.g. Arkell 1956, p. 438; Marks 1956, p. 199). There is, however, reason to doubt that this age, based on the associated ammonites, can also be applied to the belemnites (see below). Kruizinga's specimens of D. mihanus came from Wai Bona, adjacent to Wai Miha (see Boehm 1912, p. 128) and Stolley (1929 1934–5) recorded specimens of mihanus and species now placed in mihanus from Rotti, Timor, North Jamdena, and Misol. Stolley assigned a Callovian age to the 'Prodicoelites Marls' of Indonesia, which contain D. mihanus, but (1935, pp. 42, 46) recorded Prodicoelites longirostris Stolley and P. rotundus Stolley, both now included in D. mihanus, from the Basal and Lower Demú Limestone of Misol, to which he assigns a Lower Oxfordian age.

D. mihanus has been recorded from the Argentinian and Chilean Cordillera. Gottsche's specimens were collected in the Argentinian Cordillera and specimens apparently similar to D. mihanus have been identified by the writer in a collection obtained by Dr. Werner Zeil (Munich) from his Sutherland Series (locality 103) in Magallanes Province, Southern Chile (Zeil 1958, p. 431). A younger collection (Zeil's locality 91) from the same series contains *Inoceramus* similar to the galoi-haasti group of Indonesia and New Zealand and Belemnopsis fragments similar to those of the Kimeridgian of Indonesia and New Zealand.

Dicoelites lenisulcatus (Stolley)

1892 Belemnites sp., Rothpletz, p. 106, pl. 13, fig. 5.

1929 Prodicoelites lenisulcatus Stolley, pp. 189-90, pl. 6, figs. 1-6.

cf. 1913 Belemnites subblainvillei Deslongchamps (partim); Soergel, p. 621, pl. 24, fig. 5 (non pl. 24, fig. 4).

cf. 1929 Prodicoelites rothpletzi Stolley, pp. 192-3, pl. 6, figs. 28-34.

Diagnostic features. Ventral groove shallow and narrow. Dorsal groove extremely weak, and confined to alveolar region. Even in the alveolar region the dorsal groove is merely a flattening of the cross-section. Cross-sections throughout the guard are slightly compressed.

Lectotype. Stolley figured six specimens, only one of which (1929, pl. 6, fig. 1) is reasonably complete. This specimen, however, is poorly illustrated in Stolley's plate and is a juvenile. The originals of figs. 1 and 2 (fig. 2 a guard split longitudinally) were recorded as being in the Boehm Collection at Freiburg, but they cannot now be traced (pers. comm., Prof. Dr. M. Pfannenstiel, 1957). The originals of figs. 3–6 are alveolar fragments ranging from 16 to 23 mm. long and are preserved in the Wanner Collection, Geologisch-palaeontologisches Institut und Museum, Rhein. Friedrich-Wilhelms-Universität, Bonn. The longest fragment of these, the original of fig. 3, is designated lectotype of Dicoelites lenisulcatus (Stolley). The originals of figs. 3–6 were collected from Jefbie, south-east Misol Archipelago, Indonesia. Geographic and stratigraphic distribution. The species occurs in Stolley's 'Prodicoelites Marls' and has been recorded from three regions in Indonesia: Jefbie (south-east Misol Archipelago), Rotti, and Timor.

Other *Dicoelites*, also included in *Prodicoelites* by Stolley, are known from the Himalayas and are described below. A probable *Dicoelites* has been described from Somaliland by Dacqué (1905, p. 153, pl. 15, figs. 11, 12) and Cottreau (1925) recorded a similar belemnite from Ethiopia.

Dicoelites bisulcatus (Stoliczka) s. str. Stolley 1929

1866 Belemnites bisculcatus (partim) Stoliczka, pp. 78–79, pl. 8, fig. 1 (non figs. 2-4).

1929 Prodicoelites bisulcatus (Stoliczka); Stolley, p. 210.

non 1935 Prodicoelites bisulcatus (Stoliczka); Stolley, pp. 44–46, pl. 5, figs. 1–3.

