The ontogeny, palaeobiology and systematic palaeontology of some lower liassic belemnitida

Bolton, J. T. F. S.

Bolton, J. T. F. S. (1982) *The ontogeny, palaeobiology and systematic palaeontology of some lower liassic belemnitida*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7901/

ERRATA

page	line	
15	30	For "geophysical members" read "geophysical marker members".
18	15	For "Sellwood 1922" read "Sellwood 1972".
29	13	For "of Belemnites longissimus, B.bharmouthensis" read "of Belemnites (B.longissimus, B.charmouthensis)".
34	16	Underline "Belemnites".
35	19	For "Jeletsky" read "Jeletzky".
36	3	Underline "Belemnites".
41	18	For "plate 8" read "plate 13".
42	16	Underline "Pseudohastites".
43	1	Underline "Pseudohastites".
43	2	Underline "stonebarroensis".
43	3	Underline "B.longissimus".
43	4	Underline "Pseudohastites junceus".
75	32	For "beds 11b-d" read "beds 111b-d".
79	9	For "Barskov (1972, 1973)" read "Barskov (1973a,b)".
184	29	Underline "H.stonebarroensis".
234	22	For "more or well" read "more or less well".
246	19	For "mars" read "mass".
facing 252	8	For "fig. 7" read "fig. 3".
255	27	For "regeneration (of" read "regeneration of".

The ontogeny, palaeobiology and systematic palaeontology of some Lower Liassic Belemnitida

by

J.T.F.S. Bolton

Abstract

The Belemnite Marls of the Dorset coast constitute the _jamesoni_ and _ibex_ Zones of that area. This study is essentially a revision of the total belemnite fauna of these beds, with a preliminary appraisal of the belemnites from the overlying basal Green Ammonite Beds (_davoei_ Zone). Twelve morphospecies are described which are defined by their rostral ontogeny and other morphometric data.

Probable sexual dimorphism into relatively stout and slender rostra is demonstrated for four species (_Belemnites longissimus_ Miller, _B. charmouthensis_ Mayer, _B. imus_ (Lang) and _B. cricki_ (Lissajous)).

It is recognised that, at different localities and horizons, single species may be represented by assemblages that vary with respect to age and sex of individuals, and it is concluded that such belemnite assemblages are at least partly due to local population structures analagous to those that are found in modern cephalopods.

Early ontogeny, rostral form and function, epirostra and surface ornamentation are briefly discussed with reference to the species described.

The ontogeny, palaeobiology and systematic palaeontology of some Lower Liassic Belemnitida

by

John Tarquin Frank Sanders Bolton, B.Sc.(Dunelm)

A thesis submitted to the University of Durham
for the degree of Doctor of Philosophy.

Department of Geological Sciences 1982
University of Durham

Contents

Page

Page

List of figures

List of plates

[At back of volume]

Acknowledgements

I would like to thank the following for their assistance in producing this thesis: my supervisors, Dr. J.R. Senior and Dr. G.P. Larwood; my typists, Mrs. M. Senior and Ms. O. von Lyncker; Mr. M. Atkinson for invaluable assistance with the photography; Mr. D. Phillips and Dr. M.K. Howarth of the British Museum (Natural History); the staff of the Science Library and the technical staff of the Department of Geological Sciences, University of Durham, and finally the University of Durham for sponsoring the research with a Research Studentship.

Chapter I

History of research

This chapter is divided into two parts. The first deals with the more remarkable misconceptions concerning the nature of the belemnite rostrum that have existed in both folklore and scholarship since ancient times. The second documents the more viable, if less colourful, idea of the belemnite as a molluscan animal, and includes a brief survey of those works that are directly pertinent to the scope of this thesis.

Antique notions

In the European Renaissance there were several widely divergent and fantastical hypotheses that sought to account for the origin of fossils in general and belemnites in particular. With the exception of the insights of enlightened individuals such as Leonardo da Vinci and his contemporary Girolamo Fracastoro (Edwards 1967) the majority of early proposals were variants on the theme of lusus naturae. However, belemnite rostra, presumably because they have no easily recognizable modern counterparts, tended to be regarded with rather more ambivalence. The majority of their supposed identities are easily comprehended: thunderbolts, faery fingers, spectres' candles and teeth (praeternatural and mundane), are all consistent with the projectile or digit shape that is characteristic of most rostra. Such beliefs are found especially in the folklore of areas which have the appropiate geology, and may perhaps be detected in the works of various Classical authors. It is also easy to understand the many rational authors of the sixteenth to eighteenth centuries who were of the opinion that belemnites were natural concretions of some sort. More mysterious is the recurrent conviction that belemnites were to be identified with the lyncurium, lyngourion or lyncourion of ancient authors. To avoid confusion at the outset, the classical sources that are relevant to Renaissance scholarship are outlined below. The earliest reference is in De Lapidibus of Theophrastus (c. 315 - 305 B.C.):

> "...the lyngurium, which is carved into signets and is as hard as any stone, has an unusual power. For it attracts other objects just as amber does, and some people maintain that it acts not only on straws and leaves, but also on thin pieces of copper and iron, as Diocles maintained. The lyngurium is cold and very clear. A wild lynx produces better stones than a tame animal, and a male better ones than a female... The stone is discovered only when experienced searchers dig it up, for when the lynx has passed its urine, it conceals it and scrapes soil over it. Moreover, the lyngurium needs considerable working. Similarly, amber is a stone (for the amber of Liguria is dug from the earth), and of this likewise a power of attraction is an attribute. ...Then there are some [stones] which ...differ from each other although they share the same name. For instance, there is the "sard", of which the transparent, ruddier kind is known as the "female", while the transparent but darker variety is known as the "male". The same is true of the lyngurium, the female being the more transparent and paler."
> (V, verses 28 - 31; transl. & ed. Eicholz 1965, p. 67 - 9)

Ovid (43 B.C. - 17 A.D.) was probably drawing on Theophrastus when he attributed to Pythagoras this statement:

"Conquered India gave his lynxes to Bacchus, god of the vine cluster. Men say that whenever these animals empty their bladders, the contents turn to stone and harden in contact with the air." (Metamorphoses, Book XV 391 - 430, transl. Innes, 1955, p. 345) (Pythagoras died about 150 years before Theophrastus was born.)

Pliny The Elder (23 - 79 A.D.), having translated from Greek to Latin Theophrastus' article on precious stones, denied both that there was a stone called lyncurium and that the urine of an animal could become converted to a stony mass. However, he does report that Demostrate gave the name lyncurion to amber, since he believed it to have formed from lynx urine.

Other early authors who mention petrified lynx urine, often in connection with amber, include Dioscorides (late 3rd century B.C.), Solinus (3^{rd} century A.D., "an unprincipled plagiarist, popular in the Middle Ages for his brevity.") and Isidore of Seville (c. 570 - 636 A.D.).

This curious motif resurfaced during the Renaissance, when, in de Blainville's words,

> "the first authors who spoke of it were those who were concerned with mineralogy, and particularly with medical materials, and, as often happened in this period, the virtues attributed to these were equivalent to their supposed origins. Hence, as Theophrastus had said that the _lyncurium_ was the urine of the lynx converted to stone, it was concluded that this stone, when dissolved in a solvent, was very effective in acting contrary to gravel [of the urinary tract], no doubt by some kind of affinity. Thus it became merely a matter of finding the _lyncurium_. But, as with Theophrastus himself, there was some confusion between _lyncurium_ and amber, and when the latter was found in alluvial terrain in Prussia along with fragments of belemnite from the Chalk which had hitherto been regarded as amber, one begins to see how the transition was made from _lyncurium_ to belemnite." (1827, p. 5 - 6, my transl.).

Unfortunately, adequate documentation of this idea does not become available until the middle of the sixteenth century. However, since the more sober authors of this period found it necessary to refute the correspondence of belemnite, _lyncurium_ and lynx urine, it is apparent that this distinctly Mediaeval prophylactic must have had some popularity before this time. It is also telling that, as late as 1696, Jacobaeus denied that belemnites from the island of Møn (just south of Zealand) were petrified lynx urine on the grounds that there were no lynxes in Denmark! On the other hand, Chretien Encelius (1557), in his treatise on metals, was convinced that the large number of stories on the subject were proof that lynx urine solidified to form _lyncurium_, although he was probably not cognizant of belemnites.

Most authors subsequent to Encelius firmly reject the concept of petrified urine, but, probably because of the confusion between amber and fragments of orange Cretaceous belemnites (eg. Libavius (1601), they often believed belemnites to be hardened amber;

Elsholtz (1678) compared belemnites with amber), the belief that ancient authors were referring (at least in part) to belemnites when they spoke of lyncurium has continued to plague classical commentators and palaeontologists up to the present day. De Boodt (1609) gives lyncurius as a synonym for belemnite. Miller (1826) writes, with no apparent justification,

> "The ancients observed these fossils; and in Ovid's Metamorphoses it is stated that the urine of the Indian lynx became converted into stone before it reached the ground, and thus formed the Belemnites, which were therefore named Lapides Lyncis, Lyncurium etc." (1823, p. 46).

Other authors impute this identification to pre-scientific authors, Roger (1958, p. 701) being one of the most recent.

The most likely identity of lyncurium would appear to be a clear, unflawed amber, bearing in mind the properties given by Theophrastus of electrostatic attraction, transparency and implied similarity to yellow and red sard. This view has been iterated by other workers (Caley and Richards 1956, p. 109).

The clue to the whole situation is perhaps to be found in Theophrastus' mention of Diocles (see quote above), who was probably the same Diocles as the fourth century B.C. physician who made a close study of the kidneys and urinary tract (Eichholz 1965, p. 67 - 9). We may suggest that in a dissected lynx he encountered some kidney stones of a yellow colour, and that he concluded that some natural stone of similar appearance had a similar origin. This idea was disseminated amongst various early authors in a somewhat garbled fashion, starting with Theophrastus, and was quoted a thousand or so years after Isidore (6th to 7th century) in the works of Western European natural historians, although, as already implied, there seems to have been some undocumented tradition spanning this interval. Owing to a fully justified confusion between lyncurium and amber, and an understandable confusion between amber and the orange belemnite fragments which are derived from the Chalk, a number of authors regarded lyncurium as a synonym for belemnite; the final stage of the irony is the definitive statement in several more or less modern works that the ancients believed belemnites to be the petrified urine of the lynx.

Some of the less enigmatic misconceptions will now be considered, but in rather less detail than the foregoing.

"Thunder was always more dreadful to uneducated people than lightning, and all over the world there has been a great desire to find the source of that mystical power - the "thunder-bolt"." (Taylor 1885, p. 297). This exalted office has probably been filled by the belemnite rostrum ever since people noticed them washed out on field surfaces or from clayey hill and cliff outcrops after heavy storms. Pliny wrote of several varieties of "thunderstone", or "ceraunia", one of which is elongated. Presumably, "ceraunia" means "single horn". Of another variety, he reported that, "the Magi hunt for it zealously because it is found only in a place that has been struck by a thunderbolt." (Nat. Hist. Book 37, transl. Eichholz 1962). Some "cerauniae" were said by Pliny to resemble axe-heads, which has led to a modern identification of them with flint implements (Edwards 1967, p. 40), which need not be exclusive of other interpretations.

References to thunderbolts by various authors since the Renaissance imply that belemnites were widely believed to be thunderbolts, thus Césalpin (1596) regards certain stones that were believed to have fallen with thunder as owing their origin to some kind of marine shell; Platt (1764), who knew that belemnites were shells allied to nautili, writes of two "species", one of which is "common im most counties of this kingdom, and vulgarly known by the name of "Thunderbolt"." (p. 40). Taylor (1885) had "a vivid remembrance of of a veterinary surgeon, of such eminence that I dared not contradict him then, who triumphantly brought a real "thunder-bolt". A cow had been killed by lightning, and this "thunder-bolt" was found just underneath her." (pp. 298 - 9). This was an Oolitic belemnite from the boulder clay of the Eastern counties. I have encountered a farmer in the Midlands who was similarly convinced.

This fancy is not confined to Europe: a modern Sioux medicine man speaks of the South Dakota Badlands as harbouring the bones of monsters, petrified sea shells and turtles, along with "many kangi tame - bolts of lightning which have turned into black stones shaped like spear points." Of tonwan, the thunderbolt, he says, "Sometimes it hits a horse. You see all the veins burn up, like an X-ray. Afterward you find one of these black stones embedded in the earth where the lightning struck." (Fire and Erdoes 1972, p. 238 - 241). This is a striking contemporary repetition of both Pliny and the Victorian vet.

An early popular belief in belemnites as stony fingers may perhaps be detected in Pliny, who wrote that, "Idaei dactyli or Fingers of Ida, have the colour of iron and reproduce the shape of the human thumb." (Nat. Hist., Book 38, Section LI. transl. Eichholz 1962, p. 303). Since the Renaissance (eg. Belon, 1553), it has been regarded as likely that these stones were belemnites; a modern translator of Pliny endorses this view (Eichholz 1962, p. 303). De Blainville (1827, p. 25), gives digiti diaboli, or devil's fingers, as a rare name for belemnites used in Germany. An esoteric use of belemnite rostra is reflected in the terms "Alpfescht", "Alpschos" and "Alpschosstein", meaning respectively "incubus arrow", "incubus shot" and "incubus shot stone". These were supposed to be "an excellent remedy against the incubus, ...a supposition as veritable as the malady".

Other strange epithets reported by de Blainville from German authors include Spectrorum candela ("spectres' candles"), Oxyrhynchi ("sharp beaks"), which was applied only to sharp, pointed species and Corvinus lapis, derived from Rabenstein ("raven stone"), which was applied to those species that were more or less recurved at the apex.

A number of authors up to the 18th century regarded belemnites as being of inorganic origin, often as some sort of stalactite (eg. Imperato 1599; Grew 1681; Scheuchzer 1702; Lang 1708; Kindmann 1737; all in de Blainville 1827). In conflict with such authors were those who maintained an organic origin, although a number of phyla were invoked: Cesalpin believed they were shells of some sort; Mercati (1541 - 93), a pupil of Cesalpin, suggested they might be petrified dates; Lhwyd (1699), who coined the term "alveolus", appears to have regarded them as concretions formed inside various marine tubular organisms; Helwing (1717) placed them amongst the "zoophytes"; Volkmann (1720) supposed that they were spines or even vertebral columns of fishes, partly because he considered only the phragmocone which he confused with orthoceratid nautiloids, whose chambers very superficially resemble vertebrae; Klein (1731, 1740), although he regarded most belemnites as chambered cephalopods, insisted that slender, fusiform varieties (which are often found without the alveolus) were echinoid radioles. The accepted view of the belemnite as a squid-like cephalopod arose in the early 18th century, and by the end of the century had virtually ousted all other scholarly interpretations. The next section of this chapter briefly traces the development of the concept up to the present day, with particular reference to those authors who refer to belemnites from the Lower Lias.

Belemnites as cephalopods

The term "belemnite" was apparently first used in print by Agricola (1546) (Edwards 1967, p. 40), but the first author to realise the correct affinities of these "figured stones" was Ehrhart (1724). He demonstrated, 1) that they were marine shells related to the nautili and Spirula 2) that the rostrum grew by addition of external layers and 3) that their chemical composition strongly indicated their organic origin. His conclusions were admitted by various other natural historians, including Klein (1731, 1740), Linnaeus (1747), Brander (1754) and Platt (1764). Platt, having quoted from Brander, "the belemnite belongs to the testaceous part of the animal kingdom and to the family of the nautili", adds,

> "And I would beg leave further to add, that this gentleman's statements are greatly strengthened by the surprising analogy which the belemnite bears to the little peerly concamerated shell, or cornu Ammonis; and the orthoceratites, to the large nautilus; the former having its siphunculus on the verge, as the latter has it in the centre of the diaphragm, or partition of each cell or chamber." (p. 41).

However, he regarded the siphuncle as housing a "little gutt or ductus, by dilating or contracting of which the animal, it should seem, may go out or into its cell at pleasure" (p. 45). While he appreciated that the rostrum must have formed by superposition of layers from external tissues, having observed a specimen "whose laminae were in a manner dissected and laid open by the vague acid, or some other corroding menstruum, which everywhere pervades the earth," he suggested the following picturesque mode of formation: the animal

> "very likely goes out in quest of food, but travels only upon the guard or rampart, leaving a trail behind, as all snails do; which hardening into a testaceous substance, increases the dimensions of the outer walls, both in length and thickness, from the cell or chamber, to the bottom of the point of the whole belemnite. The

animal in its progress and return clasps the whole guard, as a snail does a small branch of a tree in the gardens, and where the two sides meet, there the sulcus is formed." (p. 45).

Note the attempt to explain the significance of the commonly occurring ventral rostral furrow.

By analogy with fossil and living nautili, Platt suggested that belemnites might still inhabit the seas, and concluded his paper with the reasonable exhortation,

> "strictly to examine the coasts where nautili are found. Persons commissioned to collect shells and other curiosities, generally grasp at such things as feast the eye; not regarding those of less beauty and lustre, which would help us in our researches... A premium, offered by a Society of Vertuosi, might encourage our seafaring gentlemen to search the several coasts, upon which they touch in their long voyages, and to use dragnets as they do in drudging for oysters... And great improvements might be expected, if their inquiries should be successful." (p. 52).

Lamarck published the first taxonomically formal description of a belemnite in 1801. His single genus, Belemnites, which he had described without figures or type species in 1799, contained only one species, B. paxillosa (sic) and was based on figures by Klein (1731) and Breynius (1732), which unfortunately represent several species.

The earliest formal description of material from the Belemnite Marls is due to Miller (1826), to whit B. longissimus, and possibly B. elongatus, both from the "Lyas and lyas clay" of "Lyme in Dorsetshire" (p. 60, Pls VII, VIII). He made detailed observations on the phragmocone and rostrum, which led him to conclude that the skeleton was internal and that the rostrum was initially crystalline and dense rather than porous and bouyant; the latter view was promulgated by various authors, including Lamarck, who assumed the rostrum to have the texture of the modern Sepia phragmocone. In support of his conclusion, Miller found that the size of a cone of oiled paper necessary to support a rostrum in water (the cone being glued into an empty alveolus) was " of no larger size than from some known fine specimens we may fairly conclude the outer chamber to have attained". (p. 49).

De Blainville (1827) published a 136 page treatise on belemnites, which, amongst other things, contains an excellent history of ideas on the subject, including a conprehensive annotated catalogue of authors ranging from the 16th century to his own time.

His classification encompasses about 50 species, including those of Miller. A few species are recorded from the "blue Lias" (broadly equivalent to the Lower Lias rather than the Blue Lias sensu stricto) of Britain and the Continent.

Various other classifications were erected over the next half century. These are conveniently summarised by Phillips (1865 p.25) whose monograph provides an excellent synthesis of Jurassic belemnite taxonomy up to that date. Several new species from the Dorset Lower Lias are included.

Simpson, an enthusiastic museum curator at Whitby, described 24 species from the Lower Lias of Yorkshire, 19 of which were new; unfortunately, no figures were published (1855, 1884).

In 1842, d'Orbigny recognized sexual dimorphism in belemnite rostra, but his conclusions were generally ignored or refuted.

Other 19th century authors of note include Voltz (an Engineer-in-Chief in Paris, who published an important monograph, "Sur les Belemnites" (1830)); Buckland (1837); Owen (1844); Mantell (1848, 1849); Quenstedt (1852); Mayer (1863); Huxley (1864) (who gave a very detailed account of belemnite structure and coined the term "pro-ostracum"), Tate and Blake (1876) (who provided descriptions and good figures of Liassic belemnites from Yorkshire) and Douvillé (1892).

The study of belemnites in the early 20th century was largely the province of Continental workers. It could be said that their principal concern was the gross phylogeny of the group, and to this end large numbers of genera, usually with few species, were erected and made to evolve from each other. Nevertheless, phylogenetic speculation apart, practical taxonomic systems were developed; in particular, Naef (1922) proposed a supra-generic classification which in modified form (Jeletzky 1966) is probably the most widely accepted.

Other significant studies are those of Lissajous (1907, 1925, 1927), Werner (1912), Pavlow (1913), Abel (1916) and Stolley (1919), but the single most important paper from the point of view of this thesis is that by Lang (1928) on the Belemnite Marls of Charmouth. He provided a detailed stratigraphical column and described 26 species of belemnite, 19 of which were new. Although this number is here considerably reduced, most of his observations on the changing forms of rostra from bed to bed are valid but require elaboration and reinterpretation.

More recent works which deal with or include references to Lower Liassic material are those of Roger (1952), Schwegler (1961 - 1965), Jeletzky (1966) and Schumann (1974). Schumann's paper, on the belemnites of the North German Lias gamma, is of particular relevance.

The microstructure of the belemnite skeleton, and especially of the phragmocone, has been exhaustively described and discussed, notably by Christinsen (1925), Muller-Stoll (1936), Mutvei (1964) and Jeletzky (1966). The information obtained by the use of the light microscope has been augmented and modified by recent SEM studies (Barskov 1973 a & b; Spaeth, 1975).

Following the pioneering work of Urey (1947, 1951) and Epstein et al (1953), oxygen isotope analysis on belemnite rostra became popular, but the effectiveness of this technique for absolute palaeotemperature determination is dubious (Longinelli 1969; Spaeth 1971; Veizer 1974). However, isotopic studies have helped to elucidate the primary structure and composition of belemnite skeletal parts.

The ocurrence or not of sexual dimorphism in belemnites (mainly as manifested in the rostra), although often discussed, is still disputed. Attempted demonstrations of its existence are rare in the literature; I have noted only one published paper (Delattre 1956) which takes it as its main theme.

Chapter 2

Stratigraphy

The Lias of North West Europe

Sedimentation in North West Europe during Liassic times took place in an epeiric sea whose broad extent remained constant. Lithofacies variation may be viewed within the context of an active system of basins and swells upon which may have been superimposed the effects of eustatic changes in sea level.

Basins were areas of more or less continous argillaceous sedimentation, in contrast to swells which are recognized by condensed sequences. Principal Liassic basins were, on the present Continent, the North West German and Paris Basins, and, in the British Isles, the Hebridean, North Eastern and Wessex Basins (Hallam 1961). The principal British swells were those of Market Weighton, the Vale of Moreton and the Mendips (Arkell 1933, p. 31).

Lithological cycles of various scales occur, related at least partly to eustatic oscillations in sea level. Hallam (1961) proposed eleven main cycles for the Lias, independent of the basin-swell system, which were at first regarded as being due to gradual shallowing followed by rapid deepening. It was later recognized, however, "that asymmetrical sedimentary cycles of various types might be expressions of symmetrical eustatic controls" (Hallam 1975, p. 164) and a pattern of rapid rise - long stand - rapid fall was favoured for most large cycles (Hallam 1978, pp. 25 - 6).

The mechanism controlling these apparent changes in sea-level is debatable; they have tentatively been related to changes in the volume of the ocean ridges (Hallam 1969, 1978). However, as Donovan and Jones (1979) have pointed out, large scale sea level changes due to this are "likely to be related to phenomena manifested over spans of about 10 - 30 million years" (p. 191), which may at least partly account for the general transgression that occurred during Lower Liassic times, but the rather smaller scale cycles recognized by Hallam are probably too rapid to be thus explained.

Small scale cycles (of the order of 1 m, see below) have been attributed to a combination of eustatic and local epeirogenic control (Sellwood 1970, p. 503; Hallam 1978, p. 16), but again there is the problem of finding a suitable mechanism that would operate quickly enough. Donovan *et al* (1979), pointing out that the length of these small scale cycles was of the order of 10^5 years, suggest that, "Rather than such rapid oscillations in sea level, we favour a more complex process possibly involving the development and destruction of thermoclines. These changes could both change the concentrations of mineral salts and so affect biological productivity on the surface waters, the production of skeletal calcite, and also the type of biological activity on and below the depositional interface. They would also influence the distribution of clay particles." (p. 172).

The Lower Pliensbachian and cyclic sedimentation

The Lower Pliensbachian was a time of transgression over lands that now border the North Atlantic (Hallam 1969) and related to this are major changes in invertebrate faunas that occur over the Sinemurian - Pliensbachian boundary. Groups which were particularly affected are the brachiopods, ammonites, belemnites, ostracods and foraminifera (Hallam 1961, pp. 142 - 51).

Sellwood (1970, 1972) has considered in detail the boundary between the Sinemurian and Pliensbachian in Britain. "In northern Britain, the commencement of the Pliensbachian is generally marked by a loss of quartz sand, and in southern Britain by an increase in the carbonate content of the sediment." (1972, p. 125). He was concerned mainly with the small scale sedimentary cycles that occur in the raricostatum and jamesoni Zones, defining three major types, each consisting of "coarsening upwards sequences in which the sediments, trace and body fossils indicate increasing environmental energy toward the cycle tops." (1970, p. 489).

Type 2 cycles, 0.15 - 0.9 m thick, characterize the Belemnite Marls (jamesoni and ibex Zones) of Dorset and are therefore described here. Basically, they consist of limestone - marl rhythms, the "limestones" typically containing 50 - 75% carbonate with a large clay fraction, whilst the "marls" are still more argillaceous with a carbonate content of 30 - 60%. The carbonate in the "limestones" consists partly of bioclastic debris (small echinoid spines, faecal pellets and ostracods) which forms about 40% of the rock. SEM studies have shown that the fine grained matrix consists largely of coccoliths and microcrystalline calcite growing on clay flakes. The clay mineral composition of both "marls" and "limestones" is about 95% illite and 5% kaolinite (Sellwood 1970, p. 497).

Trace fossils include Rhizocorallium, Thalassinoides Chondrites and Diplocraterion, which occur in various relations to the "limestone" and "marl" units, as described by Sellwood (1970, p. 497). Bituminous shales may occur within the"marls", their lower boundaries being gradational while the tops are well defined and penetrated by small "marl" filled Chondrites burrows. As stated above, Sellwood favoured combined eustatic and epeirogenic oscillations in sea level to account for these cycles, but their origin is still obscure.

Returning to somewhat larger scale cycles in the Lower Pliensbachian, Donovan et al (1979), in their discussion of the Lower Liassic transgression of the London Platform, postulated three stillstands corresponding to three comparatively highly calcareous layers which form geophysical members (the "70","85" and "100") in the uppermost Lower Lias of the Chipping Norton district. Each standstill was followed by a period of more argillaceous sedimentation.

The "70" marker occurs in the brevispina Subzone of the jamesoni Zone and is correlated by Donovan et al with a series of calcareous beds in the Dorset coast Belemnite Marls quoted as the "Lower Paler Marls" (beds 106 - 109), which belong, however, to the taylori Subzone, and presumably the "Lower Pale Band" (beds 111a - e) is intended.

The "85" is probably in the upper valdani Subzone of the ibex Zone, and in the Chipping Norton area corresponds to beds representing slow deposition and containing a diverse fauna. No Belemnite Marl horizon is suggested as a correlate, but in fact bed 120c (see below) corresponds very well.

The "100" is tentatively related to the Belemnite Stone (bed 121, ibex Zone, luridum Subzone). Furthermore, "The deposition of this marker and the clay sedimentation of maculatum Subzone age may represent the last stage of the transgression of the Lower Lias, followed by shallowing and increasing amounts of calcareous and silty or sandy beds grading up into the silts and sands of the Middle Lias (margaritatus Zone)" (Donovan et al, p. 171).

In the Belemnite Marls, each of the above mentioned stillstand horizons is sandwiched between more argillaceous beds, the Belemnite Stone in particular being succeeded by the soft, clayey Green Ammonite Beds (mostly davoei Zone), the topmost few metres of which are somewhat sandy and form the base of the margaritatus Zone.

The Belemnite Marls of the Dorset coast

"Anyone standing on the beach between Charmouth and Lyme, and looking up at the bluffs and precipices of Black Ven, is struck by the contrast between the pale, blue-grey colour of the third, and highest, Lias precipice and the deeper shade of the underlying Black Marl. These pale marls, about 75 ft (23 m) thick, soon pass off the eastern shoulder of Black Ven, but are readily picked up again as the eye follows the line of stratification eastwards, and across the valley to Stonebarrow Cliff. There the pale marls make the second precipice, but soon dip to the beach to form most of the long, low cliff reaching from Westhay to the Ridge fault." (Lang 1928, p.179).

These are the Belemnite Marls, which consist predominantly of alternations of argillaceous calcilutite and calcareous clay, with occasional bituminous shales (Sellwood 1972). The sequence is shown in figure 2.

Day (1863) produced the first detailed description of this formation, which he defined as the beds succeeding strata containing Ammonites raricostatus (= Echioceras raricostatum) and including as its roof formation the easily recognizable Belemnite Stone. His term for the formation, the "Belemnite Beds", was abandoned by Lang (1913, p.408; 1928, p.182) to avoid confusion with the term "Belemnite Bed" which was used by several authors (eg. Phillips, 1865-70) to refer to a short series of richly fossiliferous beds near the top of the Belemnite Marls.

In 1906, Woodward published an account in the Geological Survey Memoir on the Lias which closely resembled Day's; as Lang (1928, p.183) states,

"What emerges from Day's and Woodward's sections is that the beds below the Belemnite Shales [bed 119 of Lang] are somewhat indefinite; but (1) that there are pale, hard 'limestones' in the middle of the series; (2) that towards the base there are about 30 ft. of darker marls and (3) that there are limestones at the base of the marls."

In the second edition of the Memoir (1911), Woodward suggests the term "Stonebarrow Beds", but it is Lang's term that has gained general acceptance.

In a series of papers (1913, 1914, 1917) culminating in his definitive description of 1928, Lang divided the Belemnite Marls into no fewer than 41 horizons ranging in thickness from ½" to 27'6". With the assistance of Spath (1928; also in Lang, 1928), fourteen ammonite zones were superimposed on this stratigraphic sequence;

this zonal scheme has been superseded by that of Dean, Donovan and Howarth (1961), slightly revised by Palmer (1974) and confirmed in Cope et al (1980). Lang's lithological sequence has been adopted with little modification.

Although the Apoderoceras Limestone (bed 105) makes an easily recognizable mapping base for the formation, there has been some doubt as to exactly where the base of the jamesoni Zone - and hence of the Pliensbachian - should be drawn. This depends on pinpointing the non-sequence responsible for the absence of the top of the raricostatum Zone (macdonelli and aplanatum Subzones) in this area (Lang et al 1926, pp. 148 - 9, 155). Lang placed the non-sequence just above the base of the Hummocky Limestone (bed 103) due to the last occurrence of Echioceras raricostatum on the base of this bed, but it is now believed to be represented by the impersistent layer of nodules 2 cm above bed 103 (Sellwood, 1922, p. 145), and the lowest bed of the jamesoni Zone is thus the few centimetres of shale between this nodule horizon and bed 105. Below the nodule band are small, intraformational clasts of limestone, which occur both in the shales and in the top part of bed 103, indicating an erosive phase.

The taylori Subzone

The Apoderoceras Limestone, which contains large deroceratid ammonites, is the first member of a series of argillaceous calcilutite and calcareous clay rhythms that make up most of this subzone, which includes the beds from 104 (top, see above) to 109. Bed 108, which was not further divided by Lang, includes two horizons of bituminous shale. Only the one at the base was recorded by Sellwood (1972). The second, about 0.3 m below bed 109, was found by the present writer to contain fairly common vertebrate remains, including ganoid fish (fragmental and more or less complete), ichthyosaur fragments and one fairly well articulated skeleton; this suggests a low energy environment, which is consistent with the lithology. Like the rest of the Belemnite Marls, the fossil assemblages of this subzone are of rather low diversity, consisting mainly of ammonites, belemnite rostra, brachiopods, thin shelled pectinid bivalves (*Chlamys* spp.), crinoid fragments and occasional nautiloids (in the Apoderoceras Limestone), together with trace fossils typical of Sellwood's type 2 cycles.

The *polymorphus* and *brevispina* Subzones

Due to the overlapping of the index ammonites, these subzones cannot usually be separated (Cope *et al* 1980, p. 48). Together they span beds 110 - 114, commencing with about 8.5 m of dark calcareous clay, bed 110a of Lang, with faint alternations of more and less calcareous layers in its middle portion and bituminous shales near the base. For the purpose of the present work, bed 110 (a and b) is divided into five units (I to V), based on belemnite assemblages, which are matched with the twenty-four lithological units into which Sellwood (1972, p. 143) divided this bed. (These lithological units are generally difficult to make out in the field, being best seen when the rock is clean and just damp.)

Beds 110b and 111 comprise three well-defined type 2 cycles, (perhaps corresponding to a regional stillstand - see above) whilst bed 112 consists of darker, less calcareous alternations, with a bituminous shale near the top.

Bed 111 is to some extent characterized by the terebratulid *Cincta*, which is also quite common in the similar group of rhythms that form bed 113.

Ichthyosaur remains occur sporadically in bed 110; of particular interest was a small articulated skeleton from near the middle of the bed which after partial cleaning has revealed several arm hooks, presumably belemnitid, in the stomach-rib cage region.

The fauna of beds 113 and 114 consists mainly of ammonites and brachiopods, belemnites being rather less prolific relative to most of the Belemnite Marls.

The jamesoni Subzone

This subzone encompasses about twenty calcilutite-clay rhythms, most of whichare thinner and less visibly obvious than those below. They constitute beds 115 to 118a (or b) of Lang. Bed 115 is not readily accessible in the cliffs, and was not recognized in any beach exposures. Lang comments that, "The bed appears to be thinner at Ridgewater than at Westhay Water" (1928, p. 193). He gives its thickness as 8 ft. (2.4 m) which is in fact the thickness at Westhay Water; at Ridgewater, the bed has thinned to about 1.5 m, although in both places it seems to consist of about ten calcilutite-clay pairs. Apart from this horizon (and not counting the discontinous Belemnite Stone), all the beds of the Belemnite Marls appear to be of constant thickness between Black Ven and Golden Cap. (The overlying Green Ammonite Beds, however, show quite marked variations in thickness over the same area.)

Bed 116, a dark calcareous clay, is characterized by an absence of belemnites, but is otherwise similar in fauna to the rest of the formation. Belemnites occur in bed 117 (which is not accessible in the cliffs and is only occasionally bared of sand on its beach exposures) and become abundant in bed 118a.

The remainder of the Belemnite Marls are placed in the ibex Zone.

The masseanum Subzone

This subzone includes five faint cycles of argillaceous calcilutite and calcareous clay, beds 118b and c of Lang. Lang's bed 118b was one inch thick, lithologically indistinguishable from bed 118c, and constituted for him a zone of Coeloceras pettos which is now obsolete (Dean et al 1961, pp. 463 - 4).

The valdani Subzone

Beds 118d to 120e constitute the valdani Subzone. Bed 119 marks a change from the pattern of calcilutite-clay rhythms that prevail from bed 111 upwards, consisting instead of alternations of more or less calcareous shale (the "Belemnite Shales" of various authors). Bed 120a - b (combined by Lang himself, 1928, p. 191) is a dark, pyritic bituminous shale capped by a layer of pyrite nodules, with sporadic pyrite nodules occuring throughout the bed.

Bed 120c, as previously remarked, is a condensed bed, being a dark grey, often indurated, pyritic calcareous shale which is packed with belemnites and other molluscs to such an extent that the majority of specimens are cracked and diagenetically deformed. The belemnite fauna is unusual, including specimens with epirostra (probably mostly Belemnites nitidus), and is particularly interesting on account of the occurrence of B. longissimus (q.v.). A possible hastitid also occurs (?Hastites sp. nov. (q.v.)) which is unique to this horizon. Bed 120c forms the centre of the vaguely defined "Belemnite Bed" of various nineteenth century authors and of local collectors (probably including Mary Anning) up to the present day; the rest of bed 120 is usually included in this term, and on occasion it probably connoted beds as far down as 118 and as far up as the basal Green Ammonite Beds. Beds 120d and e are lithologically similar to 120a - b, although pyrite nodules are less common.

The luridum Subzone

The Belemnite Stone, bed 121, is an irregular, discontinous limestone, which is easily recognized both in situ and in fallen blocks by virtue of its creamy weathering and contained fauna. It is a condensed rock, being the only representative in Dorset of the luridum Subzone. As its name implies, it is full of belemnites, usually undeformed (this perhaps being due to early lithification, cf. bed 120c above) but difficult to extract, and also contains well preserved ammonites (particularly Liparoceratids, Lytoceras sps and Tragophylloceras sps), gastropods and bivalves.

The comparatively long shallow phase represented by the Belemnite Stone was apparently followed by a consistently deep water period of sedimentation represented by the soft, highly argillaceous Green Ammonite Beds that represent the davoei Zone and basal margaritatus Zone in this area. Lang's (1936) bed numbers are again utilized, the belemnite fauna of the basal members (beds 122a-c) being briefly considered in relation to the Belemnite Marls (see Belemnites nitidus, B. aduncatus, ?Coeloteuthis sp. and H. microstylus).

Outcrops of the Belemnite Marls and basal Green Ammonite Beds

The only good outcrops of the Belemnite Marls are on the coast between Lyme Regis and Seatown. A number of small, usually temporary, inland exposures were recorded by Lang (1932) for mapping purposes. Most of these are in the upper part of the formation, and especially in the Belemnite Stone which tends to form a small but well-marked feature and may have been occasionally quarried. The belemnites recovered from these exposures have all been recognized from corresponding horizons on the coast.

In situ collecting is impracticable on Black Ven as the formation occurs in rather precarious slopes. As Lang said, "except for verifying the similarity of the western with the eastern sequence, there is no point in collecting with difficulty from the third precipice of Black Ven." Further to the west, the formation has been removed by the Cretaceous Gault/Upper Greensand overstep. To the east, the formation is brought down to beach level between the eastern end of Stonebarrow Hill and the eastern end of Golden Cap; both the dip of the strata and a number of faults give rise to a nearly complete set of beach and foreshore exposures, the only beds difficult of access being 115 and 116. The distribution of these exposures is shown on the accompanying map; it must also be remembered that their extent fluctuates drastically as a result of the distribution of beach sand and pebbles; also, erosion is fairly rapid, so that since Lang published his definitive papers on the Charmouth Lower Lias, the beach exposures of all of the beds with appreciable dip have moved several metres from where he mapped them.

The basal Green Ammonite Beds are well exposed in wave cut platforms below Golden Cap; when the tide is out, belemnites can easily be picked or prised out of the sticky wet clay. No good collecting stations exist in the higher reaches of the formation, although occasional in situ specimens can be recovered from the low cliffs to the west and east of Golden Cap.

South West Germany

Material from various localities in the Swabian Alps was examined in the Staatliches Museum für Naturkunde in Ludwigsberg (near Stuttgart), and some specimens were collected from the Pliensbachian (mostly ibex and davoei Zones) in the classic exposures in the Wutach valley area, near Aselfingen, South West Germany, at the western end of the Swabian Liassic outcrop (fig.4). Due to extensive scree cover, in situ collecting is not possible from many beds, and more weight is given in the present work to material in the museum collection, especially that figured by Werner (1912).

The Sinemurian-Pliensbachian boundary in this area may in some places be marked by a non-sequence as it is in some parts of Britain (Arkell 1956, p.129).

The term "Pliensbachian" or "Pliensbachgruppe", introduced by Oppel in 1858, was named after the village of Pliensbach on the northern edge of the Swabian Alps. This rather overgrown type section is exposed in a stream, and, by dint of excavation, Schlatter

(1977) has elucidated the stratigraphy of the Lower Pliensbachian portion of it. He regards it as unlikely that there is a non-sequence at the base, and points out that at other localities (including Aselfingen), the macdonelli and aplanatum Subzones are present (1977, p. 7 - 8).

In this area, the Lower Pliensbachian is represented largely by limestones and calcareous clays that closely resemble the more indurated horizons of the Belemnite Marls. Similar rhythms are present, but are only apparent when weathered. If this generally more calcareous regime represents conditions corresponding to the more calcareous part of the Dorset sequence, thenmeaningful comparisons between the respective belemnite faunas can be made, since certain belemnites that areconspicously absent from the more calcareous portions of the Belemnite Marls appear to be nearly completely absent from the Swabian Pliensbachian.

The Aselfingen outcrop, which consists of a continous section from the Upper Sinemurian to the base of the Aalenian, is exposed in a ravine formed by a small stream (the Aubach). Here, the Pliensbachian is somewhat condensed, the Lower Pliensbachian consisting of about 3 m of limestone and calcareous clay. Nevertheless, all the subzones appear to be present.

FIG. 1

Map of localities

D - Dorset coast, Charmouth and Seatown
Y - Yorkshire coast
A - Aselfingen
O - Ostercappeln

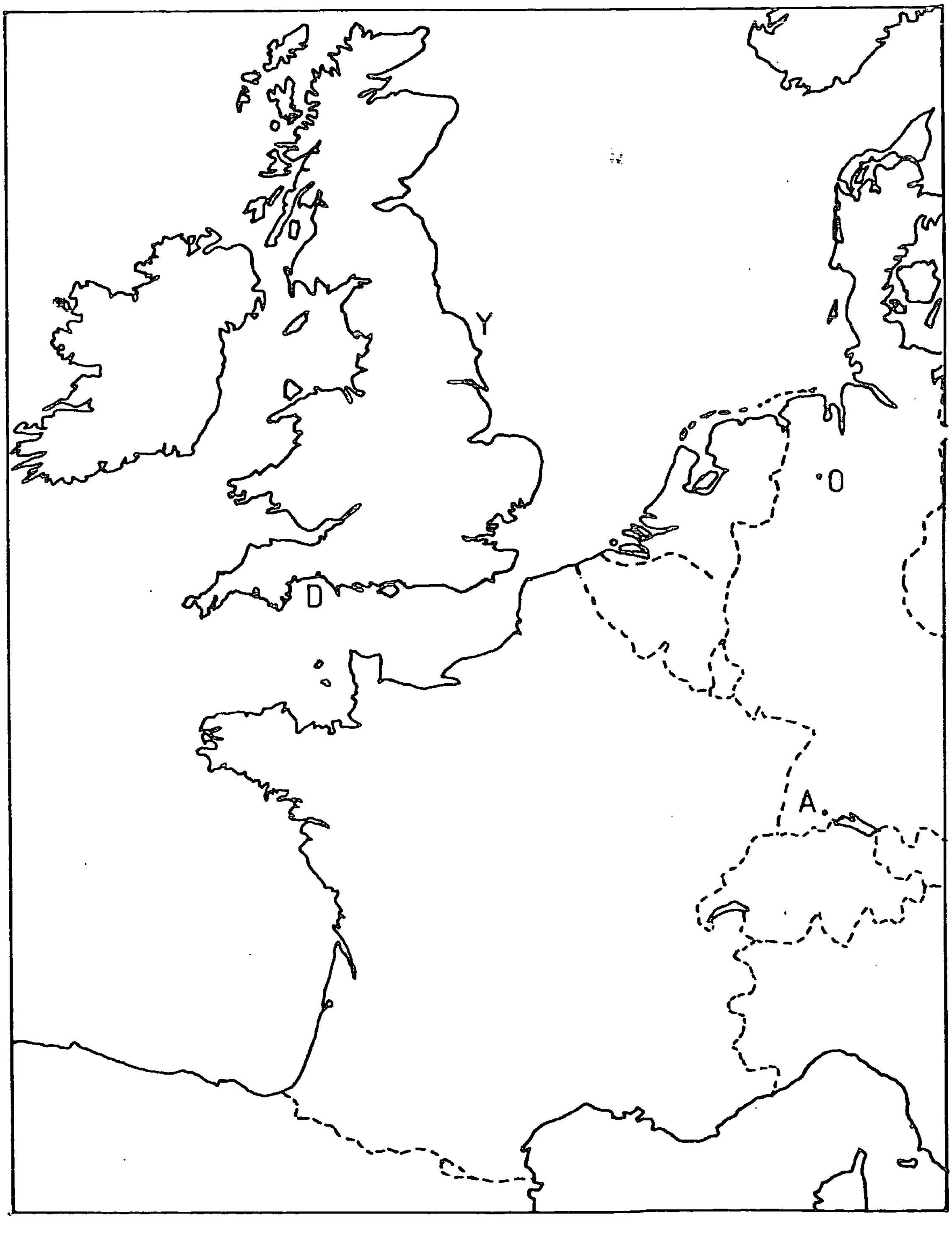
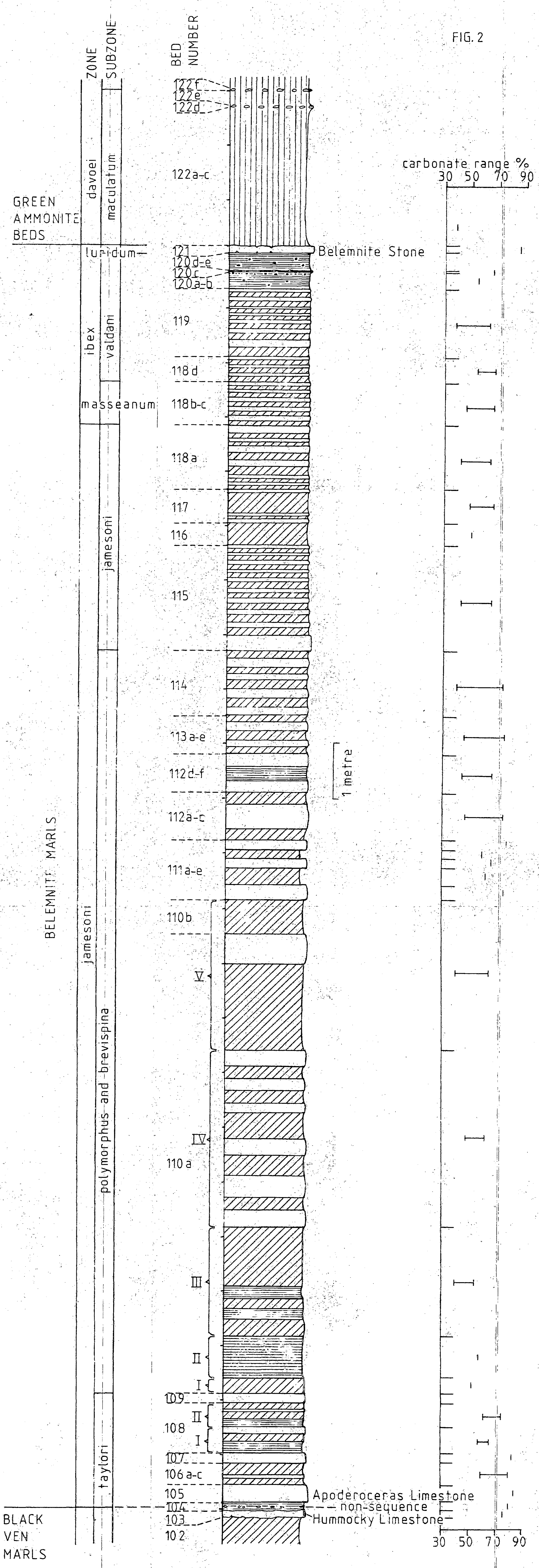


FIG.2 Section through the Belemnite Marls and basal Green Ammonite Beds exposed between Charmouth and Seatown, Dorset. Carbonate percentages after Sellwood, 1972.

<u>key</u>

□ argillaceous calcilutite
▨ calcareous clay
▤ bituminous shale
○○○ limestone nodules
••• pyrite nodules
▥ clay

FIG. 2


ZONE
SUBZONE
BED NUMBER
carbonate range %
30 50 70 90
GREEN AMMONITE BEDS
davoei
maculatum
luridum
ibex
valdani
masseanum
jamesoni
polymorphus and brevispina
taylori
BELEMNITE MARLS
BLACK VEN MARLS
122f
122e
122d
122a-c
121
120d-e
120c
120a-b
119
118d
118b-c
118a
117
116
115
114
113a-e
112d-f
112a-c
111a-e
110b
V
IV
110a
III
II
I
109
II
108
I
107
106a-c
105
104
103
102
Belemnite Stone
1 metre
Apoderoceras Limestone
non-sequence
Hummocky Limestone
30 50 70 90

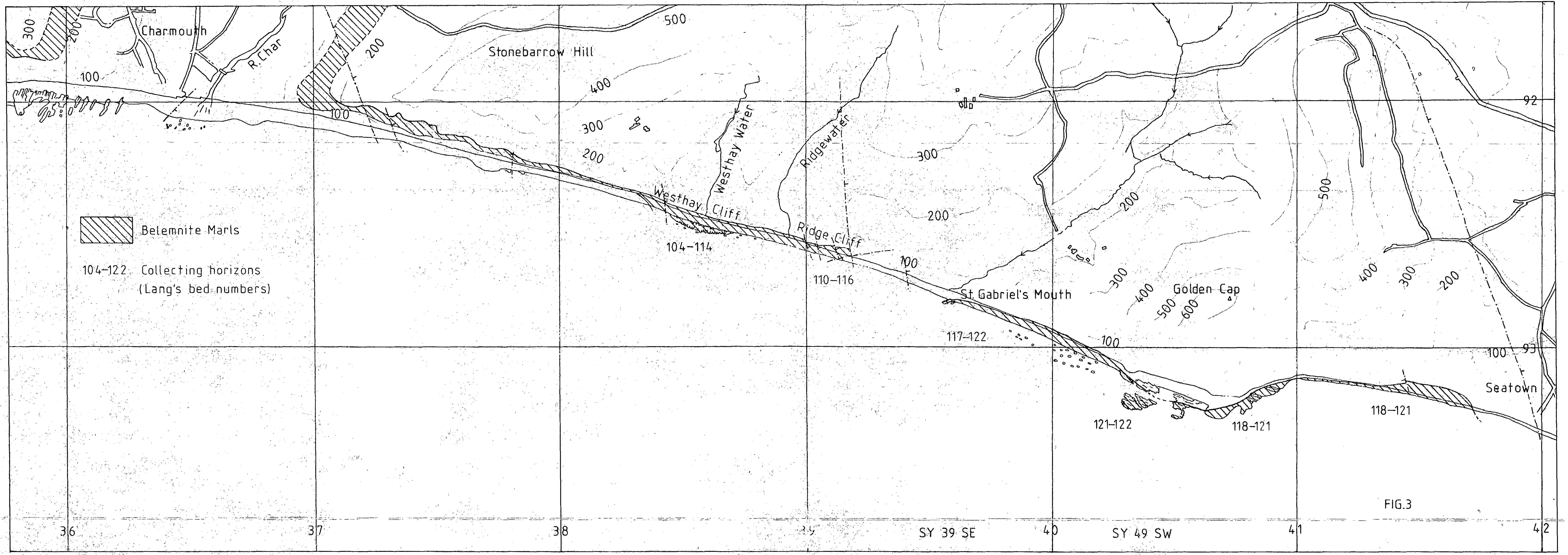


FIG.3

SCALE: 6" to 1 mile
contours in feet

Chapter 4

Systematic Palaeontology

The belemnites of the Lower Pliensbachian of the Dorset coast were found to be naturally divisible into three genera, *Belemnites*, *Hastites* and *Coeloteuthis*, of which representatives of the first are by far the most abundant and diverse.

All the species described are also regarded as natural taxa, being based on bed-by-bed morphometric study which usually clearly and objectively delimits discrete groups that constitute the adopted morphospecies and also often reveals a subsidiary dimorphism that is probably sexual. Furthermore, there emerges a picture of stratigraphically fluctuating morphology for some of the species that is largely responsible for the proliferation of taxa previously described from these beds.

Twelve species were recognized in the Belemnite Marls, (*jamesoni* and *ibex* Zones) all of which are described, the greatest attention being given to those included in Belemnites.

Four species (*Belemnites nitidus*, *B. aduncatus*, *Hastites microstylus* and *Coeloteuthis* sp.) were recognized in a comparatively small sample from the Green Ammonite Beds (*davoei* Zone), all of which also occur in the Belemnite Marls.

Supra-generic classification follows that proposed by Jeletzky (1966).

Class CEPHALOPODA Cuvier, 1794

Subclass COLEOIDEA Bather, 1888

Order BELEMNITIDA Zittel, 1895

Family BELEMNITIDAE d'Orbigny, 1845

Type genus Belemnites Lamarck, 1799

Subfamily BELEMNITINAE d'Orbigny, 1845

Genus BELEMNITES Lamarck, 1799

Type species Belemnites paxillosus Lamarck, 1801; Pliensbachian

Revised description

Rostrum highly variable, subconical and sturdy to very slender, subfusiform (clavate). Transverse section usually compressed. Apical line goniolineate, somewhat closer to ventral side of guard.