Lectotype. The original of Stoliczka, pl. 8, fig. 1. This specimen has not been traced but is adequately illustrated in three views: ventral, dorsal, and cross-sectional. The specimen was collected from the south-west of Gieumal (= Giumal), 32° 10′ N. lat., 78° 14′ E. long. in the Spiti Valley, north-west Himalayas (see Hayden 1904, pl. 18).

Diagnostic features. Characterized by a robust cylindrical guard, with a depressed cross-section, a long ventral groove and very short dorsal groove. The massive guard of this species contrasts with the slender elongate *Dicoelites* found elsewhere.

Geographic and stratigraphic distribution. The exact stratigraphic position of the species in the Spiti Valley, its only known occurrence, is not well defined. As stated on p. 617 Stoliczka collected belemnites from both the Liassic Tagling Limestone and the Kimeridgian–Tithonian Spiti Shales. However, there are extensive outcrops of Spiti Shales in the vicinity of Giumal and there is a strong possibility that Stoliczka's figured specimens came from the Spiti Shales.

Dicoelites sp.

1866 Belemnites bisulcatus (partim) Stoliczka, pp. 78-79, pl. 8, fig. 4 (non figs. 1-3).

cf. 1929 Prodicoelites cf. bisulcatus (Stoliczka); Stolley, pp. 195–6, pl. 6, fig. 46.

cf. 1935 Prodicoelites bisulcatus (Stoliczka); Stolley, pp. 44–46, pl. 5, figs. 1–3.

Material. The original of Stoliczka, pl. 8, fig. 4, has not been traced but it is illustrated by four views: ventral, dorsal, anterior, and posterior cross-sectional. The specimen was collected from the southwest of Gieumal, Spiti Valley, north-west Himalayas.

Diagnostic features. Guard similar to that of *D. mihanus* Boehm, but with a depressed apical and stem cross-section, which becomes compressed in the alveolar region. The bifurcation of the ventral groove in the stem and apical regions shown in Stoliczka's specimen is abnormal and probably the result of an injury, which displaced the structure forming the groove (? posterior aorta).

Geographic and stratigraphic distribution. As stated above and on p. 617 there is a strong possibility that Stoliczka's specimen came from the Kimeridgian–Tithonian Spiti Shales The Indonesian specimens doubtfully grouped with the Himalayan specimen are from the 'Prodicoelites Marls' of Rotti and the base of the Demú Limestone in the Misol Archipelago, the latter dated as Lower Oxfordian by Stolley.

Genus CONODICOELITES gen. nov.

1906 Dicoelites Boehm (partim), p. 389 (non Belemnites dicoelus Rothpletz and Belemnites sp. of Dacqué, 1905, p. 153).

1927 Dicoelites Boehm s. str. Stolley; Stolley, pp. 121-2.

1929 Dicoelites Boehm s. str. Stolley (? partim); Stolley, p. 196 (? non Dicoelites impar Stolley).

Type species. Dicoelites keeuwensis Boehm. Upper Jurassic, Keeuw, Wai Miha, Taliabu, Indonesia. Boehm 1912, p. 138, pl. 32, figs. 6, 7*a*, *b*.

Diagnosis. Guard short and conical or subconical and moderately elongate. Length (protoconch-apex) ranges from less than maximum transverse diameter up to between

two and four times. Outline symmetric; profile usually asymmetric, ventral surface of guard more inflated than dorsal. Apex usually excentric and dorsally placed. Cross-sections of guard circular, compressed or slightly depressed. Median dorsal and ventral grooves either equally well developed or with the ventral groove slightly broader. Dorsal groove not extending as far posteriorly as ventral groove. Both grooves narrow but relatively deep. Apical line and alveolus excentric towards venter. Alveolus penetrating deeply into guard.

Species. Apart from the type species, *C. keeuwensis*, at least three previously described species are considered to belong to *Conodicoelites*. The diagnostic features of these species are given below. Two, and possibly a third, *Conodicoelites* species occur in the Lower Kimeridgian of New Zealand and are to be described in a forthcoming publication (Stevens, in press). The species of *Conodicoelites* may be distinguished on the basis of two main features. The depth of penetration of the guard by the alveolus is characteristic, and the length of the guard (protoconch–apex) may be compared with the maximum transverse diameter, and the ratio of total length of guard (anterior–posterior) to alveolus also compared. Elongation of the guard is also a valuable feature—varying from short and conical (*keeuwensis*), elongate and conical (*sulcacutus*), subconical with a sharp apical region (*meyrati*) and subconical and slightly hastate (*waageni*).

Conodicoelites keeuwensis (Boehm)

Plate 94, figs. 1-4, 7-10

- 1912 Dicoelites keeuwensis Boehm, D. cf. keeuwensis Boehm, p. 138, pl. 32, figs. 6, 7a, b, 8a-c.
- 1920 Dicoelites keeuwensis Boehm, D. cf. keeuwensis Boehm; Bülow-Trummer, p. 134.
- 1922 Dicoelites keeuwensis Boehm; Naef, p. 254.
- 1927 Dicoelites keeuwensis Boehm; Stolley, p. 121.
- 1929 Dicoelites keeuwensis Boehm, D. cf. keeuwensis Boehm; Stolley, pp. 183-4, 196, 211-12.
- 1931 Dicoelites keeuwensis Boehm, D. cf. keeuwensis Boehm; Kruizinga, p. 371.
- 1931 Dicoelites keeuwensis Boehm; Wanner, p. 591.
- 1934 Dicoelites keeuwensis Boehm; Stolley, pp. 479, 480.
- 1956 Dicoelites keeuwensis Boehm; Marks, p. 199.

Diagnosis. Guard short and conical. Length (protoconch-apex) between 1.5 and 2.0 times maximum transverse diameter. Outline symmetrical; conical, sides of guard gradually converging towards posterior. Apical angle about 25°. Profile similar to outline, but markedly asymmetric, with ventral surface more inflated than dorsal. Apex excentric, dorsally placed. Cross-sections of guard circular, or slightly compressed in alveolar region. Median ventral and dorsal grooves equally well developed. Ventral groove shallowing and disappearing just before reaching apex. Dorsal groove extending posteriorly for about two-thirds total length of guard. Alveolus excentric towards venter and occupying more than half total length of guard. Alveolar angle about 25°.

Lectotype (here designated). Original of Boehm 1912, pl. 32, figs. 6, 7a, b. No. G676.1905, van Nouhuys Collection, Mineralogisch-Geologisch Instituut, Utrecht. Upper Jurassic, Keeuw, Wai Miha, Taliabu, Sula Islands, Indonesia. Figured here as Plate 94, figs. 1–4. The original of Boehm's pl. 32, figs. 8a–c, also in the van Nouhuys Collection, Utrecht (No. G677.1905), is figured here as Plate 94, figs. 7–10. Upper Jurassic, Betino, Wai Miha, Taliabu.

Geographic and stratigraphic distribution. The specimens which were the basis of Boehm's original description (van Nouhuys Collection, Utrecht) form the only record of the species. They came from three localities (Keeuw, Betino, Tangi) on the river Wai Miha, Taliabu, Sula Islands (see Boehm 1912, p. 128). On the basis of the associated ammonites a Callovian age (Lower or Middle) has been assigned to *D. keeuwensis* by Boehm and later workers (Boehm 1912; Stolley 1929; 1934, p. 478; Wanner 1931, p. 591; Marks 1956, p. 199; Arkell 1956, pp. 438–9) but this is assuming that the ammonites and belemnites were derived from the same beds. The associated belemnites, however, apart from *Conodicoelites*, suggest that most stream-bed collections from Taliabu, especially those of van Nouhuys from Wai Miha, are drawn from a number of distinct horizons. The ammonites have probably been derived from upstream horizons and transported downstream as concretions.

Though there is evidence that *Conodicoelites* is older in Europe (see below), in Indonesia it is more likely to be of about the same age as in New Zealand, where it has been dated as Lower Kimeridgian by Arkell from associated ammonites (Fleming and Kear 1960, p. 25; '*Dicoelites*' = *Conodicoelites*). A Lower Kimeridgian age for the Indonesian *Conodicoelites* agrees with age determinations for succeeding Indonesian belemnites based on ammonites associated with similar belemnites in New Zealand (see Stevens, in press).