Dorsolateral apical furrows and paired lateral furrows nearly always present, although degree of development varies. Alveolar angle remarkably invariable, between 25° and 30°. Epirostrum may be present.

Discussion

The present usage of Belemnites is that of Jeletsky (1966) but subgenera (B. (Belemnites) Lamark, 1799 and B. Pseudohastites Naef, 1922) are not utilized. As with subspecies, the present writer believes that, at least in the case of the belemnites studied here, these additional taxa are too arbitrary to be of any practical value or biological significance. The above description is based on Jeletzky's diagnoses of these two subgenera (B. Belemnites being "sturdy to fairly slender" and B. Pseudohastites being "slender to very slender"). Jeletzky (1966, p.141) believed paired lateral lines to be well developed only in "Pseudohastites and allied forms"; certainly they tend to be best developed in the more slender species, but all the species described here under Belemnites possess paired lateral furrows in some degree, these tending to be wider and shallower in the more robust species.

Lang [1928] utilised four genera to describe material from the Belemnite Marls and Green Ammonite beds that is here all included in *Belemnites*; these were *Clastoteuthis* gen. nov., *Passaloteuthis* Lissajous, 1915, *Angeloteuthis* gen. nov. and *Pseudohastites* Naef, 1922. Respectively two, eleven, four and five species were described under these genera, which, were these genera to be retained, would here be reduced to one, four one and two species. Instead, eight species of *Belemnites* are defined, *Clastoteuthis* and *Angeloteuthis* representing the stoutest species and *Pseudohastites* the slenderest. As implied above, the morphological continuity of this series precludes the effective use of subgenera.

The forms assigned to *Pseudohastites* by Lang [1928] do show some affinities with *Hastites*, in which genus they were included by Schumann [1974]. In particular, *Belemnites longissimus* [= *Pseudohastites* *cultellus*, *P*. *arundineus*, *P*. *junceus* and *P*. *longissimus* in Lang [1928]] often displays characters which are regarded as hastitid, although morphologically it is probably best regarded as a slender end member of *Belemnites*. *B*. *longissimus* is a likely ancestor of *Hastites*, first appearing at the base of the *jamesoni* Zone whilst the earliest true *Hastites* [*H*. *microstylus*] first appears in the upper *jamesoni* Zone [*jamesoni* or, possibly, *brevispina* Subzone]. Relevant characters of the rostra of typical *Belemnites* [such as *B*. *nitidus*, *B*. *aduncatus* and "*B*. *paxillosus*"], *B*. *longissimus* and typical *Hastites* [*H*. *microstylus* and

"H. clavatus") are qualitatively compared below.

	Belemnites	Belemnites longissimus	Hastites
1)	Moderate to large size, stout to fairly slender.	Moderate to large size, fairly to very slender.	Small size, very slender.
2)	Cylindrical to slightly clavate.	Cylindrical to moderately clavate.	Very clavate.
3)	Apical furrows well developed.	Apical furrows poorly developed.	Apical furrows absent.
4)	Paired lateral furrows variably developed.	Paired lateral furrows usually well developed.	Paired lateral furrows usually well developed.
5)	Apical line fairly straight, goniolineate slightly excentric.	Apical line fairly straight, goniolineate slightly excentric.	Apical line curved, cyrtolineale strongly excentric.
6)	Epirostrum sometimes developed.	Epirostrum sometimes developed.	Epirostrum never observed.
7)	Well calcified.	Well calcified.	Frequently poorly calcified in alveolar region.

Stratigraphical range of Belemnites

Pliensbachian

Belemnites longissimus Miller, 1826

Plates 1-3; Plate 4, figs. 6, 7.

1826 *Belemnites longissimus* sp. nov.; Miller, p.60, pl8, figs. 1 and 2.

1827 *Belemnites longissimus* Miller; de Blainville, pp.95-96, pl.4, fig.7, cop. Miller 1826.

1867 *Belemnites longissimus* Miller; Phillips, p.66, pl.13, fig.32.

1867 *Belemnites junceus* sp. nov.; Phillips, p.67, pl.13, fig.33.

?1869 *Belemnites longissimus* Miller; Dumortier, p.44, pl.4, figs. 7-11.

?1927 *Hastites junceus* (Phillips); Lissajous, pp.33-35, pl.3, figs. 20, 20a, 20b.

v.1928 *Pseudohastites cultellus* sp. nov.; Lang, p.211, pl.15, fig.1.

v 1928 *Pseudohastites longissimus* (Miller); Lang, pp.211-212, pl.15, fig.5; text fig. 3, no.8.

v.1928 *Pseudohastites junceus* (Phillips); Lang, pp.212-213, pl.15, fig.5; text fig.3, no.4

v.1928 *Pseudohastites arundineus* sp. nov.; Lang, pp.213-215, pl.15, fig. 4; text fig. 3, no.9.

1962b *Belemnites junceus* Phillips; Schwegler, pp.155-157, text fig. 40.

?1974 *Hastites junceus* (Phillips); Schumann, pp.36-37, pl.5, figs 14 and 15.

Neotype

BMNH C29037 (*Pseudohastites longissimus*), Belemnite Marls, bed 110a (110 V), Westhay Cliff, near Charmouth, Dorset.

Established by Lang (1928), pp.211-212, pl.15, fig.5.

<u>Other material</u>

Author's collection, Belemnite Marls, Charmouth: 156 specimens

bed 104: TB1032, TB1033, TB1035, TB1036

bed 110 II: D81, D92, TB276, TB282, TB287, TB292, TB293, TB297-300, TB303, TB791

bed 110 III: D83, TB160-164, TB174, TB175, TB189, TB306-313, TB327-336, TB346

bed 110 IV: TB176-179, TB181-188, TB190, TB351, TB357-359, TB362-372, TB374, TB390-395, TB406, TB407, TB409, TB411-415, TB424-429

bed 110 V: D100-104, D111, D112, D118, D124, D125, TB43, TB45, TB56-59, TB165-170, TB172, TB173, TB441-457, TB498, TB501-506, TB521, TB524, TB1046, TB1047

bed 120c: TB125, TB127, TB1122-1127, TB1129, TB1136

Belemnitiferous Marls, road cutting on A303, near Tintinhull, Dorset. OS ref. SY497205: uncatalogued fragmentary material.

BMNH, coll. and/or det. W.D. Lang, Belemnite Marls, Charmouth: 41 specimens.

bed 104: (<u>Pseudohastites</u> <u>cultellus</u>) C29045 (holotype), C29046, C29490-29492, C29494, C29495

bed 110a: (<u>Pseudohastites</u> <u>longissimus</u>) C29033, C29034, C29035, C42138, C42139; (<u>Pseudohastites</u> <u>junceus</u>) C29008 (neotype), C29009, C29111-29119, C43907-43909, C42563, C43911; (<u>Pseudohastites</u> <u>arundineus</u>) C29021-29025, C29026 (holotype), C29028-29030, C35564

bed 110b: (<u>Pseudohastites</u> <u>longissimus</u>) C29032, C29036,

bed 120c: (<u>Hastites</u> cf. <u>stonebarroensis</u>) C29512

BMNH, material other than Lang's; labelled with various genera, larger specimens junceus, smaller longissimus: 13 specimens.

bed 110: C6051, C29505, C42550, C45719, C45746-45749

bed 120c: C45840

horizon indet.: C42552-42554, C46319

Description

Rostrum very slender and greatly elongated, profile markedly clavate to tapering. Section compressed, sub-circular to sub-quadrate, typically most quadrate towards anterior of rostrum. In clavate rostra, compression is often most pronounced in the narrowed anterior portion.

Apical furrows weakly developed. Paired lateral furrows usually well developed; typically, the upper furrow commences near the apex as a fairly deep groove, widening into a shallow depression or concave facet in the anterior half of the rostrum. The lower furrow commences as a thin deep groove which is usually bowed downwards. This merges into a facet in the middle portion of the rostrum, and then narrows and deepens again into a fairly wide anterior groove which is separated from the upper furrow by a ridge (fig.111A).

Apical striae may be present.

Alveolus very short in relation to rostrum, typically 12-17% of total rostral length.

Epirostrum may be present.

Dimorphism is well developed.

A few specimens were found in which the phragmocone extends beyond the rostrum, although it is invariably badly crushed. As with the alveolus, it is short compared with other species, the preserved ante-rostral length not exceeding 33% of the total rostral length.

Discussion

The neotype selected by Lang for his Pseudohastites longissimus closely agrees with the lost specimen figured by Phillips (1867, pl.8, fig.32); this lost specimen is presumably that which Phillips believed might have served Miller as his holotype (Phillips 1867, p.66), although Lang evidently believed Phillips' and Miller's figured specimens to be separate, saying that he had been unable to trace either of them (Lang 1928, p.212).

The interpretation of Belemnites longissimus Miller must take into especial consideration three previous works: Miller (1826), Phillips (1867) and Lang (1928). Lang's utilisation of the generic name Pseudohastites is a separate problem which is considered at the beginning of this chapter.

Miller's plate 8, figure 1 is a reasonable representation of a half grown rostrum of the species as here defined, thus his specific name is given priority over any names subsequently applied to the rostra of fully grown specimens. Phillips' plate 8, figure 32 is a more detailed print, possibly of the same specimen (see above). Miller's specimen was from the "Lyas and lyas clay" of Lyme Regis, and Phillips gives the same locality. Of particular importance is Phillips' further statement (p.66), "I have a few examples from the Belemnite-bed under Golden Cliff, but none of these specimens are sufficient for good description." Furthermore, the fragmentary type material of his new species, B. junceus, is also ascribed to "Golden Cliff, near Lyme Regis" (Phillips 1867, p.67).

When Phillips and other 19th Century authors mention the "Belemnite-bed" of this part of the coast, they invariably refer to the very fossiliferous top few feet of the Belemnite Marls, from about bed 118 upwards, and especially bed 120c which is a thin condensed band packed with more or less broken and crushed rostra. These beds outcrop on the shore below Golden Cap and have long constituted a classic collecting ground. Due in part to the nature of his material, Phillips did not realise that his *B. junceus* is the fully grown rostrum of *B. longissimus*, a delusion also shared by Lang who erected neotypes for both of these species, collected furthermore from the abundant, well preserved material in the lower part of the Belemnite Marls (bed 110), which on the coast are only exposed well to the west of Golden Cap. Lang erected two further species of *Pseudohastites*, to whit *P. cultellus* (bed 104) and *P. arundineus* (bed 110), that are here regarded as conspecific with *Belemnites longissimus*.

Lang was firmly of the opinion that the forms he grouped as "Pseudohastites" were confined to the lower part of the Belemnite Marls (1928, pp.211-213), so that he defined *P. longissimus* on the basis of Phillips' figure but excluded those specimens of Phillips from "the Belemnite Bed under Golden Cliff, which are necessarily from a higher horizon than bed 110". Of *Pseudohastites junceus* he said, "... the locality mentioned by Phillips does not include bed 110. But the fact that Phillips quoted Golden Cap as 'Golden Cliff' suggests a vagueness which might easily have extended the connotation to the cliffs at Westhay ... I know of no belemnite from Golden Cap that could be identified with Phillips' fig.33; whereas ... it is a good representation of the longer of two forms mentioned as common in Bed 110a" (Lang 1928, p.213).

In fact, the present author has collected unequivocal specimens of *B. longissimus* from bed 120c below Golden Cap (pl.3,fig. Although it is fairly scarce at this horizon (and usually crushed), Lang himself collected a particularly slender, tapering specimen (BMNH C29512) which, in his determination to restrict

Pseudohastites to lower horizons, he named as "Hastites cf. stonebarroensis" (1928, p.191). Also in the BMNH is a more typical specimen of B. longissimus, C45840, which, according to the label is Pseudohastites junceus from the Crumbly Bed (=120d-e), from the J. Harrison collection, purchased 1865. Judging from its distorted preservation, it probably came from the top surface of bed 120c; in common with several other specimens from this horizon, it appears to have an epirostrum.

Thus Phillips' records of "B. longissimus" and "B. junceus" from the "Belemnite-bed" below "Golden Cliff" upon which the interpretation of B. longissimus Miller must largely rest, do not need to be regarded as vague. It is moreover apparent that he was not much aware of the outcrops in the lower part of the Belemnite Marls that appear only to the west of Golden Cap, as he could not otherwise have failed to collect good complete specimens of B. longissimus from the excellent exposures below Westhay Cliff. Another clue to his lack of knowledge of these exposures is his mention of a squat belemnite from the "Lias of Lyme Regis", "allied to B. insculptus" (from the Inferior Oolite) to which he does not give a name and which he regards as very rare (Phillips 1867, p.46, diag.18; pl.5, fig.13). This specimen can definitely be ascribed to B. abruptus (Lang) (q.v.) which occurs in beds 110 to 114; it is scarce, but hardly "very rare", most in situ specimens being collected from below Westhay Cliff.

To summarise, Phillips' own poorly preserved material of "B. longissimus" and "B. junceus" came from bed 120c, including his figured type of B. junceus. The figured specimen of B. longissimus was not his; it might have been Miller's original specimen, and almost certainly came from bed 110. Phillips was not aware of the faunas from this horizon upon which Lang (1928) defined his species. On the other hand, Lang did not acknowledge the presence of "*Pseudohastites*" in beds higher than 110, claiming that Phillips' locality for *B. junceus* was vague enough to include Westhay Cliff and therefore beds much lower than 120c, and that specimens of *B. longissimus* from bed 120c (including both Phillips' and his own) were to be assigned to *Hastites*.

We may conclude that Lang's immature neotype of *Pseudohastites longissimus* from bed 110 is a reasonable duplicate of the type specimen (or specimens) employed by Miller and Phillips, and that the species may be interpreted on this basis.

Use of Phillips' specific name, "*junceus*", has continued until recent times; notable instances apart from Lang (1928) are *Hastites junceus* (Phillips) of Lissajous (1927) and Schumann (1974). Both authors apply the term to a comparatively robust belemnite that is similar to but even more stout than certain specimens of *B. longissimus* from bed 104 (= *Pseudohastites cultellus* Lang) and the lower part of bed 110. Lissajous' figured specimen from the "zone a Polymorphites Jamesoni de Lime Regis" is probably a specimen of *Belemnites charmouthensis* Mayer (q.v.); he also records the species from the *jamesoni* Zone of Limas (Rhone) (Lissajous 1927, pp.33-35, pl.3, figs 20, 20a, 20b). Schumann's plate 5, figure 14 is similar whilst his figure 15 represents an even stouter form that is similar to *B. nitidus* Phillips. Both of these figured specimens are from the *taylori* Subzone of Ostercappeln, North Germany (this subzone at Charmouth includes beds 105-109).

However, Schumann did recognize that Lang's four species (*Pseudohastites arundineus*, *P. cultellus*, *P. junceus* and *P. longissimus*) are conspecific; uncertainty about the status of *B. longissimus* Miller *et auctorum* led him to employ the specific name _junceus_ (Schumann 1974, p.36).

Ontogeny

The ontogeny of this species is particularly interesting in that a number of specimens display exceptionally clear primary spherules (fig.9) (see p.238), representing early loci of calcite growth in the aborally developing mantle. These spherules seem to control the initial elongation of the rostrum after the first few saucer-like layers (corresponding in part to the "primordial guard" of Jeletzky (1966)) have been deposited on the protoconch. The number of spherules observed in this region varies between one and six.

By the time that the post-alveolar length of the rostrum is 1-2mm, the profile of the whole rostrum is quite even, the convolutions imposed on the earliest layers by the spherules having been smoothed out by non-concentric deposition of subsequent lamellae. At this point, there often occurs the earliest strong growth line, suggesting that a hiatus in growth is characteristic at this stage of development. This line clearly delimits a more or less conical profile, which may be constricted in front of the protoconch to produce a very thick claviform profile (fig.10A). The apex of this growth stage is frequently of a sub-mucronate or drawn out appearance; this can sometimes be seen to be due to deposition of the lamellae at the apex around another calcite spherule (fig.10A). The alveolus is approximately half of the total length of the rostrum in these earliest stages of growth.

Until it has achieved a post alveolar length (Lp) of 4-6mm, diameter (Dp) 1.2-1.4mm, the rostrum only gradually becomes more slender. Then, a sudden change in the slope of Dp:Lp occurs [fig.8] elongation occurring at a relatively greater rate than thickening, compared with any other species of Belemnites from these horizons. Growth continues with no further sharp changes in slope until full size is attained. The relative length of the alveolus gradually decreases to less than 20% of the total rostral length.

When rostral growth curves are plotted for a number of specimens, it becomes apparent that, when post alveolar length exceeds 30-40mm, a narrow but distinct morphological gap appears, separating more robust from relatively slender individuals. With smaller specimens, although robust and gracile adults tend to have respectively robust and gracile early growth stages, there is a degree of overlap which prevents positive differentiation between them.

The degree of dimorphism is enhanced by a gradual increase in the slope of the curves of most robust specimens. This commences at a post alveolar length of 40-60mm, corresponding to an increase in rate of thickening relative to increase in length. Contrasted with this is the almost linear growth of the gracile form which commences at the early stage [Lp = 4-6mm] mentioned above [cf. the similar but more pronounced dimorphism in B. charmouthensis]. This allometry of growth in the robust form is responsible for the high degree of variation shown by the larger specimens from beds 110 IV-V, as depicted in the scatter diagram in figure 7B. The effect is less noticeable in beds 110 II-III, figure 7A, as some of the robust specimens in their early stages continue to increase rapidly in girth for longer then usual, i.e. to a post alveolar length of 8-14mm rather than 4-6mm. Subsequent to this, their curves flatten off more than is usual, so that eventually they intersect the curves representing the rest of the robust individuals, after which the usual slight increase in slope occurs. Specimens of this sort occur particularly in bed 110 II, but are not uncommon up to bed 110 V; it is impractical to separate them as a different species, although they are distinguished as triangles in the scatter and growth diagrams.

A series of specimens illustrative of dimorphism is shown in plate 3.

Stratigraphical variation

This species first appears in the upper half of bed 104, which marks the base of the Pliensbachian in the Charmouth area. Because it is here more robust than the majority of specimens from bed 110, Lang placed it in a new species, Pseudohastites cultellus, which was confined to bed 104 alone. However, as it is indistinguishable from some of the more robust specimens of Belemnites longissimus from bed 110 (especially 110 II-III), it is not practicable to raise it to the status of a separate species. Specimens from bed 104 are rarely clavate, but this also is in accord with a large minority of those from bed 110. BMNH specimen C29494, collected by Lang and labelled "Pseudohastites ?cultellus", is distinctly clavate (1.17 in vertical plane); the holotype of P. cultellus, C29045, although it may be clavate, is deformed, both by apparently abnormal growth resulting in an uneven, "lumpy" profile, and by a post-mortem breakage (common at this horizon) about half way along the rostrum (see Lang 1928, pl.15, fig.1). The present author's specimens from this horizon are not clavate; three other specimens of P. cultellus recorded by Lang (1928, p.195) could not be located in the BMNH collections).

The next appearance of B. longissimus is in bed 110 II, whence it persists to the top of bed 110 V, giving an unbroken record through nearly 9m of the sequence. In bed 110 II, only the robust form appears to be present.

Dimorphism is first apparent in bed 110 III, is particularly noticeable in bed 110 IV and is still clearly manifested in bed 110 V. The longest and most slender specimens occur in bed 110 IV.

Figure 13 shows that there is a general increase in clavateness from bed 104 upwards. Both gracile and robust forms exhibit the same range of variation in this character at a given horizon. The fact that this character changes equally in each dimorph throughout the three horizons where dimorphism occurs could be regarded as circumstantial evidence that they belong to one species, i.e. degree of clavateness is, in this case, a specific character, not sex linked, that fluctuates in time.

The degree of compression of the rostrum changes only very slightly from horizon to horizon (fig.12); again, gracile and robust forms are identical in this character.

Lang (1928) erected *Pseudohastites arundineus* to include the stouter forms of *Belemnites longissimus* from bed 110. The chronological and sexual variations described above are responsible for his rather confused attempt to distinguish two species on this basis: "The somewhat clavate and much elongated belemnites common throughout bed 110 , though ... varying considerably and, to some extent, continuously in shape and proportions, yet group themselves around two modes ... It is convenient, since any complete specimen can generally be referred without hesitation to one of these two forms *P. arundineus* and *P. junceus*, respectively more and less stout , to regard them, at least provisionally, as distinct species." (pp.213-214).

Specimens of *B. longissimus* from bed 120C are for the most part so crushed and fractured as to preclude accurate measurement. However, they appear to resemble closely those from bed 110, and apparently include both gracile and robust forms although the sample is too inadequate to establish the definite presence or absence of dimorphism. Well developed epirostra are common at this horizon; specimens with short epirostra sometimes occur in bed 110. Epirostra are further discussed on p.253.

It is at once noticeable that *B. longissimus* in the Belemnite Marls is confined to beds of comparatively low carbonate content (see fig.2). The upper part of bed 104 is composed of a soft, dark shale which belies the high carbonate content given by Sellwood (1974, text fig.12); the impersistent layer of calcareous nodules in the middle of bed 104 may be responsible for this figure.

Between beds 104 and 110, the carbonate content oscillates between 60 and 80%. Throughout bed 110, it is nearly always less than 60%, *B. longissimus* reappearing in bed 110 II and continuing in abundance to the roof of bed 110 V. Thereafter, its only recorded occurrence is in bed 120C (carbonate approx. 65%), which in the Belemnite Marls is the only markedly condensed horizon other than the Belemnite Stone. The sequence between beds 110 and 120C consists of very pronounced alternations of dark, soft and light indurated marls, carbonate content rapidly oscillating between about 40 and 75%.

The comparatively stout form (Lp = 110mm, Dp = 9.5mm) from North Germany assigned by Schumann (1974) to *Hastites junceus* (Phillips), which is possibly a geographical variant of *B. longissimus*, ranges, according to him, from the *taylori* to the *valdani* Subzone. This corresponds to beds 105-120 of the Belemnite Marls. His material (11 specimens) is from two localities, Rottorf and Ostercappeln and is most similar in appearance to *B. longissimus* from bed 104 of the Belemnite Marls. At Rottorf, the sequence is unlike the Belemnite Marls, consisting as it does of alternations of oolitic ironstone, limestone and marl, while at Ostercappeln undifferentiated marls only are present (thus resembling bed 110 of the Belemnite Marls).

Very few belemnites assignable to *B. longissimus* have been recorded from South Germany (the only probable record noted being Schwegler 1962b, p.155, fig.40, from Dürnau); examination of material in the Staatliches Museum für Naturkunde in Stuttgart and of the well represented Lower and Middle Lias of Aselfingen failed to produce any specimens. The lithologies of the Lower Lias in this region are very similar to those sequences in the Belemnite Marls from which *B. longissimus* is absent. On the other hand, species do occur commonly which in the Belemnite Marls show no facies dependency (*B. nitidus*, *B. charmouthensis* and *B. abruptus*).

Thus the available evidence suggests that *B. longissimus* preferred an environment or environments represented by a regime of sedimentation comparatively low in carbonate and high in argillaceous material; this probably corresponds to the deeper, and therefore less turbulent, phases of deposition at this time, which may have been more suitable for the animal bearing one of the most slender and perhaps most delicate of belemnite rostra in the whole of the geological record.

Distribution

1. Charmouth, Dorset: Belemnite Marls, *jamesoni* and *ibex* Zones, beds 104, 110 II-V, 120C.
2. Tintinhull, Dorset: Belemnitiferous Marls, ?lateral equivalent of beds 110 IV-V.
3. Dürnau, Württemberg, South West Germany: Lias gamma (Schwegler 1972b).

?4. Rottorf and Ostercappeln, North Germany: Lias gamma 1-2b

(Schumann 1974).

?5. Limas, Rhone, France: jamesoni Zone (Lissajous 1927).

FIG.7 key

A: ▽ author's coll., bed 110 II
⊙ robust
○ gracile author's coll., bed 110 III
○ indeterminate
◇a holotype *Pseudohastites arundineus*
◇j neotype *P. junceus*
🄹 BMNH coll. "*P. junceus*"

B: ◈ NEOTYPE
▽ author's coll., robust, cf. bed 110 II
⊙ robust
○ gracile author's coll.
○ indeterminate
🄹 BMNH coll. "*P. junceus*"
🄰 BMNH coll. "*P. arundineus*"

FIG. 7

Belemnites longissimus

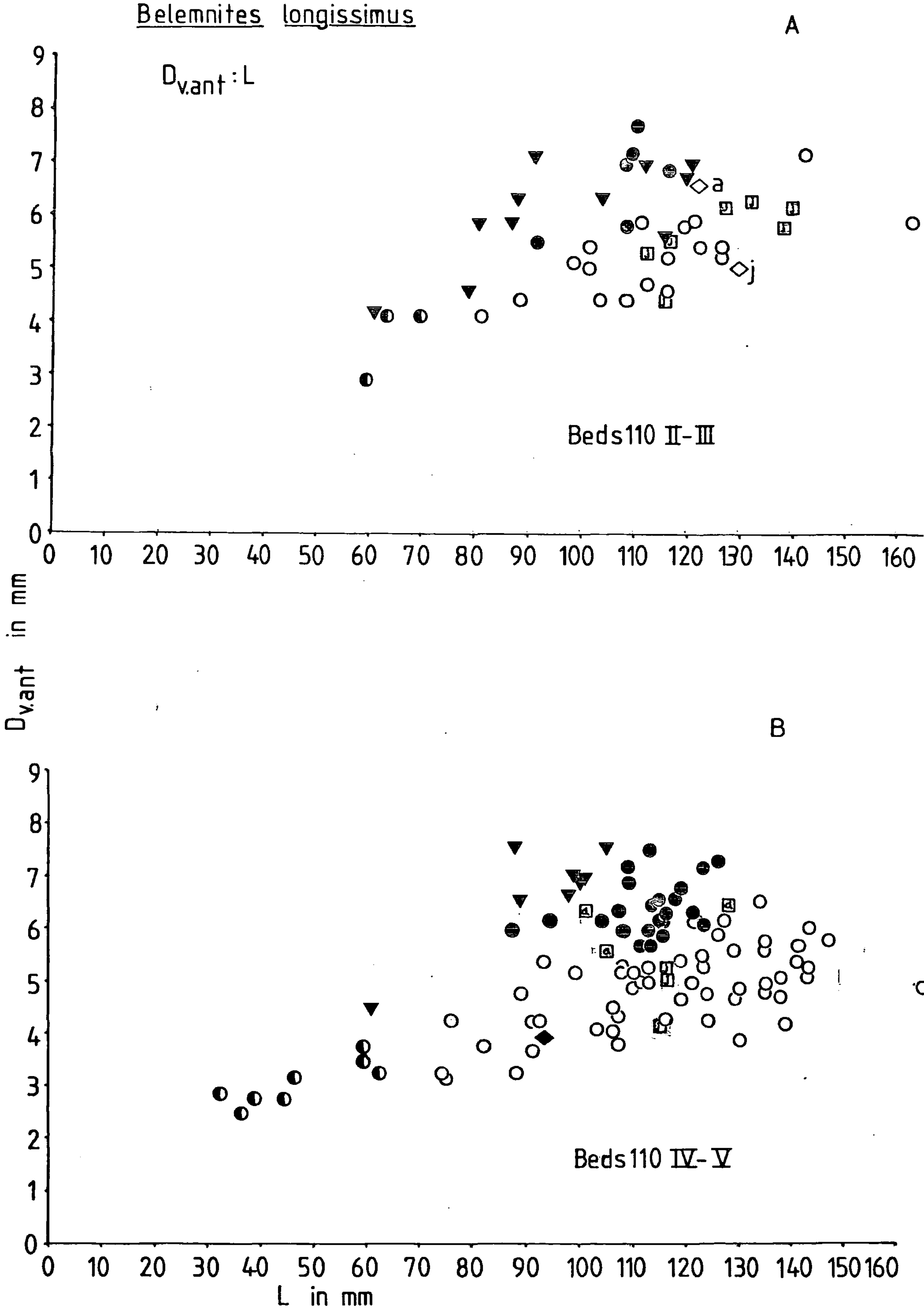


FIG.8 *key*

A: ▽ author's coll., bed 110 II
o author's coll., bed 110 III
◇a holotype *Pseudohastites arundineus*
◇j neotype *P. junceus*
🄹 BMNH coll. "*P. junceus*

B: ◇ NEOTYPE
o author's coll.
🄰 BMNH coll., "*P. arundineus*"

FIG. 8

Belemnites longissimus

$D_p : L_p$

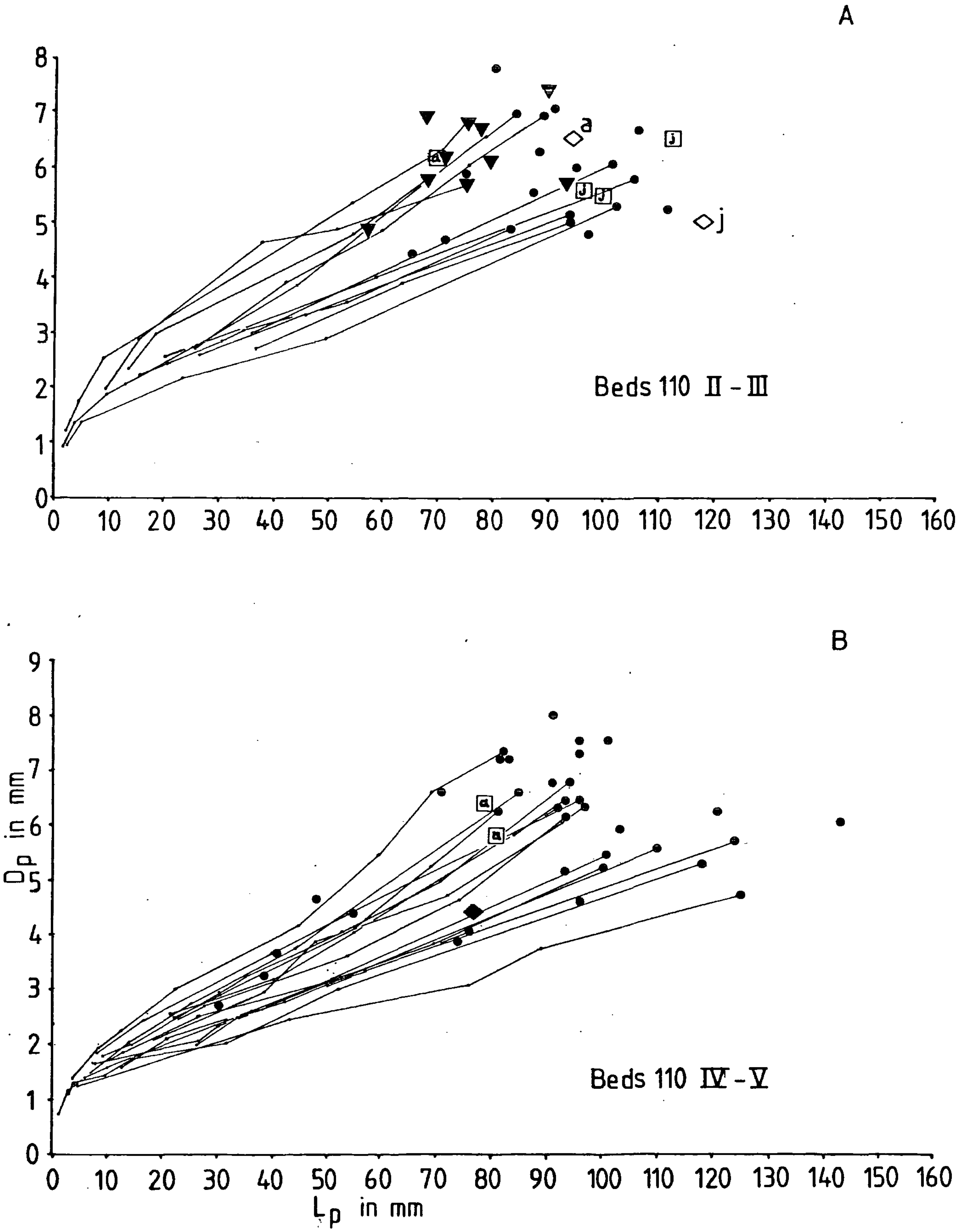


FIG.9 Belemnites longissimus: camera lucida drawings of median longitudinal polished sections.

A: TB367 (robust) bed 110 IV, x50
(with photograph)

B: TB506 (juvenile) bed 110 V, x50

C: TB173 (gracile) bed 110 V, x50

p - protoconch
l - rostral lamellae
s - primary spherules
v - sparry calcite-filled void between prismatic and nacreous layers of protoconch
f - fracture

FIG.10 Belemnites longissimus: camera lucida drawings of median longitudinal polished sections.

A: TB357 (gracile) bed 110 IV, x24

B: TB329 (robust) bed 110 III, x24

C: TB188 (robust) bed 110 IV, x24

D: TB363 (robust) bed 110 IV, x24

p - protoconch
r - earliest clear rostral growth line
s - primary spherule

FIG. 9

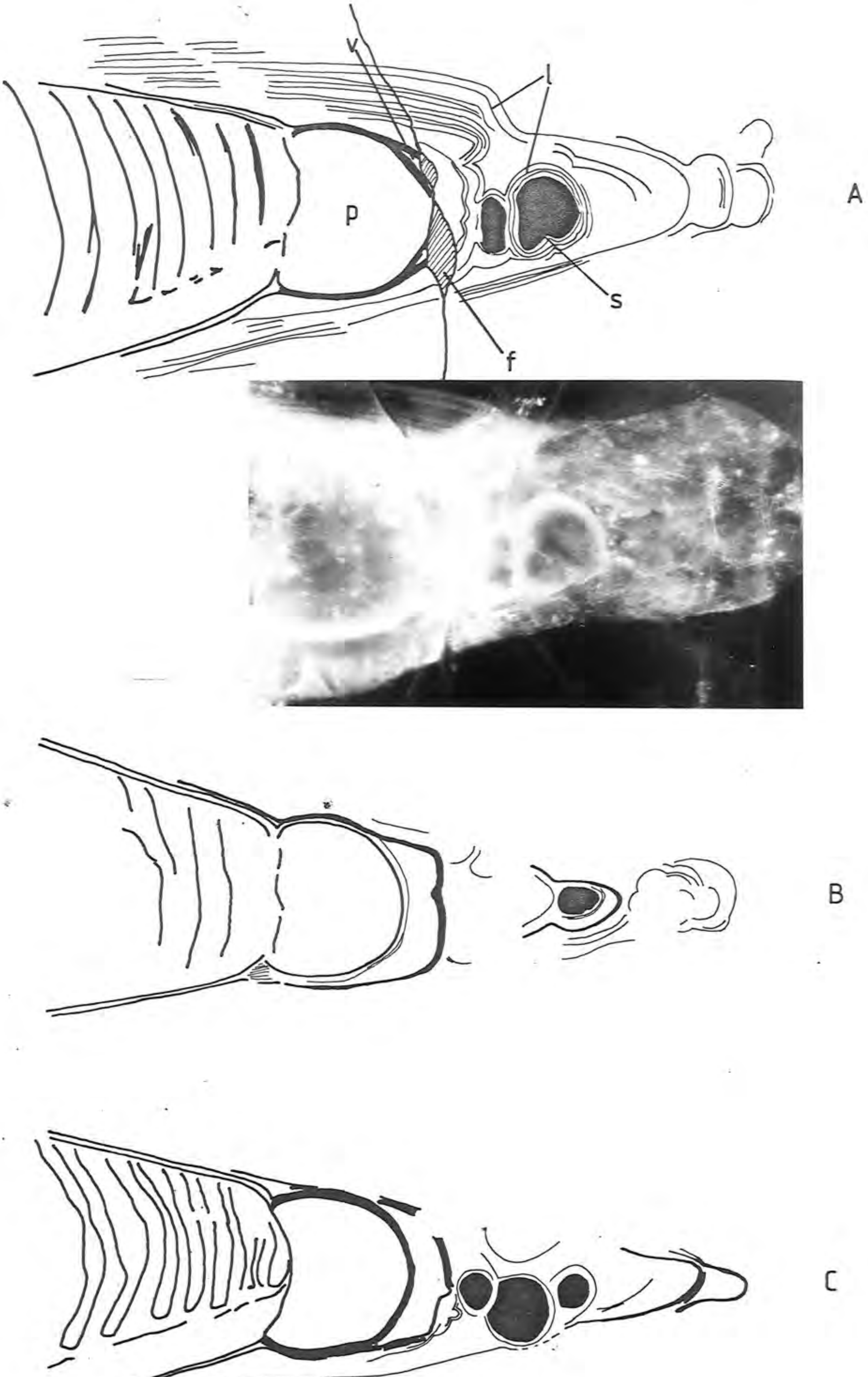


FIG. 10

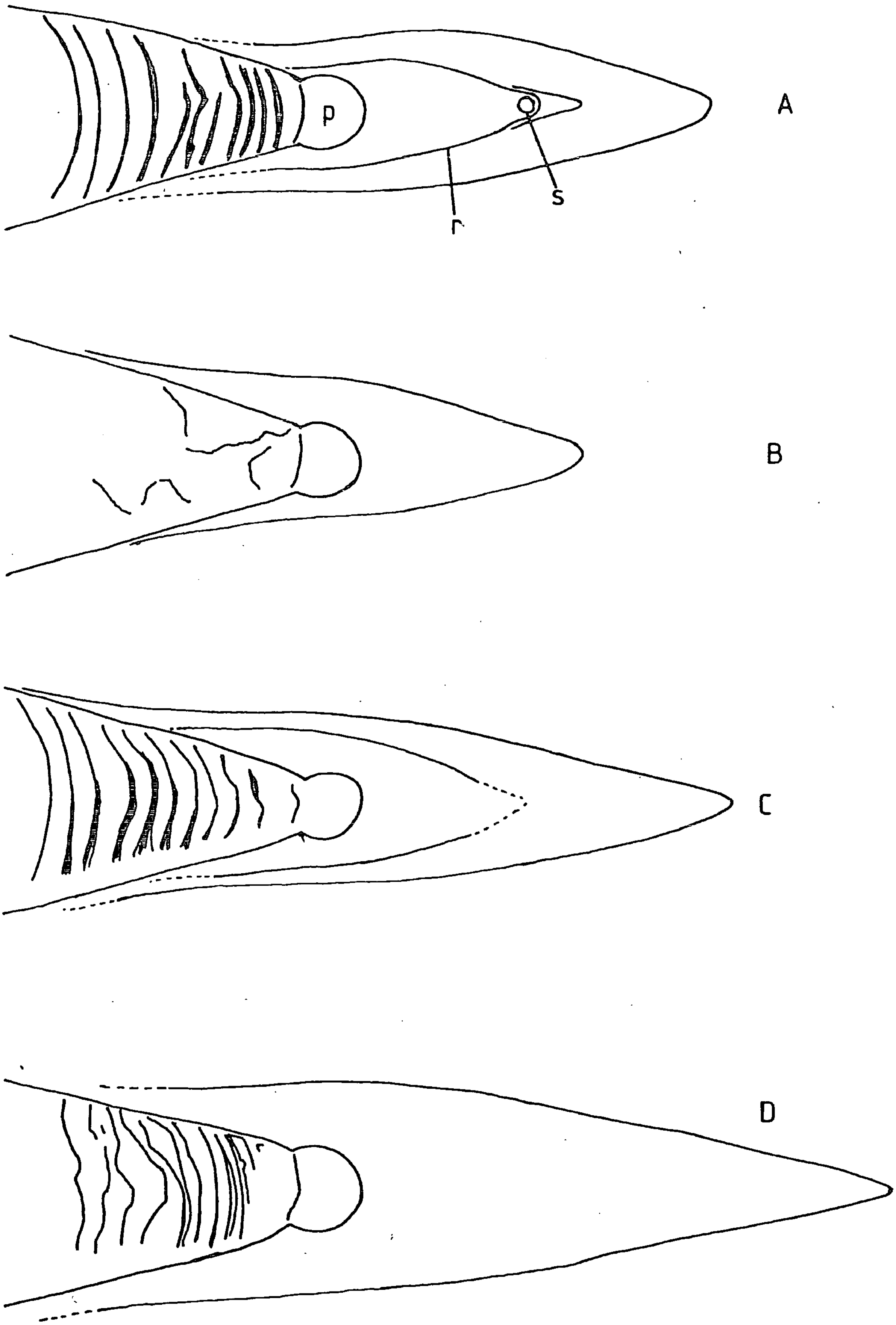


FIG.11 Belemnites longissimus: camera lucida drawings of median longitudinal polished sections.

A: TB363 (robust) bed 110 IV, x6

B: TB188 (robust) bed 110 IV, x6

C: TB357 (gracile) bed 110 IV, x6

r - earliest clear rostral growth line
o - outer surface of rostrum

FIG. 11

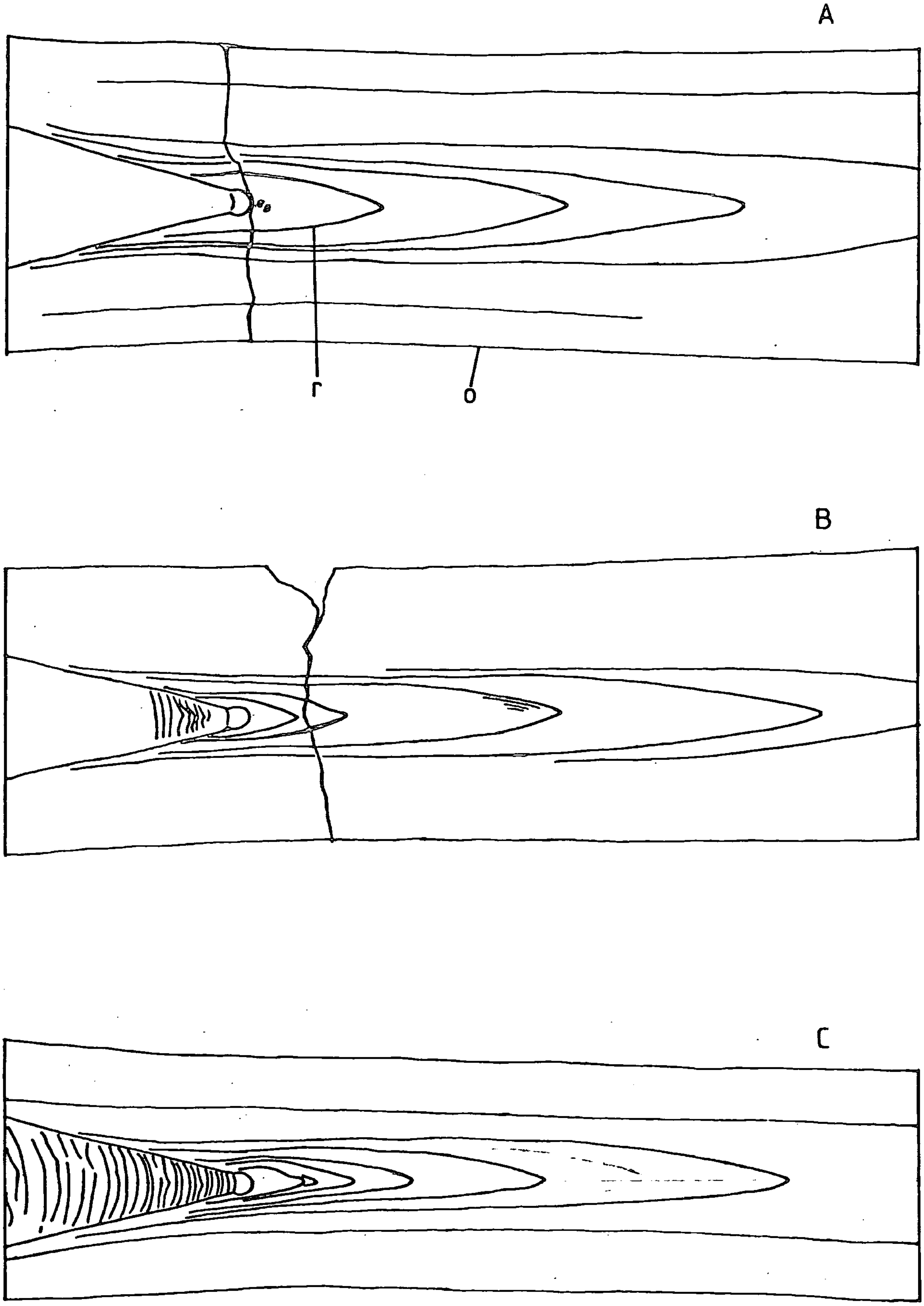
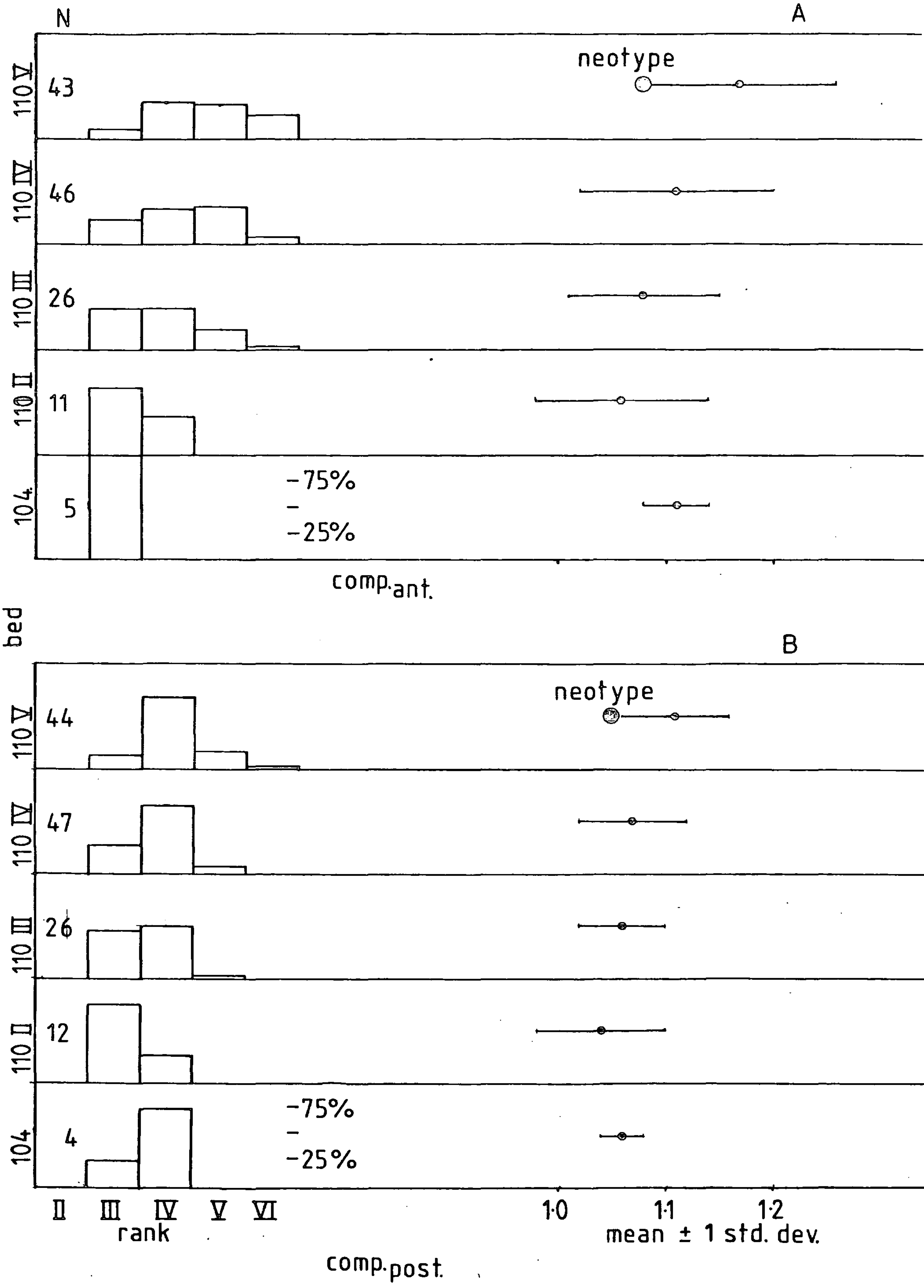


FIG. 12

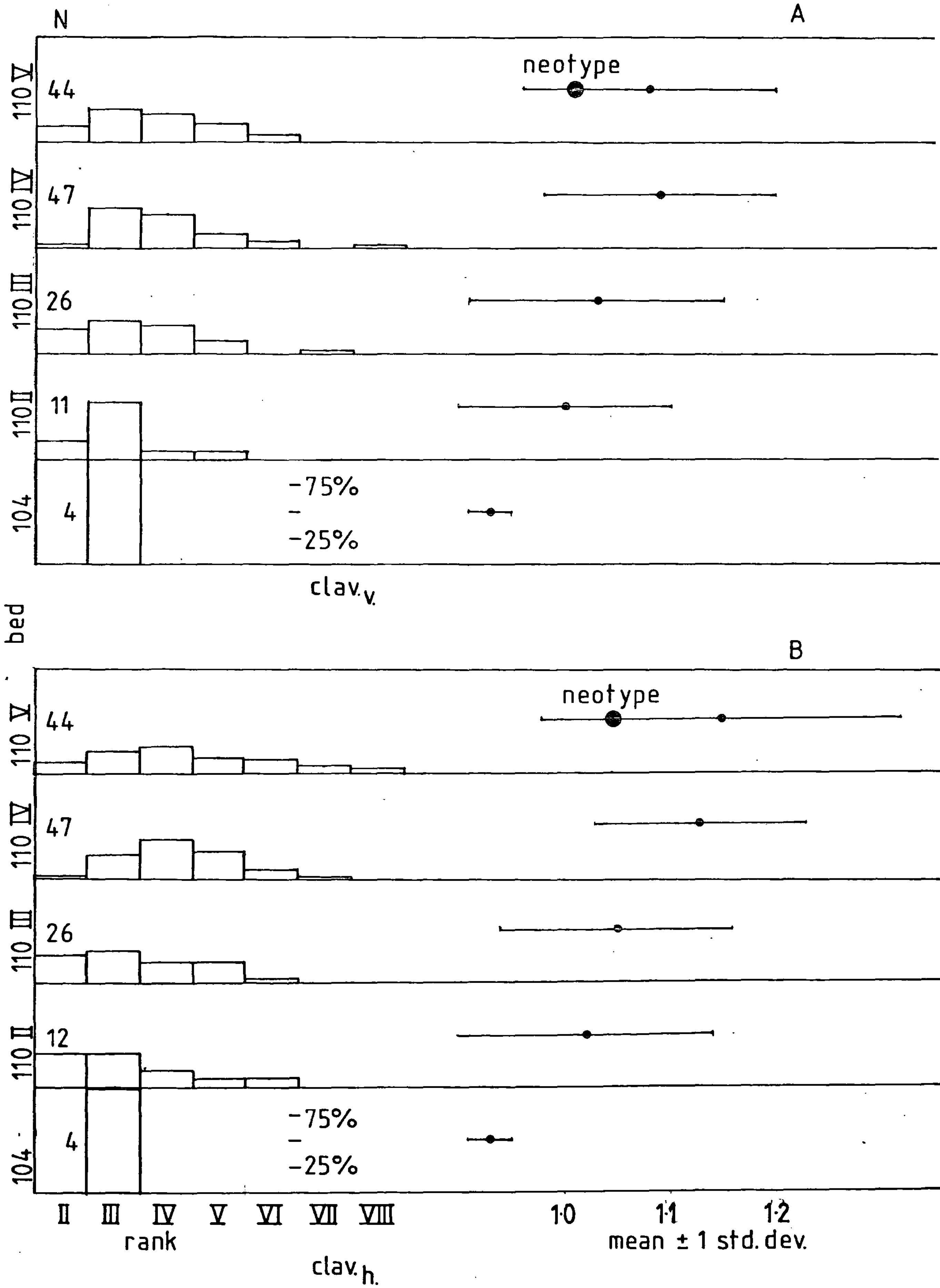


Belemnites longissimus

compression

FIG.13

Belemnites longissimus
clavateness



Belemnites charmouthensis Mayer, 1864

Pl.4 figs.1-5 ; Pl.5, figs.1-6.

? 1827	Belemnites umbilicatus sp. nov.; de Blainville, p. 97, pl. 3, fig, 11.
? 1840	Belemnites umbilicatus de Blainville; d'Orbigny, p. 86 - 87, pl. 6, figs. 6 - 11.
1864	Belemnites charmouthensis sp. nov.; Mayer, p. 364 (no figure), jamesoni Zone, Charmouth.
non 1864	Belemnites charmouthensis sp. nov.; Mayer, p. 364 (no figure), fimbriatus beds, Saint Fortunat, Rhône.
non 1869	Belemnites charmouthensis Mayer; Dumortier, p. 50, pl. 5.
? 1876	Belemnites charmouthensis Mayer; Tate and Blake, p. 317, pl. 4, fig. 5.
? 1884	Belemnites charmouthensis Mayer; Simpson, p. 55.
? 1912	Belemnites charmouthensis Mayer; Werner, p. 116, Taf. 10, fig. 16.
? 1910	Belemnites charmouthensis Mayer; Thompson, p. 102.
1925	Hastites charmouthensis (Mayer); Lissajous, p. 69.
? 1927	Hastites junceus (Phillips); Lissajous, p. 33 - 35, pl. 3, figs. 20, 20a, 20b.
v. 1928	Pseudohastites charmouthensis (Mayer); Lang, p. 215, pl. 15, fig. 2; text fig. 3, no. 3.
vp. 1928	Passaloteuthis argillarum sp. nov. Lang; p. 200.
? 1962 b	Belemnites charmouthensis Mayer; Schwegler, p. 97 - 98, figs. 36, 37.
?p 1974	Hastites clavatus charmouthensis (Mayer); Schumann, p. 32 - 33, Taf. 6, figs. 8 - 14, 16.
?p 1974	Hastites junceus (Phillips); Schumann, p. 36 - 37, Taf. 5, fig. 14 only.

Neotype

BMNH C29042 (*Pseudohastites charmouthensis*), Belemnite Marls, bed 110a (110 I), 28 ft. 6 in. below 111, Westhay Cliff, near Charmouth, Dorset. Established by Lang (1928) p. 215, pl. 15, fig. 2.

Other material

Author's collection, Belemnite Marls, Charmouth: 89 specimens

- bed 108 I: TB215, TB216, TB217, TB590 - 593, TB601 - 611, TB853 - 857
- bed 108 II: TB614 - 625, ?TB626 (? *B. nitidus*), TB627 - 633, TB636
- bed 109: ?TB646
- bed 110 I: 138, D85, TB271 - 275, TB277 - 280, TB288, TB290, TB291
- bed 110 III: TB315, TB316, TB317, TB322, TB340, TB341, TB342, TB347, TB348
- bed 110 IV: TB180, TB222, TB225, TB373, TB375, TB377, TB378, TB379, TB396, TB397, TB398, TB401, TB402, TB405, TB408, TB410, TB418, TB419, TB420, TB422, ?TB516 (? *B. nitidus*)

BMNH, coll. W.D. Lang, Belemnite Marls, Charmouth: 8 specimens

- bed 107: C33174
- bed 110a, 29 ft. below top (=110 I): C28873 ("*Passaloteuthis argillarum*"), C29041
- bed 110a, exact horizon not specified (=110 I - V): C29043, C43906, C43910, C43913, C44931

Description

Rostrum fairly slender (usually somewhat more so than that of *B. nitidus*), profile variable, distinctly clavate to slightly tapering. Section nearly always compressed, sometimes highly so, particularly in the anterior portion of the rostrum. Paired lateral furrows well developed.

Dimorphism apparent when sufficient size is attained, adult rostra being readily separable into gracile and robust forms.

Alveolus short, typically 25 to 35% of the total rostral length.

Discussion

Mayer's original description (1864, p. 364; no figure) of Belemnites charmouthensis as a moderate sized, clavate, elongated and markedly compressed belemnite with paired lateral lines and a small alveolus was matched by Lang (1928, p. 215) to a form occurring in bed 110 of the Belemnite Marls, with particular mention of the subclavate forms from the lowest part of that bed. He assigned the species to Pseudohastites. In actual fact, Mayer's designated material, consisting perhaps of only two specimens, came from the "fimbriatus beds" of Rhône (equivalent to the topmost beds of the Belemnite Marls) (collected by Dumortier) as well as from the jamesoni Zone of Charmouth. As Lang pointed out, it is obviously desirable to base the species on type material from the latter source, especially as it is probable that the Rhône material is of a different species (see below).

In the absence of Mayer's holotype or syntypes, Lang selected as neotype a specimen collected 28½ ft. from the top of bed 110, which places it in bed 110 I. (I assume that he measured 1 ft. up from the base of the bed and subtracted this from his estimate of 29 ft. 6 in. for the complete thickness of bed 110; to measure accurately 28½ ft. of strata exposed in wave-cut platforms and irregular cliffs would be well nigh impossible.)

Although this neotype, which closely matches Mayer's measurements, is acceptably a specimen of B. charmouthensis, it is more slender than any other conspecific specimens collected by either Lang or the present author, illustrating the tendency to nominate types that caricature rather than characterize the species in question. Mayer stated the length to be 81 mm and the diameter (position unspecified) as 6.5 mm; Lang's neotype has a length of 78 mm (with a slightly damaged apex) and a maximum diameter of 6.7 mm.

In accord with Mayer's diagnosis, samples ascribed to B. charmouthensis have consisted largely of clavate belemnites of modest size. Without detailed analyses, material from other localities and horizons described by various authors can only be placed in tentative relation to the material from the type locality.

Werner's figured specimen (1912, Taf. 10, fig. 16) from the Lias gamma of Balingen, South West Germany, is not clavate but is similar to some Charmouth specimens (eg. TB516, pl.5 , fig.5, a fairly large, gracile specimen from bed 110 IV).

Schumann (1974, p. 36) acknowledges Lang's neotype, but his figured material of Hastites clavatus charmouthensis (Taf. 6, figs. 8 - 14, 16), from Rottorf and Ostercappeln, North Germany, is all from a higher stratigraphical level (equivalent to beds 113 - 120 in the Belemnite Marls) than that in which Belemnites charmouthensis occurs in Dorset. However, the figured specimens from Ostercappeln (from Lias gamma 1d, equivalent to Belemnite Marls beds 113 - 114) certainly are strikingly similar to those from Charmouth, and are very likely to be of the same species. On the other hand, the Rottorf specimens (from Lias gamma 2c, equivalent to Belemnite Marls beds 118c - 121) reveal an uncompressed transverse section and a strongly curved and excentric axial line which is characteristic of certain Hastites like forms which occur frequently from the ibex Zone upwards at localities throughout Europe; the present author possesses comparable specimens from the ibex and davoei Zones of Dorset (see p.193). It is probable that the Rhône specimen mentioned by Mayer belonged to this group, which only superficially resembles B. charmouthensis sensu Lang and even then can usually be distinguished from it by its comparatively uncompressed rostral section. The correct affinities of this material were realized by Schumann when he assigned it to the genus Hastites.

One slightly earlier clavate specimen from Lias gamma 1a (equivalent to Belemnite Marls beds 105 - 109) is a possible candidate for inclusion in B. charmouthensis; Schumann (Taf. 5, fig. 14) called it Hastites junceus (Phillips), and it could indeed belong to B. longissimus (q.v.) which in the present work includes B. junceus (Phillips). Again, a specimen figured by Lissajous (1927, pl. 3, fig. 20) as Hastites junceus (Phillips) from the jamesoni Zone of "Lime Regis" may be a short B. longissimus from the upper part of bed 104 (it is slightly deformed, as are most rostra from this horizon) or a slender B. charmouthensis, perhaps from bed 108.

Doubts similar to those outlined above apply to other references cited in the synonomy. Thus B. umbilicatus de Blainville is insufficiently stratigraphically localised (clayey limestones with Gryphaea arcuata of Basse-Normandie, and Vieux Pont, nr. Bayeux (1827, p.97)), but as it occurs with "la bélemnite bicanaliculée" (1827, pl. 2, fig. 7) which is probably to be identified with one of the common belemnitids from the ibex and davoei Zones which have prominent apical furrows (Belemnites aduncatus (q.v.)) it is likely to be one of the true hastitids already alluded to.

As realised by Lang (1928, p. 215), Dumortier's figure (1869, p. 50, pl. 5) is supposedly based on the specimen mentioned by Mayer as being from the Rhone fimbriatus beds, and so is probably not valid.

B. charmouthensis may occur in the jamesoni Zone of the Yorkshire coast; appropiate material was described under this name by Tate and Blake (1876, p. 317, pl. 4, fig. 5), although Lang regarded the figured specimen as too stout to be of the same species.

One specimen (C28873) regarded by Lang as a small example of Passaloteuthis argillarum belongs to B. charmouthensis; this was the only specimen from the base of bed 110 which he attributed to P. argillarum.

In common with most belemnititds, B. charmouthensis is somewhat difficult to characterize due to its lack of distinction from the mainstream of belemnite forms, represented at this stratigraphical level (jamesoni Zone) mainly by B. nitidus (q.v.); it may also occasionally be confused with B. longissimus; elsewhere, as has been shown, it has been confused with later hastitids (ibex and davoei Zones) - indeed, Mayer himself was partly responsible for this, and despite the general acceptance of the validity of Lang's neotype and redefinition, subsequent misinterpretations are frequent.

To conclude, B. charmouthensis sensu Lang lies within the limits of variation of a form that is not always markedly clavate, it being mainly the specimens from bed 110 I at Charmouth that most satisfactorily fulfil Mayer's criteria. At other horizons, it is most likely to be confused with slender, incompletely grown specimens of B. nitidus, particularly if samples contain few rostra. Scatter and growth diagrams derived from carefully collected assemblages provide the most reliable means of differentiation between these two species.

Ontogeny

Few specimens were found to show clear early growth stages in longitudinal section. Those that do (fig.15) reveal the early rostrum, post-alveolar length about 2.5 mm, to be a fairly slender cone, slightly inflected posterior to the position of the protoconch. The alveolus is somewhat excentric and occupies slightly more than half of the total length of the rostrum. An axially positioned spherule (see p.238)is enclosed by the earliestclear growth laminae in the specimen shown in fig.15A, but the generally poor preservation of shell detail in all the sectioned specimens of <u>B. charmouthensis</u> does not disclose whether or not primary spherules play much part in early rostral formation.

A distinct change in the growth curve at a post- alveolar length of 5 to 10 mm marks an increase in rate of lengthening relative to thickening. This continues in a linear fashion in those forms that eventually become recognizable as gracile rostra, whereas the comparative rate of thickening gradually increases again to give rise to robust rostra; the rate of divergence between the two forms is commonly accelerated by a sudden marked increase in rate of thickening in the robust specimens, hence the growth curves for these may be comparatively complex. The combination of these effects produces the most striking graphical example of dimorphism out of all the observed Belemnite Marls material; in section, robust and gracile specimens are distinguishable at a post-alveolar length of 40 - 50 mm. It is perhaps surprising that this dimorphism does not really show up in the scatter diagram of total length/diameter (fig.14A). This is mainly due to the inaccuracy inherent in measuring the alveolar component of the rostral length, so that, although gracile and robust specimens plot in the appropiate parts of the diagram, the rift between them is obscured.

The rostrum becomes compressed at a fairly early stage, although the aforementioned paucity of clear growth lines conceals the size at which this would first be noticeable. The six smallest whole specimens collected (total length 17 - 36 mm), which incidentally are all from bed 108 (see below), are all at least slightly compressed, so this character probably develops before a post-alveolar length of about 10 mm is attained. Three of these specimens are clavate and the other three are nearly so (vertical clavateness = 0.97 - 1.09), so it appears that the transition between a gently tapering, conical and a clavate profile occurs between post-alveolar lengths of about 10 - 20 mm.

Both robust and gracile forms achieve similar degrees of clavateness and compression. It should be noted that, as compression is nearly constant throughout most of the rostral length, so the clavateness is roughly the same whether measured in a horizontal or vertical plane.

Stratigraphical variation

Lang (1928, pp. 195, 215) considered Pseudohastites charmouthensis to be confined in the Belemnite Marls to bed 110a, listing firmly identified specimens only from the bottom foot of this bed (=110 I). However, BMNH C33174, identified by him as P. charmouthensis subsequent to the 1928 paper, is from bed 107, thus extending the range down into the taylori Subzone. It is surprising that he missed it in bed 108 (consisting of about 1 m of soft, dark, calcareous clay) where it is common and easily collected; in fact, he only recorded two belemnite rostra (of Passaloteuthis ima) from this horizon, so his examination of it was probably rather cursory. Material from higher in bed 110 was at least partly confused with B. nitidus, his samples being very small (fig. 5).

As previously stated, B. charmouthensis is at its most characteristic in bed 110 I, where it is unlikely to be mistaken for anything else. Below this, specimens do not reach as large a size and are also not usually as clavate or compressed (fig.16) (this being only in small part due to the combination of smaller size and allometric growth). In beds 110 III - IV, it attains its largest size and consequently its clearest degree of dimorphism, although, unlike B. longissimus (q.v.), both sexes are probably present at each horizon. Again, it is not so strongly clavate or compressed, and is very likely to be confused with similar sized (up to about 50 mm total length) rostra of B. nitidus . The most effective way of distinguishing between them is by graphing post-alveolar length (L_a) against diameter at the protoconch (D_p); this reveals the interesting fact that, in bed 110 IV, B. nitidus is present only in juvenile form (fig.105). If B. nitidus had not thus been present, I would probably have regarded the fully grown B. charmouthensis material from this horizon as a somewhat slender (although not remarkedly so) stratigraphical variant of B. nitidus . Both species fluctuated chronologically with regard to slenderness, clavateness and compression, so that analysis of reasonably sized assemblages is required to distinguish them clearly at a given horizon.

Distribution

1) Charmouth, Dorset: Belemnite Marls, jamesoni Zone, taylori and polymorphus Subzones, beds 107 - 110 I, 110 III, 110 IV.
2) ?Yorkshire coast, various localities (Tate & Blake 1876): jamesoni Zone.
3) ?Balingen, Huttlingen and Hinterweiler, Württemberg, West Germany: Schwarjura gamma, ?jamesoni Zone (Werner 1912).
4) ?Rottorf and Ostercappeln, North Germany: jamesoni Zone, Lias gamma 1c - 1d (Schumann 1974).

FIG.14

Belemnites charmouthensis

beds 108–110 IV

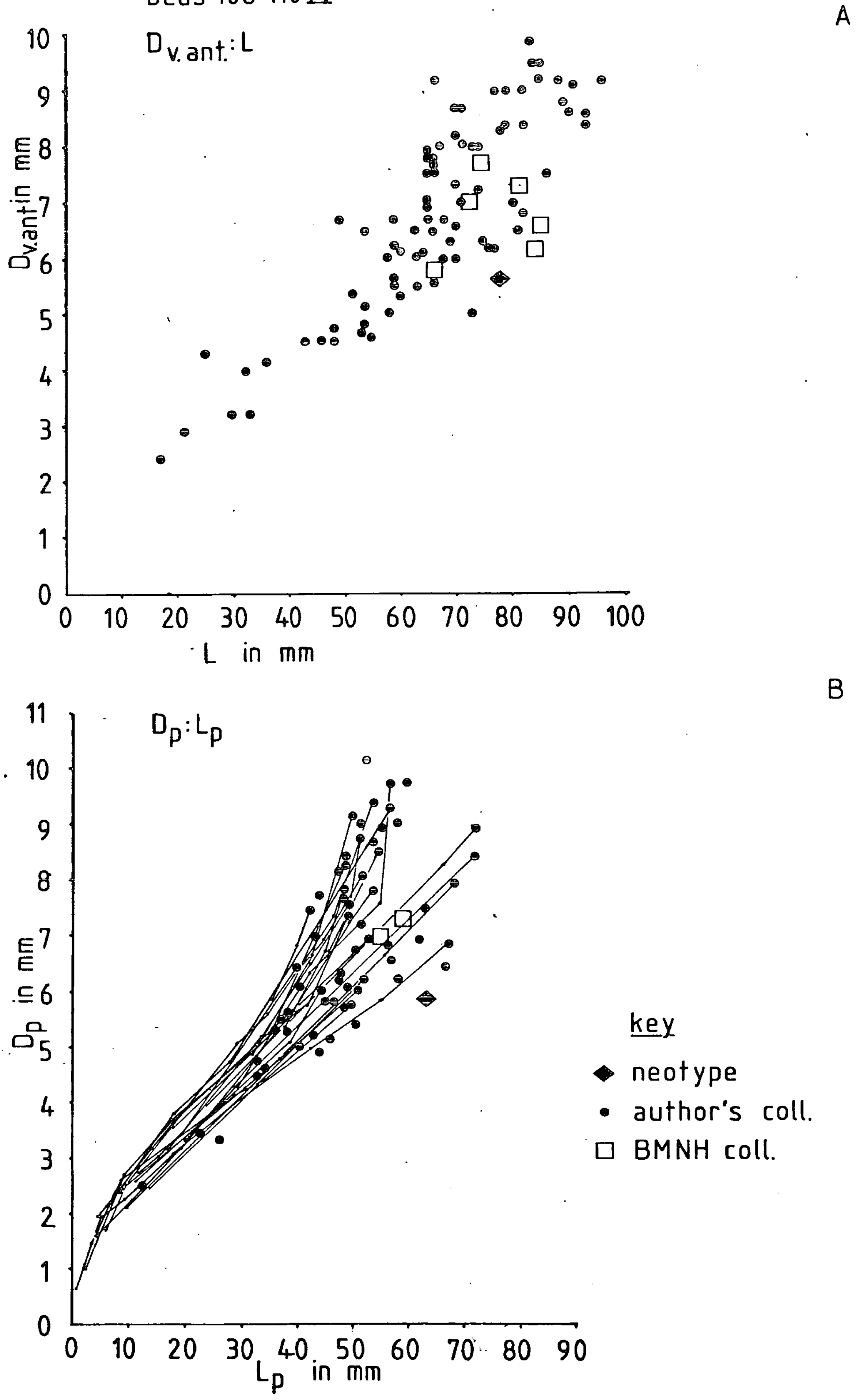


FIG.15 Belemnites charmouthensis: camera lucida drawings of median longitudinal polished sections.

A: TB615 (indeterminate) bed 108 II, x12

B: TB602 (indeterminate) bed 108 I, x12

C: TB410 (gracile) bed 110 IV, x12

D: TB348 (robust) bed 110 III, x24

p - protoconch
r - earliest clear rostral growth line
s - primary spherule

FIG. 15

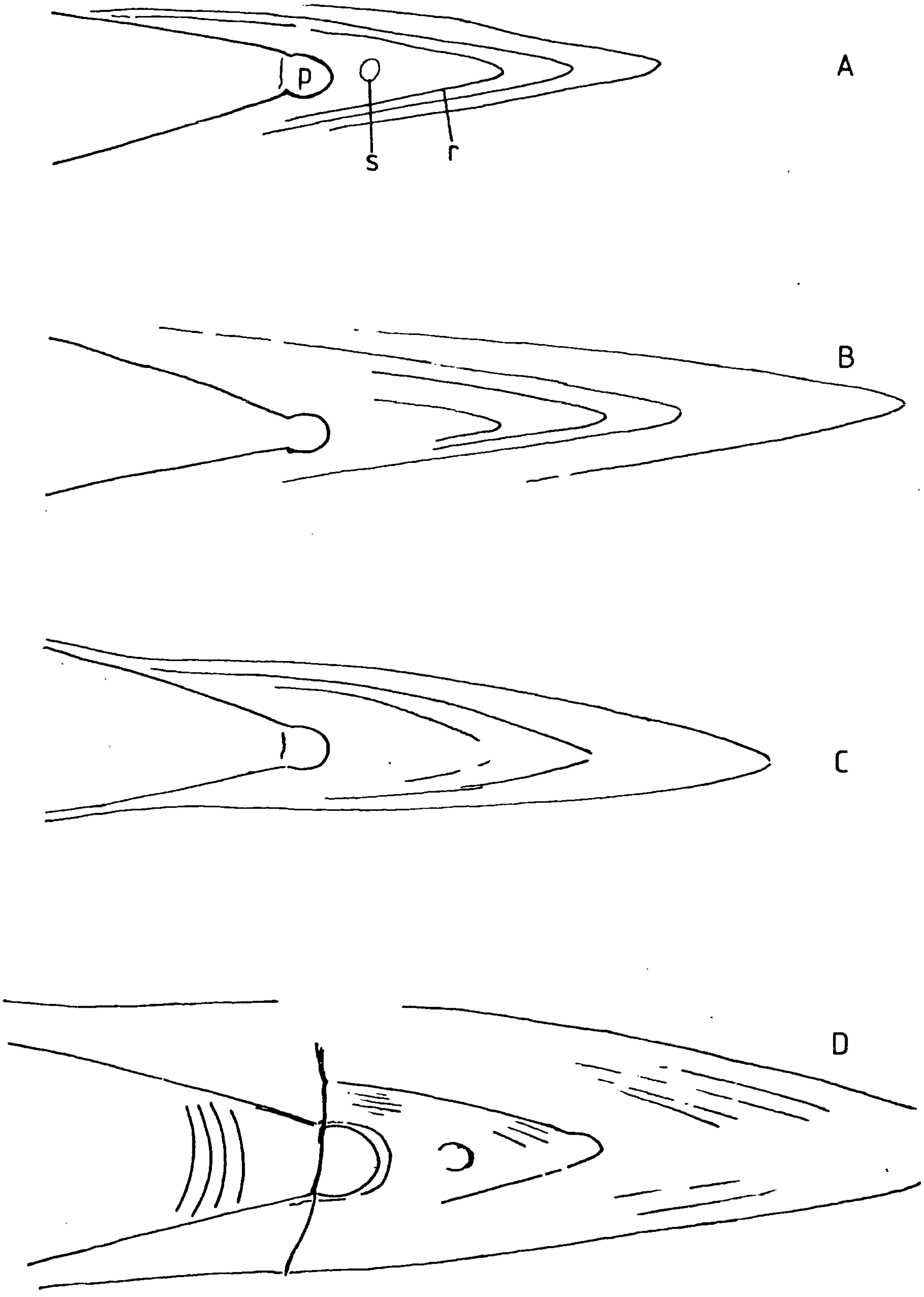
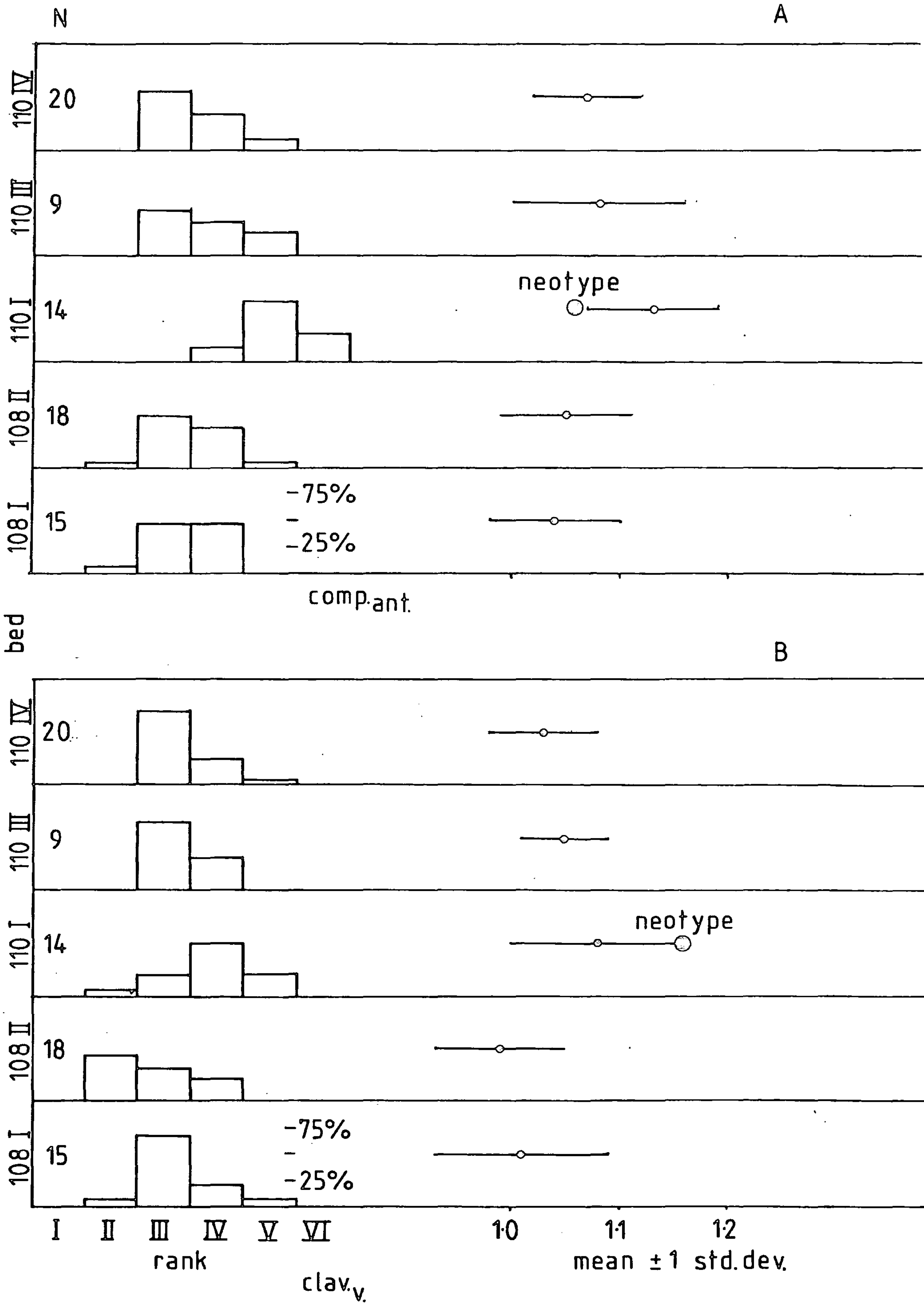


FIG. 16

Belemnites charmouthensis

compression and clavateness



Belemnites *nitidus* Phillips, 1867

Plates 6-16.

?p1836 *Belemnites* *ovalis* sp.nov.; Buckland, vol.ii, p.69, pl.44', figs 7, 8.

?1855 *Belemnites* *elegans* sp.nov.; Simpson, p.31 [no fig.].

?1863 *Belemnites* *virgatus* sp.nov.; Mayer, pp.190-191 [no fig.].

?p1867 *Belemnites* *bucklandi* sp.nov.; Phillips, p.53, pl.8, fig.18 [specimens from Golden Cap, Belemnite Bed only].

.1867 *Belemnites* *nitidus* sp.nov.; Phillips, p.67, pl.13, figs 34a, b.

?1867 *Belemnites* *elegans* Simpson; Phillips, p.84, pl.20, fig.50.

?1869 *Belemnites* *armatus* sp.nov.; Dumortier, p.40, pl.1, figs 13-16.

?1876 *Belemnites* *virgatus* Mayer; Tate and Blake, p.318, pl.4, fig.7.

?1883 *Belemnites* *armatus* Dumortier; Mayer-Eymar, p.641 [no fig.].

?1884 *Belemnites* *armatus* Dumortier; Mayer-Eymar, p.55 [no fig.].

v.1912 *Belemnites* *virgatus* Mayer; Werner, p.120, pl.11, fig.4.

v.1928 *Passaloteuthis* *argillarum* sp.nov.; Lang, p.200, pl.13, fig.7; text-fig.3, no.5.

v.1928 *Passaloteuthis* *stonebarroensis* sp.nov.; Lang, pp.200-201, pl.13, fig.6; text-fig.2, no.2.

v.1928 *Passaloteuthis* *elongata* [Miller]; Lang, pp.201-202, pl.13, fig.8; text-fig.3, nol.

v.1928 *Passaloteuthis* *westhaiensis* sp.nov.; Lang, p.202, pl.13, fig.9; text-fig.2, no.1.

v.1928 *Passaloteuthis woottonensis* sp.nov.; Lang, pp.202-203, pl.14, fig.1.

v.1928 *Passaloteuthis seatownensis* sp.nov.; Lang, p.203, pl.14, fig.3.

v.1928 *Passaloteuthis dayi* sp.nov.; Lang, p.204, pl.14, fig.2; text-fig.2, no.5.

p.1928 *Passaloteuthis apicicurvata* de Blainville; Lang, p.205-206, specimens from bed 120c only.

?1962b *Belemnites virgatus* Mayer; Schwegler, pp.127-129, fig.21.

1974 *Belemnites paxillosus elongatus* Miller; Schumann, pp.23-24, pl.2, fig.14; pl.3, figs 3-5.

1974 *Belemnites armatus armatus* Dumortier; Schumann, p.26, pl.3, fig.6; pl.4, figs 1, 2, 7, 8.

1974 *Belemnites armatus dayi* (Lang); Schumann, pp.26-27, pl.4, figs 3-6.

Type material

The incomplete rostrum of *Belemnites nitidus* figured by Phillips (1867) plate 13, figure 34a, has not been traced; Oxford University Museum specimen number J15071, identified by J.A. Jeletzky (J. Powell pers. com.) as that figured by Phillips (1867) in plate 13, figure 34b, is here chosen as lectotype. Phillips gave the horizon and locality as "Belemnite-bed, Golden Cliff, Lyme Regis", i.e. the topmost beds of the Belemnite Marls exposed below Golden Cap. Both of his figured specimens are typical of material from beds 117 and 118a.

Other material

The following BMNH specimens, designated as types by Lang (1928), form a convenient suite of topotypes of *B. nitidus*; they are all from the Belemnite Marls exposed between Charmouth and

Seatown:

C28880 holotype *Passaloteuthis argillarum*; bed 110b (110IV).
C28889 holotype *P. stonebarroensis*; bed 110a (110 V).
C28902 neotype *P. elongata* (Miller); bed 111c.
C28894 holotype *P. westhaiensis*; bed 112 (middle).
C11414 holotype *P. seatownensis*; bed 120.
C11407 holotype *P. dayi*; bed 120.

Due to its size, the list of material studied is given as an appendix.

Total numbers are:

Author's collection, Belemnite Marls and Green Ammonite Beds, between Charmouth and Seatown, Dorset: 572 specimens.

BMNH, collected and/or determined by W.D. Lang, Belemnite Marls, near Charmouth: 85 specimens.

Staatl. Mus. Nat., Stuttgart, *jamesoni* and *ibex* Zones, Wurttemberg: 4 specimens.

Description

Rostrum of generalized belemnitid form, moderately slender to moderately stout, profile clavate to tapering. Apex acute to somewhat rounded, not usually recurved (cf. *B. aduncatus*). Section variable, usually more or less compressed. Paired lateral furrows usually present, often strongly developed especially in more elongate specimens. Dorsolateral apical furrows well developed. Possibly dimorphic (i.e. possible gracile rostra occur rarely).

Alveolus of moderate length relative to rostrum, typically 30-50% of total rostral length, the longer alveoli being associated with stouter rostra.

Well developed epirostrum sometimes present.

Discussion

The corpus of belemnites here placed in B. nitidus has in the past yielded forms that became the types for a surprisingly large number of species. This can be attributed to the generalized but variable belemnitid form assumed by the rostra of B. nitidus, which provides a somewhat vague and featureless field upon which authors have projected their own particular predispositions towards belemnite taxonomy.

The data assembled in the present work suggest strongly that a large majority of the "conventional" belemnites from the whole of the Belemnite Marls and probably from the lateral equivalents in the rest of N.W. Europe, are best regarded as constituting one species whose morphology fluctuated slightly but frequently in time.

Unless accompanied by precise stratigraphical information, references to forms that should perhaps be included in this species are apt to be too ambiguous to be of much taxonomic value, hence the question marks in the synonymy. The earliest unequivocal description of a belemnite belonging to the species as here defined is Phillips' B. nitidus (1867, p.67, pl.13, fig.34a) whose untraced figured specimen, although incomplete, quite closely matches Lang's holotype of Passaloteuthis woottonensis and similar material in the BMNH and present author's collections from beds 117 and 118a. The well developed paired lateral furrows shown in the figure of Phillips' specimen appear to be more marked than is usual, but this is due to his method of illustrating belemnite rostra with strongly oblique lighting and is characteristic of many of his plates. The "shorter variety" of B. nitidus figured by him as plate 8, figure 34b, particularly resembles several specimens from bed 117, and is a suitable lectotype.

It is possible that a detailed analysis of material from the *jamesoni* and *ibex* Zones of the Yorkshire coast would show that *B. elegans* Simpson [1855, p.31] [figured in Phillips 1867, pl.10, fig.50] is conspecific with *B. nitidus*. Phillips himself states, "Specimens occur at Lyme Regis, referred by me to *B. nitidus* [p.67], and figured as a short variety [Pl.XIII, fig.34b], which are much like this fossil, but have not the apical striae, and always present more or less of the double lateral grooving" [op. cit., p.85]. He also comments on the variation in degree of compression of the rostra of *B. elegans*, which is an important feature in the present treatment of *B. nitidus* . Similarly, *B. virgatus* of Mayer and other authors, from various European localities and horizons, may include some comparatively slender clavate specimens of *B. nitidus*. In particular, material figured under this name by Werner [1912, p.120, Taf.11, fig.4] from the Lias gamma of Durnau, Wurttemberg and by Tate & Blake [1876, p.318, pl.4, figs 7a, 7b] from the *jamesoni* Zone of the Yorkshire coast is almost certainly conspecific with *B. nitidus*.

Lang's [1928] description of various species of *Passaloteuthis*, mostly from the Belemnite Marls, provides a useful standard for consideration of the stratigraphical variation of *B. nitidus*. In his treatment of this genus, he utilised eleven specific names, nine of which were new. Two are here retained [as *Belemnites imus* [Lang] and *B. ridgensis* [Lang]], two are incorporated into *B. aduncatus* Miller [*Passaloteuthis auricipitis* Lang and *P. apicicurvata* [de Blainville], principally from the Green Ammonite Beds, *davoei* Zone] and the remaining seven are incorporated into *B. nitidus* Phillips [to which Lang did not refer]. Of these seven, six names were new whilst *B. elongatus* Miller was considered to be applicable [as *Passaloteuthis elongata*] to forms from beds 11b-d which Lang [1928, p.202] considered

Miller's figures to resemble. However, Miller's figures show a specimen with a well preserved ante-rostral phragmocone and he also states the rostrum to be of a dark brown colour (1823, p.60, pl.7, figs 6-8). Neither of these conditions is met in specimens from beds 111b-d; on the other hand, brown rostra are characteristic of the Green Ammonite Beds and complete phragmocones are sometimes associated with them, so it is more likely that this was the source of Miller's type; it is possibly a comparatively featureless specimen of B. aduncatus Miller (q.v.). The term elongatus is thus not available for the species under discussion, otherwise it would have priority over nitidus.

The diagnostic bases of Lang's seven species must now be considered in order to justify the taxonomy here proposed. In ascending stratigraphical order and with their diagnostic features summarised, they are:

1) Passaloteuthis argillarum, beds 110a-b: slender, resembling P. elongata, but smaller and not as slim.

2) P. stonebarroensis, beds 110a-b: stout, resembling P. ridgensis and P. auricipitis, but less stout; less pronounced dorsolateral furrows.

3) P. elongata, bed 111: large, slim rostrum, exceeded in slimness by P. westhaiensis, P. woottonensis, P. dayi and P. seatownensis; rather marked dorsolateral furrows.

4) P. westhaiensis bed 112: resembles P. elongata, but more slender and tapering; shallow but marked dorsolateral furrows.

5) P. woottonensis, beds 115-118a: resembles P. westhaiensis but still more elongate.

6) P. seatownensis, beds 120a-d: resembles P. woottonensis but still more slender.

7) P. dayi, beds 119-120c: about as slender as P. westhaiensis

which it resembles, but less tapering than P. westhaiensis or P. elongata; dorsolateral furrows obscure.

Obviously, relative slenderness was the major criterion used by Lang; however, unless quantified, this parameter is rather vague. If figure 77 is examined, it will be seen that "slenderness" in B. nitidus as measured by the ratio of total rostral length (L) to vertical diameter fluctuates chronologically in a seemingly directionless manner, thus belying Lang's statement that, when placed in stratigraphical order, P. argillarum, P. elongata, P. westhaiensis, P. woottonensis and P. seatownensis are in order of increasing slenderness (1928, p.199). However, when horizontal diameter is considered, there is a remarkable directional series from beds 110 V to 117 - ten samples in all - where "slenderness" does increase. This is another way of saying that the degree of compression increases throughout this series (figs 45-46). The degree of change from bed to bed is slight and is not here considered to be sufficient to distinguish separate species; thus quantification of Lang's diagnostic criteria suggests that his species cannot be considered to be valid. When other parameters are examined (clavateness, form of juvenile rostra, growth curves) a pattern of slight bed by bed fluctuation again emerges. Furthermore, in the cases of Passaloteuthis argillarum and P. stonebarroensis from bed 110 and P. dayi and P. seatownensis from bed 120, each bed was found to contain only one variable form.

Specimens from bed 120c ascribed by Lang to P. apicicurvatus (= B. aduncatus q.v.) are probably B. nitidus; they closely resemble material from beds 120a-b. From the present author's collection, a number of smaller crushed specimens bearing epirostra, also from bed 120c, are more tentatively assigned to B. nitidus;

they appear to resemble epirostrid specimens from beds 117-118a.

Schumann's (1974) study of belemnites from the North German Lias gamma incorporated six of Lang's species (*P. argillarum* not being mentioned) in two species, three sub-species of the genus *Belemnites* from the *jamesoni* and *ibex* Zones: *P. elongata* (Miller) became *B. paxillosus elongatus* Miller; *P. stonebarroensis* Lang became *B. armatus armatus* Dumortier; *P. dayi* Lang became *B. armatus dayi* (Lang), and possibly included *P. westhaiensis*, *P. woottonensis* and *P. seatownensis*. (Schumann 1974, pp.23-27).

Whilst it is probable that Schumann's material represents a series similar to that occurring in the Belemnite Marls, the present writer feels that this utilisation of sub-species is unnecessary and obscures a simpler relation between successive assemblages. There is certainly no justification for separating *P. elongata sensu* Lang at species level when all the other forms are only separated as sub-species; in the Belemnite Marls, it occurs in the middle of the sequence, and is a morphological and chronological bridge between lower and higher assemblages of *B. nitidus*.

Lang's main purpose in delimiting so many species was to provide zonation by means of belemnites, and in this context it could be useful to retain his species as sub-species or varieties; biologically speaking, this may be misleading, and it seems best to regard *B. nitidus* as a long ranged, slightly fluctuating but essentially static species of conservative form.

Ontogeny

Development of the rostral profile normally follows a simple pattern, with a more or less linear increase in length relative to diameter after a post-alveolar length of 5-10mm is attained.

The earliest visible growth laminae reveal a sub-conical rostrum, post-alveolar length about 1mm, being more cylindrical in the alveolar portion. At this stage, the alveolus itself is approximately half the total length of rostrum, noticeably excentric but not nearly so much so as in, for example, B. imus or B. abruptus.

A few specimens are well enough preserved to display clearly the crescentic structure immediately posterior to the protoconch (fig.39a), interpreted by Barskov (1972, 1973) as a primary void between the inner, prismatic and outer, nacreous layers of the protoconch, diagenetically filled with sparry calcite and often interpreted as a solid "pri mordial rostrum". This is further discussed on p.240.

Calcite spherules, believed to be primary, are sometimes visible within the earliest distinguishable rostrum.

Growth usually continues to produce the characteristically unremarkable rostrum that typifies this species. There is a tendency for a gradual increase in relative rate of thickening to occur in the later stages, which, coupled with a period of early concentric growth around the earliest conical lamellae, produces a gently sinuous growth curve (e.g. in beds 108-110, fig.29). Also in bed 110, there are a few specimens where growth is more nearly linear, but only three specimens were observed which attain sufficient size (post-alveolar length greater than about 55mm) to separate them from the others. A number of smaller specimens share this growth style, and it is possible that this is an instance of dimorphism. It is suggestive that a similar pattern (i.e. linear growth leading to gracile forms, an upward curve leading to robust forms) is a clear feature of B. charmouthensis (q.v), where the numbers of each form are more nearly matched. (However, equality of numbers is not a necessary test of sexual dimorphism in cephalopods, especially when collected from a single locality: see p.197.

To make matters more confusing, these linear growth curves closely match what appear to be the prevalent modes of growth of the species at other horizons (e.g. 112d-f, 119-120), which could be held to justify the existence of two separate species. On the other hand, the morphological gap between the two forms in bed 110 is occupied by forms from other horizons, and so it is most feasible to regard the morphology of the one species to be subject to irregular oscillations from bed to bed, perhaps with dimorphic forms being variably represented. It is entirely feasible that male or female forms predominate at particular horizons, and even that, in view of the oscillating morphology, robust rostra at one horizon are homeomorphic with gracile rostra at another - relatively clear cases of dimorphism in other species involve a difference in diameter of only 2mm or so.

A number of specimens of B. nitidus from beds 115, 117 and, especially, 118a (and possibly 120c) have well developed epirostra, which, as figure 35 shows, are only formed after the normal rostrum has reached a post alveolar length of at least 30mm. The size grouping suggests that, where present, the epirostrum develops in different specimens at about the same point in their ontogeny. (Note that the specimens plotted in figure 35 came from several bedding planes, and so this feature is not related to a unique population.) Up to the development of the epirostrum, there is in section no perceptible difference between these and non-epirostrid specimens.

Epirostra are discussed in more detail on p.253, but it may as well be stated here that their function remains enigmatic. It may be significant that from bed 118a, approximately equal numbers of specimens of comparable size with and without epirostra were obtained (21 with, 23 without) suggesting that this may be a special case of sexual dimorphism with, for once, each sex equally represented.

Epirostra do not appear to have been previously recorded from these beds.

In some assemblages, for example those from beds 108-110, 11b-d, 112 and 117, rostra of B. nitidus occur in two or three distinct size groups (figs 18-23). This mortality pattern could be due to a combination of several factors, such as (1) yearly mortality of one, two and three year old individuals with the low mortality of certain sizes due to rapid seasonal growth and/or seasonal migration; (2), as (1), but with year groups replaced by several spawning groups from different times of one year; (3) post-reproductive mortality of mature populations.

Seasonal migration is further suggested by the occurrence at certain horizons of juvenile B. nitidus only (e.g. 110 IV, fig.87) or larger specimens only (e.g. 111e, 112d-f, figs 91, 93). The composition of belemnite populations is further discussed on p.197.

Growth is variably allometric with respect to clavateness and compression of the rostrum (fig.50). There is a tendency for individuals to become noticeably clavate and compressed at a fairly early stage (post-alveolar length 15-20mm, total length 20-30mm). Clavateness then normally decreases throughout ontogeny but does not usually change much after a total rostral length of 40mm is reached, thus justifying the use of, where possible, specimens over this length in constructing the diagrams of degrees of clavateness in different beds (figs 47-49).

Compression usually increases slightly throughout ontogeny, although in some cases this is preceeded by a fairly sharp drop between a total rostral length of about 20-40mm [fig.50b; this is somewhat illusory, as the drop corresponds to the mortality gap between juveniles and the rest of the assemblage; so that specimens of intermediate size and compression do not occur]. Again, specimens over 40mm long were utilised for the diagrams of compression [figs. 44-46].

Stratigraphical variation

The fluctuations in morphology alluded to above, consisting mainly of slight non-directional changes in slenderness and compression and in degree of clavateness, are documented in figure 77 and figures 44 - 49. Size distribution also fluctuates [figs. 41-43], which has a slight effect on measurement of mean values of the above parameters as these features display some allometry in their ontogeny. That the effect of size distribution on these characters is slight is shown by figure 50, which reveals the actual differences in compression and degree of clavateness for equivalent size groups from five different horizons.

The most remarkable feature of this variation is the "trend" towards increasing compression in beds 110 V to 117, [although there is one slight reversal between beds 111e and 112d-f] before and after which apparently random fluctuations occur. No definite explanation can be suggested for this trend; perhaps selection was occurring for some streamlining advantage. It is interesting [and typical of the rather ambiguous hints often encountered in belemnite research] that another quite different species [B. cricki q.v.] with high compression should appear immediately after the curtailment of this apparent directional series.

Assuming that the forms here grouped under the heading of B. nitidus do represent one species, then it has been found in nearly all of the lithological units of the Belemnite Marls, and a few specimens have been collected from the basal Green Ammonite Beds, mostly where exposed below Golden Cap (beds 122a-c of Lang (1936)). In the Green Ammonite Beds, it is numerically subordinate to B. aduncatus, which may be the result of competition. B. aduncatus first occurs, rarely, in the top few beds of the Belemnite Marls and becomes fairly common in beds 120d-121. The belemnite fauna of bed 121 (the Belemnite Stone, a condensed bed representing the luridum Subzone and usually regarded as the top bed of the Belemnite Marls) is in general like that of beds 122a-c, with B. aduncatus and Hastites microstylus predominating and with only small numbers of B. nitidus.

Distribution

B. nitidus probably has a wide geographical distribution, and there is good evidence in the literature (see list below) that it occurs at other localities with a similar range of morphological variation to that shown in the Belemnite Marls of Dorset.

1. Charmouth, Dorset: Belemnite Marls, jamesoni and ibex Zones, beds 104-121; Green Ammonite Beds, davoei Zone, maculatum Subzone, beds 122a-c.