Conodicoelites meyrati (Ooster)

1857 Belemnites meyrati Ooster, pp. 18-19, pl. 3, figs. 1-17.

1908 Belemnites (Duvalia) meyrati Ooster; Roman, pp. 10-14, pl. 1, figs, 1-5.

1909 Dicoelites meyrati (Ooster); Boehm, pp. 565-6.

1915 Dicoelites meyrati (Ooster); Lissajous, pp. 26-27, pl. 1, fig. 2.

1920 Dicoelites meyrati (Ooster); Bülow-Trummer, p. 134.

1922 Dicoelites meyrati (Ooster); Naef, p. 254.

1925 Dicoelites meyrati (Ooster); Lissajous, p. 40, fig. 22.

1927 Dicoelites meyrati (Ooster); Stolley, p. 121.

1929 Dicoelites meyrati (Ooster); Stolley, pp. 183-4, 211-12.

? cf. 1932 Dicoelites cf. meyrati (Ooster); Krimholz, pp. 38-39.

1952 Dicoelites meyrati (Ooster); Roger in Piveteau, pp. 715-16, fig. 41.

1961 Dicoelites meyrati (Ooster); Pugaczewska, pp. 184-8, pl. 24, figs. 1-4.

Type specimens. In 1958 the writer made inquiries at the museums at Bern and Geneva but Ooster's original specimens were not traced. Upper Jurassic (? Callovian) of the Swiss Alps.

Diagnosis. Guard subconical, elongate in alveolar region, its sides then rapidly converging to form a sharp apical region. Apical angle about 18°. Length (protoconchapex) about four times maximum transverse inflation. Outline symmetrical, profile asymmetrical. Cross-sections of guard slightly compressed. Ventral groove prominent, extending from apex to alveolus without change. Dorsal groove generally slightly broader than ventral groove and extending posteriorly for about two-thirds total length of guard. Alveolus excentric towards venter and occupying a little less than half total length of guard. Alveolar angle 19–24°.

Geographic and stratigraphic distribution. C. meyrati was described by Ooster from three localities in the Bernese Alps (Hohmad, Sulzgraben, and Schwefelberg). The stratigraphic position of these localities is unknown. A Callovian age has been accepted by later workers (e.g. Bülow-Trummer 1920, p. 134; Pugaczewska 1961, p. 188), but according to Dr. B. Ziegler (Zürich, pers. comm.) the strata at Sulzgraben are uppermost Bajocian (zone of Parkinsonia parkinsoni) and the beds at Hohmad are Upper Oxfordian (zone of Gregoryceras transversarium or Epipeltoceras bimammatum). Pugaczewska (1961) described specimens which she has assigned to C. meyrati from the Callovian of the Holy Cross Mountains (south-east Poland) and Krimholz (1932) compared specimens from the Callovian of Crimea to meyrati.

Conodicoelites waageni (Neumayr)

Plate 94, figs. 13-16; text-fig. 1

1871 Belemnites waageni Neumayr, pp. 26, 51 (postscript), pl. 9, fig. 1.

1909 Dicoelites waageni (Neumayr); Boehm, pp. 565-6.

1920 Dicoelites waageni (Neumayr); Bülow-Trummer, p. 134.

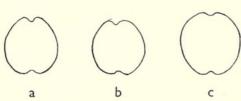
1922 Dicoelites waageni (Neumayr); Naef, p. 254.

1961 Dicoelites waageni (Neumayr); Pugaczewska, pp. 188-9, pl. 6, figs. 5-6.

Lectotype (here designated). Original of Neumayr 1871, pl. 9, fig. 1. Bayerische Staatssammlung für

Paläontologie und historische Geologie, Munich. Lower Callovian, Balin, Polish Carpathians (district Chrzanów).

Figured here as Plate 94 figs. 13-16.