Other probable localities, jamesoni and ibex Zones, include:

2. Yorkshire Coast (especially Robin Hood's Bay) (Phillips 1867; Tate and Blake 1876).

3. Durnau, Balingen, Boll and Aselfingen, Wurttemberg, West Germany (Werner 1912; pers. obs.).

4. Rottorf and Ostercappeln, North Germany (Schumann 1974).

5. Rhone basin, France (Mayer 1863; Dumortier 1869).

Belemnites nitidus

$D_{v.ant.}$: L

beds 104, 106, 107

key

▼ author's coll., bed 104

● " " beds 106, 107

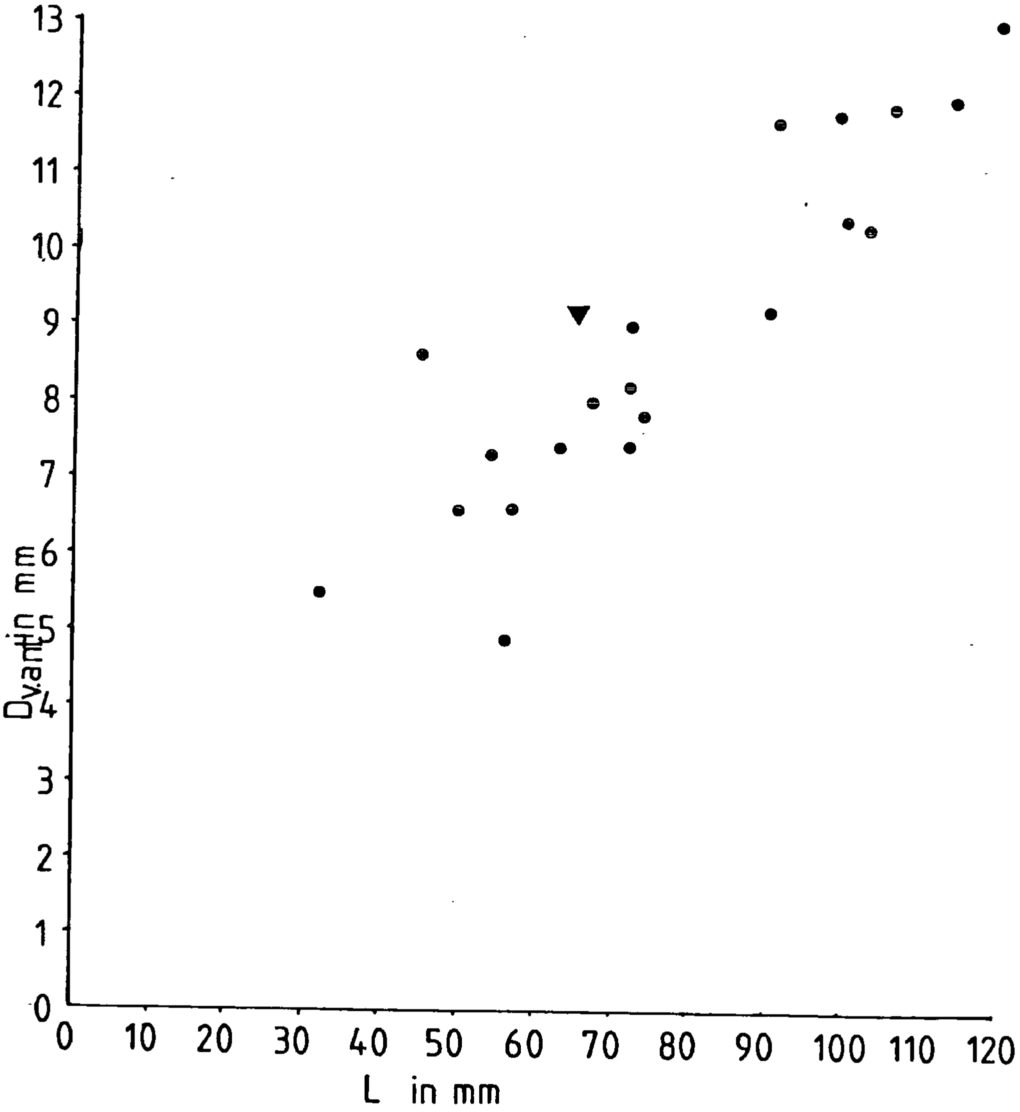


FIG.18

B. nitidus

$D_{v.ant.}:L$
beds 108–110

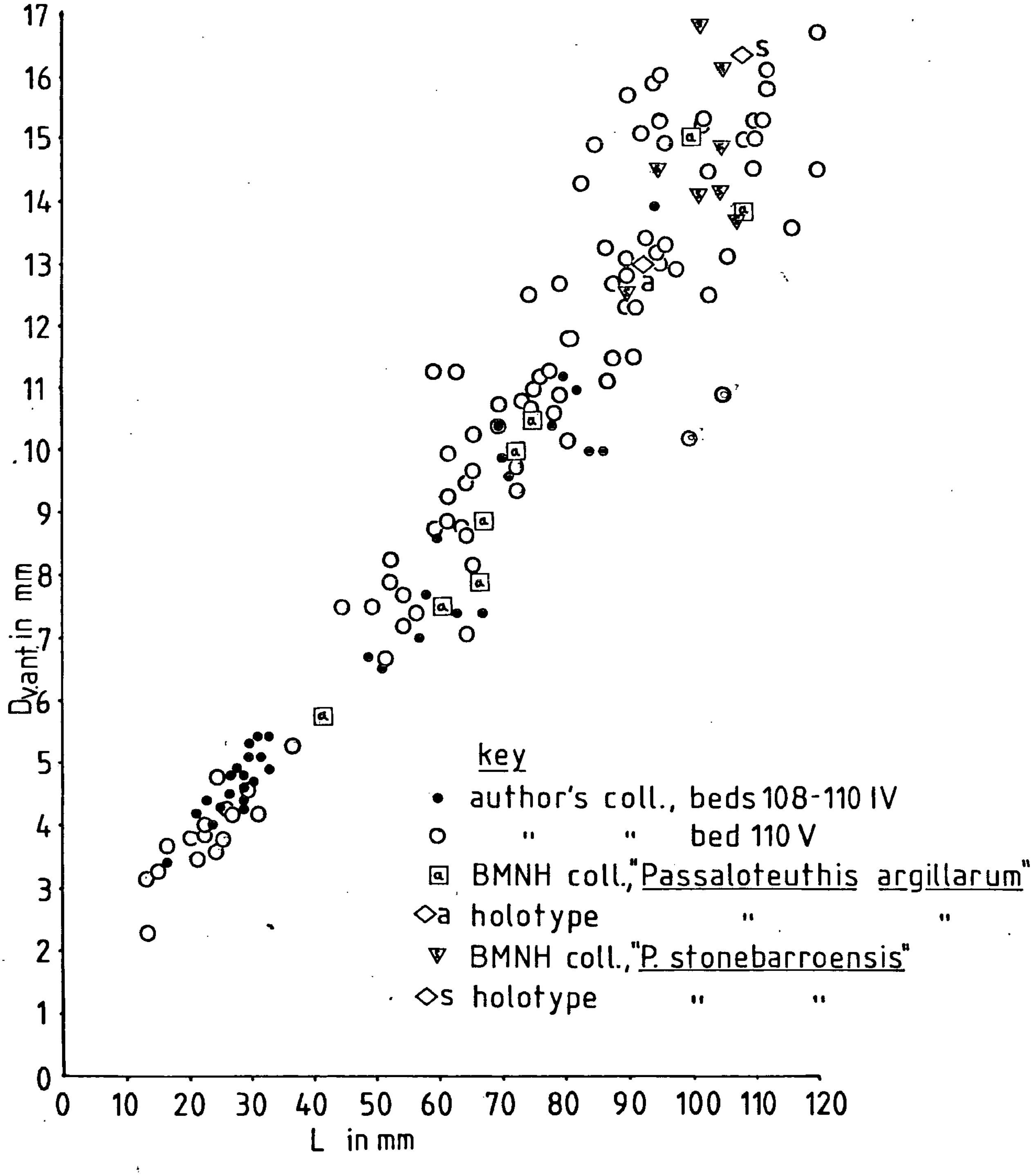


FIG. 19

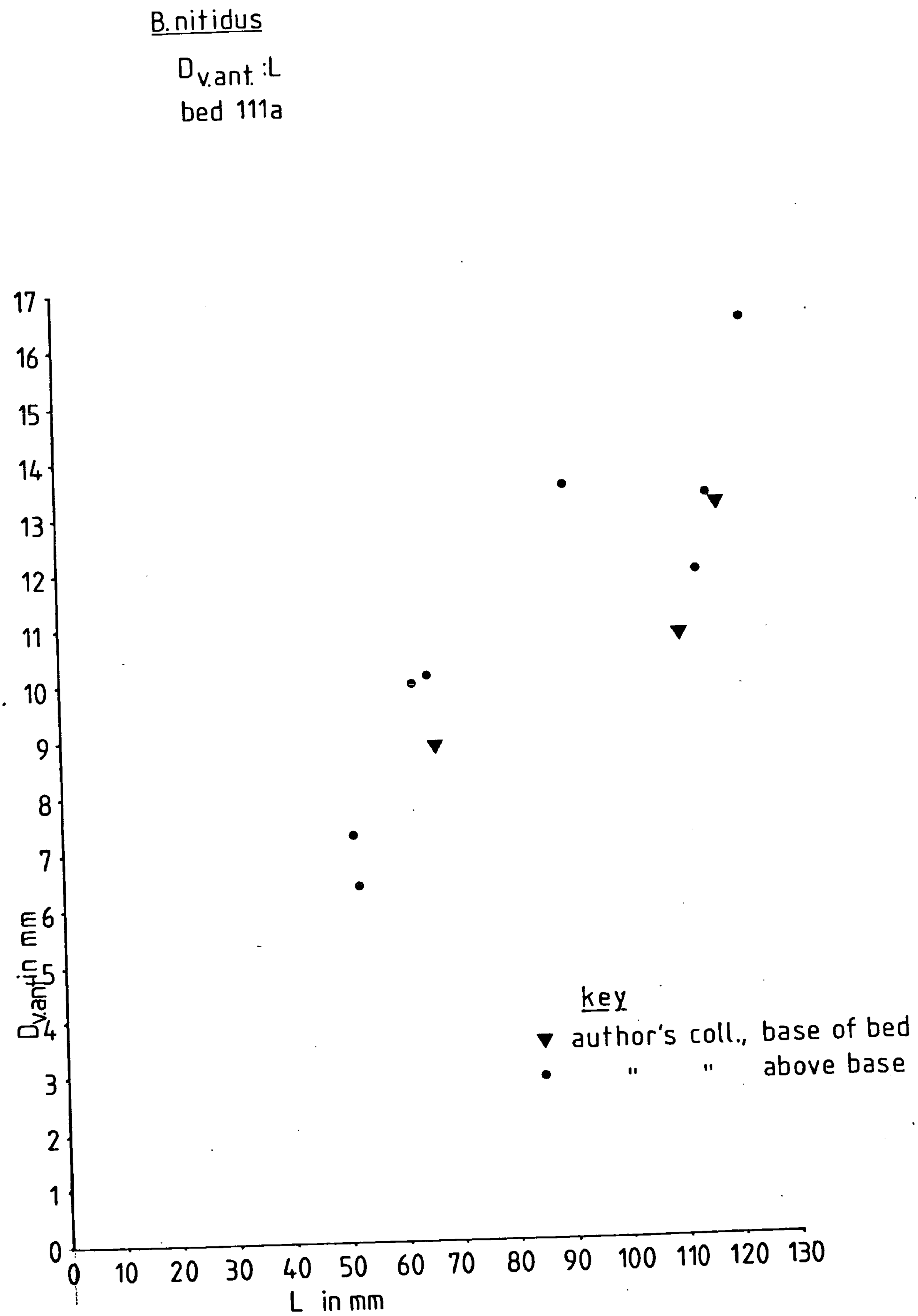

B. nitidus
$D_{v.ant.}$: L
bed 111a
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
$D_{v.ant.}$ in mm
0
10
20
30
40
50
60
70
80
90
100
110
120
130
L in mm
key
▼ author's coll., base of bed
● " " above base

FIG. 20

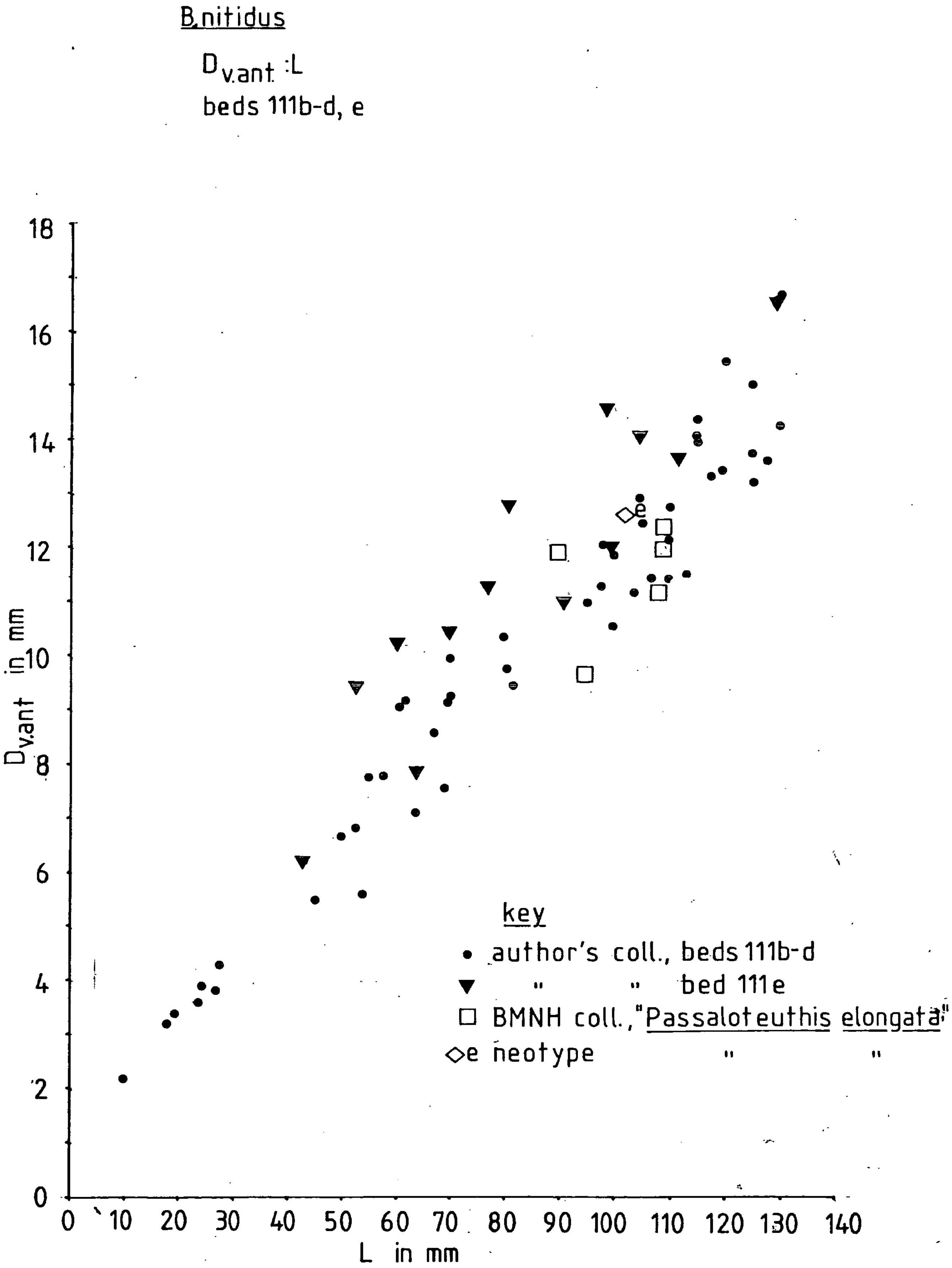
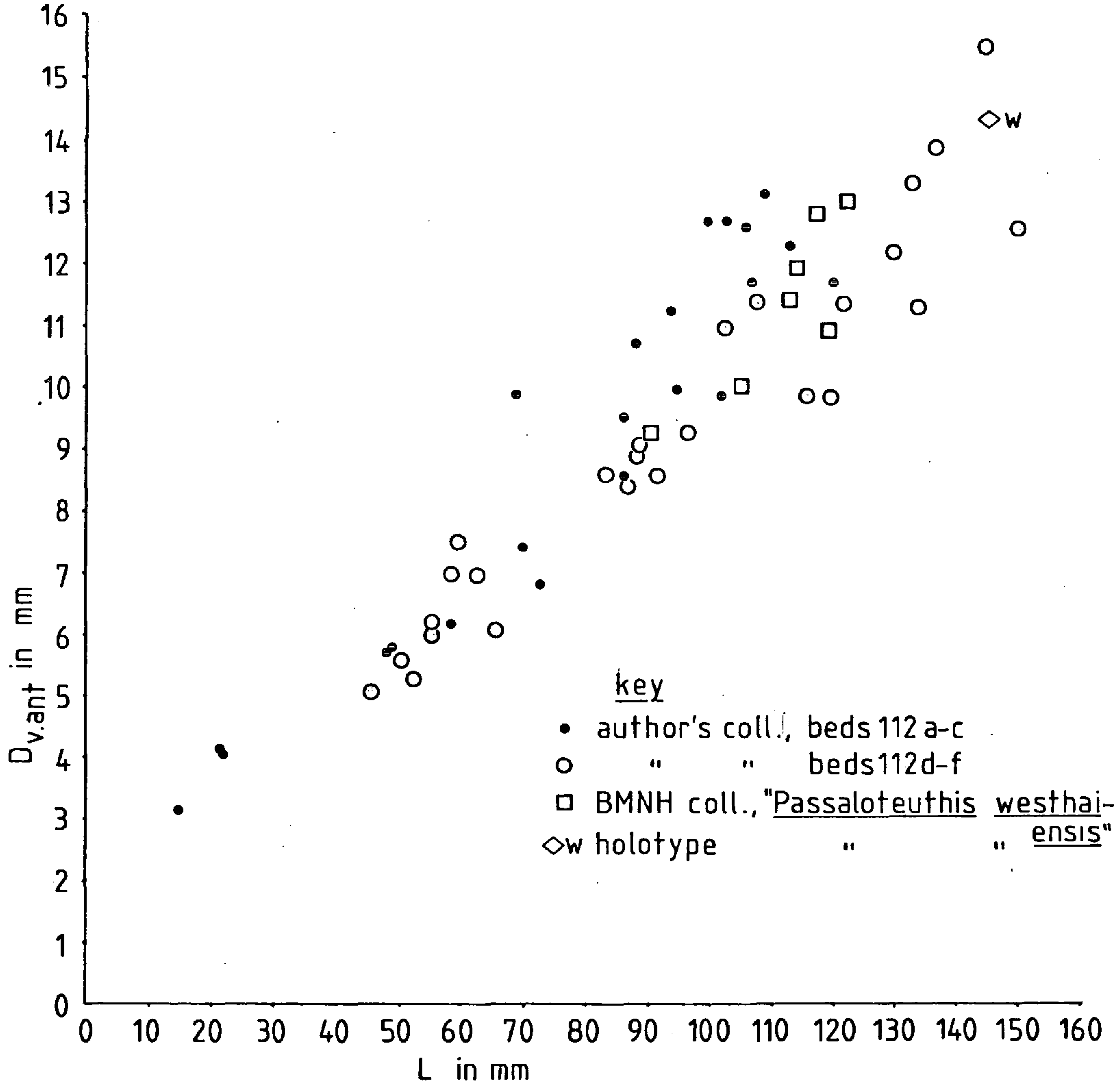

B.nitidus
$D_{v.ant}$:L
beds 111b-d, e
18
16
14
12
10
8
6
4
2
0
$D_{v.ant}$ in mm
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
L in mm
key
● author's coll., beds 111b-d
▼ " " bed 111e
□ BMNH coll., "Passaloteuthis elongata"
◇e neotype " "

FIG. 21

B. nitidus

$D_{v.ant} : L$

bed 112



<u>B. nitidus</u>

$D_{v.ant.}:L$
beds 113–115

<u>key</u>

▼ author's coll., bed 113b
● " " bed 114
○ " " bed 115

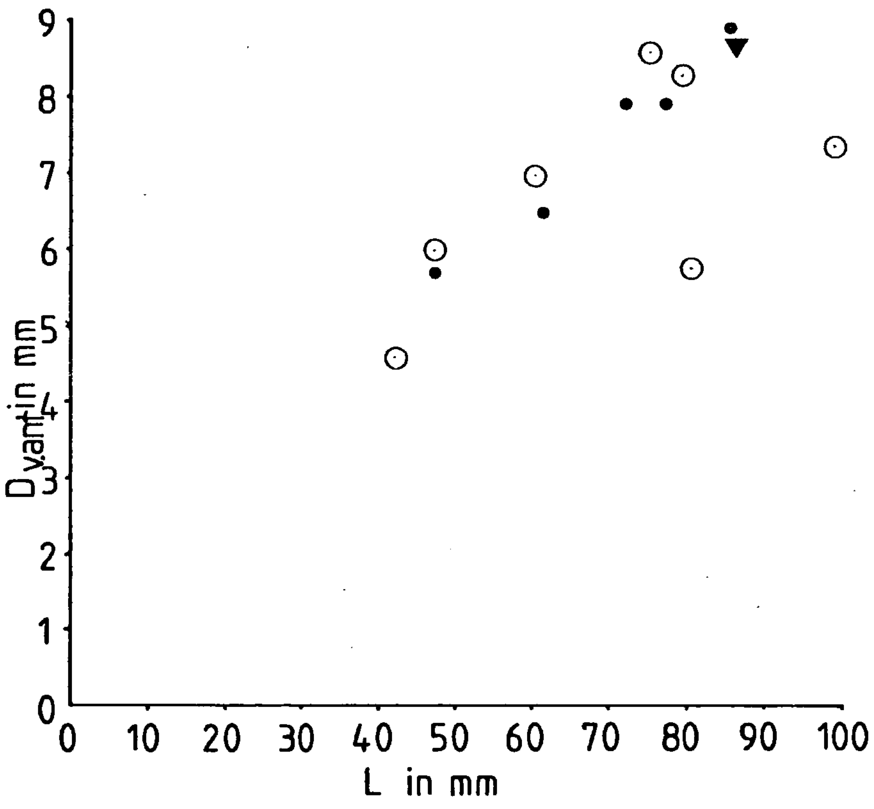


FIG.2 3

<u>B. nitidus</u>

$D_{v.ant.}:L$
bed 117

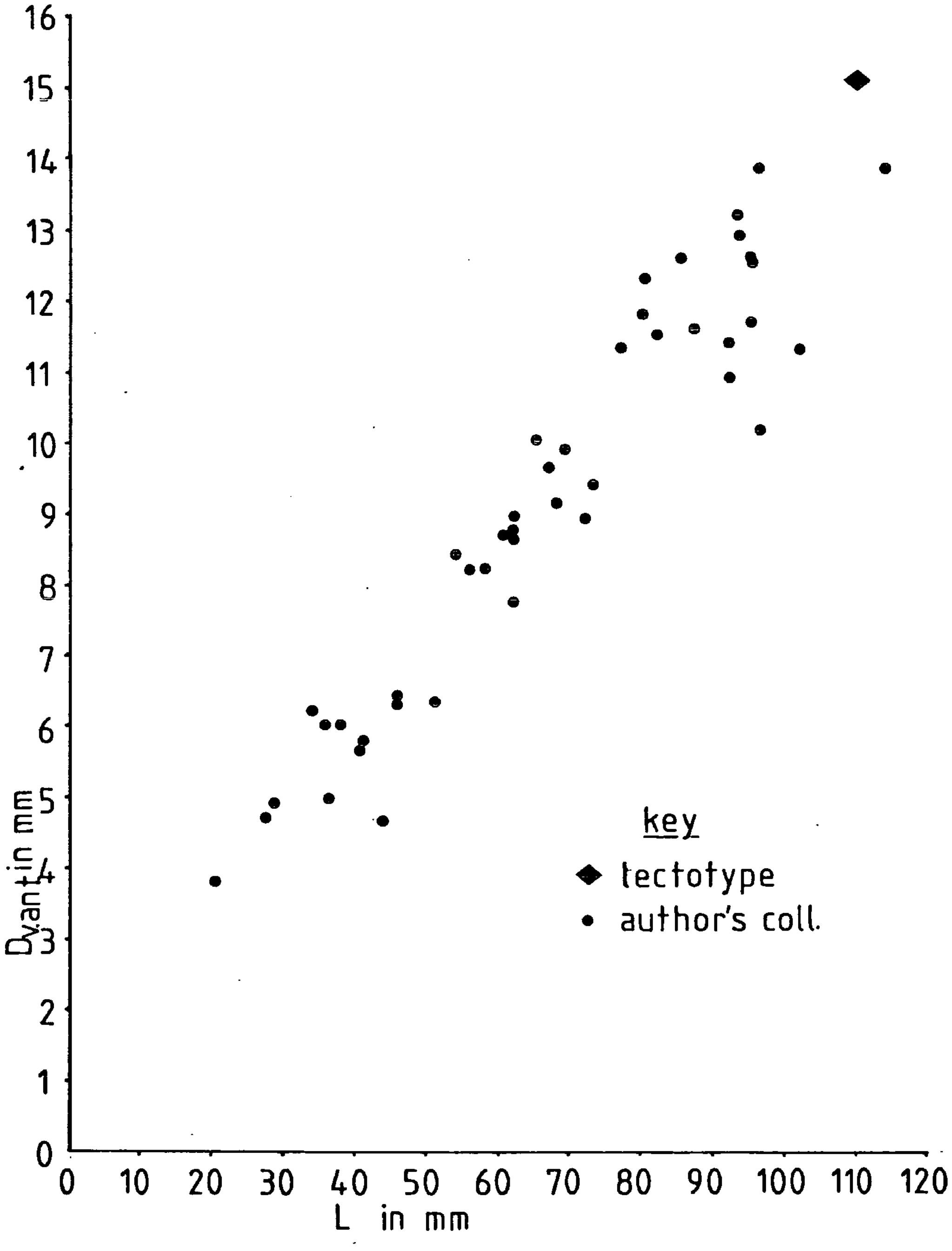


FIG. 24

B. nitidus

$D_{v.ant.}$:L
bed 118

key
- ● author's coll., bed 118a
- ▼ " " " epirostrids
- ○ " " beds 118b-d
- ◇w holotype *Passaloteuthis woottonensis*

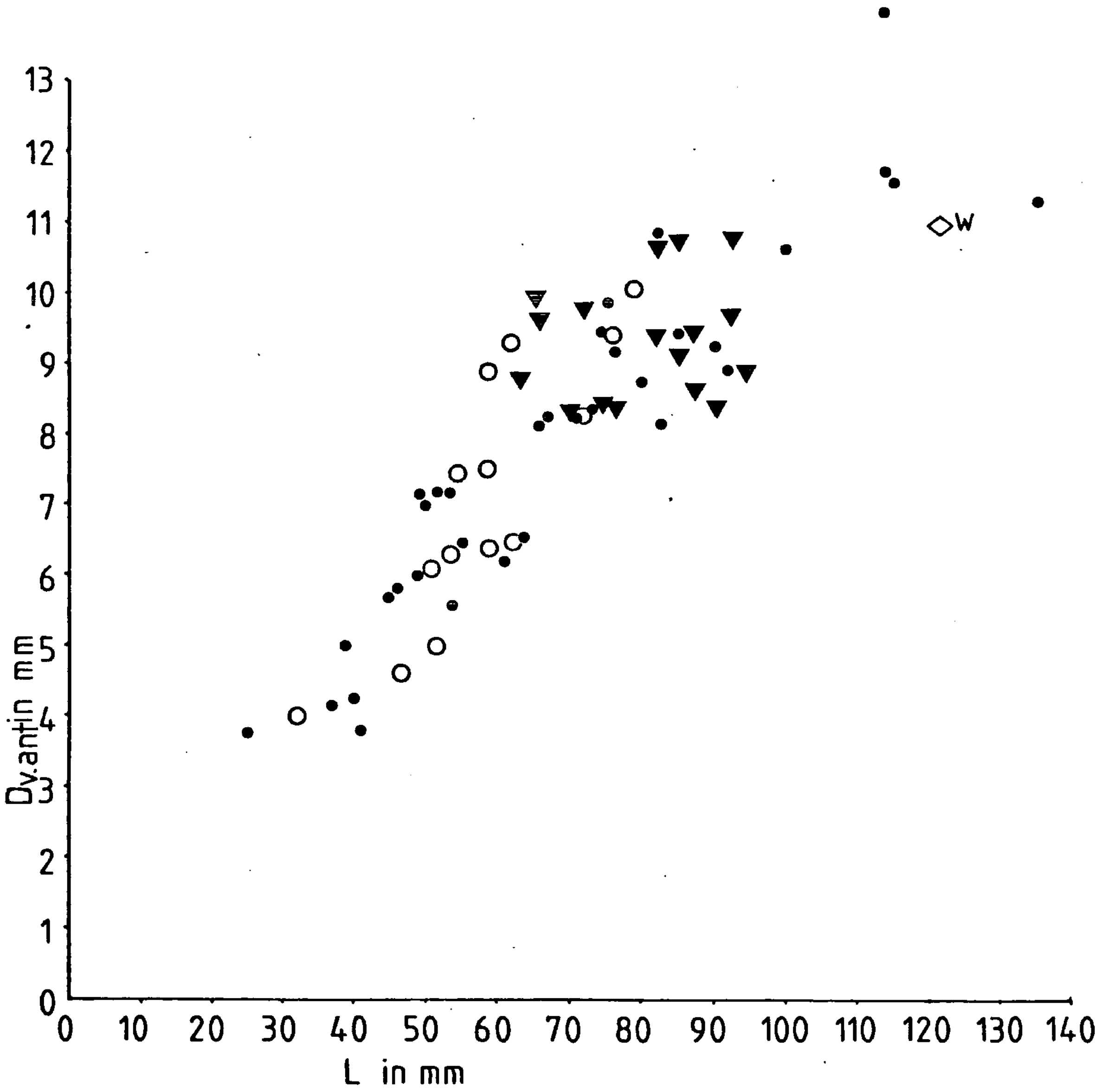


FIG. 25

B. nitidus

$D_{v.ant.}:L$
bed 119

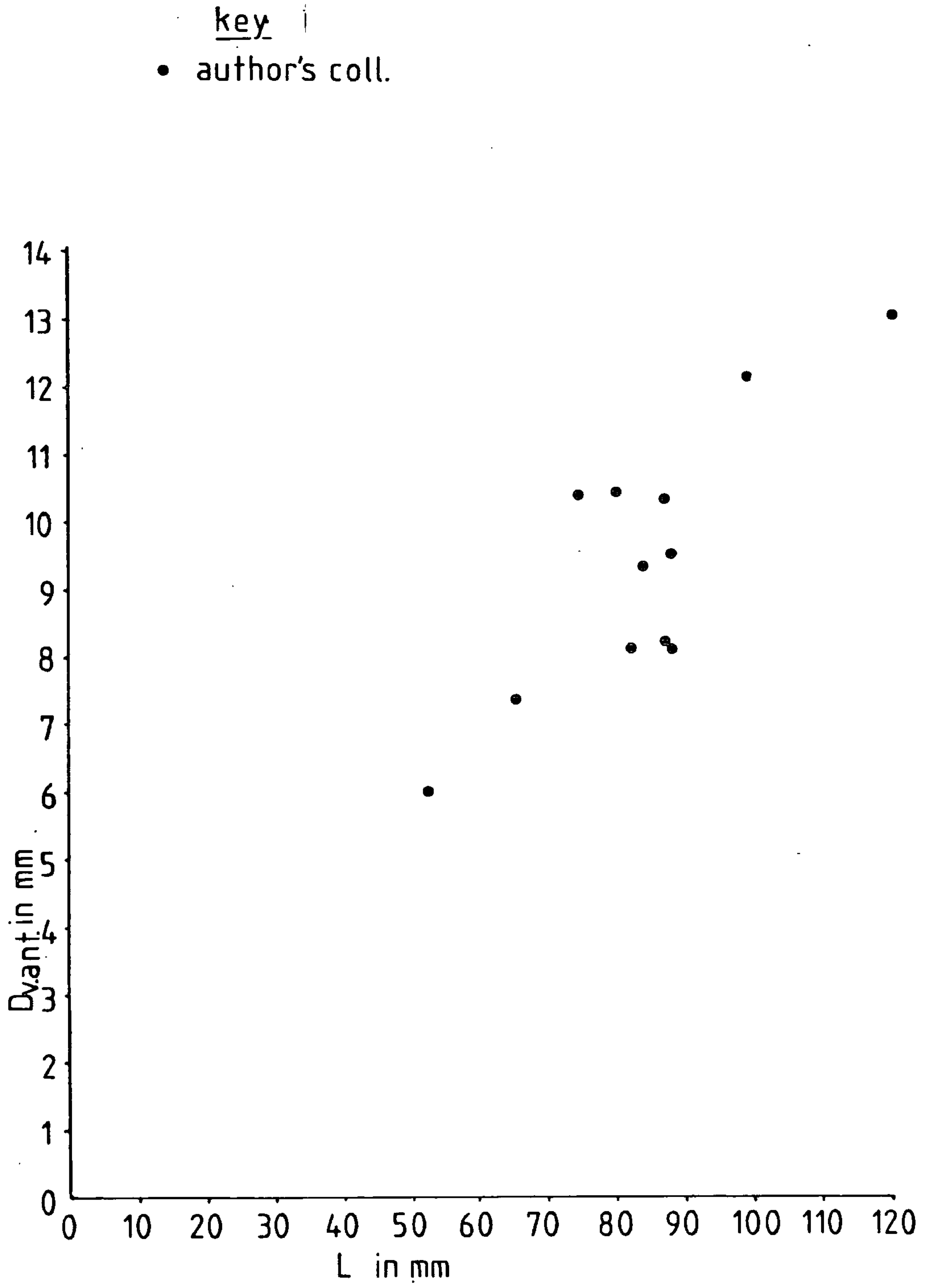


FIG. 26

<u>B. nitidus</u>

$D_{v.ant.}$:L
beds 120 a–b

<u>key</u>
- author's coll.

◇s holotype *Passaloteuthis seatownensis*

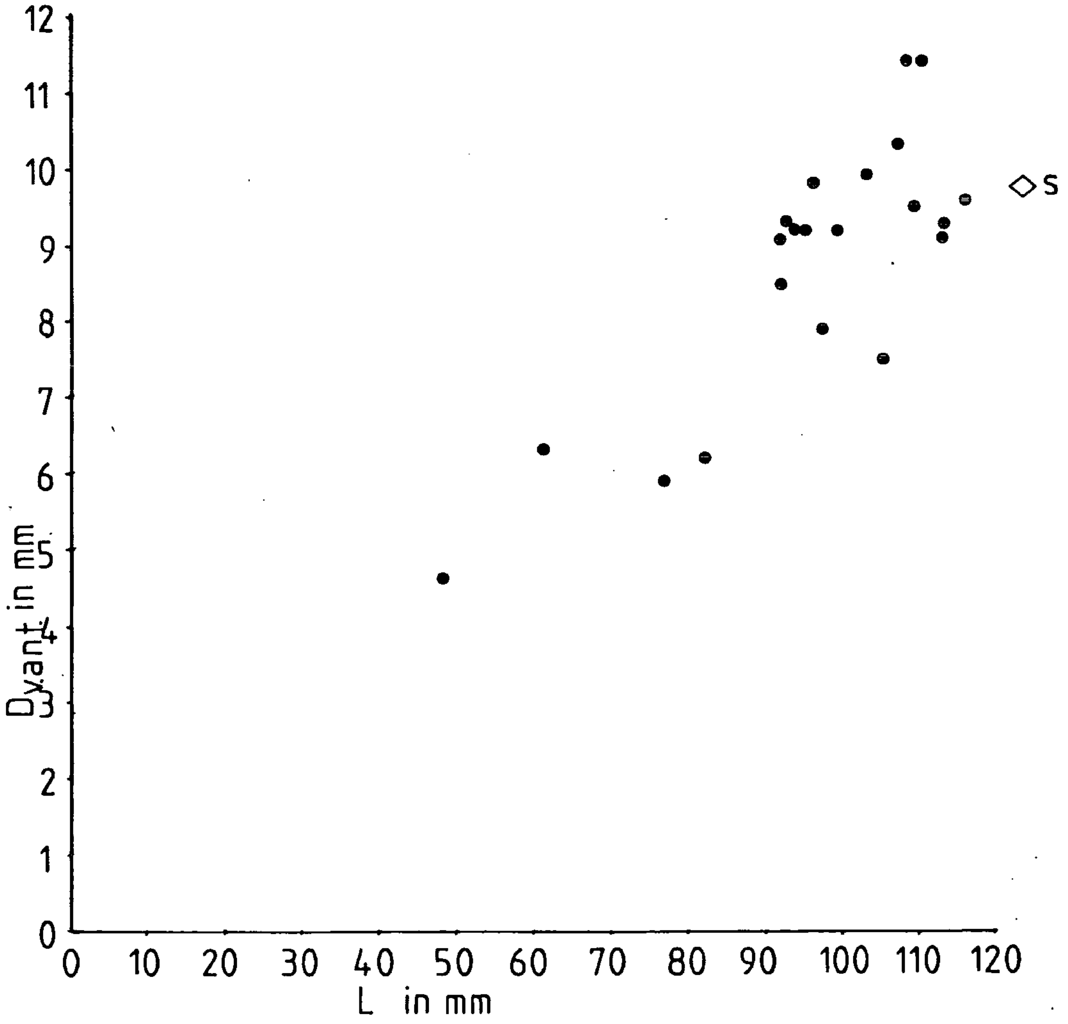


FIG. 27

B. nitidus

$D_{v.ant.}:L$

beds 120c–122c

key

▼ author's coll. bed 120c

● " " beds 120d–121

○ " " beds 122a–c

◇ holotype Passaloteuthis dayi

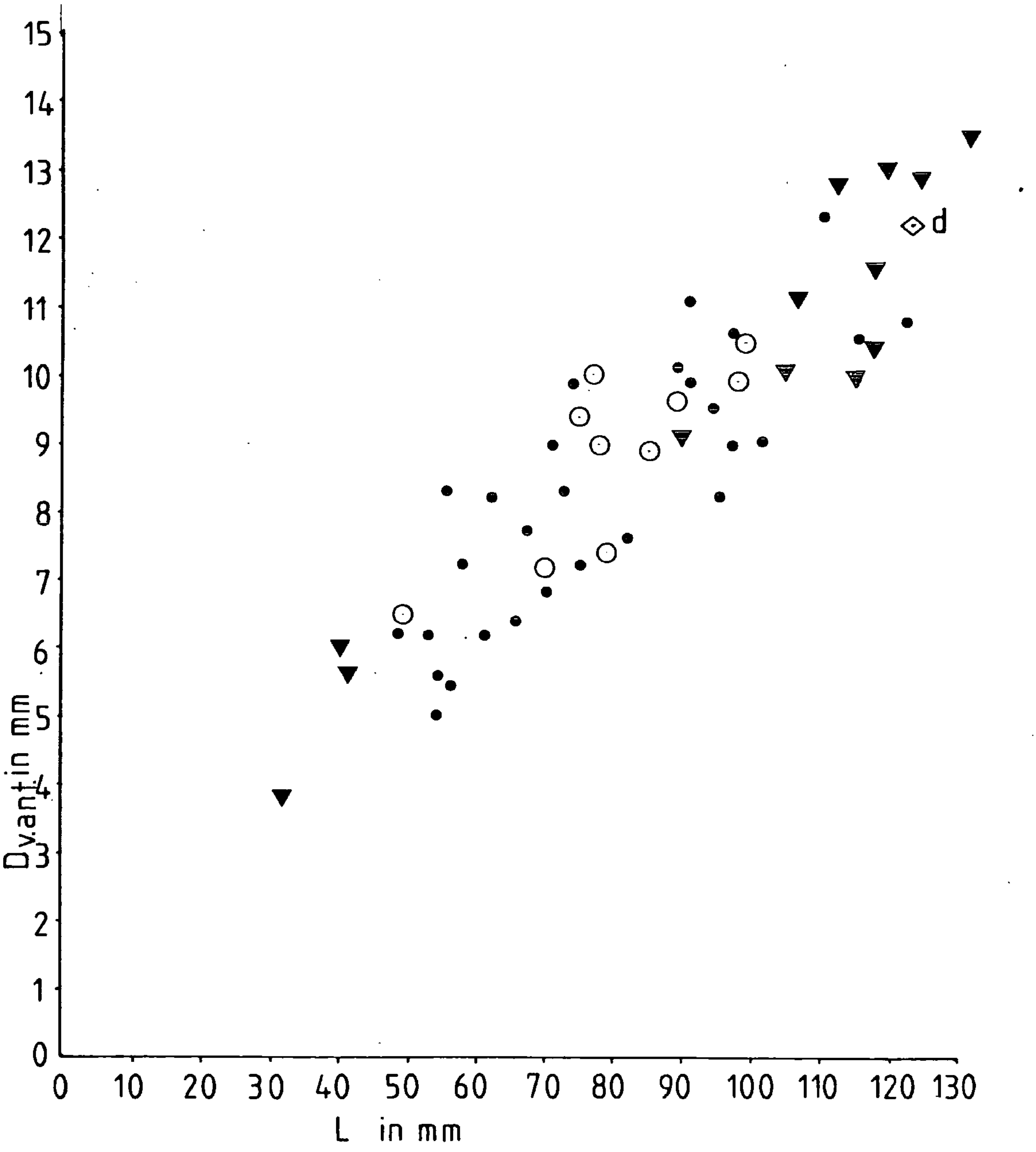


FIG. 28

Belemnites nitidus

$D_p : L_p$

beds 104–107

key

▼ author's coll., bed 104

● " " beds 106-107

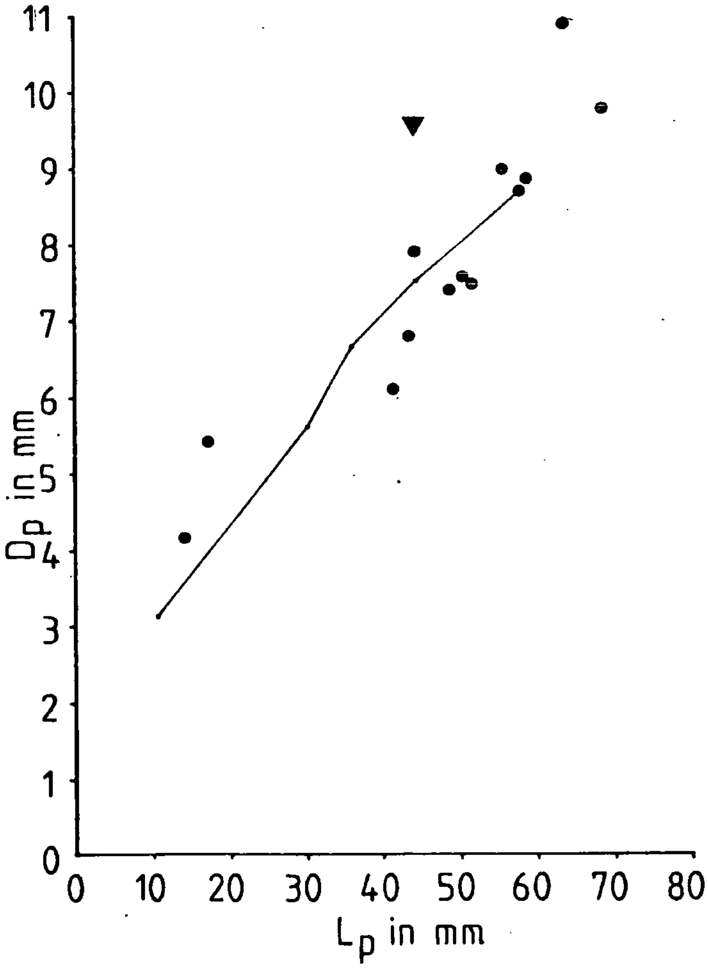


FIG. 29

<u>B. nitidus</u>

$D_p : L_p$

beds 108–110

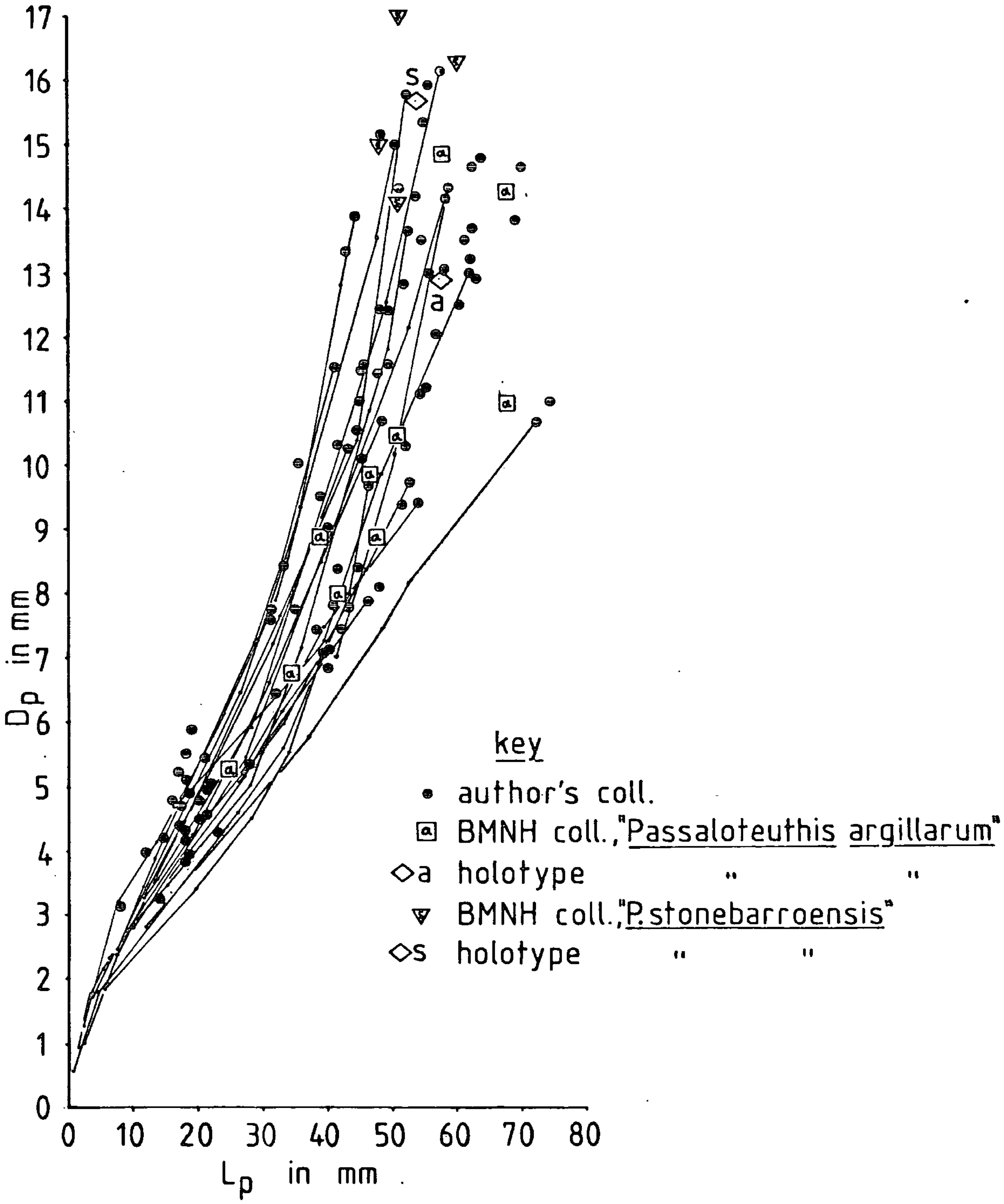
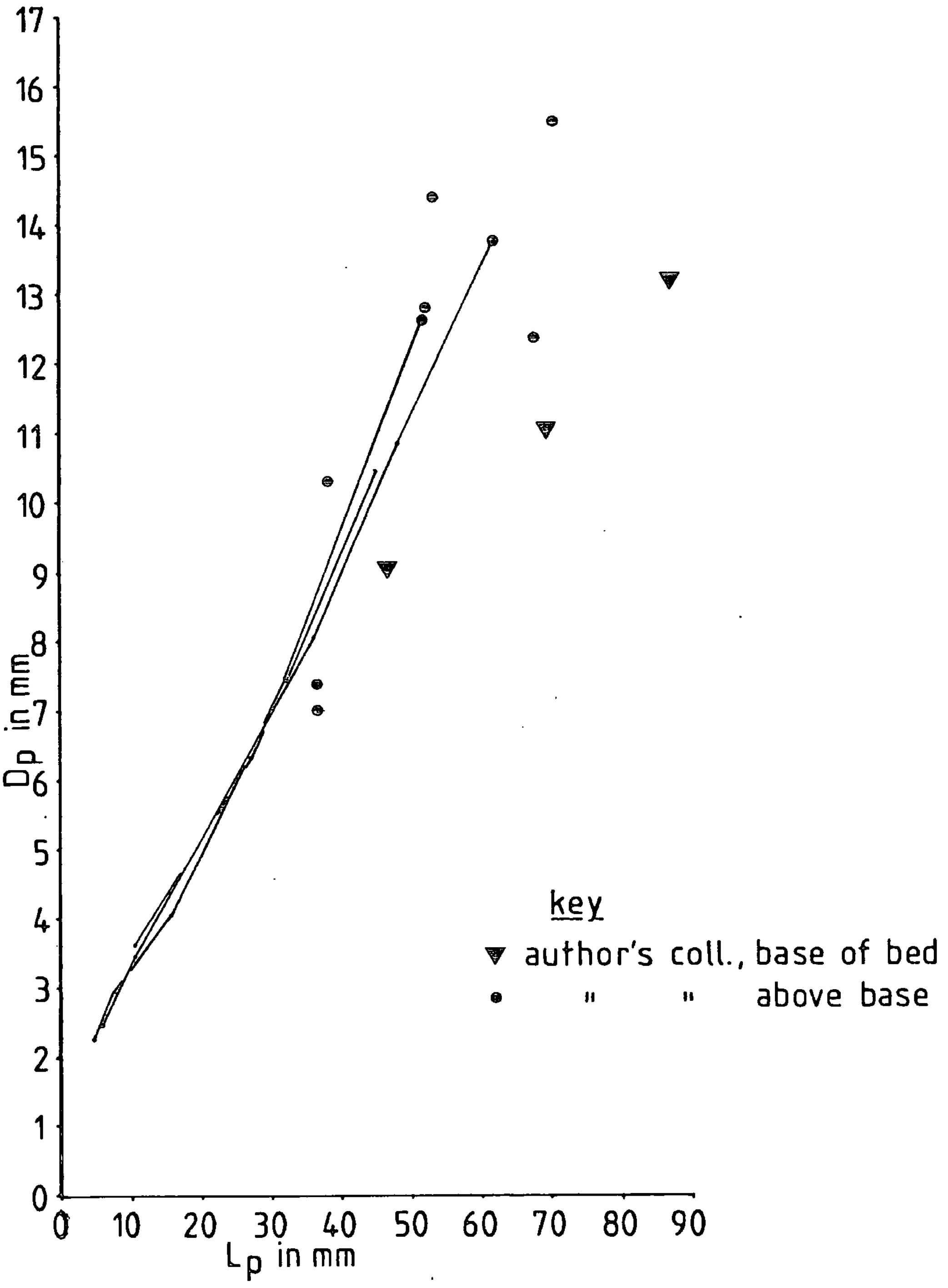


FIG. 30

B. nitidus

$D_p : L_p$

bed 111a



B. nitidus

$D_p : L_p$

beds 111 b-d

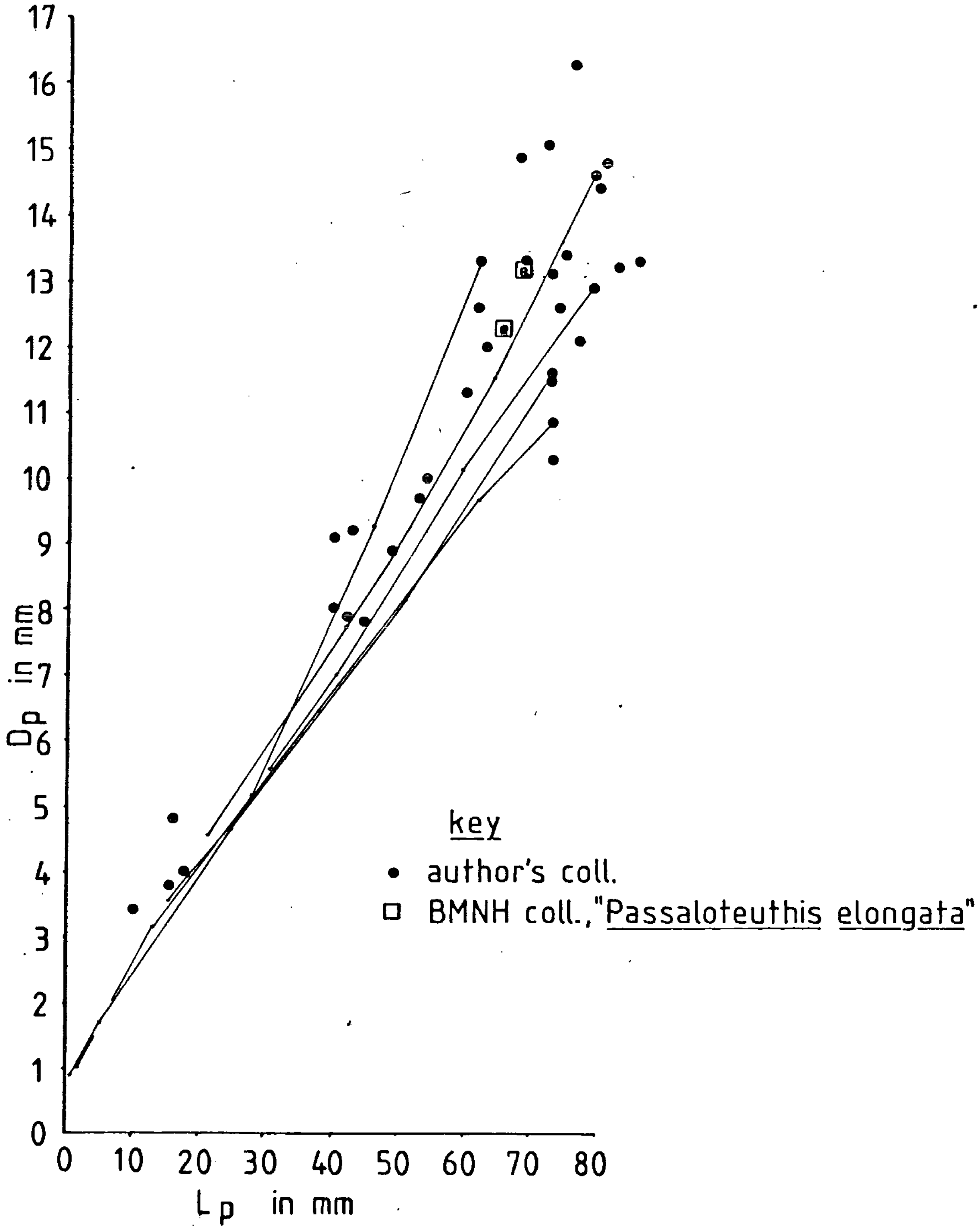


FIG. 32

B. nitidus

$D_p : L_p$

bed 112

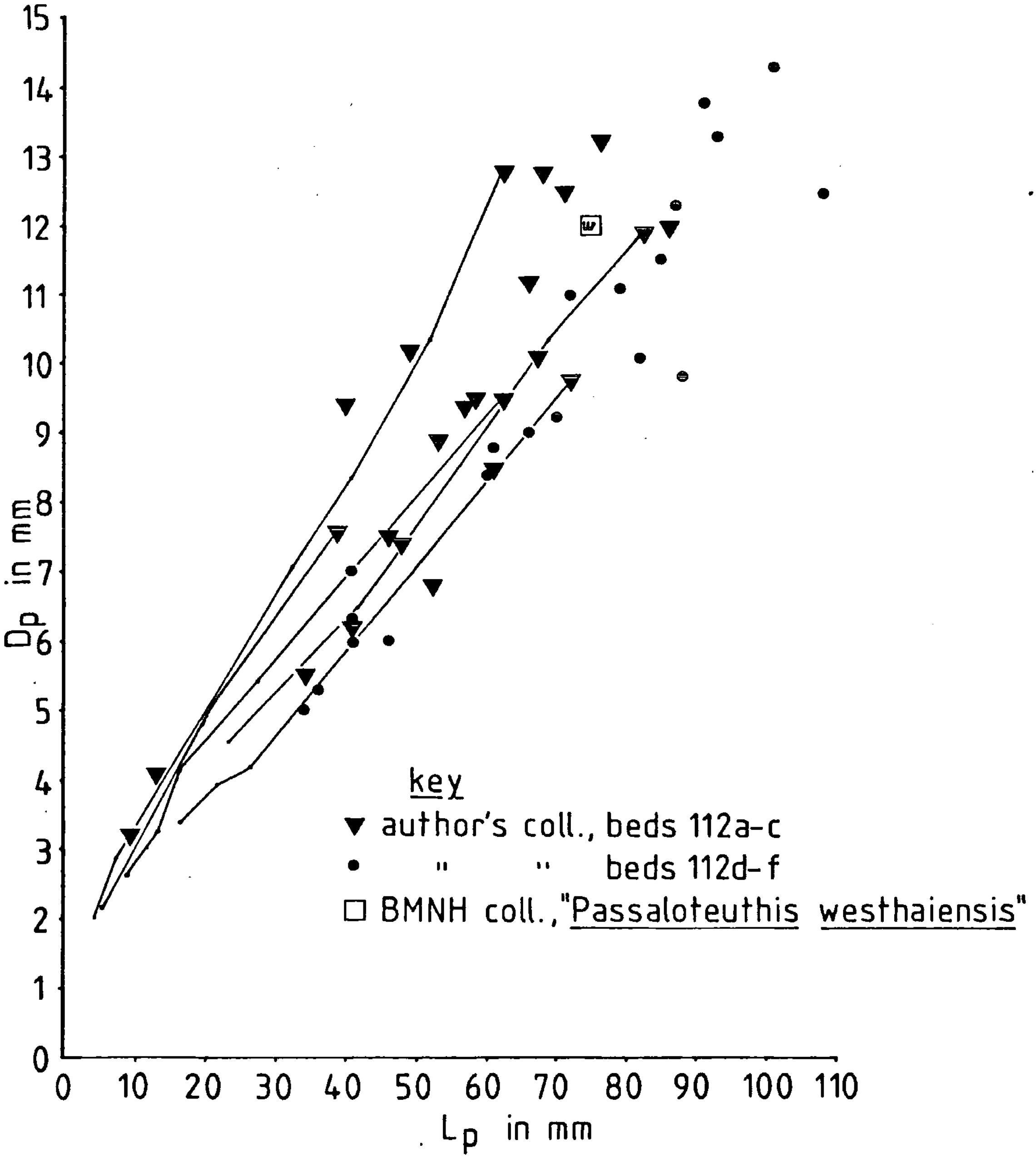


FIG. 33

B. nitidus

$D_p : L_p$

beds 113–115

key

▼ author's coll., bed 113b
● " " bed 114
○ " " bed 115

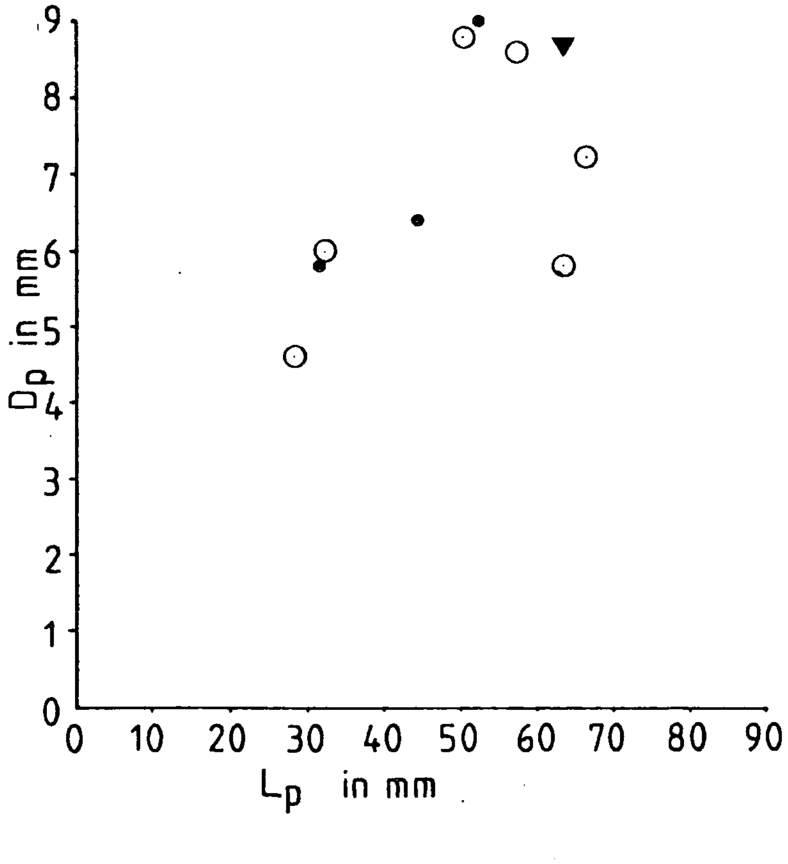


FIG. 34

B. nitidus

$D_p : L_p$

bed 117

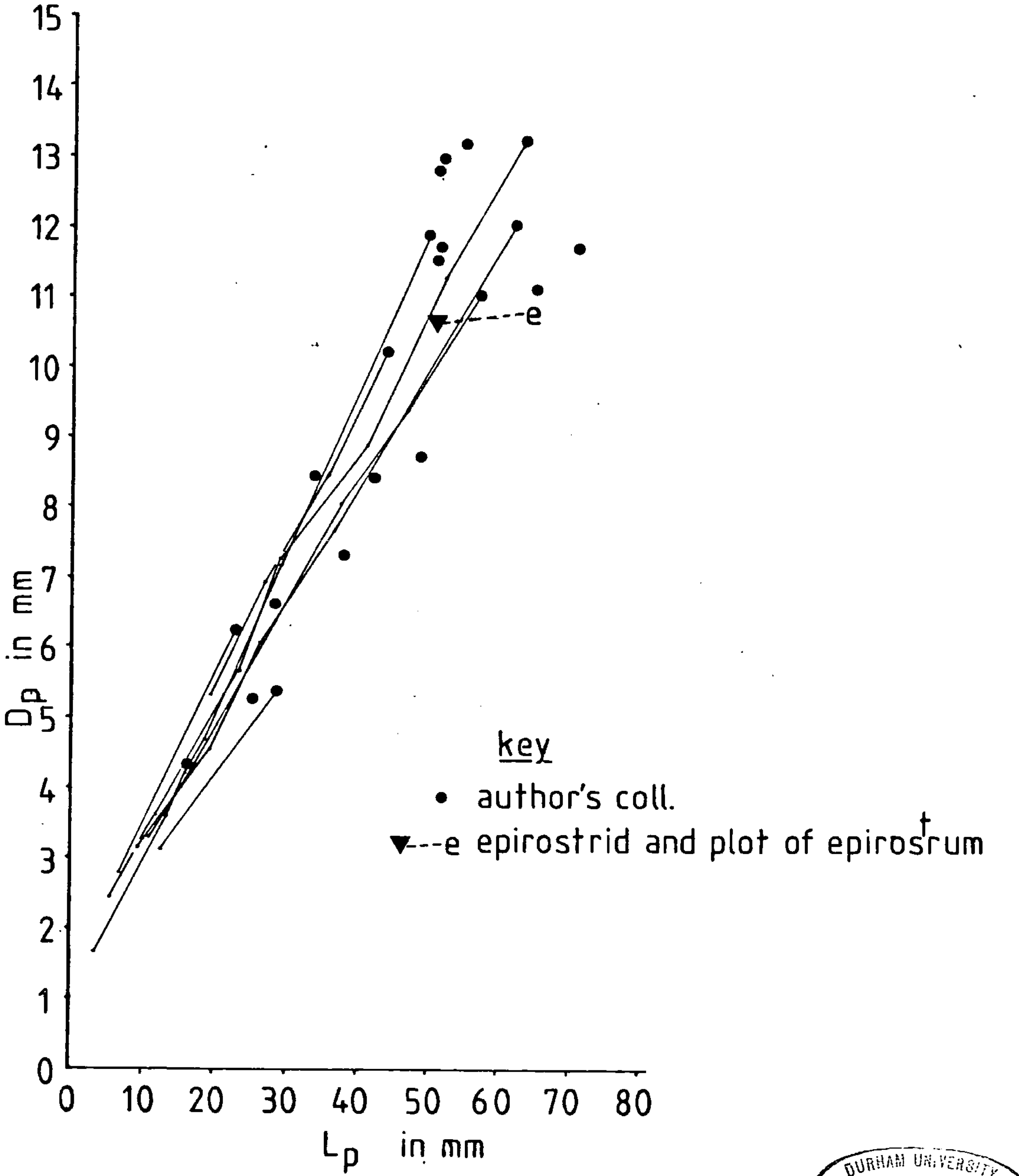


FIG.35

B. nitidus

$D_p : L_p$
bed 118

key

- ● author's coll., bed 118a
- ▼--e " " " epirostrids and plot of epirostrum
- ○ " " beds 118 b-d