TEXT-FIG. 1. Conodicoelites waageni (Neumayr). Lectotype. Balin, Polish Carpathians. Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. Cross-sections through guard (provided by courtesy of Dr. K. W. Barthel). Section *a*, 62 mm. from apex of guard (see Pl. 94, figs. 13–16); section *b*, 68 mm.; section

c, 84 mm. All natural size.

Diagnosis. Guard sub-conical. Length (protoconchapex) about four times maximum transverse diameter. Outline symmetric; profile slightly asymmetric. Apical region, elongate, pointed. Apical angle about 15°. Sides of guard tending to become parallel towards anterior and converging slightly in alveolar region to produce slight hastation some 20 mm. anterior to protoconch. Cross-sections of guard circular or slightly depressed (text-fig. 1). Ventral groove deep, extending back from alveolus but shallowing and disappearing before reaching apex. Dorsal groove deep, extending back to just

short of half total length of guard. The alveolus occupies under half of total length of guard and is slightly excentric towards venter. Alveolar angle about 24°.

Geographic and stratigraphic distribution. C. waageni has been recorded only from Neumayr's original locality, the Balin Oolite of Balin, near Cracow, south-east Poland. A Lower Callovian age is accepted for the Balin Oolite (Arkell 1956, p. 480; Pugaczewska 1961, p. 188).

Conodicoelites sulcacutus (Stolley)

1866 Belemnites bisulcatus Stoliczka (partim), pp. 78–79, pl. 8, figs. 2–3 (non pl. 8, figs. 1, 4).

1895 Belemnites sulcacutus F. E. Suess; Diener, pp. 583-4 (nomen nudum).

1906 Dicoelites sulcacutus (Suess); Boehm, p. 389 (nomen nudum).

1920 Dicoelites sulcacutus (Diener); Bülow-Trummer, p. 134 (nomen nudum).

1922 Dicoelites sulcacutus (Diener); Naef, p. 254 (nomen nudum).

1929 Dicoelites sulcacutus (F. E. Suess); Stolley, pp. 210-12.

1956 Belemnopsis sulcacutus; Arkell, p. 408.

1957 Belemnites sulcacutus Suess; Holland et al., p. 251.

Diener (1895) in describing fossils collected from the Niti area (Johar and Hundes) of the central Himalayas introduced the name *Belemnites sulcacutus*, as a *nomen nudum*, stating that the fossil identifications had been supplied by F. E. Suess and that descriptions and illustrations of species were to be published later. These, however, did not appear. Thirty-four years later Stolley (1929, pp. 210–13) gained access to Suess's manuscript and original material in the Diener Collection and indicated that Suess's name *sulcacutus* can be applied to the belemnite from the Spiti area (north-west Himalayas)

figured by Stoliczka (1866) as pl. 8, figs. 2–3. By associating Suess's nomen nudum with Stoliczka's figure Stolley therefore validated sulcacutus. The taxon Dicoelites sulcacutus Stolley (ex. F. E. Suess nomen nudum) is thus based on Diener's material in Vienna and the specimen figured by Stoliczka as pl. 8, figs. 2–3. Therefore, both Diener's and Stoliczka's material can be regarded as syntypic.

Unfortunately both Stoliczka's material (which Stolley could not trace: 1929, p. 211) and Diener's (which Stolley examined) cannot now be traced in Vienna (Dr. F. Steininger, pers. comm.). However, Stoliczka's figures are adequate for diagnosis, the guard being shown in ventral (but not dorsal) view and in two cross-sectional views.

Diagnosis. Guard conical, elongate. Length (protoconch-apex) less than maximum transverse diameter. Outline symmetrical, sides gradually converging posteriorly to form an almost perfect cone. Apical angle about 14°. Profile not known, but to judge from Stoliczka's cross-sections, probably approximately the same as the outline. Cross-sections of guard circular or compressed posteriorly, depressed anteriorly. Ventral groove narrow and deep, extending backwards from alveolus, but shallowing and disappearing before reaching apex. Dorsal groove not known, but to judge from Stoliczka's cross-sections, probably of about the same depth and breadth as the ventral groove, but extending posteriorly for less than half the total length of the guard. Alveolus extremely deep and occupying three-quarters of total length of guard. Alveolar angle about 11°.