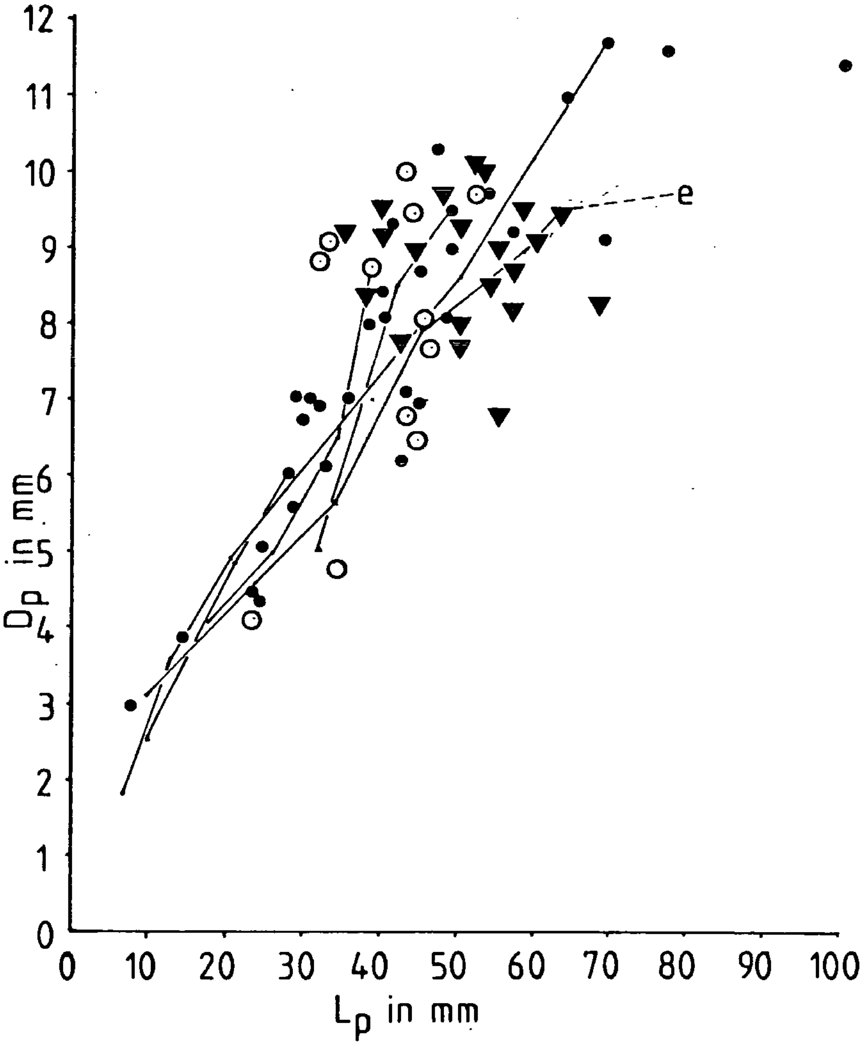


FIG. 36

B. nitidus

$D_p : L_p$

bed 119

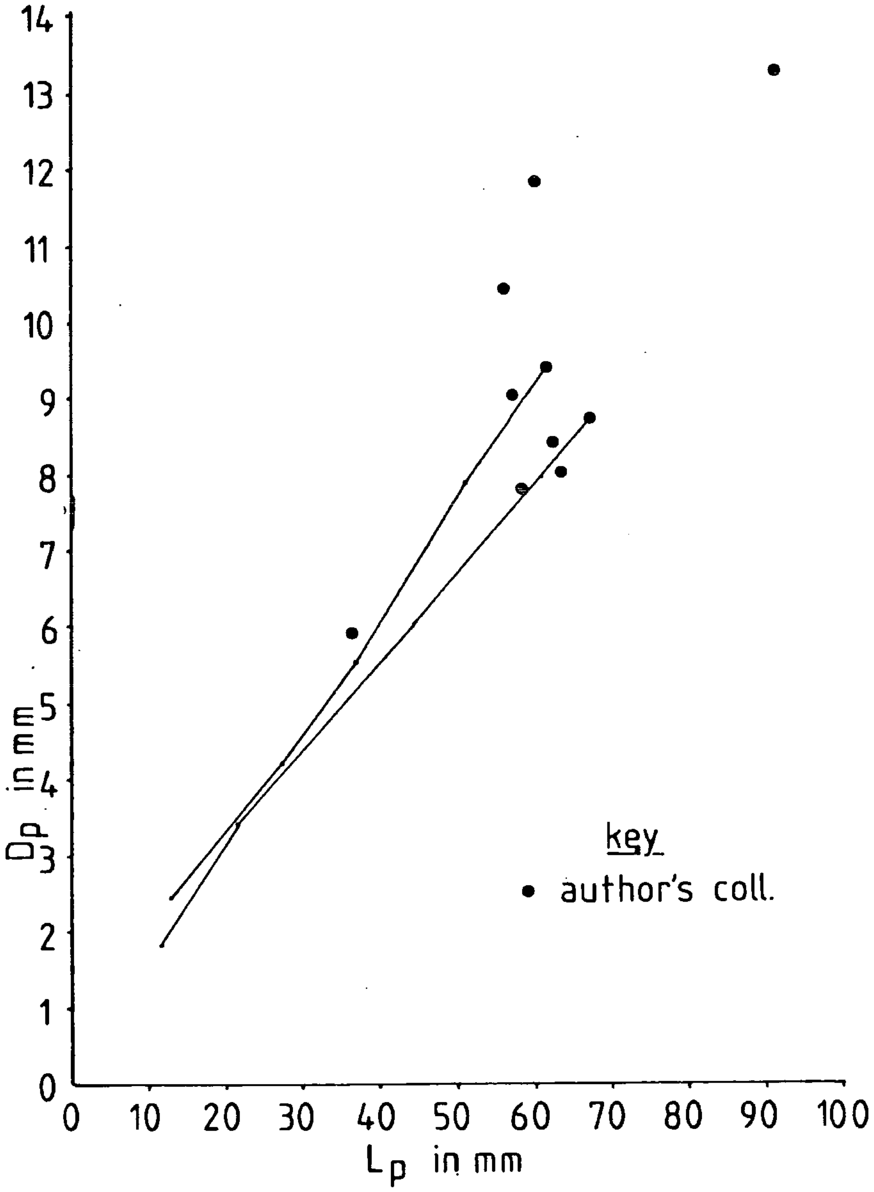


FIG. 37

B. nitidus

$D_p : L_p$

beds 120 a-b

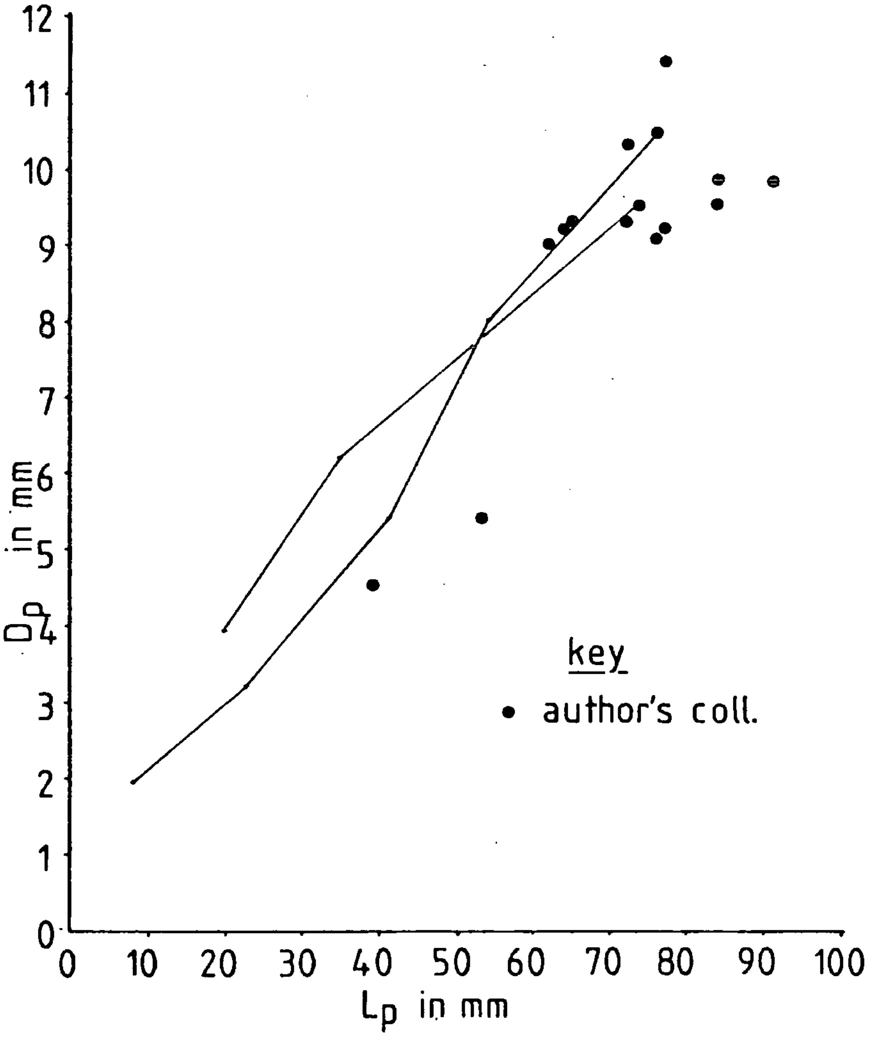


FIG.38

B. nitidus

$D_p : L_p$

beds 120c–e

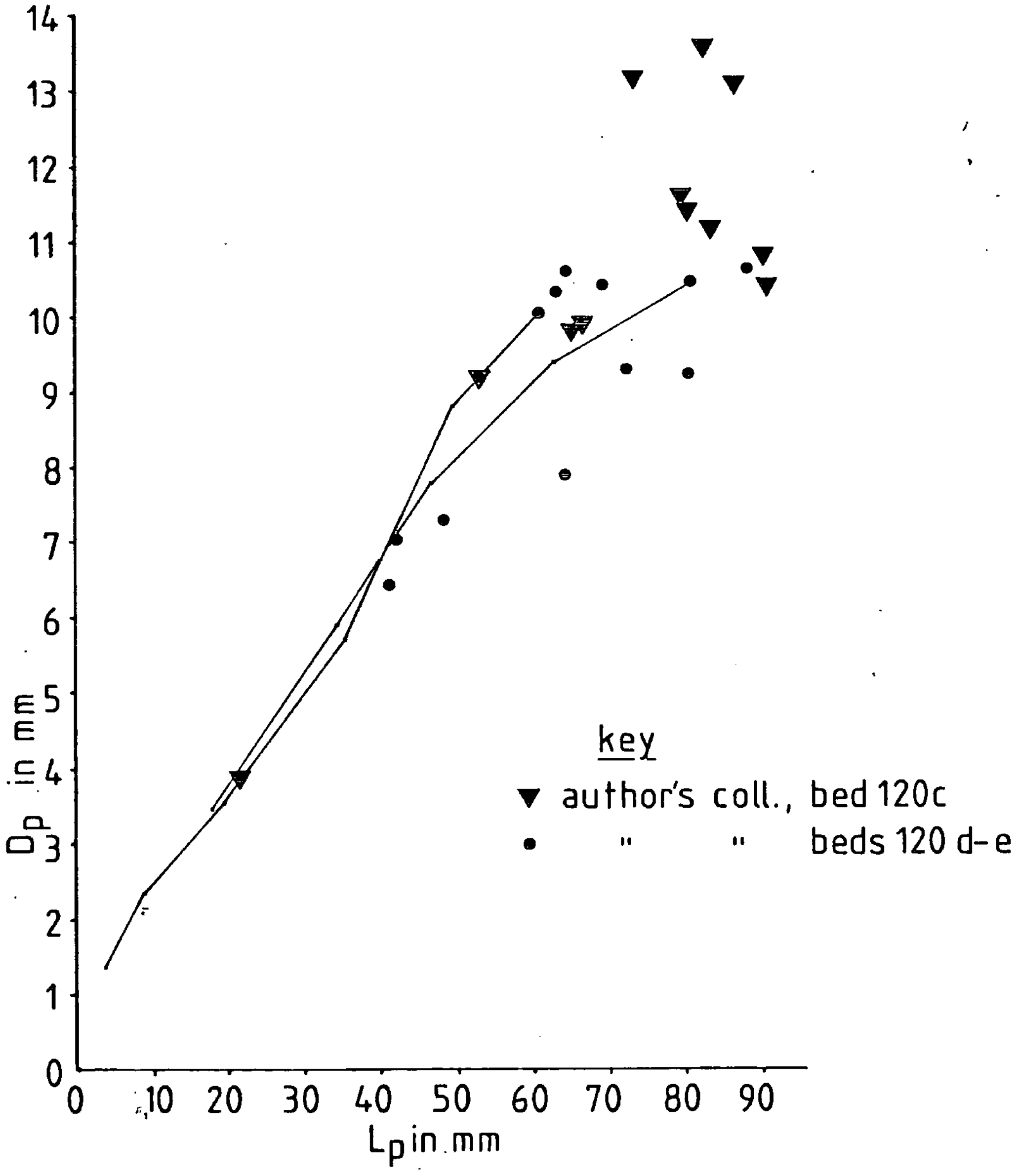


FIG.39 Belemnites nitidus: camera lucida drawings of median longitudinal polished sections.

A: TB661 bed 111b, x24
(with photograph)

B: TB270 bed 110 II, x12

C: TB661 bed 111b, x12

p - protoconch
r - earliest clear rostral growth line
s - primary spherules
v - sparry calcite-filled void between prismatic and nacreous layers of protoconch

FIG.40 Belemnites nitidus: camera lucida drawings of median longitudinal polished sections.

A: TB681 beds 112a-c, x12

B: TB117 beds 120a-b, x12

C: TB118 beds 120a-b, x12

p - protoconch
r - earliest clear rostral growth line

FIG.39

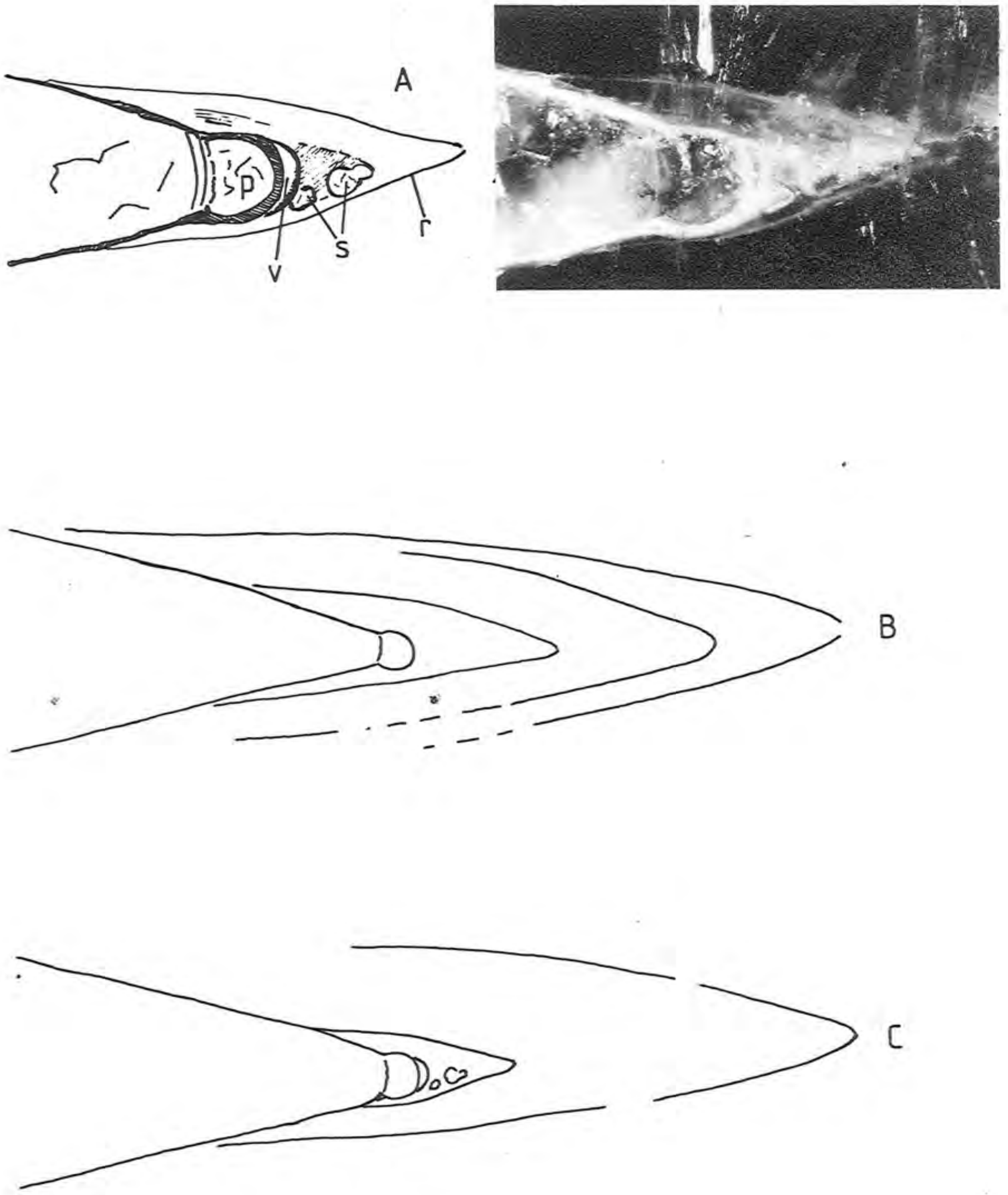


FIG.40

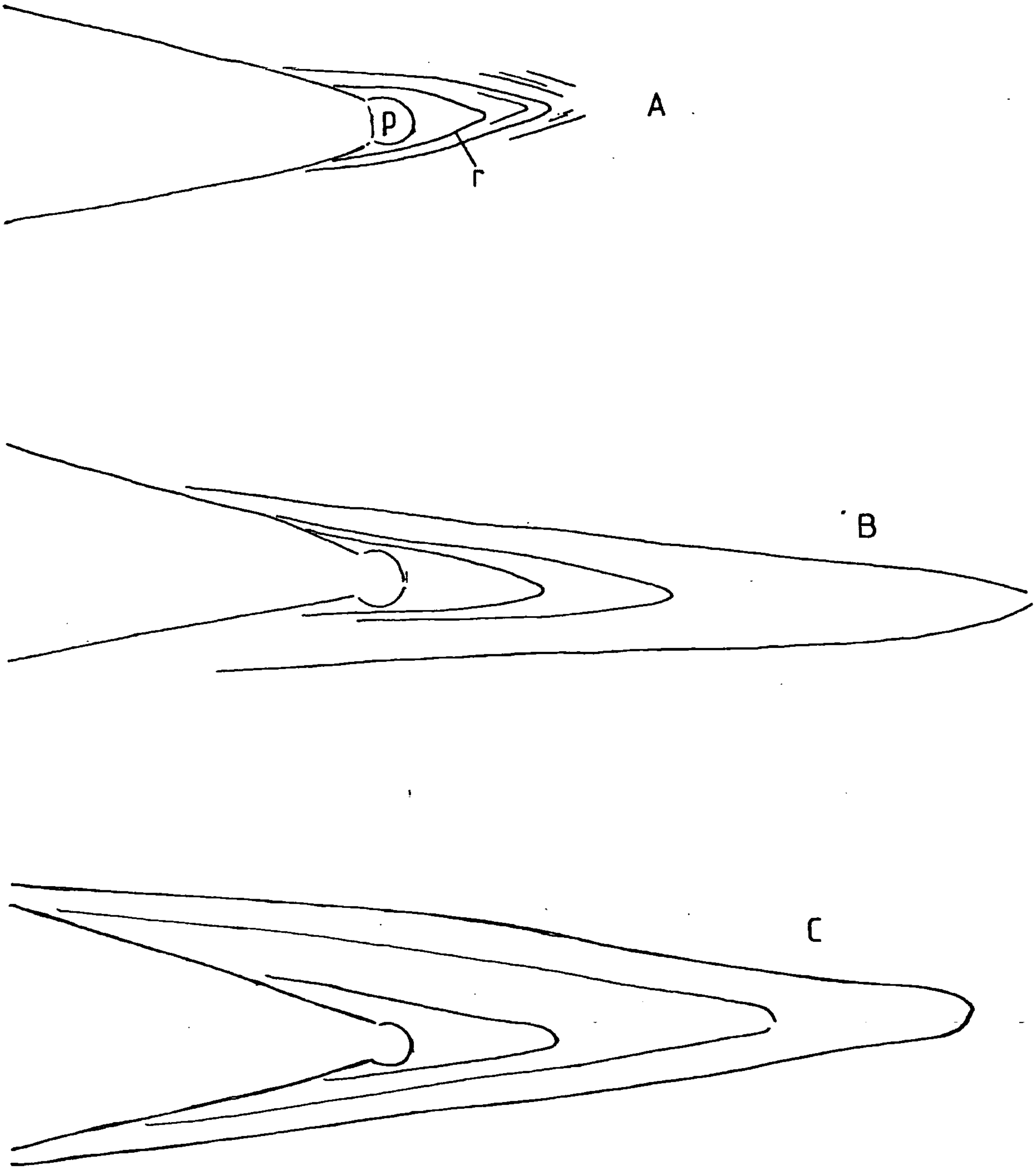


FIG. 41

<u>Belemnites</u> <u>nitidus</u>
length
beds 104–110V

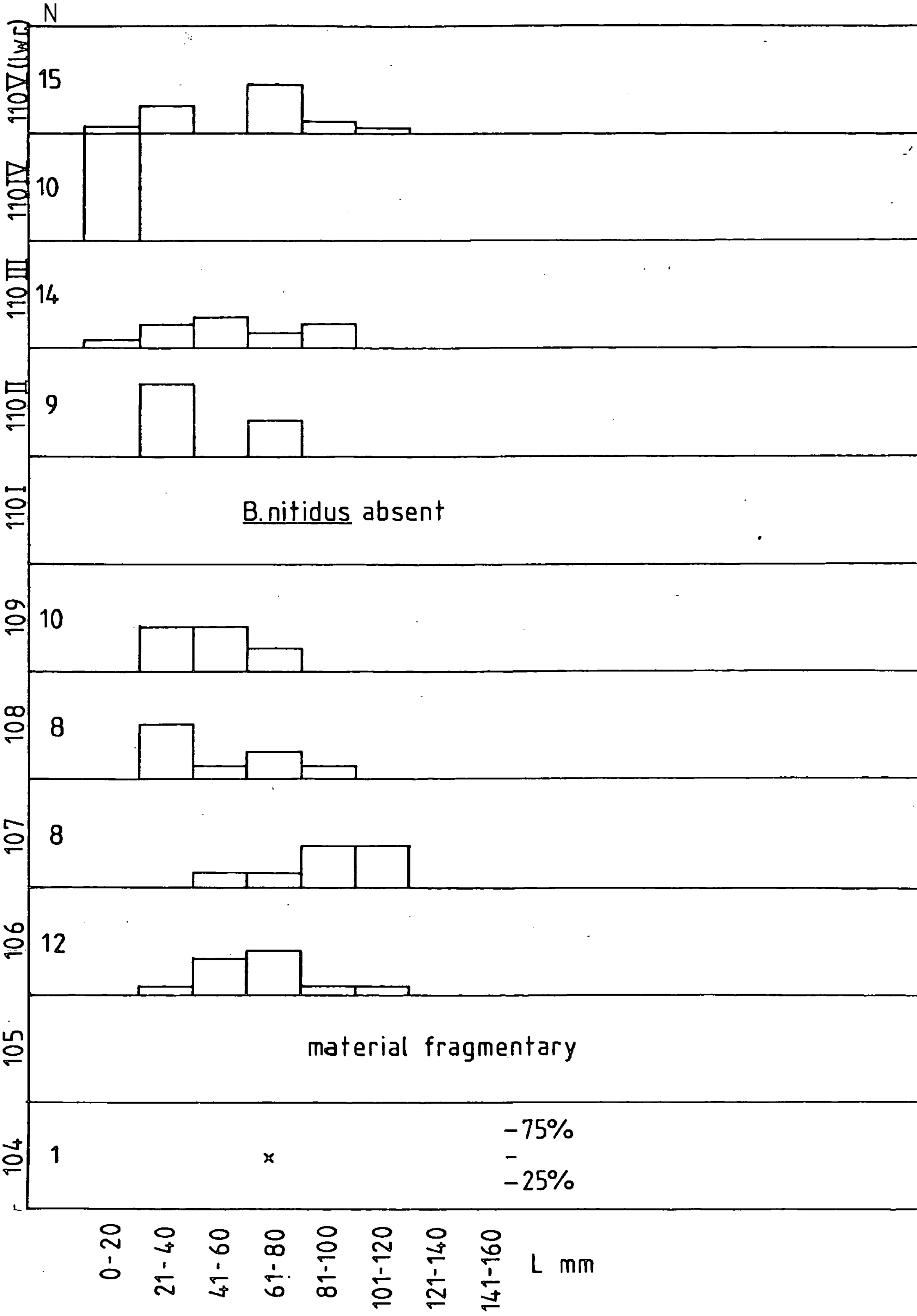
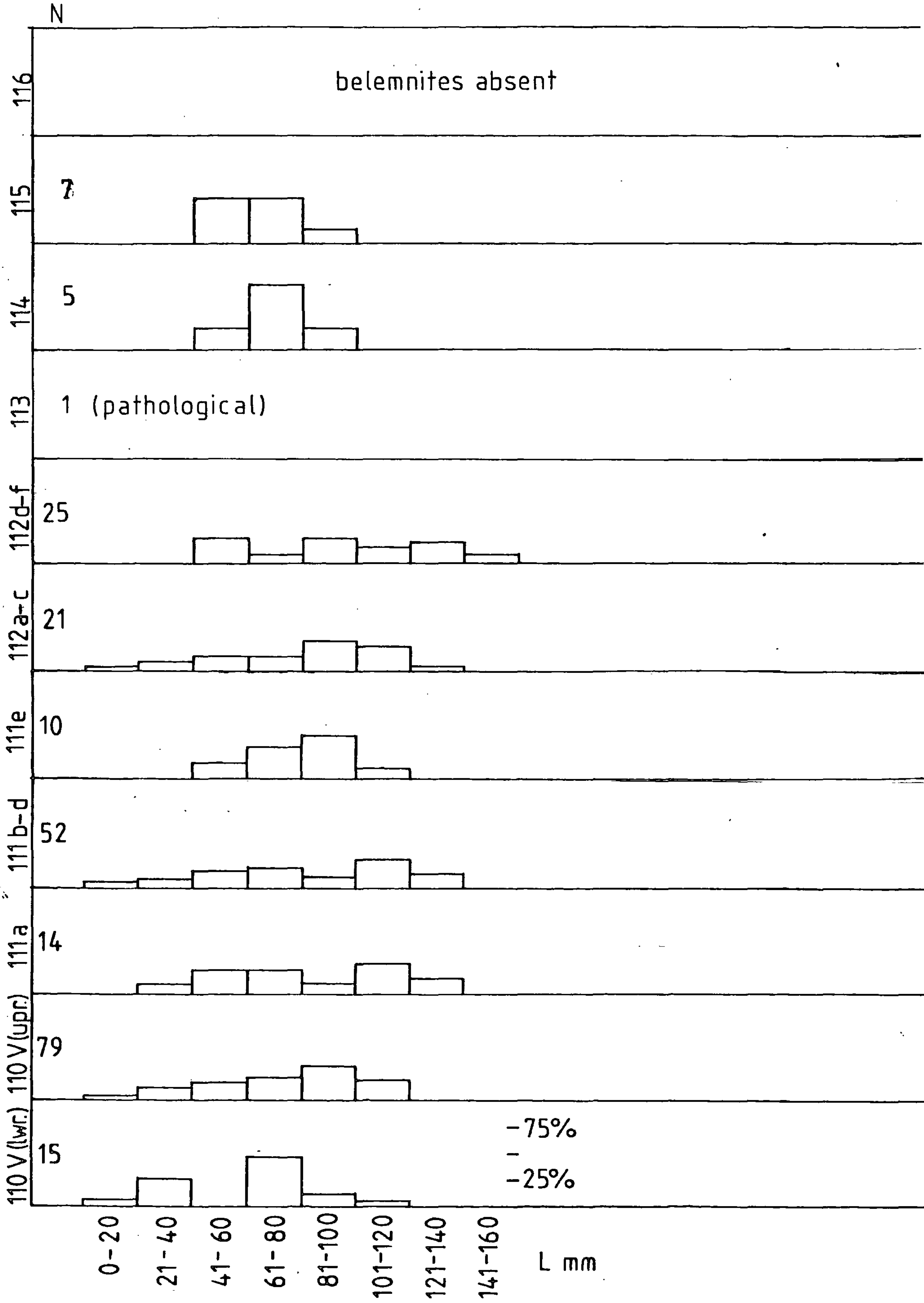


FIG. 42

B. nitidus
length
beds 110V–116



B. nitidus
length
beds 117–122c

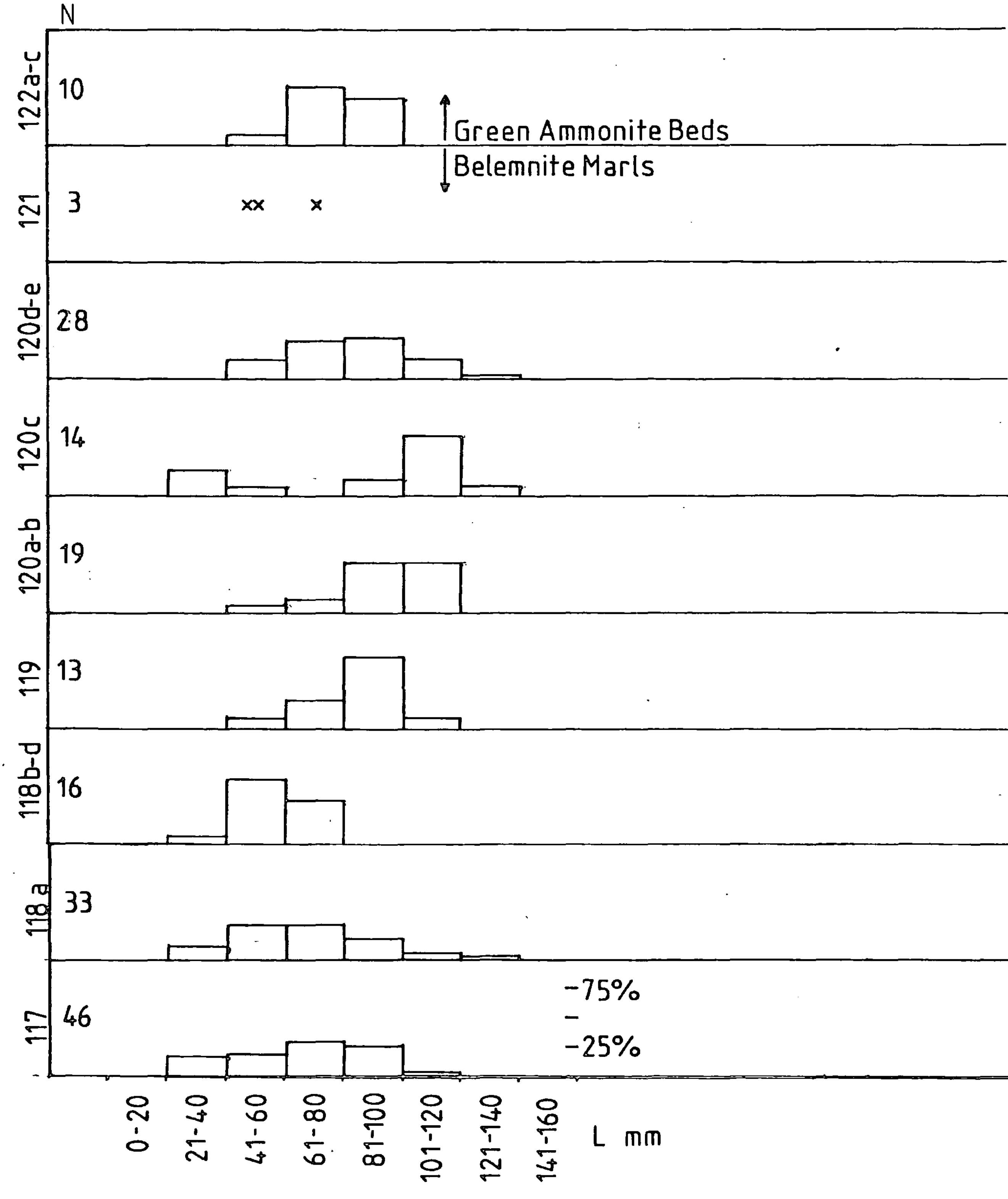


FIG. 44

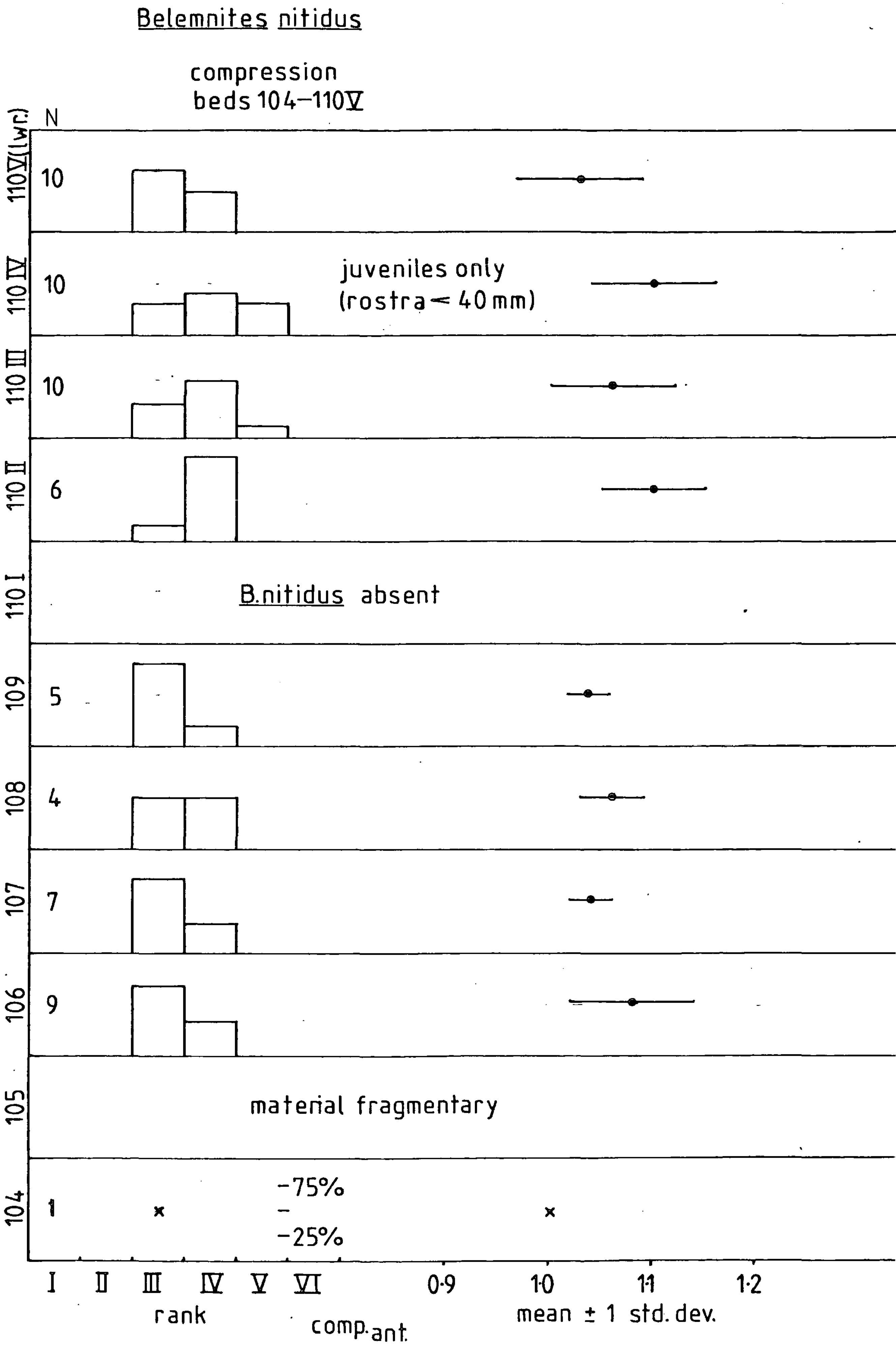

Belemnites nitidus
compression
beds 104–110V
N
110V (lwr.)
10
110IV
10
juveniles only
(rostra < 40 mm)
110III
10
110II
6
110I
B. nitidus absent
109
5
108
4
107
7
106
9
105
material fragmentary
104
1
–75%
–
–25%
I
II
III
IV
V
VI
rank
comp.ant.
0·9
1·0
1·1
1·2
mean ± 1 std. dev.

FIG. 45

B. nitidus
compression
beds 110V–116

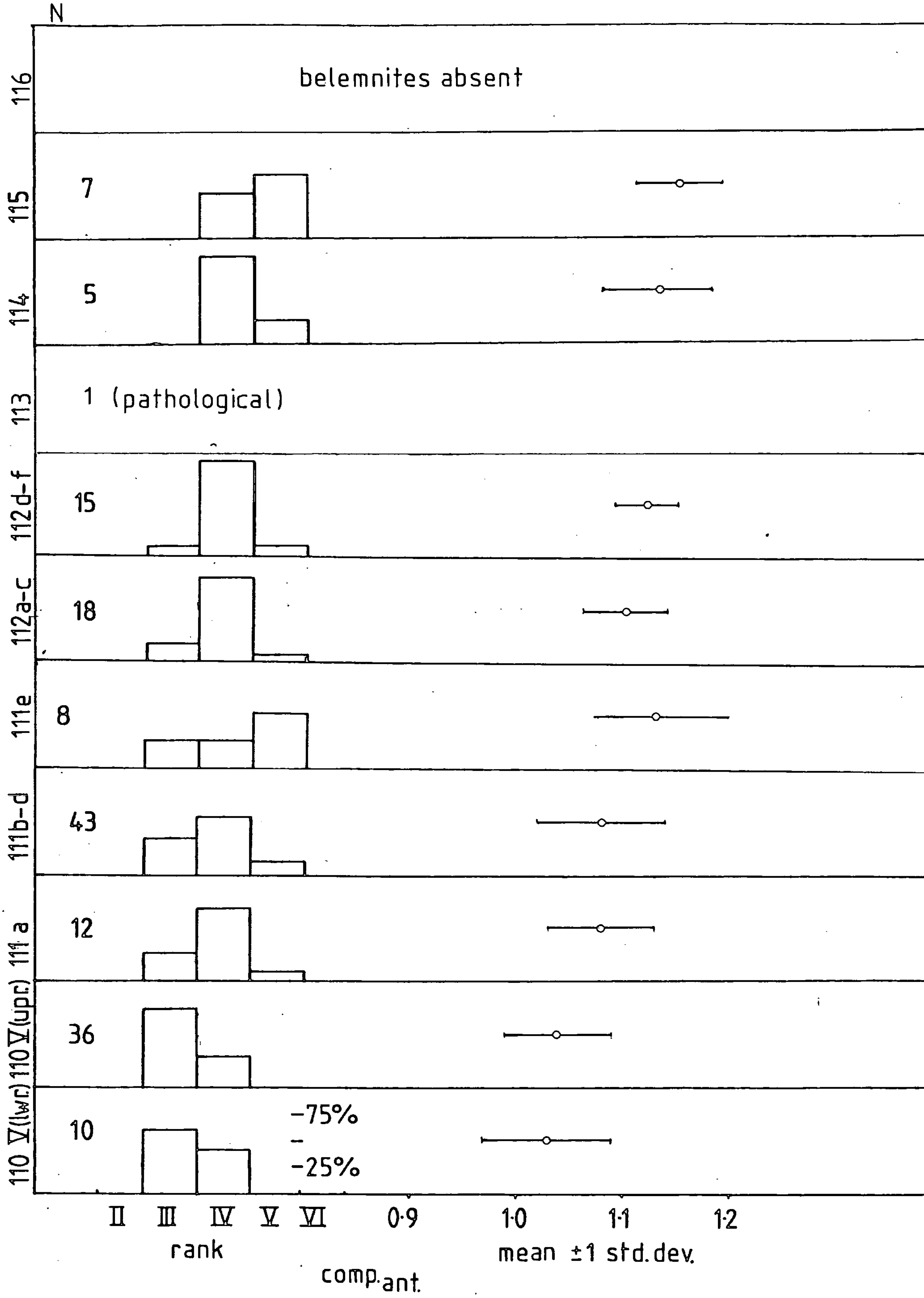


FIG. 46

B. nitidus
compression
beds 117–122c

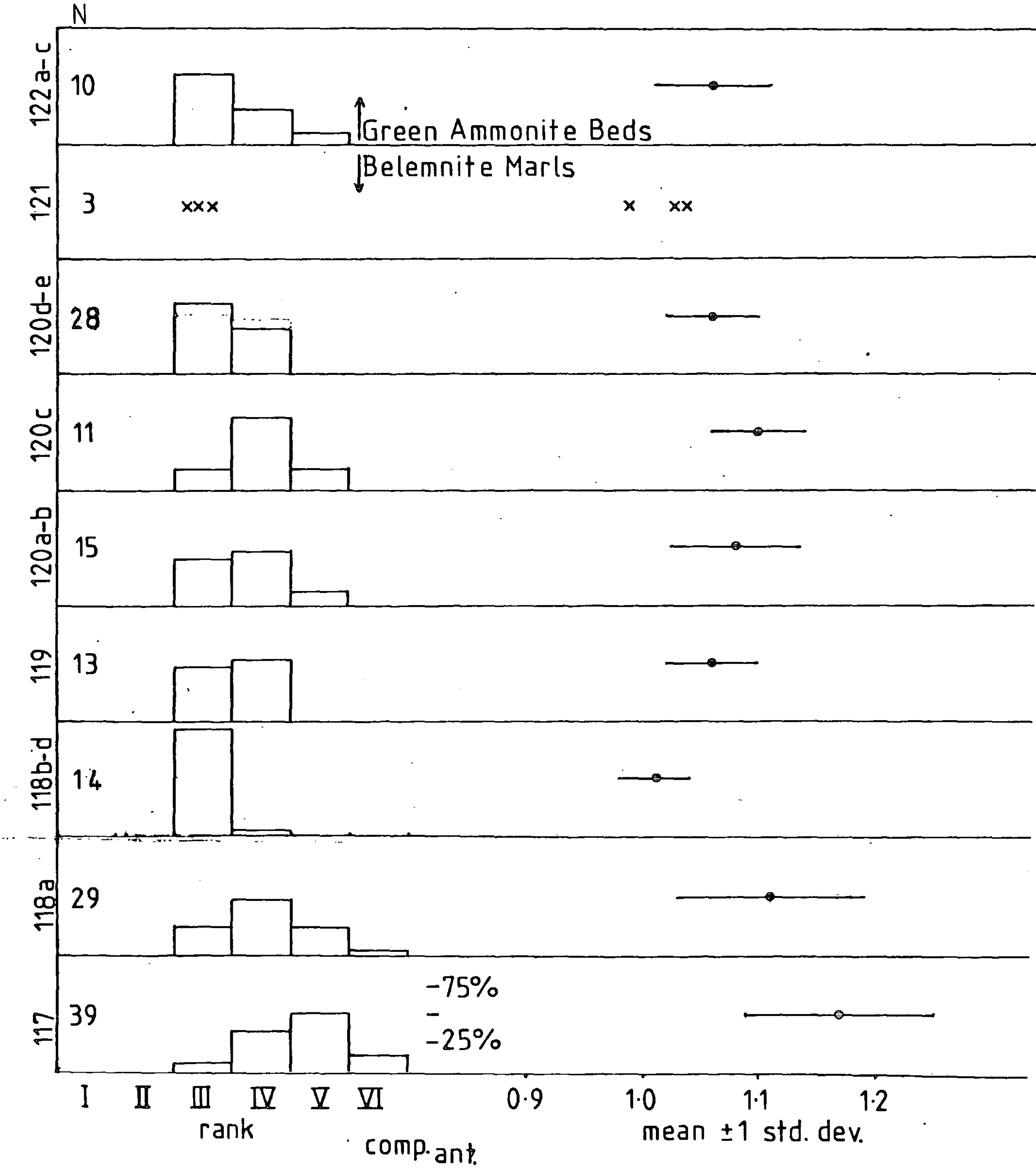


FIG. 47

<u>Belemnites</u> <u>nitidus</u>
clavateness
beds 104–110V

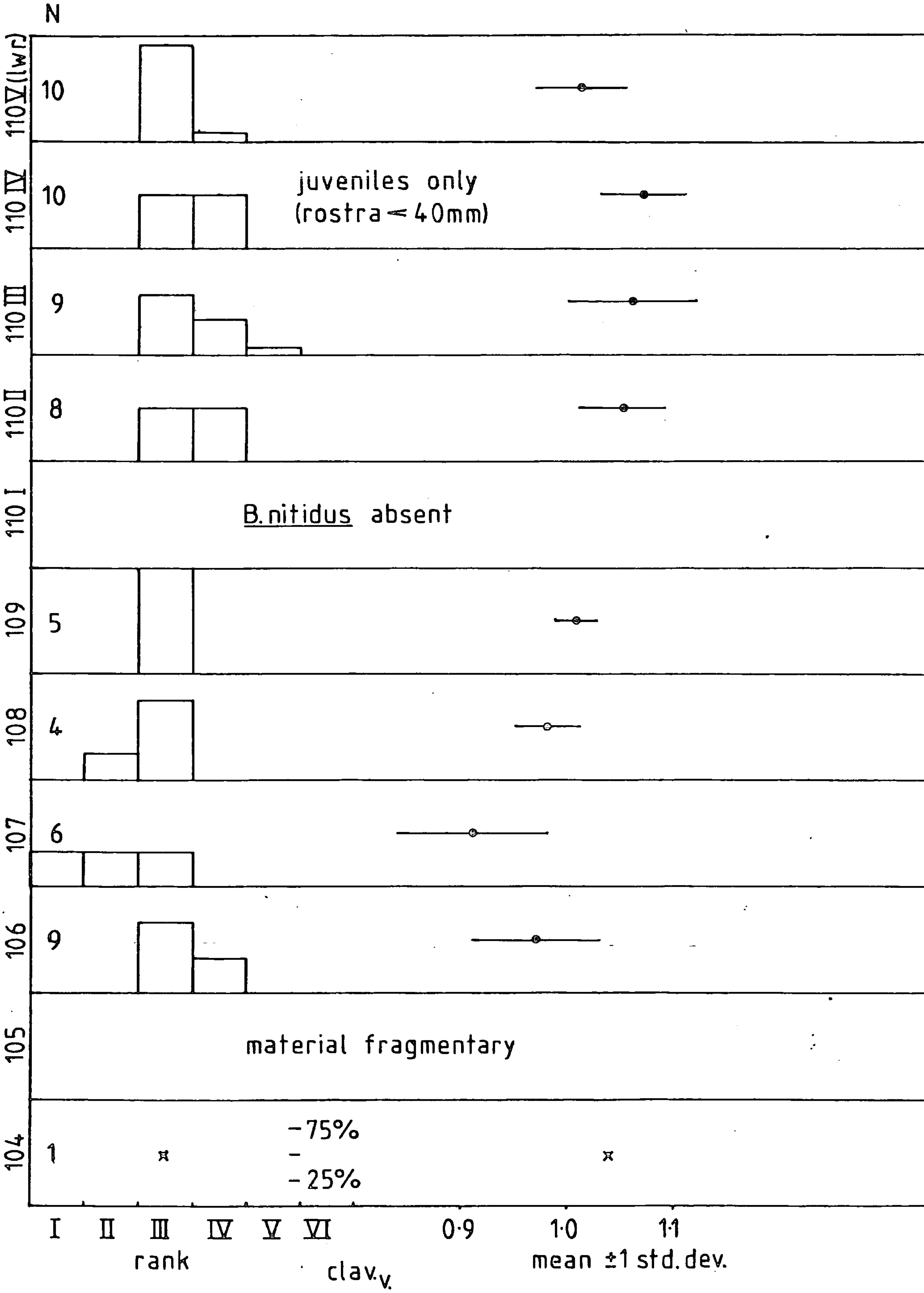


FIG. 48

B. nitidus
clavateness
beds 110V–116

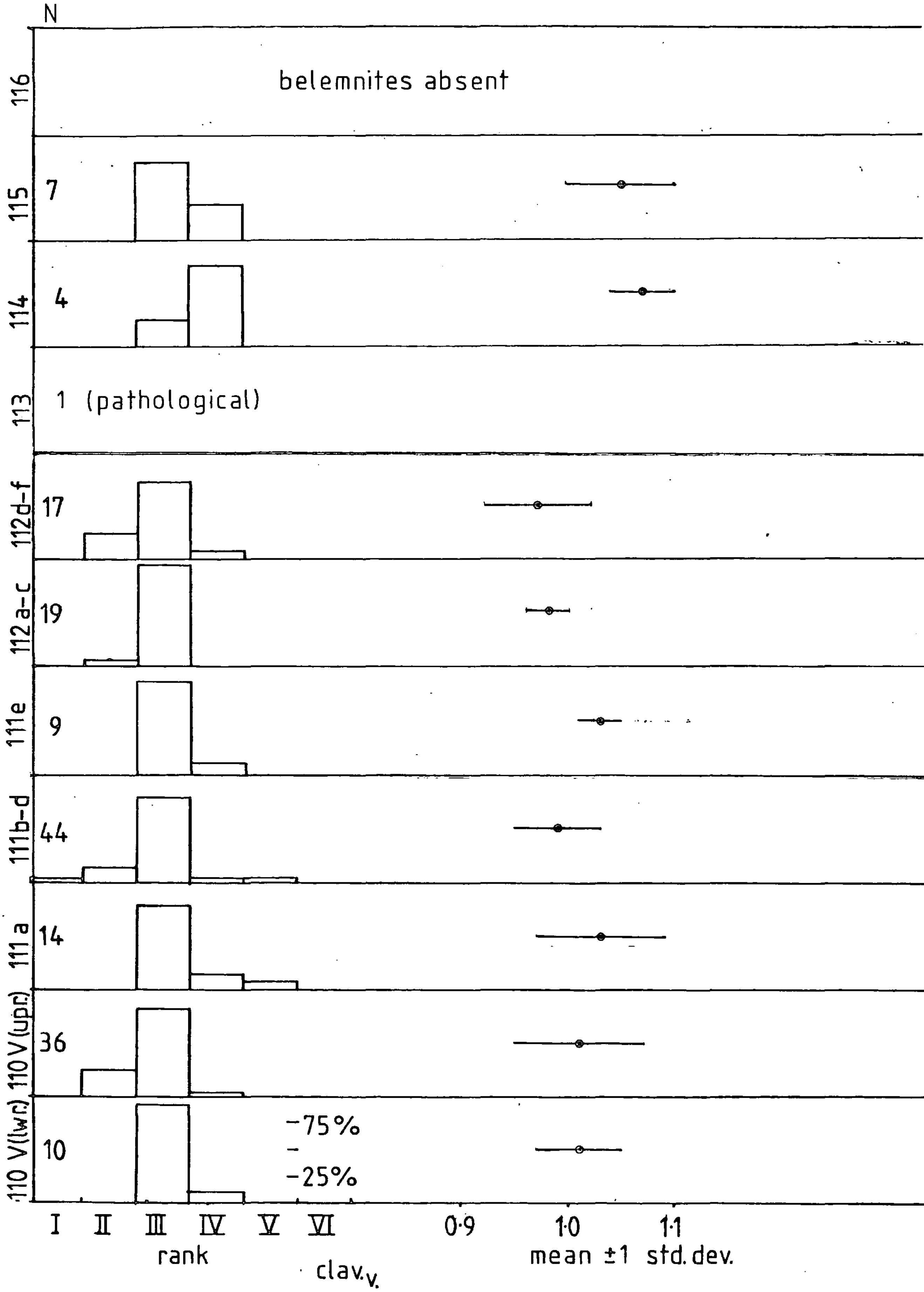


FIG. 49

B. nitidus
clavateness
beds 117–122c

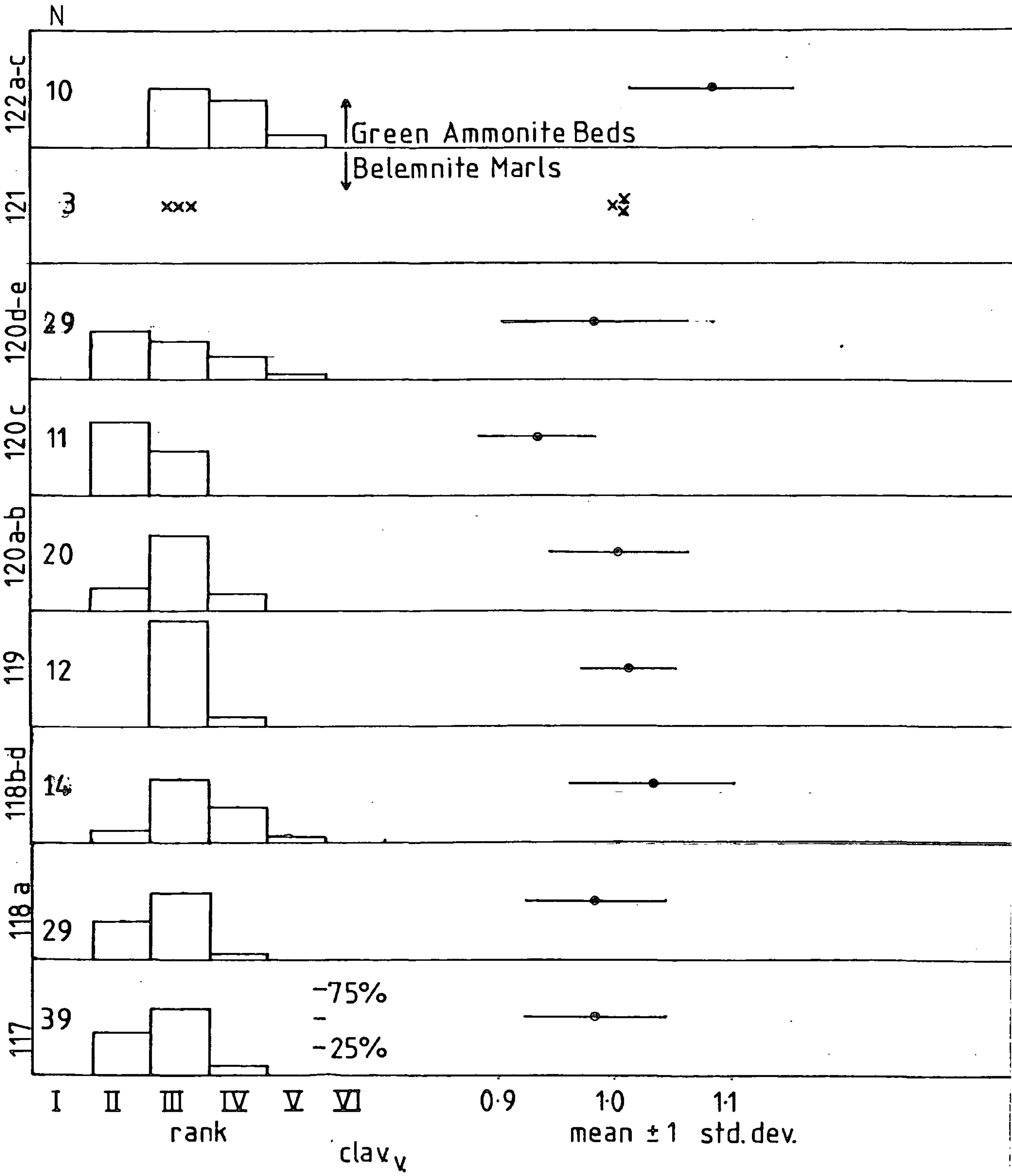
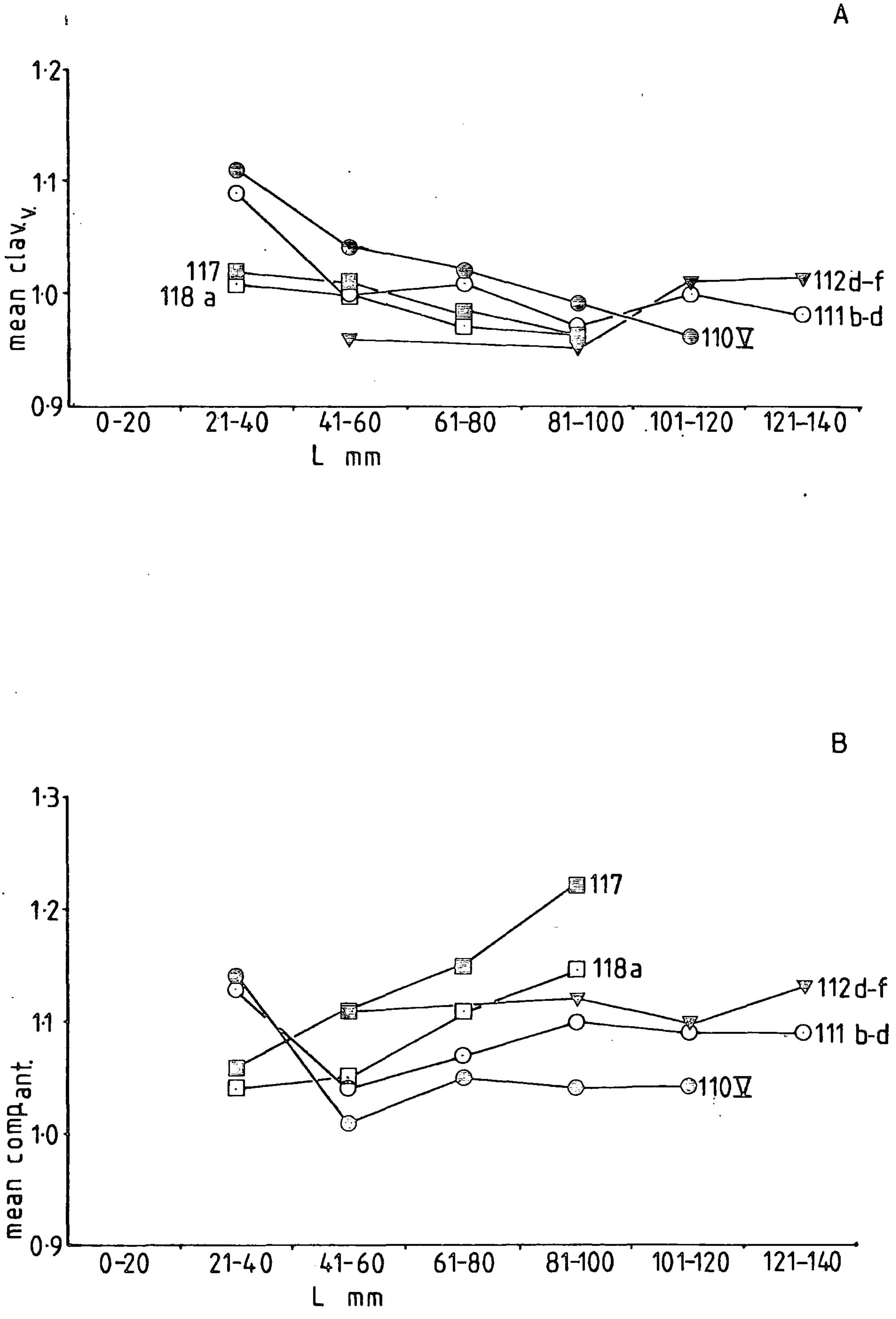


FIG.50 *Belemnites nitidus*: graphs showing changes in A) clavateness and B) compression during ontogeny for samples from five different horizons.

FIG. 50


A
1·2
1·1
1·0
0·9
mean clav.v.
117
118 a
112d–f
111b-d
110V
0–20
21–40
41–60
61–80
81–100
101–120
121–140
L mm
B
1·3
1·2
1·1
1·0
0·9
mean comp.ant.
117
118a
112d–f
111 b-d
110V
0–20
21–40
41–60
61–80
81–100
101–120
121–140
L mm

Belemnites imus (Lang 1928)

Plates 17, 18.

v 1928 Passaloteuthis ima sp. nov.; Lang, pp. 199 - 200, pl. 13, fig. 5; text fig. 3, no. 10

p. 1928 Passaloteuthis stonebarroensis sp. nov.; Lang, pp. 200 - 201

Holotype

BMNH C28989 (Passaloteuthis ima), Belemnite Marls, bed 108, foreshore below Westhay Cliff, Charmouth. Established by Lang (1928), pp. 199 - 200, pl. 13, fig. 5.

Other material

Author's collection, Belemnite Marls, near Charmouth, Dorset: 39 specimens

bed 106c: TB848
bed 107: D75
bed 108: D80, TB597, TB599, TB613, TB852
bed 110 I: no specimens collected, but impression probably of this species seen below Westhay Cliff.
bed 110 II: D84, D86, D87, D89, D94, TB284
bed 110 III: TB324, TB794
bed 110 IV: TB223, TB226, TB227, TB229, TB230, TB352 - 354, TB360, TB361, TB380, TB382 - 385, TB399, TB514, TB515, TB1044

BMNH, coll. W.D. Lang, Belemnite Marls, Charmouth: 16 specimens

bed 104: (Passaloteuthis cf. ima)?C29496
bed 105: (Passaloteuthis cf. ima)?C29498, C35561
bed 106: C28866, C29499, C29500, C42029
bed 107: (Passaloteuthis cf. ima) C29501

bed 108: C28990

bed 110 I: C43790, C43793; (Passaloteuthis cf. ima) C43860

beds 110 II - IV: (Passaloteuthis stonebarroensis) C28890 - 28892, C43801

Description

Rostrum stout, never clavate in vertical plane, occasionally very slightly so in horizontal plane. Section compressed, usually with distinctive sub-pentagonal outline in anterior portion of rostrum, caused by ventrolateral facets (fig.111D) which are especially well developed in larger specimens.

Dorsolateral apical furrows often present. Paired lateral furrows weakly developed; where present, they are integral with the ventrolateral facets.

Dimorphism into comparatively stout and slender forms is present, and is also manifest in the length of the alveolus relative to the rostrum (an effect dependent upon the diameter of the rostrum). In robust forms, the alveolus averages 53% of the total rostral length, whilst in gracile forms it averages 60%.

Epirostrum unknown.

Discussion

The holotype, from bed 108, is a small rostrum of this species but is typical of this horizon. It is fractured across the apex of the phragmocone, and measurements taken from this point firmly identify it as a gracilirostrid specimen (fig.52). In his 1928 paper, Lang regarded the species as restricted to beds 106 - 108. However, he apparently later amended this view as two specimens in the BMNH that were determined by him as Passaloteuthis ima (C43790, C43793) were collected from the base of bed 110. (The labels actually state "109 or base 110", but the comparatively dark adherent matrix suggests bed 110 I). Material classified by him as P. cf. ima is from beds 104, 105, 107 and the base of 110. Not recognizing dimorphism, his diagnosis of P. ima was based mainly on gracile rostra. Robust specimens, which are frequently considerably more massive (especially in beds 110 II - IV) were assigned by him to P. stonebarroensis (= B. nitidus Phillips of the present work). However, B. imus can be distinguished from B. nitidus by the former's comparatively conical profile, sub-pentagonal transverse section and, very clearly, by comparison of early growth lamellae in longitudinal section. Robust specimens of B. imus approach in stoutness B. abruptus, which may be closely related.

B. imus is not a common belemnite, which probably contributed to Lang's limited recognition of it. Other authors do not seem to have been aware of it at all, and attempts to recognize conspecific material in other works have not been successful.

Ontogeny

The rostral ontogeny of this species is graphically simple, essentially consisting of almost linear growth from a conical juvenile profile to a somewhat less conical adult profile, with D_p/L_p decreasing at a very low rate throughout most of the structure's development. Slight variations in this basic pattern produce an easily recognizable degree of dimorphism into robust and gracile forms.

Early growth lamellae are often poorly visible in this species, but tend to be most clearly developed in gracile specimens. For this reason, the camera lucida drawings of early growth stages were taken from these. It must be emphasized that, apart from this difference in clarity, the early stages of the two forms are indistinguishable from each other.

As with most specimens from the Belemnite Marls, details of the phragmocone are very poorly preserved.

The earliest visible rostral growth stage, with a post alveolar length of about 2 mm, is always markedly excentric, to such an extent that the ventral surface is practically contigous to the phragmocone and has to accommodate to the bulge of the protoconch (figs. 53A,B). In this respect, it is very similar to B. abruptus, and the relationship between these two belemnites is discussed under the latter's heading. The degree of excentricity rapidly decreases to a more usual level.

The specimen illustrated in figs.53A,B displays some minor convolutions in the post-alveolar ventral portion of this early growth stage which may be due to deposition around primary calcite spherules (see p.238). However, in B. imus, early rostral form cannot be seen to be noticeably influenced by such deposits, and convoluted lamellae were not observed in other examples of the species.

Growth continues in the uniform manner previously indicated, with a slight decrease in the gradient D_p/L_p occurring at a post-alveolar length of 35 - 40 mm in those individuals here regarded as gracilirostrid members of the species. The resultant dimorphism is readily apparent in the growth curves shown in fig.52. Subsequent to the appearance of dimorphism, some specimens, both gracile and robust, show a more marked flattening of this curve before their final shape is assumed: that is to say there is a sudden late elongation of the rostrum which, although comparatively slight, brings to mind the formation of an epirostrum. This feature, which results in a more gentle taper to the apex, was not observed in any other species, with the possible exception of B. aduncatus (q.v.).

(Forms with "true" epirostra (notably B. nitidus) occur rarely in the upper beds of the Belemnite Marls but bear little resemblance to B. imus.)

Dimorphism in B. imus is also manifested in the length of the alveolus, the growth of which relative to the post-alveolar length is plotted in fig.52B. As stated elsewhere (p.29), measurement of alveolar length is liable to greater error than the other parameters, and in species with comparatively short alveoli (eg. B. charmouthensis, B. longissimus) it is too inaccurate to be of much use in this respect. However, in B. imus, it may generally be stated that the alveolus is longer in robust specimens; this is due to the greater thickness and hence length of the anterior (alveolar) portion of the rostrum. There is no evidence that the phragmocones themselves are different. Both gracile and robust forms achieve similar post-alveolar lengths.

In both forms, lateral facets gradually develop to produce the sub-pentagonal cross-section which is characteristic of the species. Specimens fractured across or near to the protoconch reveal that the earliest visible stages are circular in transverse section.

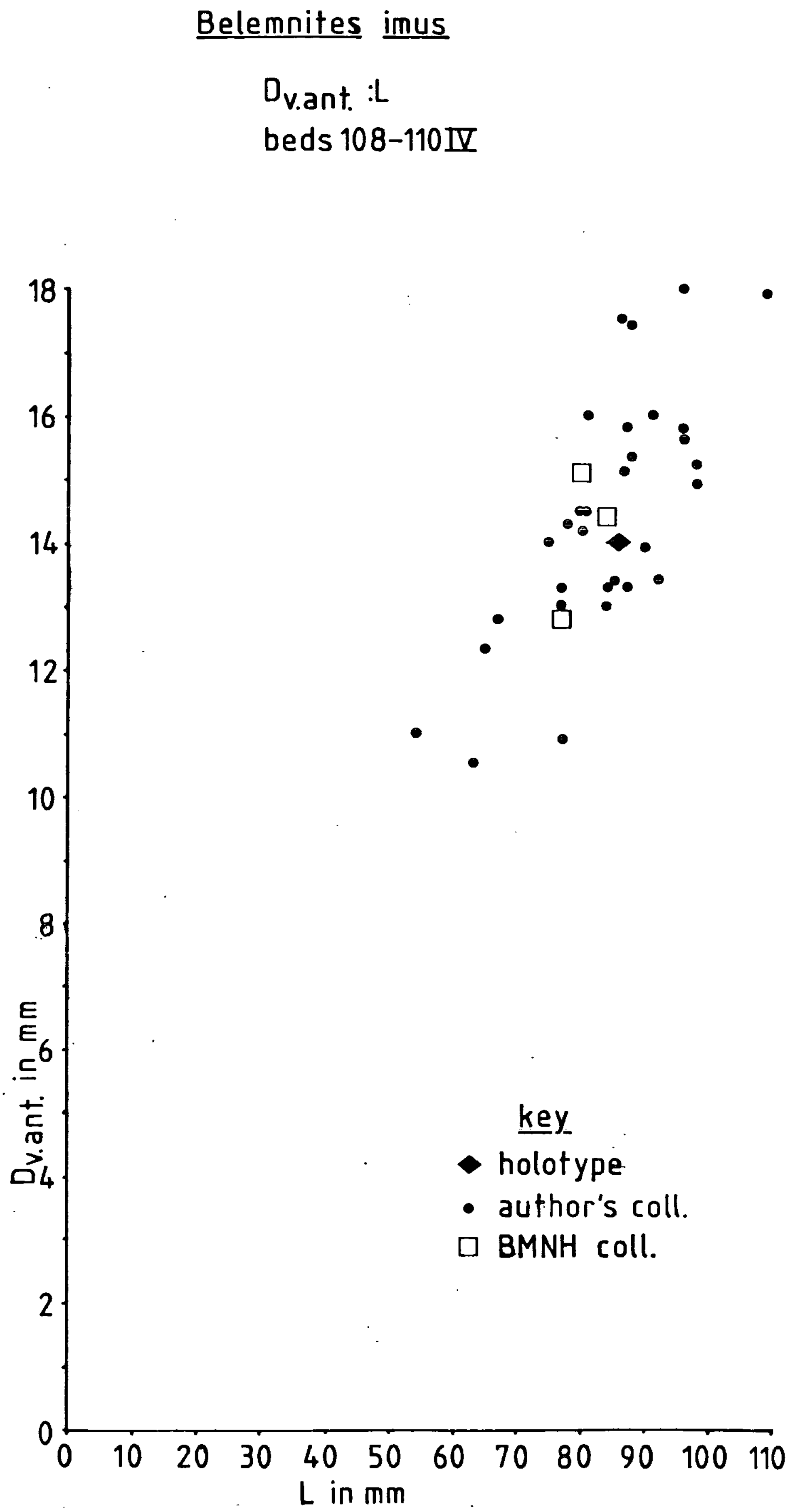
It is interesting that no rostra of juvenile B. imus were found; that this is not an artifact of post mortal distribution or preservation is suggested by the occurrence of B. imus at several horizons in the company of species showing more complete age variation (figs.79-87). The implications of this and comparable observations on other assemblages are discussed on p.197.

Stratigraphical variation

B. imus is stable in form throughout its occurrence in the Belemnite Marls, although it tends to achieve a larger size in bed 110. Since its growth is less allometric than that of most belemnite species, this does not produce the common apparent effect of a morphological change. The species is also remarkable for the overall low degree of variation in its morphology, which could be related to the apparently small size of its population, which in turn is possibly connected with the speciation of B. abruptus (q.v.).

Distribution

Charmouth, Dorset: Belemnite Marls, jamesoni Zone, taylori and polymorphus Subzones, beds ?104, ?105, 106 - 110 IV.


Belemnites imus
Dv.ant. :L
beds 108–110 IV
18
16
14
12
10
8
6
4
2
0
Dv.ant. in mm
0
10
20
30
40
50
60
70
80
90
100
110
L in mm
key
◆ holotype
● author's coll.
□ BMNH coll.

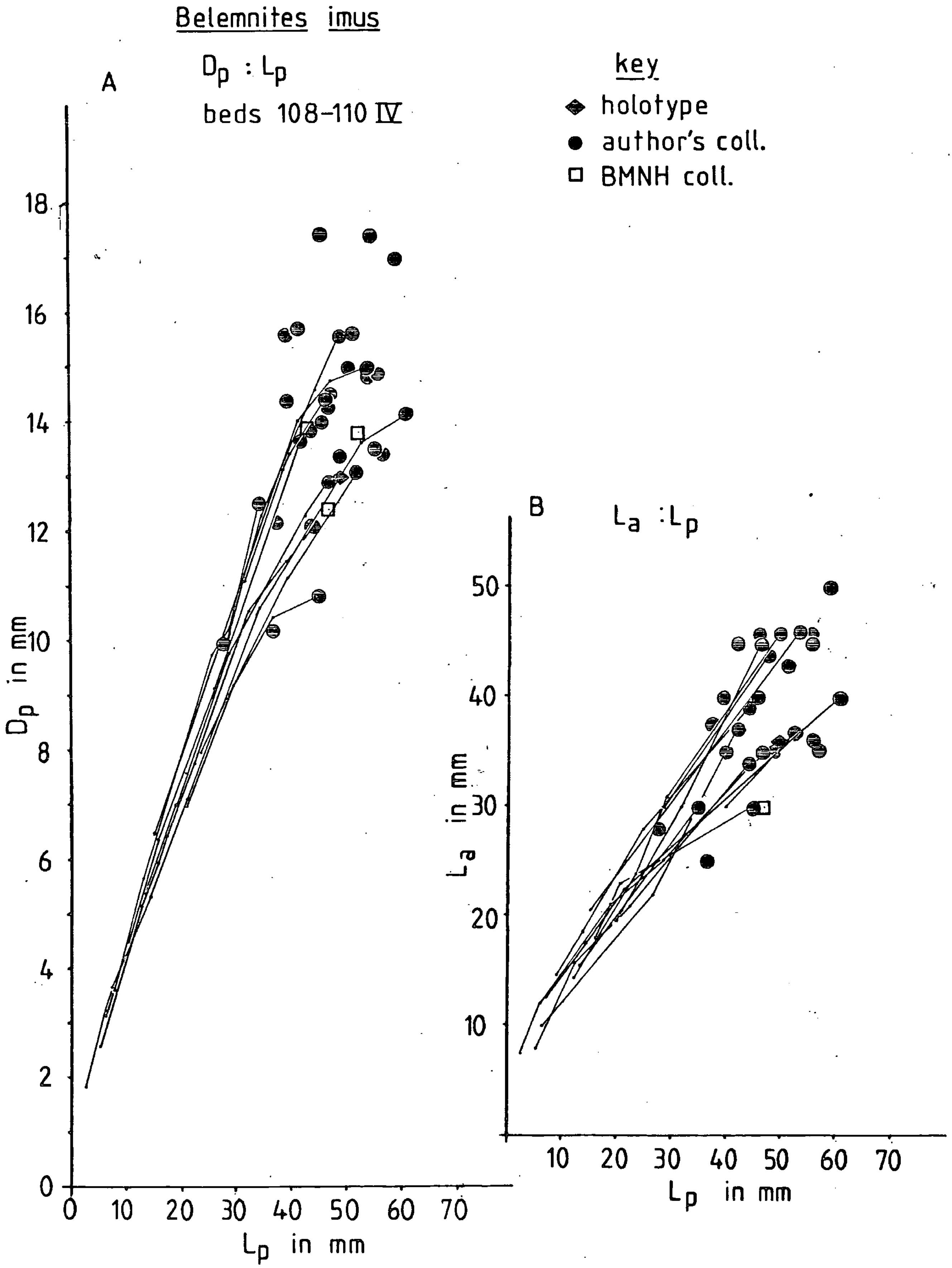

Belemnites imus
A
$D_p : L_p$
beds 108–110 IV
key
◆ holotype
● author's coll.
☐ BMNH coll.
D_p in mm
0
2
4
6
8
10
12
14
16
18
0
10
20
30
40
50
60
70
L_p in mm
B
$L_a : L_p$
L_a in mm
10
20
30
40
50
10
20
30
40
50
60
70
L_p in mm

FIG.53 Belemnites imus: camera lucida drawings of median longitudinal polished sections.

A: D86 (gracile) bed 108 II, x24

B: D86 (gracile) bed 108 II, x12

C: TB352 (gracile) bed 110 IV, x12

p - protoconch
r - earliest clear rostral growth line
v - sparry calcite-filled void between prismatic and nacreous layers of protoconch

FIG. 53

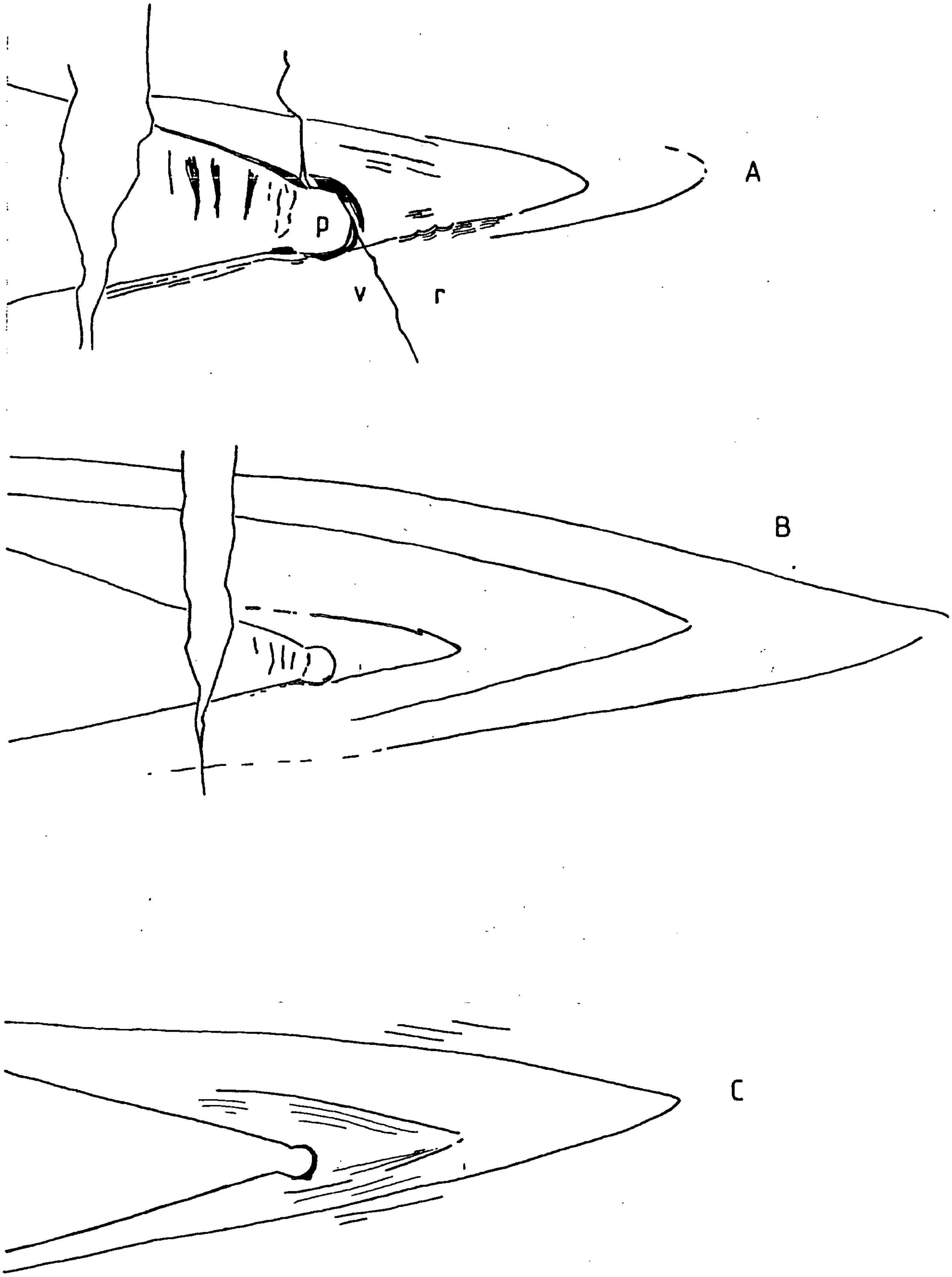
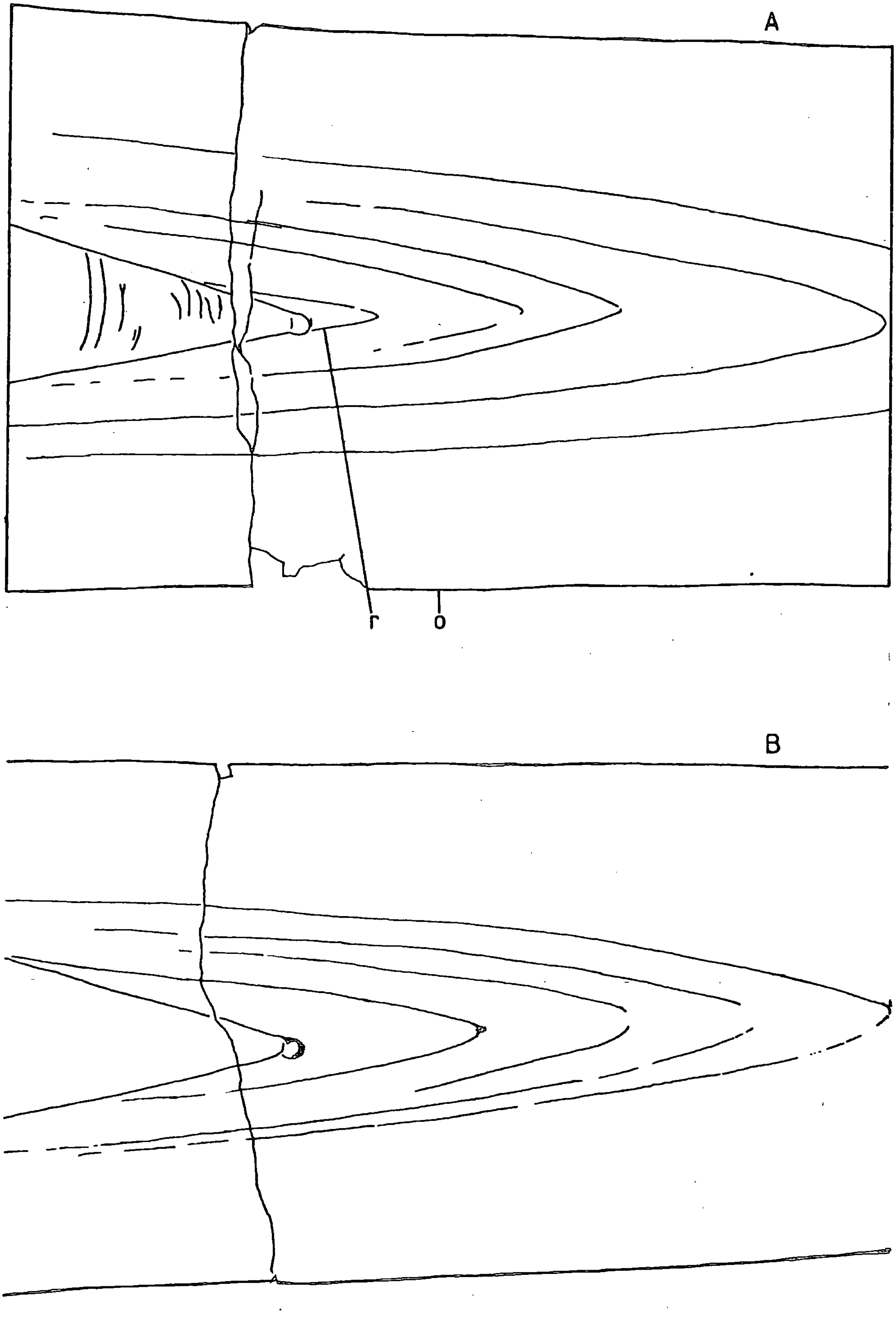


FIG.54 Belemnites imus: camera lucida drawings of median longitudinal polished sections.

A: D86 (gracile) bed 108 II, x6
B: TB380 (gracile) bed 110 IV, x6

r - earliest clear rostral growth line
o - outer surface of rostrum

FIG. 54



Belemnites abruptus (Lang, 1928)

Plate19, figs.1-4; Plate20, figs.1-3; Plate21, figs.1-4.

? p. 1827 *Belemnites brevis* sp. nov.; de Blainville, pp. 86 - 88, pl. 3, figs. 1 - 3.

non 1836 *Belemnites ?brevis* de Blainville; Buckland, vol. 2, p. 70, pl. 44', fig. 14.

cf. 1858 *Belemnites brevis* de Blainville; Quenstedt, pp. 72, 74, pl. 8, fig. 14.

cf. 1866 *Belemnites infundibulum* sp. nov.; Phillips, pp. 36 - 37, pl. 1, fig. 3; diag. 17.

? p. 1866 *Belemnites excavatus* sp. nov.; Phillips, pp. 37 - 38, pl. 2, fig. 4. v,s'',s'L only.

cf. 1866 *Belemnites calcar* sp. nov.; Phillips, p. 38, pl. 2, fig. 5. non fig. 5.1''' .

. 1866 "Belemnite from the Lias, allied to *B. insculptus*"; Phillips, p. 46, pl. 5, fig. 13; diag. 18 .

non 1906 *Coeloteuthis calcar* (Phillips); Lissajous, p. 265 not traced, but fig. reproduced in Roger 1952 .

? 1907 *Belemnites (Coeloteuthis) calcar* Phillips; Lissajous, p. 75, pl. 1, fig. 26.

v . 1912 *Belemnites excavatus* Phillips; Werner, p. 112 - 3, pl. 10, fig. 6.

non 1922 *Coeloteuthis excavata* (Phillips); Naef, pp. 229 - 230, figs. 84 i,k cop. Phillips 1867.

non 1925 *Coeloteuthis excavatus* [sic] Phillips; Lissajous, pp. 21 - 22, fig. 10 cop. Phillips 1867.

v* 1928 *Clastoteuthis abrupta* sp. nov.; Lang, pp. 196 - 197, pl. 13, fig. 1; text fig. 3, no. 7.

v . 1928 *Clastoteuthis stantonensis* sp. nov.; Lang, pp. 197 - 198, pl. 13, fig. 2; text fig. 3, no. 6.

p. 1950 *Coeloteuthis excavata* (Phillips); Bairstow, pp. 226 - 227.

non 1952 *Coeloteuthis calcar* (Phillips); Roger 1952, p. 709 - 710, fig. 21. cop. Lissajous 1906

cf. 1962 *Belemnites calcar* Phillips; Schwegler, pp. 17 - 18, fig. 12.

1962 *Belemnites aff. calcar* Phillips; Schwegler, pp. 18 - 19, fig. 13.

v 1962 *Belemnites excavatus* Phillips; Schwegler, pp. 19 - 20, fig. 14. cop. Werner 1912

non 1974 *Coeloteuthis excavata* (Phillips); Schumann, pp. 27 - 28, pl. 4, fig. 9.

Holotype

BMNH C28864 (*Clastoteuthis abrupta*), Belemnite Marls, bed 111 b, Westhay Cliff, near Charmouth, Dorset. Established by Lang (1928) p. 197, pl. 13, fig. 1.

Other material

Author's collection, Belemnite Marls, Charmouth: 34 specimens

bed 110 IV: ?TB356 (juv.), TB795

bed 110 V (lower): D105, D106, D175, TB44, TB520, TB523, TB1045, TB1048, TB1049

bed 110 V (upper): D115, D128, TB51, TB438, TB477, TB496 (juv.), TB509, TB522, TB530, TB536, ?TB542, TB545, TB796, TB1050

bed 111 a: TB654

bed 111 b: D133, ?TB67 (juv.)

bed 111 (inferred); D177

beds 112 a - c: TB103, TB811, TB828, TB829

beds 112 d - f: TB703

bed 114: TB1051

Belemnitiferous Marls, road cutting on A303, near Tintinhull, Dorset, OS ref. SY497205: 1 specimen

TB1211

BMNH, coll. W.D. Lang, Belemnite Marls, Charmouth: 5 specimens

bed 110 b (=top 110 V): C28862, C28867

bed 111 b: C28863

bed 112 d: C28861 (holotype *Clastoteuthis stantonensis*)

bed 112 e: C28860 (*Clastoteuthis stantonensis*)

Staatl. Mus. Nat., Stuttgart: 2 specimens

One specimen labelled "*Belemnites brevis tertius*", coll. Hermann (1947) Lias gamma, Hinterweiler.

One specimen labelled "*Belemnites excavatus* Phillips", figured in Werner (1912) pl. 10, fig. 6. Lias gamma, Balingen.

Description

Rostrum very robust, very short relative to its diameter, profile tending to a conical appearance which is not so apparent in the larger specimens. Transverse section sub-trapezoidal, narrowing towards dorsal surface. Apex blunt, sometimes umbilicate; ventral surface curves round strongly to the apex; dorsal surface curves more gradually.

Wide, fairly shallow apical furrows are usually well developed. These merge anteriorly into lateral facets encompassing weak lateral grooves which are usually paired; the grooves are developed mainly in the anterior part of the rostrum. (The facets are responsible for the trapezoidal section).

Alveolus very deep, typically about 60% of the total rostral length, and is markedly excentric (excentricity = 1.5 - 2.0).

Discussion

The holotype, collected by Lang from bed 111 b at Westhay Cliff, is a large but otherwise typical example of the species. It might also be desireable to nominate as a paratype the holotype of *Clastoteuthis stantonensis* Lang (B.M. (N.H.) C28861) from bed 112; this species was founded on the characteristically small specimens of *Belemnites abruptus* that occur above bed 111.

Although the interpretation of this species on the basis of Lang's type material is quite straightforward, it is necessary to consider the past usage of other specific names, notably *excavatus* and, to a lesser extent, *calcar*, in connection with *B. abruptus* and superficially similar forms from various localities and horizons. Unfortunately, the position is further complicated by the frequent application of Lissajous' (1906) generic name *Coeloteuthis* to some or all of the forms under consideration. The confusion is exacerbated by the commonly held opinion that *Coeloteuthis* typifies a sub-family Coeloteuthinae that is to be distinguished from the Belemnitinae mainly by the comparatively large volume taken up by its alveolus within the rostrum. In this respect, *Belemnites abruptus* is morphologically intermediate between these two sub-families, although it is clearly closely related to *B. imus* (q.v.) which undeniably belongs to the Belemnitinae. The basic aim of the following discussion is to extract *B. abruptus* from this imbroglio; it can then be recognized as a discrete species, at the stout end of the morphological series regarded here as constituting the genus *Belemnites*.

The earliest unequivocal reference to B. abruptus is probably the "Belemnite from the Lias, allied to B. insculptus" of Phillips (1866, p. 46) which he regarded as a very rare belemnite from the upper part of the Lower Lias of the Dorset coast. This suggests that Phillips was not well acquainted with the lower portion of the Belemnite Marls, including horizon 110 V in which B. abruptus is quite often encountered (see also p.43). As he does not give a name to this specimen, it is clear that he regards the species to which it belongs to be distinct from his new species B. excavatus and B. calcar which are externally rather similar to it. The excellent engraving of the unnamed belemnite (pl. 5, fig. 13) in fact represents a typical specimen of B. abruptus, whilst his text fig.18 p.46 shows that its alveolus is distinctly smaller in proportion to the rostrum than in the figured section of B. excavatus (pl. 2, fig. 45).

Phillips figured two specimens under the name of B. excavatus; the longitudinally sectioned specimen referred to above is that upon which the most important points of his diagnosis are based. Buckland (1836, pl. 44', fig. 14) had published a figure of the same specimen under the tentative name of B. brevis? which reveals the rostrum as a thin sheath around the alveolus, "like the finger of a thick leather glove". (B. brevis was erected by de Blainville in 1827 as a holdall name for several species of short Lower Liassic belemnite, designating three varieties of which two (b & c) resemble B. abruptus, but more positive identification is not possible.) This was later made the type of the genus Coeloteuthis (Lissajous 1906, 1925) which was adopted by the majority of authors. The extreme rarity of such coeloteuthine belemnites is attested by the fact that most of these authors copy their illustrations of Coeloteuthis from earlier works (see synonomy) so that ultimately several figures are derived from the one specimen utilized by Buckman and Phillips, which, ironically, is lost. Bairstow (1950) suggested that, "judging from the figure, it is a non-median section, liable to be misunderstood", which might be held to account for the rarity of Coeloteuthis. However, a few corroborative specimens with true coeloteuthine internal structure have been described and figured (Lissajous (1906) copied in Roger (1952); Schumann 1974).

Therefore Phillips' description and figure can be taken to demonstrated an intention to apply the name B. excavatus to what was subsequently to be described as a coeloteuthine belemnite.

Phillips' other figured specimen of B. excavatus (pl. II, fig. 4v, s", s', l), which Bairstow located in the Oxford University Museum (Bairstow 1950) and thus designated as the lectotype of Coeloteuthis excavata, is probably conspecific with B. abruptus, in which case it is distinct from B. excavatus as intended by Phillips. Bairstow attempted to establish the depth of its alveolus by means of an X-ray skiagram. However, this is an unreliable method due to the fact that an apparently alveolar outline could be due to a discontinuity in the rostrum such as a growth layer impregnated by pyrite or a change in the texture of rostral calcite (see Roger 1952, p. 709, fig. 20 (3,4) for such a specimen of Nannobelus acutus). In this case, the depth of the "alveolar" outline, with its apex about 7 mm from the apex of the rostrum, corresponds very closely to the position of a prominent and unusual change in the appearance of the lamellae that is observed in several sectioned specimens of B. abruptus (see below, and fig.57). If this X-ray outline did correspond to the alveolus, then it would, as Bairstow pointed out, "occupy more of the guard than is usual in Clastoteuthis, but less than authors have supposed it to occupy in Coeloteuthis" (1950, p. 227). However, as we have seen, Coeloteuthis does possess a proportionately deeper alveolus than this. Thus, whether or not the alveolus of this specimen is shallower than indicated by the X-ray, it is not a suitable lectotype of Coeloteuthis excavata. (It is also poorly localized - "Lyme Regis... probably in the upper part of the Lower Lias"). Bairstow was probably correct in saying that it "represents the same genus to which Dr. Lang applied the name Clastoteuthis", hence Clastoteuthis is not be regarded as a junior synonym of Coeloteuthis Lissajous; also, B. abruptus (= Clastoteuthis abrupta Lang and C. stantonensis Lang) is distinct from B. excavatus sensu Phillips.

Phillips' B. calcar (1866, p. 38, pl. II, fig. 5) more closely resembles B. abruptus, but his designated material is mostly from the Lower Sinemurian (bucklandi Zone). A single specimen from an unspecified horizon in the Belemnite Marls (fig. 5 1''') appears to be very similar to three rare examples in the author's collection (Pl.21 , fig. 5) which could be juveniles of B. abruptus - Phillips himself suggests that this specimen may not belong to B. calcar. So, unless further research should indicate that B. abruptus from the Lower Pliensbachian is an unaltered descendant of B. calcar from the Lower Sinemurian, they will be regarded as distinct species; at present, the most likely immediate ancestor of B. abruptus seems to be B. imus.

Having established that B. abruptus (Lang), B. excavatus Phillips and B. calcar Phillips are separate species automatically disposes of several works that are based on Phillips' figures and which may regard Clastoteuthis abruptus Lang and C. stantonensis Lang as junior synonyms of either of Phillips' terms (see synonymy). However, a few authors have described material under the specific names excavatus or calcar (Coeloteuthis or Belemnites) which is almost certainly conspecific with B. abruptus. This is obviously the case with material from the German Lias gamma (Werner 1912, pl. 10, fig. 6; Schwegler 1962, fig. 13), and possibly with some of Lissajous' material from

Macon, France (1907, pl. 1, fig. 26).

The above discussion essentially does no more than vindicate Lang's own remarks on the distinctness of Clastoteuthis abrupta from coeloteuthine forms. The identity of C. stantonensis with C. abrupta is revealed by morphometric study and is detailed below.

Ontogeny

Some fine detail of the shell structure around the protoconch shown in fig.56A would seem to support Barskov's (1973) model of the initial stages of belemnitid ontogeny. However, the preservation is not good enough to allow a firm description and consideration of this phase of ontogeny is deferred to p.238.

The earliest clear rostral growth stage, with a post alveolar length of about 2 mm, characteristically has an uneven conical profile and is highly excentric (fig.56). The ventral laminae of the rostrum may follow the bulge of the protoconch; B. imus is the only other belemnite observed in which this appears to be normal. Amongst the weakly defined laminae formed prior to the first clear growth stage there are sometimes clear indications of primary spherules which appear at least partly to control the initial irregularity of the early rostral profile (see p.238).

In the specimens from which longitudinal sections were prepared, prominent growth lines tend to be absent after these initial stages until a post-alveolar length of 10 - 14 mm is attained. (Fainter growth lines, if carefully traced, can be used to provide intervening points on the growth curves.) The apical region contained within the well defined lamellae at this length of rostrum consists of a jumble of calcite spherules, often partly surrounded by concentric lamellae, interspersed with darker organic material (figs.57-59).

The apex formed by the lamellae enclosing this material has a somewhat elongated profile, so that the whole structure can resemble a partly developed epirostrum in internal detail. A similar structure was observed by Jeletzky as a diagnostic feature of Megateuthis (1966, p. 70; pl. 12, fig. 1), where the axial part of the juvenile rostrum "appears to be built largely of ill-defined laminae obscurae". Such poorly organized apical material often occupies much of the axial region of B. abruptus, in which case it appears to be responsible for the apical umbilicus observed in several specimens, due probably to slight weathering (fig.59C). This was also noticed by Jeletzky in Megateuthis, and is very probably the principal cause of the occasional umbilicae observed in many other belemnites.

In B. abruptus, it is interesting that the most marked region of apical disorganization corresponds to (i.e. it is enclosed by) the aformentioned series of prominent growth lines, pale coloured and hence relatively poor in organic material, which also correspond to a distinct change of gradient in the plotted growth curves, with a relative increase in rate of thickening relative to lengthening (fig.55A). Growth subsequently remains more or less linear, giving rise to the characteristically stubby rostrum.

The distribution and possible significance of poorly organized rostral material is discussed elsewhere (p.255); what is of particular interest here is that, prior to the change in the gradient of the growth curve, the rostrum is virtually identical to that of juvenile B. imus. In effect, juvenile rostra of these two species would be indistinguishable until a post-alveolar length of about 10 - 15 mm is achieved. In actual fact, the only juvenile specimens found were associated with B. abruptus, no appropiate specimens having been found in those beds where B. imus occurs.