Geographic and stratigraphic distribution. The species occurs in the Niti and Spiti regions of the central and north-west Himalayas. Its stratigraphic position in these regions is doubtful. Diener's specimens, from the Niti region, were obtained from beds underlying the Spiti Shales (Diener 1895, pp. 583–4, fig. 10). Arkell (1956, pp. 407–8) has assigned an Upper Oxfordian–Tithonian age to the Spiti Shales and a Callovian age to the sulcacutus Beds.

The precise stratigraphic position of Stoliczka's specimen from the Spiti region is not known, as he obtained belemnites from both the Tagling Limestone (Liassic; Arkell 1956, pp. 408–9) and from talus slopes below the Spiti Shales (Stoliczka 1866, pp. 79, 83). His figured specimens are, however, from the Gieumal (Giumal) area were there are extensive exposures of Spiti Shales (see Hayden 1904, pl. 18), so there is a strong possibility that they came from the Spiti Shales. As there is reason to believe that Upper Oxfordian is not represented in the Spiti Shales (Stevens, in press) Stoliczka's specimens could be as young as Lower Kimeridgian, but this is difficult to reconcile with the Callovian age assigned to Diener's specimens, which though coming from directly below the Spiti Shales are apparently separated from them by a non-sequence representing most or all of the Oxfordian.

STRATIGRAPHIC DISTRIBUTION OF DICOELITES AND CONODICOELITES

The stratigraphic distribution of *Dicoelites* and *Conodicoelites* is difficult to determine as the ages of many of their species are not fully known.

The *Dicoelites* species recorded from Indonesia have been assigned a Callovian ('Prodicoelites Marls') and Lower Oxfordian (Basal and Lower Demú Limestone of Misol) age by previous writers. *Dicoelites* has not been recorded from New Zealand where there are well-developed Indo-Pacific belemnite assemblages of Bajocian—Bathonian and Lower or Middle Callovian age, but where the Upper Callovian and Oxfordian are not represented by belemnites. *Dicoelites* has also not been recorded from Australia, where there is a similar gap in the belemnite record. Therefore on this purely negative

evidence it is likely that the Indonesian *Dicoelites* have a range extending from at least Upper Callovian to Middle or Upper Oxfordian. The stratigraphy of the *Dicoelites* recorded from the Himalayas is unknown, but if some at least came from the Spiti Shales and were associated with *Belemnopsis gerardi* (= B. uhligi Stevens, 1963) or B. alfurica, a Lower Kimeridgian age is likely.

Stolley (1927, p. 122; 1934, p. 478) stated that *Dicoelites* (= *Prodicoelites* Stolley) appeared before *Conodicoelites* (= *Dicoelites sensu* Stolley) but that the age difference between the two was not very great. In New Zealand *Conodicoelites* is of Lower Kimeridgian age and it is thought that this age can also be applied to the Indonesian *Conodicoelites*, previously dated as Callovian. Nevertheless, a Callovian age has been accepted for *C. waageni* in Poland and also, though on less secure grounds, for *C. meyrati* in Switzerland. A Callovian age also seems likely for *C. sulcacutus* from the Himalayas. Belemnites similar to *C. meyrati* have been recorded from the Upper Toarcian and Lower Bajocian of Russia.

Thus it is likely that *Conodicoelites* appeared before *Dicoelites*, probably in the Toarcian–Bajocian of eastern Europe. Then in the Callovian it was able to spread along the northern margin of the Tethys, appearing in the Swiss Alps, the Carpathians and the Himalayas. Further migration into the Indo-Pacific region was, however, apparently impeded and *Conodicoelites* did not reach Indonesia and New Zealand until the Kimeridgian.

Dicoelites was apparently confined to the Indo-Pacific region and species ranged throughout the Callovian and Oxfordian. The European records of the genus in the Bajocian (avena Mayer, jacquoti Terquem and Jourdy, wuerttemburgicus Oppel) and Portlandian (pellati de Loriol) have not been confirmed.

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