During these early stages, both species have an unremarkable circular cross section, lateral facets first becoming noticeable a little later; in B. imus these tend to face ventro-laterally, whilst in B. abruptus they occupy a more normal slightly dorso-lateral position but otherwise are of similar extent.

At Charmouth B. abruptus first appears at the top of bed 110 IV (one specimen only), about 3.0 m below bed 111, whilst the highest specimens of B. imus are from just below this, about 3.5 m below bed 111.

In consideration of this stratigraphical distribution and early ontogenetic similarity (the subsequent divergance being heralded by a distinct ontogenetic event in B. abruptus, namely the temporary development of a peculiar apical structure), it must be regarded as a strong possibility that B. abruptus descended directly from B. imus. That this is a rapid speciation event perhaps actually occurring at this locality is circumstantially supported by the fact that each species is here present only in small numbers (see eg. Gould and Eldredge 1977, p. 121). Furthermore, B. abruptus is rare elsewhere, whilst B. imus is so far unrecognized outside the Charmouth area.

In addition, as fully grown B. abruptus rostra present juvenile features of both species (deep alveolus and coniform profile), it is tempting to suggest it as an instance of paedomorphosis; the growth curves in fig.55A are immediately distinguished by maintaining throughout their length the steep slope characteristic of early growth.

Dimorphism is not so far apparent in this species, although it might be expected in view of its apparently close relationship to B. imus. One sectioned specimen (TB1045), represented by the right-most point in fig.55A, does display a growth curve which separates it somewhat from the others. Although it shows a marked growth stage with a post-alveolar length of 12 mm, this does not presage the usual change in gradient and the complete specimen is consequently a little more slender than most of the others. External measurements on specimens of B. abruptus where the position of the protoconch is not known are of little use in this respect, due to a) the rapid variation in diameter along its length and b) the large percentage error inherent in estimating the complete length of the rostrum due to its comparative shortness.

A larger collection is required to clarify this matter; at present, the scarcity of the material makes further sectioning undesireable.

Stratigraphical variation

Lang gave the range of Clastoteuthis abrupta as beds 110 b (i.e. up to 0.6 m below 111) and 111, and of C. stantonensis as bed 112 only (1928, p. 196). The present study extends this range down to 3.0 m below bed 111 and up to bed 114.

The isolated specimen mentioned above from the top of bed 110 IV is fully grown and somewhat slender for the species, although not remarkably so - it is by no means an "intermediate" form between B. imus and B. abruptus.

Bed 110 V has yielded the majority of specimens, and from this horizon one may reasonably expect to find one or two specimens per day when collecting from the foreshore and cliff at Westhay Cliff. Above bed 110, B. abruptus is very rare; the few specimens recorded from above bed 111 are all comparatively small which led Lang to erect the species Clastoteuthis stantonensis for them. These small rostra are in fact identical to small specimens from lower horizons which all fall within the range of growthcurves of larger examples, as does the growth curve of Lang's sectioned specimen (C28860) from bed 112 e. Apart from this variation in size attained, B. abruptus appears to remain constant in form throughout its short range.

Three specimens which are probably juvenile B. abruptus were found (pl.20 21, fig.5 5), being assigned to this species rather than B. imus because of their stratigraphical position.

Four other small conical rostra, although superficially similar to B. abruptus/B. imus juveniles, have exceptionally deep alveoli invested with a thin layer of rostral material, and thus may be true coeloteuthine belemnites (see p.179).

Distribution

1) Charmouth, Dorset: Belemnite Marls, jamesoni Zone, polymorphus and brevispina Subzones, beds 110 IV, 110 V, 111 a - d, 112 a - f, 114.
2) Tintinhull, Dorset: Belemnitiferous Marls, with B. longissimus, ?lateral equivalent of beds 110 IV - V.
3) Balingen and Hinterweiler, Württemberg, W. Germany: Lias gamma
4) Macon, Saone et Loire, France: "Charmouthian" (Lwr. Pliensbachian) (Lissajous, 1907).

FIG. 55

Belemnites abruptus

beds 110IV–114

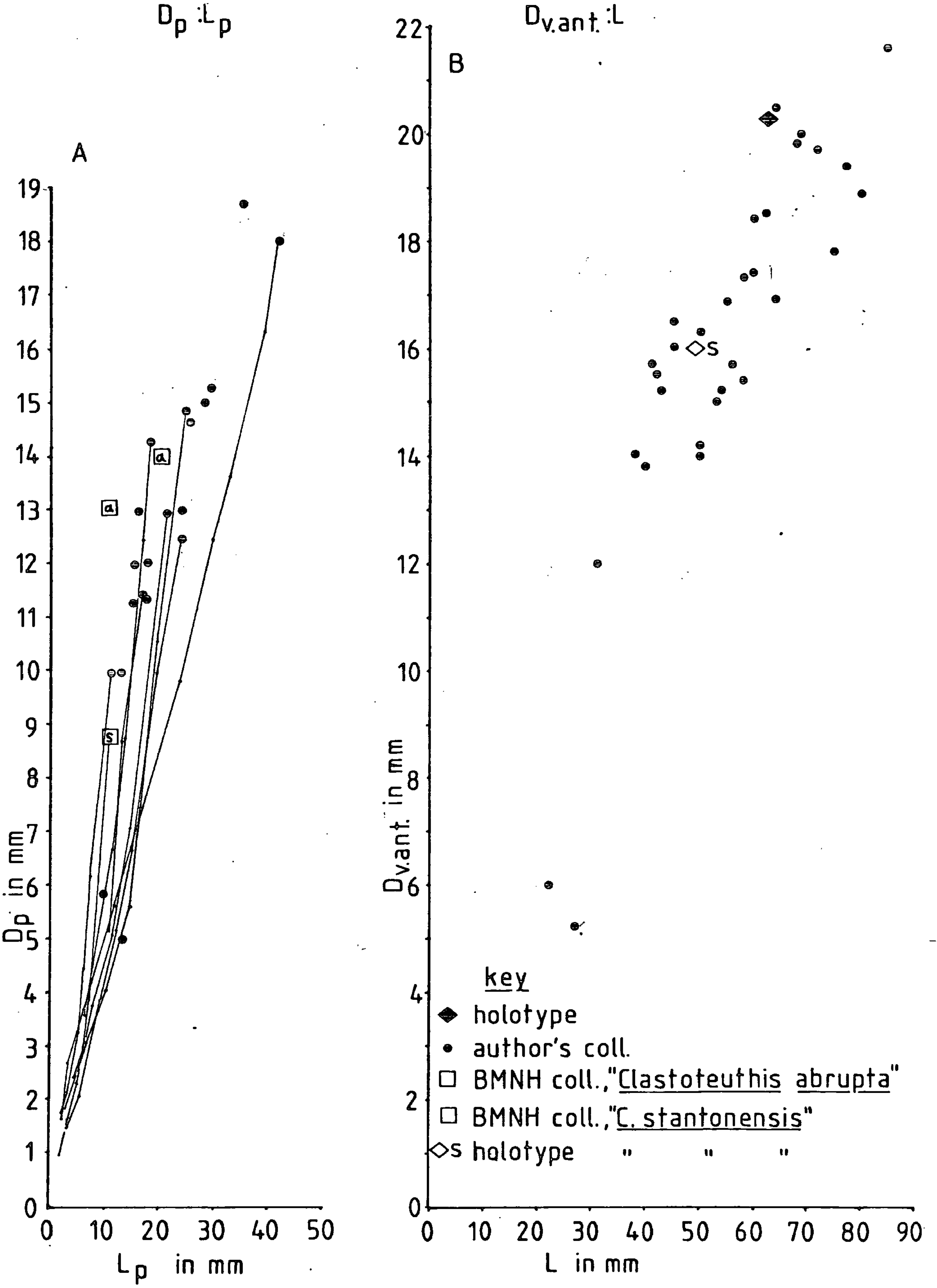


FIG.56 Belemnites abruptus: camera lucida drawings of median longitudinal polished sections.

A: D175 bed 110 V, x24

B: TB1045 bed 110 V, x24

C: TB1045 bed 110 V, x6

p - protoconch
r - earliest clear rostral growth line
s - primary spherules
v - sparry calcite-filled void between prismatic and nacreous layers of protoconch

FIG. 56

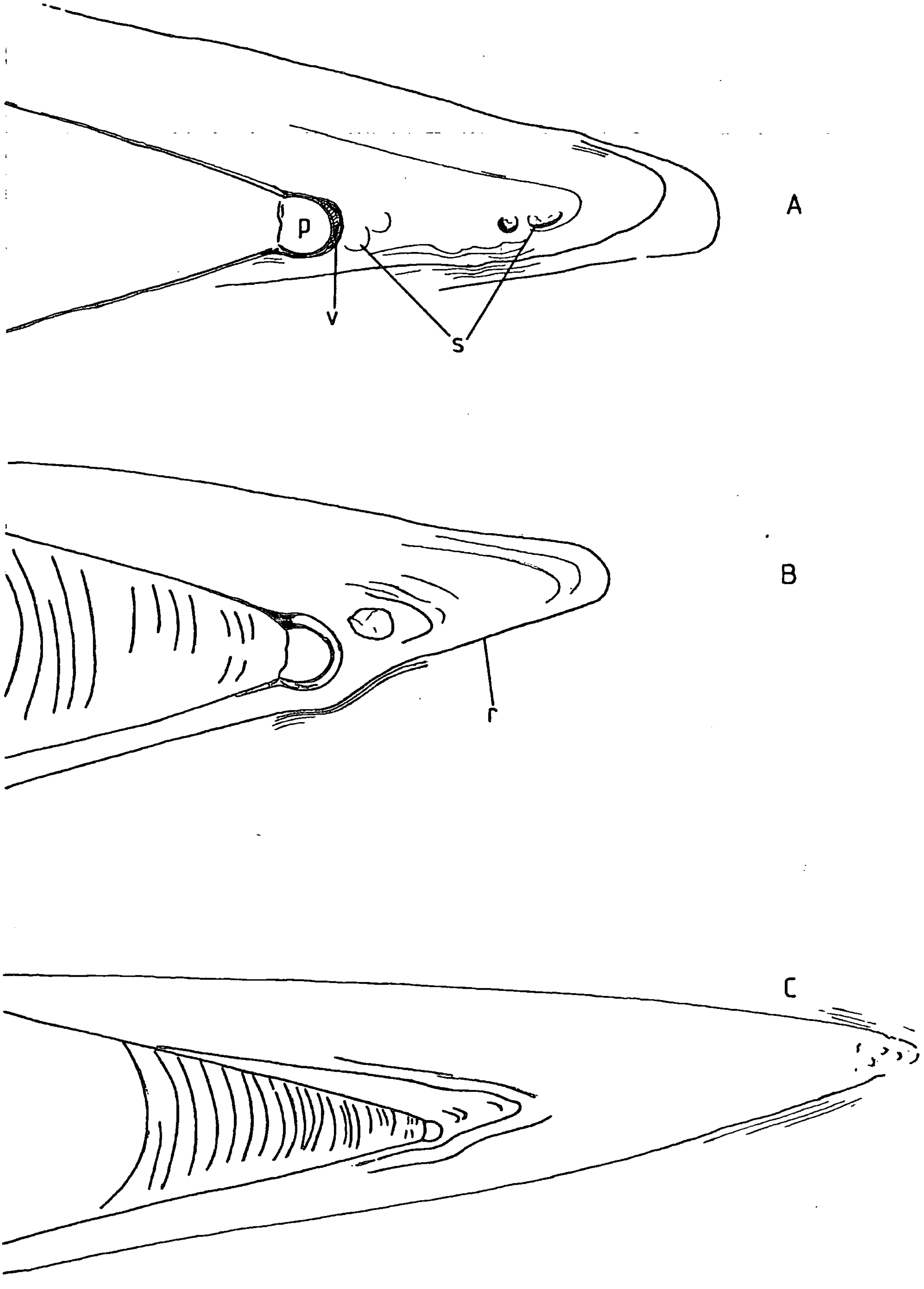


FIG.57 Belemnites abruptus: camera lucida drawing of median longitudinal polished section of specimen D175, bed 110 V, x6. (See also figs. 58 and 59A,B)

a - poorly defined material along apical line
b - prominent growth line enclosing (a) and marking change of slope in growth curve (see text)
c - region of pale lamellae surrounding (b), reflecting low original organic content

bars indicate portions of rostrum shown in figs. 58A and 59a

(The posterior part of the alveolus is filled with sparry calcite containing traces of septa; the anterior part of the alveolus is filled with argillaceous material containing well formed gypsum crystals.)

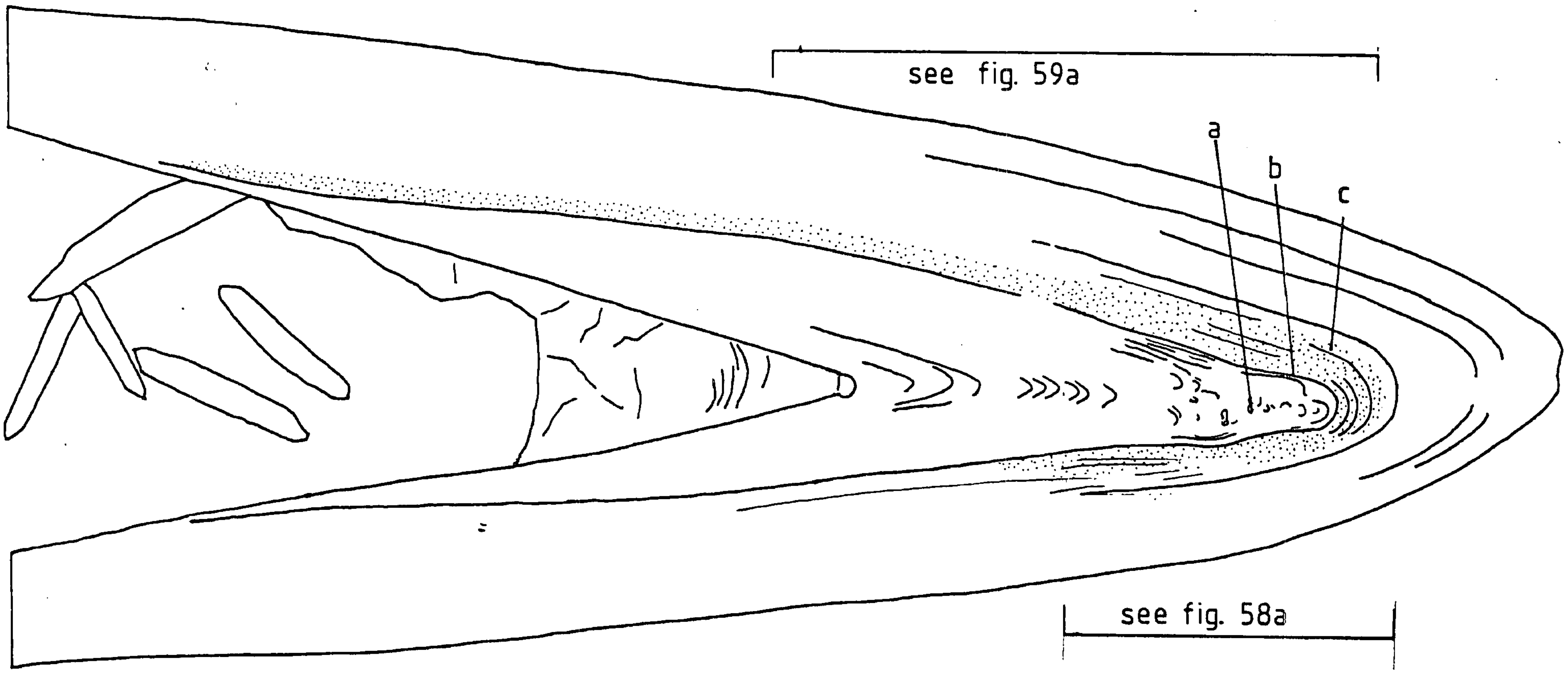


FIG. 57

FIG. 58 Belemnites abruptus: camera lucida drawings of median longitudinal polished section of specimen D175. (See also figs. 59A,B)

A: portion of rostrum indicated by in fig. 57, x12

B: part of (A), x24

Note spherulitic calcite and convoluted lamellae.

FIG.58

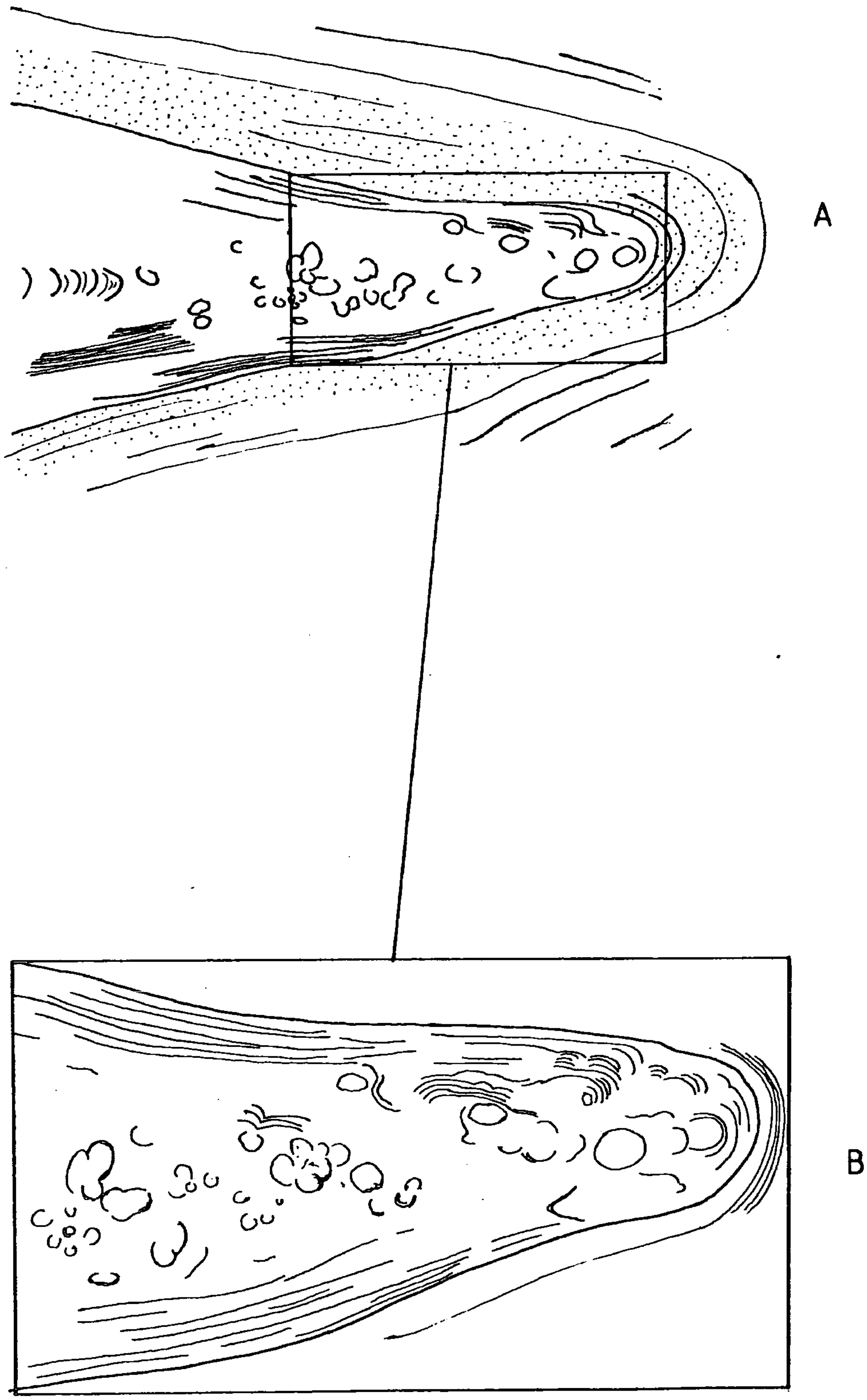


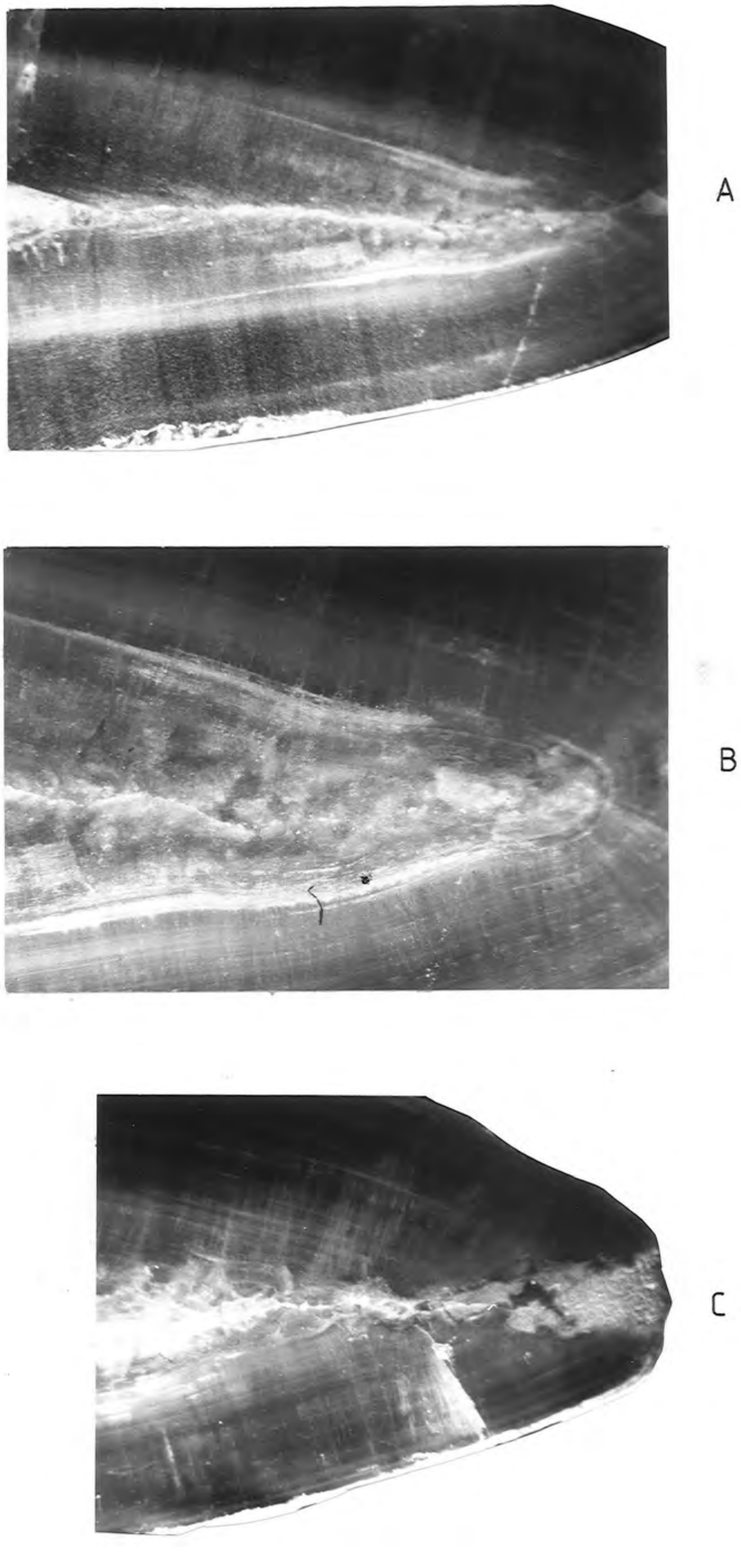
FIG.59 Belemnites abruptus: photographs of median longitudinal polished sections.

A: D175 bed 110 V, x6: part of rostrum shown in fig. 57

B: D175, x12: area shown in fig 58A

C: D106 bed 110 V, x6, showing weathered apical region filled with matrix material, producing an umbilicus at the apex

FIG. 59



Belemnites cricki (Lissajous, 1927)

Plates 22,23.

non 1820	*Belemnites penicillatus* sp. nov. Schlottheim, p. 50.
non 1827	*Belemnites penicillatus* Schlottheim; de Blainville, p. 89, pl. 3, fig. 7.
1828	*Belemnites penicillatus* de Blainville (sic); Sowerby, p. 181, pl. 590, figs. 5 & 6.
non 1830-33	*Belemnites oxyconus* sp. nov.; Hehl in Zieten, p. 27, pl. 1, fig. 5.
non 1849	*Belemnites tripartitus oxyconus* Hehl; Quenstedt, p. 419, pl. 26, figs. 19 & 20.
p. 1866	*Belemnites penicillatus* Sowerby (sic) Phillips, p. 34, pl. 1, fig. 2.
1867	*Belemnites oxyconus* Quenstedt (sic); Phillips, pp. 87 - 89, diag. 23, p. 88.
1925	*Belemnites cricki* sp. nov.; Lissajous, p. 116 (no description or fig.).
1927	*Prototeuthis cricki* sp. nov.; Lissajous, p. 7, pl. 1, figs. 1 & 2.
v .1928	*Angeloteuthis gabriel* sp. nov.; Lang, pp. 206 - 208, pl. 15, figs. 11 & 12; text fig. 2, no. 10.
v .1928	*Angeloteuthis raphael* sp. nov.; Lang, pp. 208 - 209, pl. 15, figs. 9 & 10; text fig. 2, no. 8.
v .1928	*Angeloteuthis michael* sp. nov.; Lang, p. 209, pl. 15, figs. 13 & 14; text fig. 2, no. 8.
v .1928	*Angeloteuthis uriel* sp. nov.; Lang, p. 209 - 211, pl. 13, figs. 3 & 4; text fig. 2, no. 9.

Type material

In the absence of a holotype, a lectotype should be selected from material in University of Lyon, collected by Lissajous from the "Belemnite bed" (in this case, beds 118b - 119) of Charmouth, which is probably still extant.

Failing this, BMNH C28939 (holotype Angeloteuthis gabriel Lang), from bed 118c, would be a suitable neotype.

Other material

Author's collection, Belemnite Marls, foreshore below and to west of Golden Cap, nr. Charmouth, Dorset: 120 specimens

beds 118b - c: D139, TB751 - 756, TB758, TB760, TB765 - 788, TB877 - 896, TB995 - 1024

beds 118c (top) - 118 d: TB898 - 917, TB919, TB921 - 925

bed 119: D137 - 140, TB108, TB1085 - 1090

BMNH, coll. W.D. Lang, Belemnite Marls, nr. Charmouth, Dorset: 51 specimens

bed 118b: (A. gabriel) C28937, C28938, C28961; (A. raphael) C28962, C28967, C28968

bed 118c: (A. gabriel) C28927 - 28935, C28937 - C28939 (holotype), C28947, C28961, C28971, C43850; (A. raphael) C28943 - 28945 (holotype), C28946, C28948, C28950 - 28954, C28956 - 28960, C28969, C43843, C43886; (A. michael) C28942, C28972, C28976, C29511; (A. uriel) C28983

bed 118d: (A. uriel) C28982, C28984, C28985 (holotype)

bed 119: (A. raphael) C28977, C28980; (A. michael) C2981 (holotype)

Description

Rostrum medium sized, short relative to diameter, cylindrical or slightly tapering for 60 - 70% of its length, then narrowing rapidly to the apex. Transverse section usually strongly compressed from an early stage and increasing markedly during ontogeny.

Apex variable, blunt to sharply pointed, often recurved towards the dorsal surface. Often umbilicate.

Wide, shallow apical furrows usually well developed, merging anteriorly into lateral facets which may encompass shallow lateral furrows. Prominent apical striae often present.

Epirostrum occasionally developed, usually short and/or incompletely preserved.

Alveolus slightly excentric, typically 30 - 50% of total rostral length.

Rostra almost certainly dimorphic, although bimodal distribution into comparatively stout and slender forms is not as marked as in some other species.

Discussion

The interpretation of B. cricki is based on Lissajous' posthumously published description (1927, in Roman (ed.)) of a species from the "belemnite Bed" of Charmouth that obviously corresponds to material from beds 118b - 119 which comprise part of the vaguely defined "Belemnite Bed" of earlier collectors and authors. The figures accompanying the description (1927, pl. 1, figs. 1 & 2) are of specimens in Lissajous' collection from the Lower Pliensbachian of Cheltenham (no further details are given) which were selected by the editor, Roman. This locality not being mentioned in the description, a lectotype should be chosen from Lissajous' Charmouth material, if this is still extant.

The elements of Lissajous' diagnosis (1927, p. 7) are incorporated with the description given above, with only one important difference: he regarded the degree of compression of the rostrum to be much less marked in the adults than in juveniles, whereas in fact the reverse is normally the case. It is probable that his sample was small and not representative in this respect, comparatively uncompressed larger rostra being very much in the minority. He also does not mention the occurrence of epirostra, which occur very occasionally in the species.

Earlier references to this belemnite (see synonymy) do not distinguish it from superficially similar species whose types are from widely separated horizons. Hence although this form from the Charmouth "Belemnite Bed" has been known at least since the early nineteenth century (B. penicillatus de Blainville in Sowerby, 1928 where pl. 590, figs. 5 & 6 are very good figures of B. cricki from below Golden Cap), cricki is the earliest acceptable specific name.

B. penicillatus Schlotheim, 1820, and Schlotheim interpreted by de Blainville, 1827, is from the Upper Lias or Middle Jurassic, and probably belongs to the group of B. acuarius Schlotheim (Lissajous 1925, p. 120).

Phillips' (1866, pp. 34 - 37, pl. 1, fig. 2) B. penicillatus de Blainville includes specimens from Golden Cap and nearby which are definitely of B. cricki, and from the "Lower Lias (middle part) near Cheltenham", which may be. His material from the Sinemurian (bucklandi Zone, near Bath; turneri Zone, near Taunton; obtusum Zone, near Bristol) almost certainly represents one or more other species, neither B. penicillatus nor B. cricki. Specimens from the Lower Lias of Antrim and of Robin Hood's Bay, Yorkshire, are also, probably incorrectly, ascribed to B. penicillatus, but I do not know whether B. cricki occurs in these areas. Unfortunately, Phillips' figured specimens are not individually localised.

B. oxyconus Hehl (in Zieten, 1830 - 33) is a Toarcian form (Lissajous 1925, p. 116). Phillips (1867, pp. 87 - 89, diag. 23) applied the name (attributing authorship to Quenstedt, who, however, was in accord with Zieten's publication (Quenstedt 1849, p. 419)) to probable specimens of B. cricki, showing recurved apices, from "Cheltenham, in the Belemnite Bed of the Lower Lias". Apparently Lissajous originally intended to base his Prototeuthis cricki on this material (Lissajous 1925, p. 116: Belemnites cricki is proposed, without figure or description, in place of Phillips' B. oxyconus which is preoccupied) but, as shown above, a lectotype or neotype from Charmouth is required.

Lang (1928, pp. 206 - 211) divided the single species under discussion into four species, with characteristic reservations, "The rostra of the four species of Angeloteuthis grade to some extent, being very variable, both in proportions of length to breadth and in the amount of compression." (p. 206). The species are distinguished on grounds of relative shortness and slenderness, relative amount of compression and form of the apex. In fact, the continuity of variation in these characters precludes such a separation. There is apparently a division (apparent only from internal measurements - see below) into two adult rostral forms which are here regarded as probable gracile and robust sexual dimorphs.

Lang was aware of Lissajous' (1927) paper, listing Prototeuthis cricki as a possible synonym of Angeloteuthis gabriel Lang (1928, p. 207).

After 1928, there are no fresh interpretations of the species, although Schumann (1974, p. 23) regarded Angeloteuthis raphael Lang and A. gabriel Lang as possible synonyms of Belemnites paxillosus paxillosus Lamarck, a suggestion that is not endorsed here.

Ontogeny

The rostral ontogeny of this species can be described essentially as growth from a small, only slightly compressed cone to a rather stubby adult rostrum which is normally strongly compressed. As figures 63 to 64 show, the early conical profile gives way to the adult parallel sided profile with rapidly tapering apex at an early stage (post-alveolar length about 4 mm).

Throughout ontogeny, the rate of thickening of the vertical diameter tends to increase slightly relative to rate of lengthening, which shows as the gentle upward curve of most of the growth curves in figure 62. Horizontal diameter increases at a slower relative rate, producing the marked increase in compression represented in figure 65C.

In figure 62, the distribution of growth lines and points representing whole specimens is suggestive of dimorphism, with gracile and robust specimens being distinguishable on these internal parameters at post-alveolar lengths greater than about 25 mm. This dimorphism is only manifest in the sample from bed 118b and most of 118c (see below). The degrees of compression observed within each group are identical, which is consistent with observations on other more obviously dimorphic species from the Belemnite Marls.

One or two primary spherules are occasionally visible within the area enclosed by the earliest clear growth laminae.

When the rostrum is more or less fully grown, an epirostrum is very occasionally developed (pl.22, fig.2); no complete examples were collected, the structure being represented by a few mm of crushed tube with a weathered appearance.

Stratigraphical variation

The material studied is divided into three stratigraphic samples: 1) from beds 118b and most of 118c, 2) from the topmost two units of bed 118c and all of 118d and 3) from bed 119.

Lang (1928, p. 206) commented that the length of Angeloteuthis gabriel "decreases with the height of its horizon, since the longest forms occur in 118b and the shortest high in 118c". This statement is supported by the present research which shows that specimens of Belemnites cricki over 60 mm long are common only below the top units of bed 118c (fig.65A). Lang's other three species of Angeloteuthis also fit into (and were partly based upon) this length distribution, thus A. michael (118c (top) - 119) and A. uriel (118c - d) include mostly rather stout and short specimens of B. cricki, and A. raphael (118b - 119) consists mainly of more slender, usually longer specimens and encompasses in particular specimens from beds 118b - c which are here regarded as probable gracile rostra of the dimorphic species (fig.60).

If the variation in form observed in beds 118b - c is due to dimorphism, then only the robust form is present in beds 118c (top) to 119. Intermittent occurrence of one or other dimorph is consistent with the observed vertical distributions of the other dimorphic species discussed in the present work.

In the sample measured, rostra from beds 118c (top) - d tend to be slightly more compressed than those from below and above, although a larger sample is required to determine the level of significance of this. Effectively, apart from the supposed effects of dimorphism, the species remains morphologically stable throughout its short range in the Belemnite Marls.

As yet, too little material is known from other localities for a detailed comparison to be made with that from the Charmouth area. One point which may or may not be significant is that B. cricki often has an upwardly recurved apex, which strongly resembles that commonly developed in B. aduncatus (q.v.) which is common from bed 121 upwards although it first occurs in bed 117. The two species have little else in common.

Distribution

1) Charmouth, Dorset: Belemnite Marls, ibex Zone, masseanum and valdani Subzones, beds 118b - 119.

2) Cheltenham, Gloucestershire: ibex Zone, Belemnite Bed (Lissajous, 1927, pl. 1, figs. 1 & 2).

FIG. 60

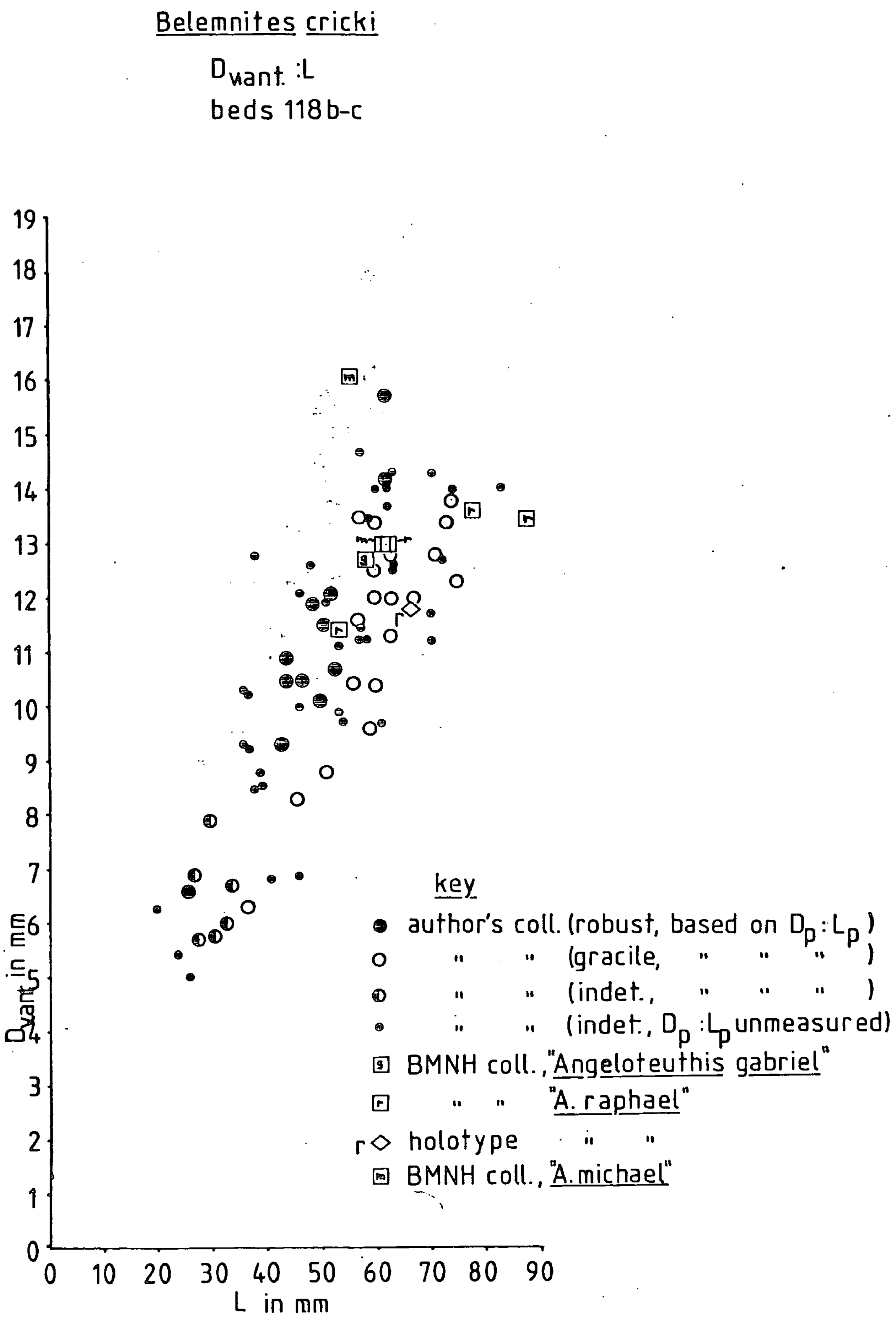

Belemnites cricki
$D_{vant.}:L$
beds 118b-c
$D_{vant.}$ in mm
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
L in mm
0
10
20
30
40
50
60
70
80
90
key
● author's coll. (robust, based on $D_p:L_p$)
○ " " (gracile, " " ")
◐ " " (indet., " " ")
• " " (indet., $D_p:L_p$ unmeasured)
g BMNH coll., "Angeloteuthis gabriel"
r " " "A. raphael"
r◇ holotype " "
m BMNH coll., "A. michael"

FIG. 61

B. cricki

$D_{v.ant.}$:L

beds 118d–119

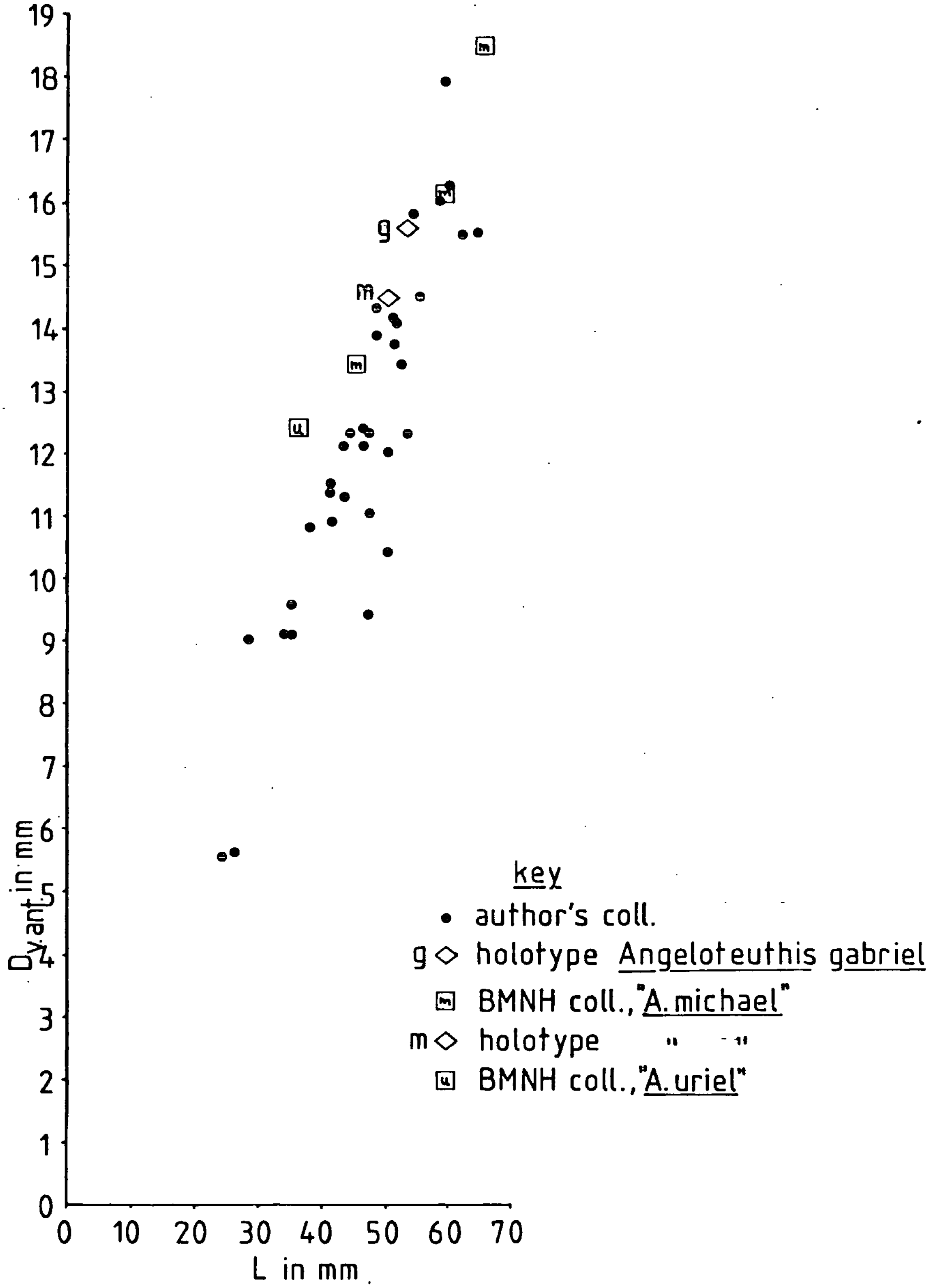


FIG. 62

Belemnites cricki

$D_p : L_p$

beds 118b–119

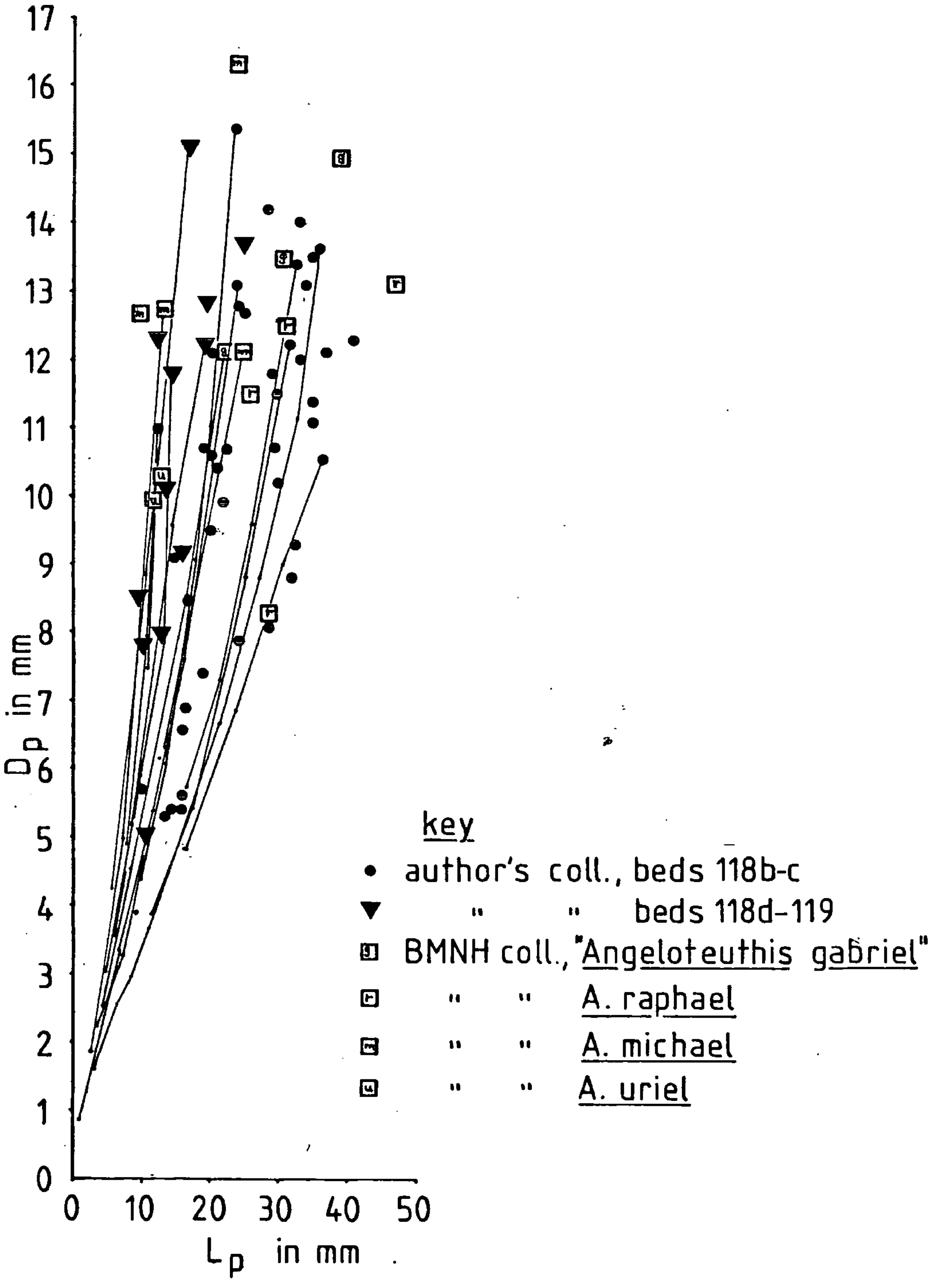


FIG.63 Belemnites cricki: camera lucida drawings of median longitudinal polished sections.

A: TB1009 (gracile) beds 118b-c, x12

B: TB909 (robust) bed 118c (top), x12

C: TB1007 (gracile) beds 118b-c, x12

p - protoconch
r - earliest clear rostral growth line
s - primary spherule

FIG. 63

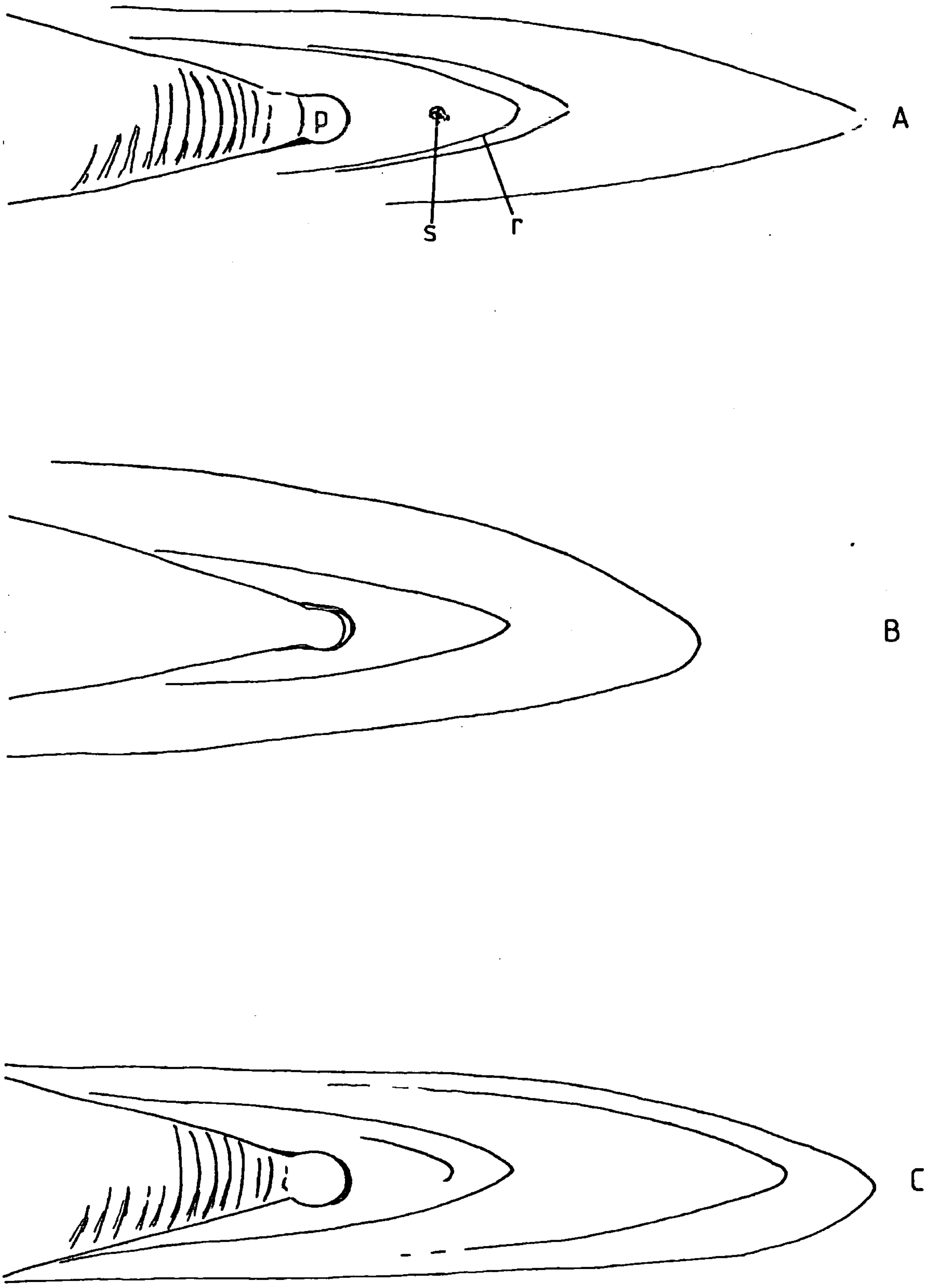


FIG.64 *Belemnites cricki*: camera lucida drawings of median longitudinal polished sections.

A: TB909 (robust) bed 118c (top), x6

B: TB1007 (gracile) beds 118b-c, x6

o - outer surface of rostrum

FIG. 64

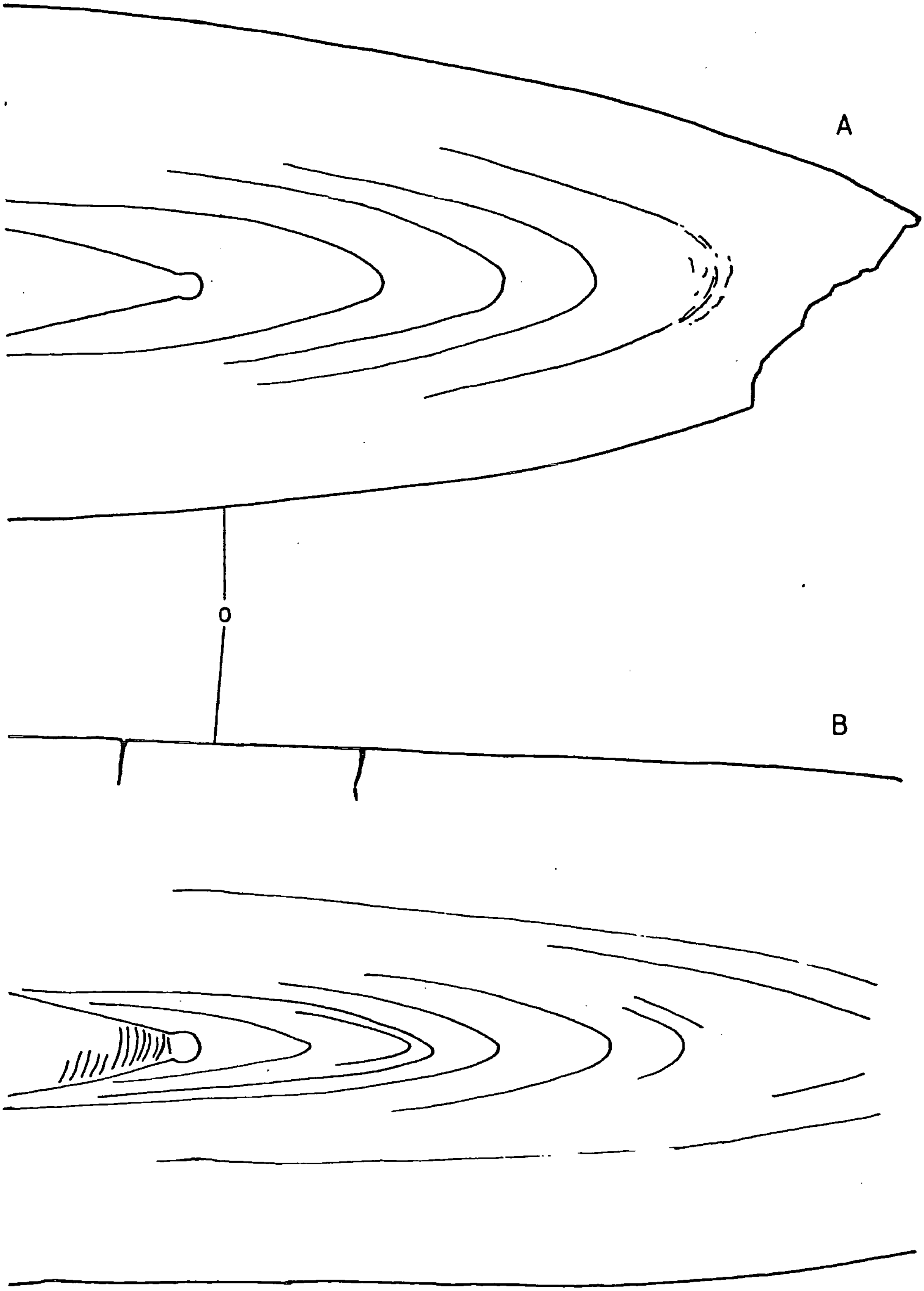
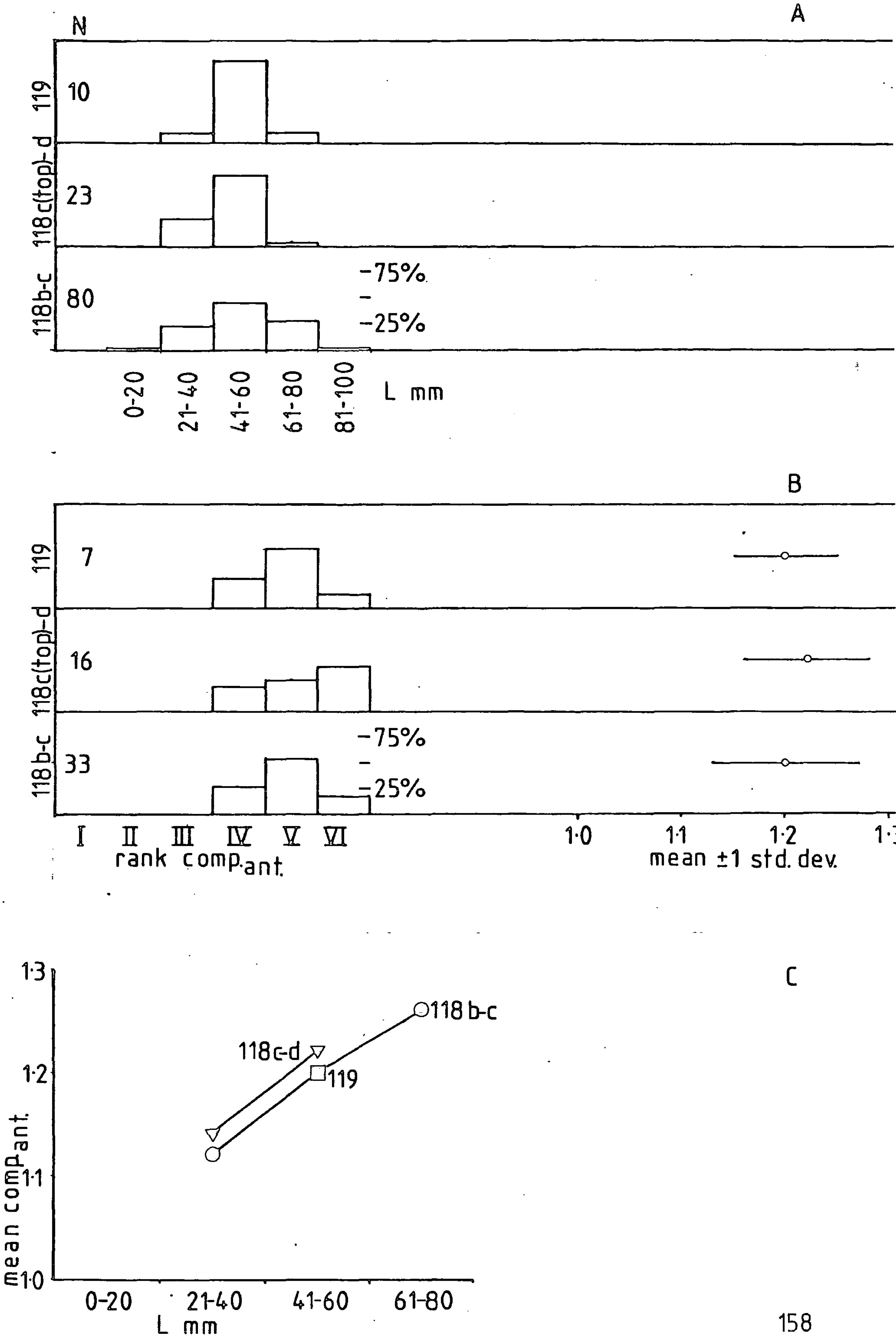


FIG. 65

Belemnites cricki
length and compression



Belemnites ridgensis (Lang 1928)

Plate 24 figs. 1, 2

1928 Passaloteuthis ridgensis sp. nov.; Lang, pp. 203 - 204, pl. 14, fig. 6; text fig. 3, no. 2.

Holotype

BMNH C28907 (Passaloteuthis ridgensis), Belemnite Marls, bed 118c, foreshore South East of Golden Cap (below Ridge Cliff), near Seatown, Dorset. Established by Lang (1928) p. 203, pl. 14, fig. 6.

Other material

Author's collection, Belemnite Marls, foreshore between Westhay Cliff and Golden Cap, near Charmouth: 7 specimens

beds 112d-f: ?TB702
bed 117: TB749, TB750
bed 118a: TB988
bed 118c: TB763, TB1030, TB1031

BMNH, coll. W.D. Lang, Belemnite Marls, foreshore below Golden Cap: 3 specimens

bed 118c: C28908 - 28910

Description

Rostra attaining fairly large size, stout, tending to be slightly clavate in the horizontal plane, not usually so in the vertical.

Section always depressed in posterior half of rostrum, often so in anterior. This depression is associated with a characteristic flattening of the ventral surface, coupled with ventro-lateral inflation, which produces a distinctive outline to the section (fig. 110C).

Paired lateral furrows variably developed; the upper ones are usually fairly prominent and merge into well developed dorsolateral apical furrows.

Alveolus occupies 40 - 60% of total rostral length, and is moderately excentric.

Dimorphism not recognized.

Epirostrum unknown.

Discussion

This rare but distinctive belemnite was defined by Lang (1928, p. 203) on the basis of its unelongated apex and stout rostrum bearing broad, well-defined dorsolateral furrows, "particularly conspicous at the apex". The unusual ventral flattening and depressed section of the rostrum were not mentioned, although the depression is apparent from the measurements given of specimen C28910.

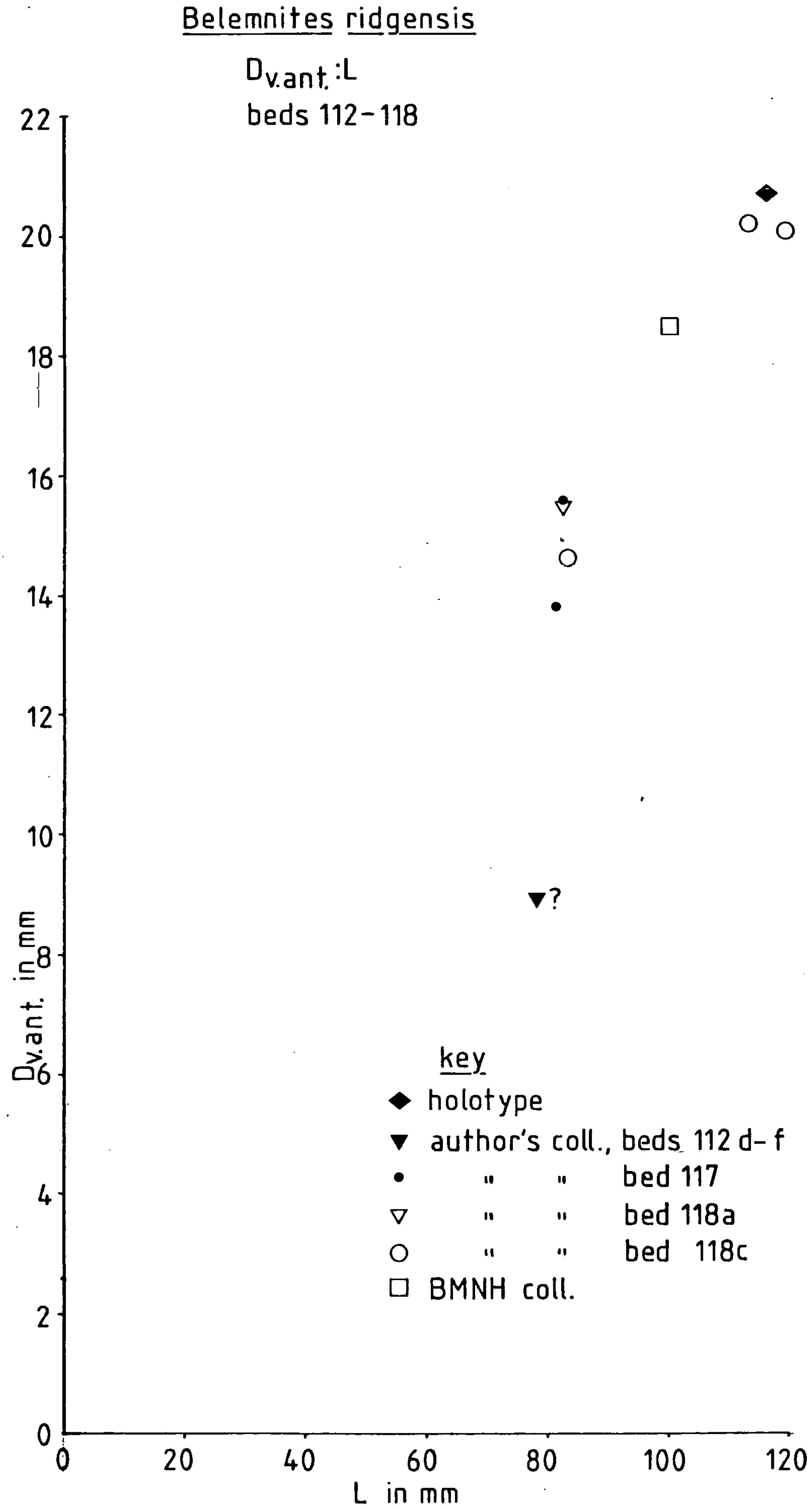
Lang's four specimens are all from bed 118c. The present author has specimens from beds 118a, 118c and 117, with a possible specimen from beds 112d-f (pl.24 fig.3); the latter is smaller than the others, comparatively slender and markedly clavate. It shares, however, the ventral flattening, rostral depression and prominent dorsolateral furrows of the much larger specimens from the type horizon, and does not resemble other material (mostly B. nitidus (q.v.)) from beds 112d-f.

Too few specimens are known to provide definitive information on ontogeny and stratigraphical variation. Due to the inadequacy of the sample, the data on compression, clavateness and length are presented for individual specimens (figs.68A-D).

The species has not been recognized outside the type area. Schumann (1974, p. 23) regarded Passaloteuthis ridgensis Lang as a possible synonym of Belemnites paxillosus paxillosus Lamarck, but, in view of the distinctive characters described above, B. ridgensis is best regarded as a separate species.

Distribution

Charmouth and Seatown, Dorset: Belemnite Marls, jamesoni Zone, brevispina Subzone, ?beds 112d-f, jamesoni Subzone, beds 117, 118a; ibex Zone, masseanum Subzone, bed 118c.


Belemnites ridgensis
$D_{v.ant.}$:L
beds 112-118
$D_{v.ant.}$ in mm
22
20
18
16
14
12
10
8
6
4
2
0
0
20
40
60
80
100
120
L in mm
?
key
◆ holotype
▼ author's coll., beds 112 d-f
● " " bed 117
▽ " " bed 118a
○ " " bed 118c
□ BMNH coll.

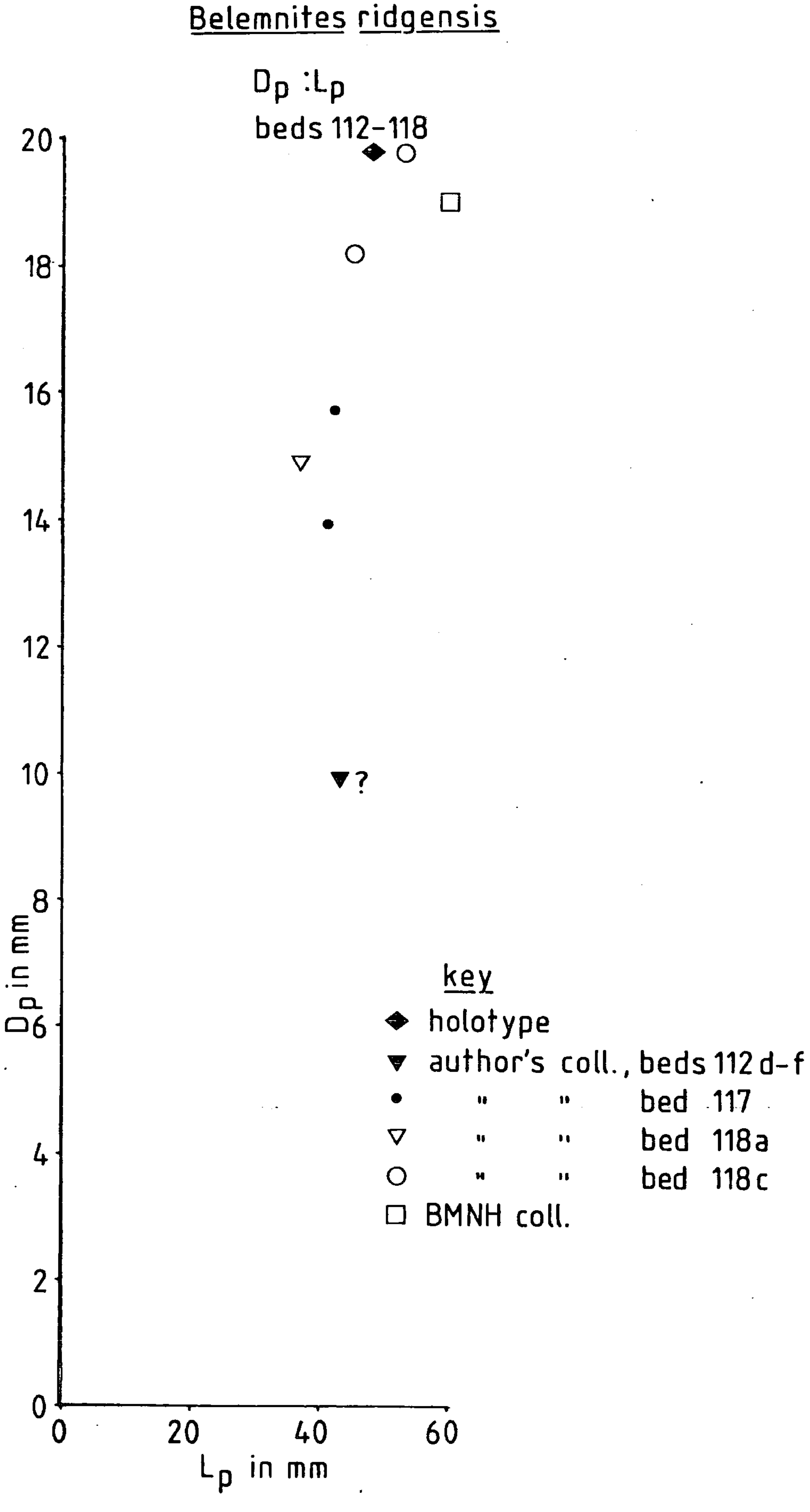
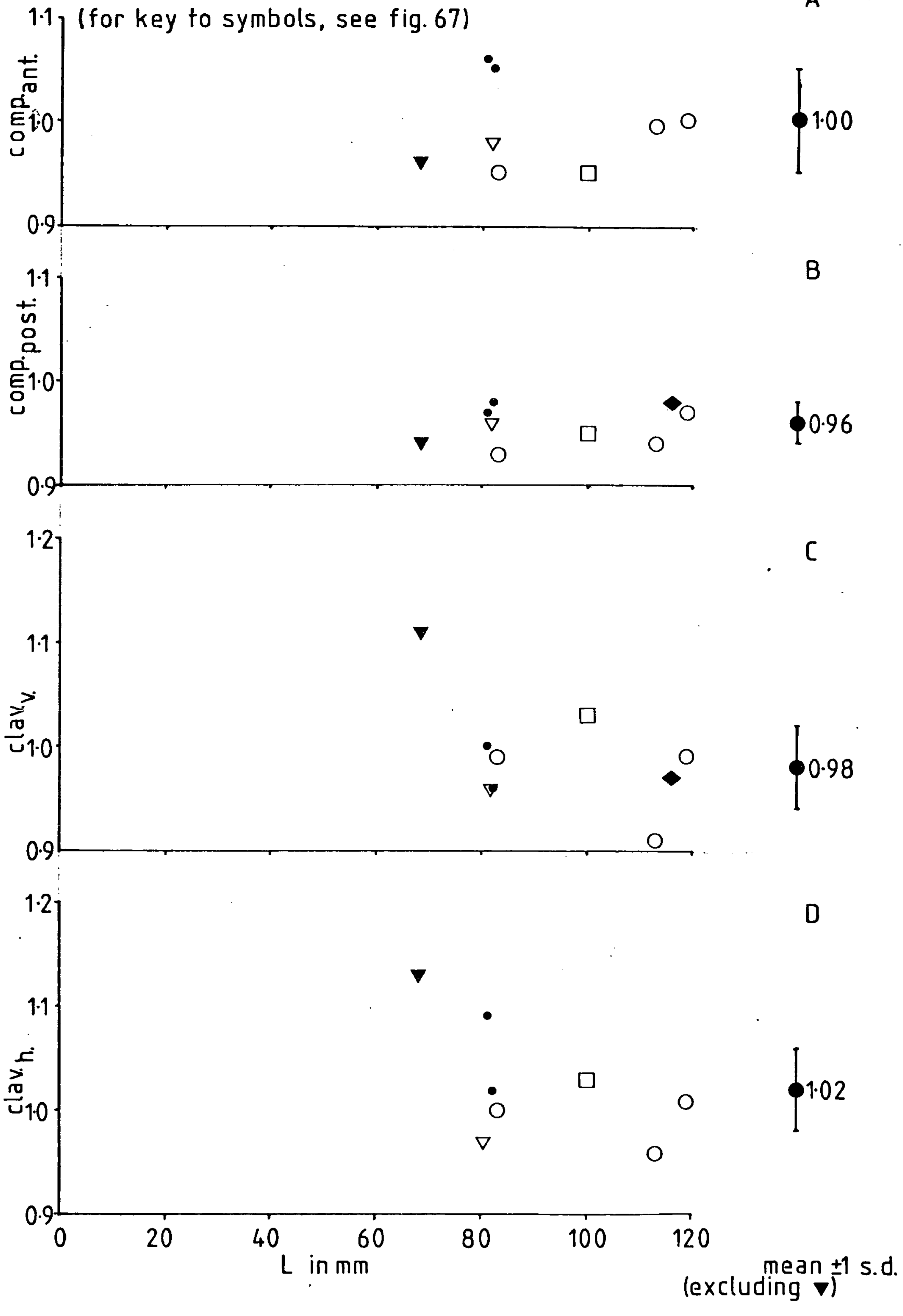

Belemnites ridgensis
Dp :Lp
beds 112-118
Dp in mm
Lp in mm
20
18
16
14
12
10
8
6
4
2
0
0
20
40
60
?
key
◆ holotype
▼ author's coll., beds 112 d-f
● " " bed 117
▽ " " bed 118a
○ " " bed 118c
□ BMNH coll.

FIG. 68

Belemnites ridgensis
compression and clavateness
(for key to symbols, see fig. 67)



Belemnites aduncatus Miller, 1826

Plates 25-27

1826	*Belemnites aduncatus* sp. nov.; Miller, p. 59, pl. 8, figs. 6, 7, 8.
? 1826	*Belemnites elongatus* sp. nov.; Miller, p. 60, pl. 7, figs. 6, 7, 8.
1827	*Belemnites apicicurvatus* sp. nov.; de Blainville, pp. 76 - 77, pl. 2, fig. 6.
1827	*Belemnites aduncatus* Miller; de Blainville, pp. 77 - 78, pl. 4, fig. 2 (cop. Miller).
? 1829	*Belemnites elongatus* Miller; Sowerby, p. 178, pl. 590, fig. 1.
? 1830	*Belemnites apicicurvatus* de Blainville; Zieten, p. 30, Taf. 23, fig. 4.
p. 1840 - 42	*Belemnites elongatus* Miller; d'Orbigny, pp. 90 - 92, pl. 8, figs. 6 - 11.
? 1846 - 49	*Belemnites paxillosus numismalis* subsp. nov.; Quenstedt, p. 399, Taf. 23, fig. 21.
? 1858	*Belemnites paxillosus numismalis* Quenstedt; Quenstedt, p. 137, Taf. 17, fig. 12.
1866	*Belemnites apicicurvatus* de Blainville; Phillips, pp. 49 - 50, pl. 6, fig. 16.
? 1866	*Belemnites elongatus* Sowerby (sic); Phillips, pp. 50 - 52, pl. 8, fig. 7.
p. 1876	*Belemnites apicicurvatus* de Blainville; Tate and Blake, p. 319 (no fig.).
1883	*Belemnites apicicurvatus* de Blainville; Mayer-Eymar, p. 611 (no fig.).
1907	*Belemnites* (*Megateuthis*) *apicicurvatus* de Blainville;

Lissajous, p. 77, pl. 1, fig. 17.

1912 Belemnites apicicurvatus de Blainville; Werner, p. 119, Taf. 11, figs. 2, 3.

1922 Passaloteuthis apicicurvata (de Blainville); Naef, p. 234, text fig. 85 b.

1925 Belemnites aduncatus Miller; Lissajous, p. 52 (no fig.).

1925 Belemnites apicicurvatus de Blainville; Lissajous, p. 54 (no fig.).

1928 Passaloteuthis auricipitis sp. nov.; Lang, p. 204, pl. 14, fig. 4, text fig. 2, no. 4.

p. 1928 Passaloteuthis apicicurvata (de Blainville); Lang, pp. 205 - 206, pl. 14, fig. 5; text fig. 2, no. 3. (not material from bed 120c).

1962 b Belemnites apicicurvatus de Blainville; Schwegler, pp. 123 - 125, text figs. 17, 18.

? 1962 b Belemnites aff. apicicurvatus de Blainville; Schwegler, pp. 125 - 126, text fig. 19.

1974 Belemnites paxillosus apicicurvatus de Blainville; Schumann, pp. 24 - 25, Taf. 2, figs. 9 - 13; Taf. 3, figs. 1 - 2.

Neotype

BMNH C29521 (Passaloteuthis apicicurvata), Belemnite Marls, bed 120d, Westhay Water, near Charmouth, Dorset. Established by Lang (1928) p. 205 (not figured).

Other material

Author's collection, Belemnite Marls, between Charmouth and Seatown, Dorset: 14 specimens bed 117: TB858

beds 118b-c: TB874, TB875

beds 120d-e: TB147 - 149, TB1137 - 1141

bed 121: TB157, TB1214, TB1217, TB1218

Green Ammonite Beds, foreshore below Golden Cap: 75 specimens

beds 122a-c: TB546 - 552, TB554 - 561, TB564 - 567, TB571 - 581, TB918, TB920, TB1156 - 1172, TB1175 - 1191

horizon uncertain: D136, D210, D211, D213 - 219

? ibex and davoei Zones, Wutach valley, near Aselfingen, South West Germany: numerous uncatalogued specimens, mostly fragmentary.

BMNH, coll. and/or det. W.D. Lang, Belemnite Marls, near Golden Cap: 15 specimens

bed 119: (Passaloteuthis auricipitis) C29421; (P. apicicurvata) C29243

bed 120d: (P. apicicurvata) C28845, C28846, C29184, C29189, C29194, C29244; (P. cf. apicicurvata) C29515; (P. auricipitis) C28949 (holotype), C28922

bed 120e: (P. apicicurvata) C28839, C28923,

bed 121: (P. apicicurvata) C29529, C29530

Green Ammonite Beds, Golden Cap: 18 specimens (after Lang, 1936)

bed 122a: (P. apicicurvata) C42172

bed 122b: (P.apicicurvata) C42173, C42202

bed 122c: (P. apicicurvata) C28924, C42010, C42166, C42167, C42176 - 42179

bed 122d: (P. apicicurvata) C42020; (P. auricipitis) C42021

bed 126b: (P. auricipitis) C42013, C42095

bed 126c: (P. auricipitis) C42180

bed 127: (P. auricipitis) C28921, C42015

Description

Rostrum usually fairly stout, approximately cylindrical for much of its length, may be slightly clavate particularly in horizontal plane. Section nearly always compressed, oval to sub-rectangular.

Apex very acute, usually recurved, "narrowed apically to a slender point which is unsymmetrical, owing to the ventral outline generally curving regularly upwards, and the dorsal outline generally at first curving abruptly downwards, and then flattening to a nearly horizontal direction." (Lang 1928, p. 205). Apex commonly deformed (i.e. bilaterally asymmetrical), sometimes hooked (aduncate).

Apical dorsolateral grooves prominent, dorsal and ventral grooves often present together with more conventional striae. Paired lateral furrows faint, the upper members sometimes continuous with apical dorsolateral grooves.

Alveolus slightly excentric, typically occupying 25 - 40% of total rostral length.

Rostral surface of larger specimens often bears a raised striated or reticulated ornamentation.

Epirostrum unknown.

Discussion

The type (now lost) upon which Miller's <u>Belemnites aduncatus</u> was based (1826, pl. 8, fig. 6) is an apically deformed example of the common and ubiquitous species usually referred to <u>B. apicicurvatus</u> de Blainville (1827). Although it may be argued that Miller's specimen is pathological and hence not a suitable holotype, apical malformation is in fact fairly common in this species, and two of the present author's specimens from the Green Ammonite Beds (pl.25, fig.3) and one from the Belemnite Stone display hooked apices that resemble that shown in Miller's figure.

De Blainville recognized that Miller's B. aduncatus differed only in slight degree from B. apicicurvatus: "This species, Belemnites aduncatus, which was established by Mr. Miller, does not appear to differ much from my Belemnites apicicurvatus, except that its apex is more pointed, more hooked, and the apical furrows are deeper and more numerous." (1827, p. 77).

A locality is not given for Miller's holotype, but he does say that the species comes from the "Lyas and lyas clay" of Lyme Regis and Weymouth. As there are no Liassic outcrops near Weymouth, it is obviously desirable to select a neotype from the Lyme Regis area. (The reference to Weymouth was perhaps based on Oxford Clay material.) The most likely sources for any specimens of B. aduncatus, apart from loose fallen material, are the outcrops in the upper Belemnite Marls and lower Green Ammonite Beds in the vicinity of Golden Cap, and Lang's neotype of Passaloteuthis apicicurvata from the nearby Westhay Water is thus an appropiate basis for interpretation of the species.

Miller's figured specimen (also lost) of Belemnites elongatus (1826, pl. 7, figs. 6 - 8) is probably a comparatively featureless specimen of B. aduncatus from the Green Ammonite Beds or, possibly, the Belemnite Stone. (It is only "elongate" by virtue of the preservation of the complete or nearly complete phragmocone.). Lack of morphological detail coupled with its vague stratigraphic position (as with B. aduncatus, "Lyas and lyas clay") do not permit positive identification, and B. elongatus must be regarded as an unavailable name.

Lang (1928), following Naef (1922), placed B. apicicurvatus in the genus Passaloteuthis Lissajous (1915) (under which name it appears in the BMNH handbook "Mesozoic Fossils" (1962)) and erected a further species, P. auricipitis (1928, p. 204, pl. 14, fig. 14), based on stout rostra from the ibex and davoei Zones of the Charmouth area, which is almost certainly conspecific with his more slender P. apicicurvata from the same horizons.

Schumann's figured material from North Germany, given subspecies status as Belemnites paxillosus apicicurvatus (1974, pl. 2, figs. 9 - 13; pl. 3, figs. 1, 2) agrees well with the material from the type area, and also includes (pl. 3, fig. 1) a specimen with a hooked apex, very similar in this respect to Miller's holotype of B. aduncatus although Schumann makes no reference to this.

Ontogeny

A more detailed discussion of the ontogeny of B. aduncatus awaits a fuller study of the belemnite fauna of the Green Ammonite Beds.

The early growth stages seen in broken or sectioned specimens are more robust and tending to conicity than in B. nitidus, with which the species is most likely to be confused. This character persists to a fairly late stage, and is apparent in many more or less half grown rostra (total length 40 - 60 mm).

Degrees of compression and clavateness tend to increase slightly with size, although they never become particularly marked.

Figure 69 shows that the rostra of B. aduncatus, from the beds examined, fall into two very clearly defined size groups, whilst a third may be represented by the two smallest specimens. This size distribution is very similar to that observed in some samples of B. nitidus, and such patterns are discussed on p.200. One extremely large specimen of B. aduncatus was collected (pl.27 , fig.1), represented by the point at L = 150 mm, $D_{v.\ ant.}$ = 19.4 mm, which it is tempting to regard as a rare survivor into its fourth year (or season).

The etiolated apex that is the most obvious feature of the species develops gradually, so that although clearly present in many specimens of the second (40 - 80 mm) size group, it is most distinctive in the third group.

Many specimens, mostly in the third group, display some surface ornamentation, usually of a reticulated or striated pattern but sometimes including areas of small longitudinally elongated pustules. These markings are quite distinct from the commonly observed ridges and depressions caused by etching and exfoliation of growth laminae, and are further considered on p.258.

Stratigraphical variation

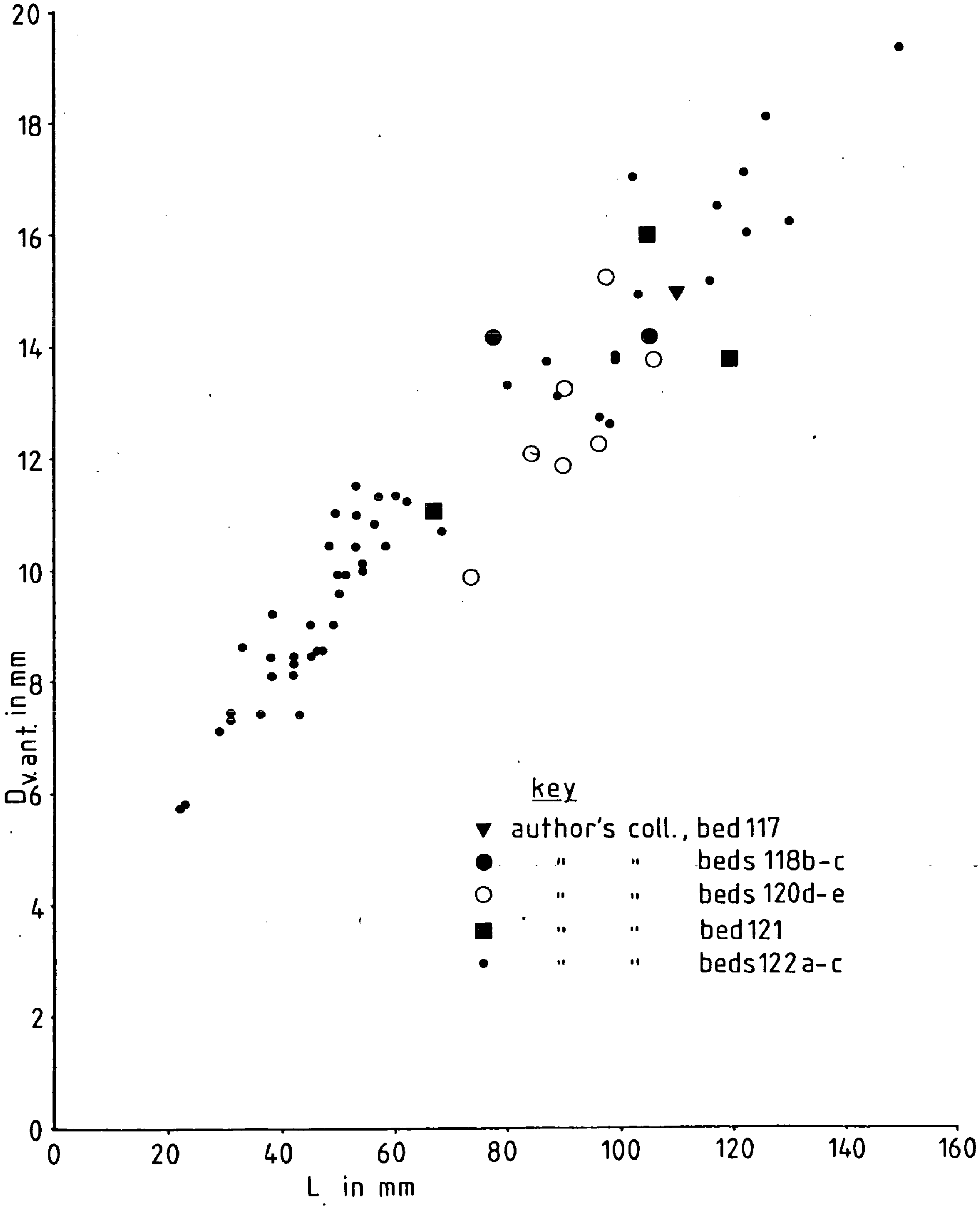
This species was only collected in reasonable numbers from the basal Green Ammonite Beds. From the limited number of specimens recovered from the Belemnite Marls, it appears that there is a slight reduction in the degree of clavateness from the Belemnite Marls to the Green Ammonite Beds. The degree of compression remains stable (figs.71A,72). A single specimen (TB858, pl.25 , fig.1), which is fairly clavate, was found in bed 117, and is the earliest specimens of B. aduncatus known to me. Occasional specimens occur in beds 118 and 119, but the species only becomes reasonably common in bed 120d. In bed 121 and the overlying Green Ammonite Beds it is numerically superior to B. nitidus which is the commonest belemnite in the Belemnite Marls.

Records of Belemnites apicicurvatus are frequent (see synonymy) and cover many localities; virtually all of them refer to material that is probably conspecific with B. aduncatus, the range of forms illustrated generally agreeing closely with the species as it occurs in Dorset. Occasionally, longer and more slender specimens have been described (eg. Werner 1912, Taf. 11, fig. 2, from Lias gamma of Eislingen, South West Germany; this specimen is very similar to that described as B. paxillosus numismalis, by Quenstedt (1858, Taf. 17, fig. 12) from Pliensbach). It is quite probable that these are variants of B. aduncatus; the single exceptionally large specimen, mentioned above under "Ontogeny", approaches these forms.

Distribution

1) Charmouth and Seatown, Dorset: Belemnite Marls, jamesoni Zone, jamesoni Subzone, bed 117 (one specimen), 118b; ibex Zone, beds 118c - 121; Green Ammonite Beds, davoei Zone, beds 122 - 127.
2) Many other European localities, ibex and davoei Zones.

FIG.69



Belemnites aduncatus

$D_{v.ant.}:L$
beds 117-122c

FIG. 70

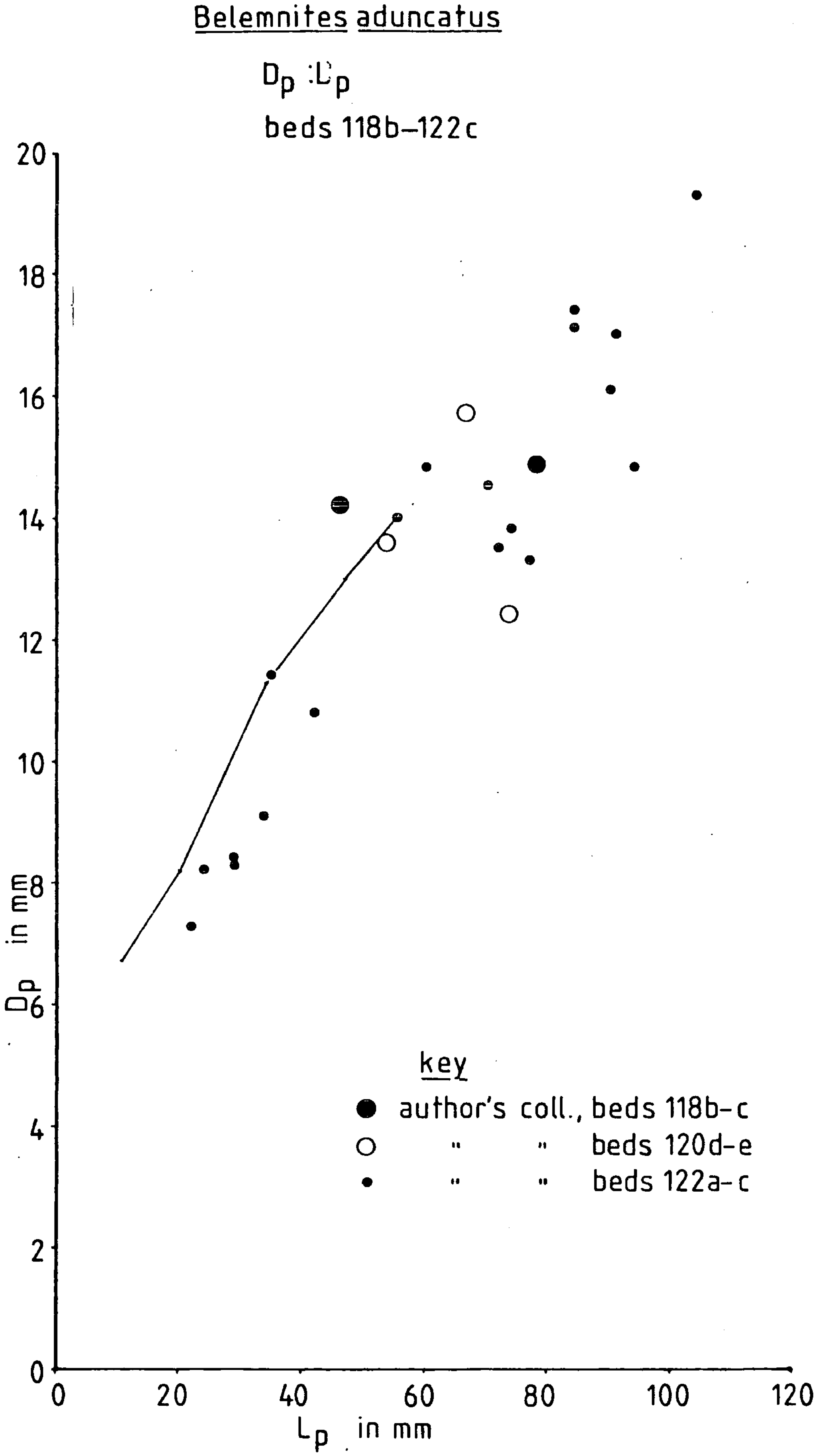

Belemnites aduncatus
$D_p : L_p$
beds 118b–122c
20
18
16
14
12
10
8
6
4
2
0
D_p in mm
0
20
40
60
80
100
120
L_p in mm
key
● author's coll., beds 118b-c
○ " " beds 120d-e
• " " beds 122a-c

FIG. 71

Belemnites aduncatus
compression and length

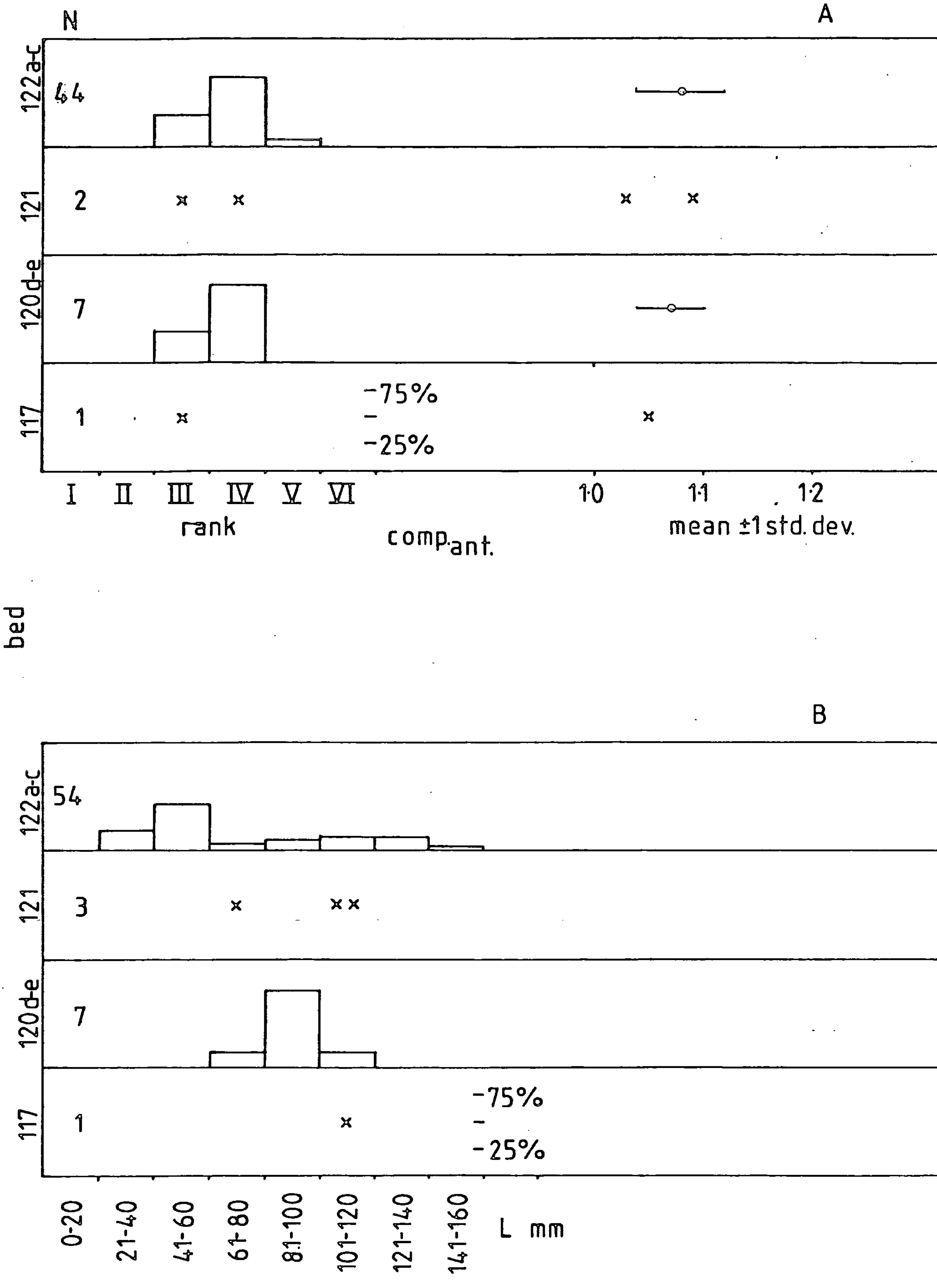
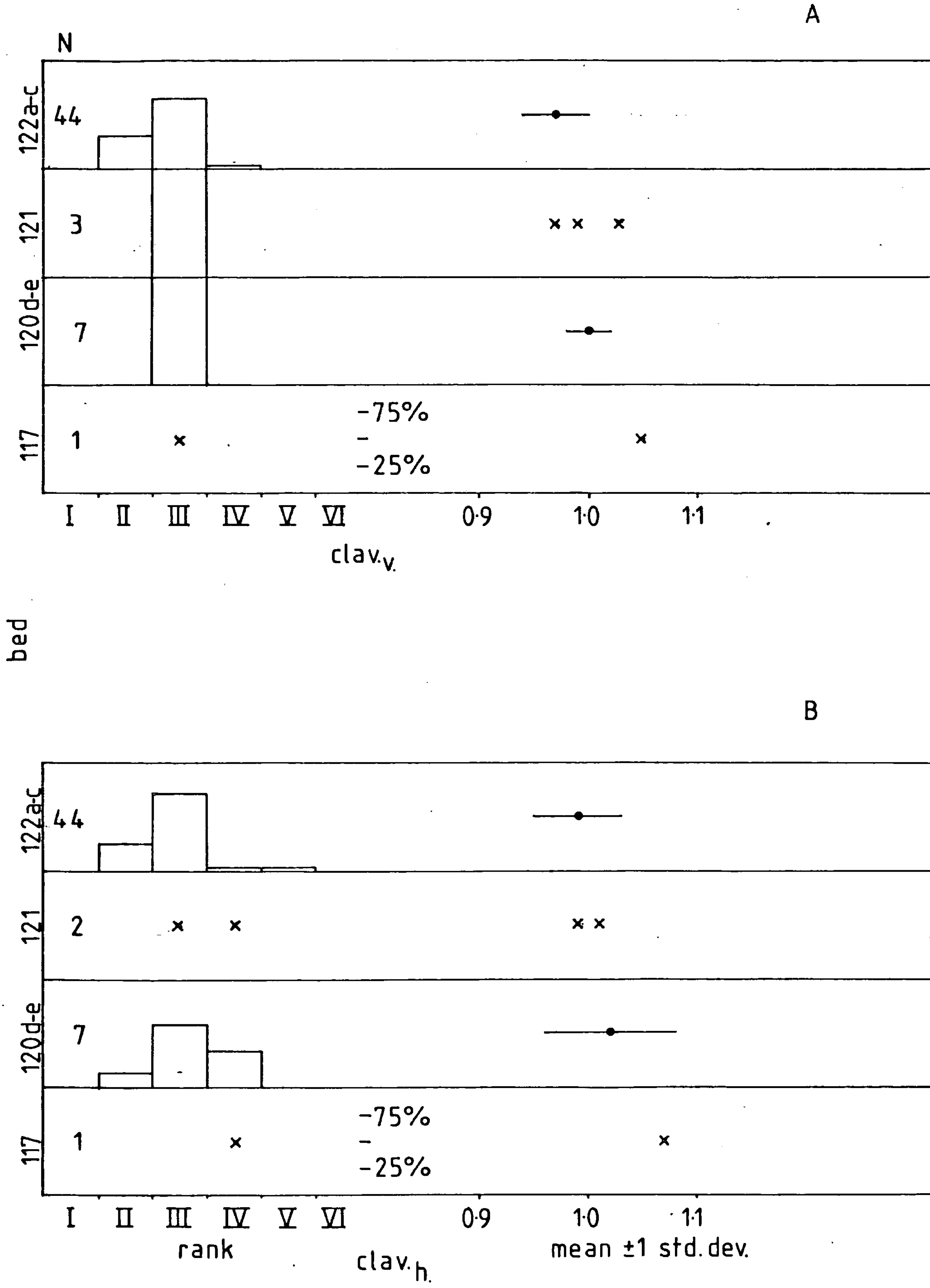


FIG. 72

Belemnites aduncatus
clavateness



Subfamily COELOTEUTHINAE Naef, 1922

Type genus: Coeloteuthis Lissajous, by monotypy.

Genus COELOTEUTHIS Lissajous, 1906

Type species: Coeloteuthis excavata (Phillips, 1866); Lower Pliensbachian, Belemnite Marls, Dorset coast.

Description

Rostrum attaining only a moderate size, profile an obtuse cone. Dorsolateral furrows present. Transverse section subcircular or subquadrangular.

Alveolar cavity occupies nearly the whole of the rostrum, which is reduced to a rather thin casing around the alveolus.

Epirostrum unknown.

Discussion

The above description is based on Lissajous (1925, p. 21).

The principal character of the genus is the extreme depth of the alveolus, and recognition is straightforward if this criterion is applied. Belemnites abruptus (q.v.), which externally resembles Coeloteuthis excavata and has often been regarded as conspecific with it, is quite clearly a stout representative of Belemnites. Once this is realised, Coeloteuthis remains as an extremely rare genus, encountered very sporadically in the Lower Pliensbachian. The few well attested occurrences of it known to the present author are of this age (Phillips 1866; Roger (after Lissajous) 1952; Schumann 1974) although Lissajous (1925, p. 22) regarded its range as Lower Pliensbachian to Aalenian. Obviously more research is desir able, the genus being likely to remain poorly understood until larger samples become available. At present, its distinctive rostral development is considered sufficient to warrant its inclusion in a separate subfamily Coeloteuthinae Naef.

The curious synonymous homonymy of Coeloteuthis Lissajous, 1906 and Coeloteuthis Stolley, 1919 was pointed out by Bairstow (1950, p. 226).

Stratigraphic range

Lower Pliensbachian - ? Aalenian.

? Coeloteuthis sp.

Pl.20 fig.5 Pl.21 figs. 6,7

cf. 1836 Belemnites ?brevis de Blainville; Buckland, vol. 2, p. 70, pl. 44', fig. 14.

cf. 1866 Belemnites excavatus sp. nov.; Phillips, pp. 37 - 38, pl. 2, fig. 4 S only.

cf. 1906 Coeloteuthis calcar (Phillips); Lissajous, p. 265 (not traced).

cf. 1922 Coeloteuthis excavata (Phillips); Naef, pp. 229 - 230, fig. 84 i only (cop. Phillips 1866).

cf. 1925 Coeloteuthis excavatus [sic] (Phillips); Lissajous, pp. 21 - 22, fig. 10 (cop. Phillips 1866).

cf. 1974 Coeloteuthis excavata (Phillips); Schumann, pp. 27 - 28, Taf. 4, fig. 9.

Material

Author's collection, Belemnite Marls, Charmouth, Dorset: 3 specimens

bed 110 IV: TB389

bed 111b: TB805

?bed 110 (fallen block): 130

Green Ammonite Beds, foreshore below Golden Cap: 1 specimen

beds 122a - c: TB562

Description

Rostrum small, conical, slightly compressed. Apex fairly blunt. Dorsolateral apical furrows present, merging anteriorly into dorsolateral facets which may be furrowed; the appearance of furrows can be due to the crushing of the very fragile guard around the alveolus.

Alveolus occupies most of the rostrum, with the post-alveolar length not exceeding about 5 mm. Total length (L) of the rostrum cannot be validly ascertained due to gradual thinning of rostral material against phragmocone wall.

Specimen TB562 (pl.21 fig.7) has part of the phragmocone preserved in a crushed state; total preserved length of phragmocone and rostrum is 40 mm, estimated post-alveolar length of rostrum is 3 mm.

Discussion

The four specimens in the author's collection are all somewhat smaller than the figured specimens of Coeloteuthis listed in the synonymy, but are generally similar to these in their conicity and relative depth of alveolus. Two specimens (TB389, TB805) from the Belemnite Marls were fractured, permitting the post-alveolar rostral length to be estimated, this being 3 - 4 mm in each case. Specimen TB562 from the Green Ammonite Beds is virtually identical in appearance to TB389.

Ontogeny

No attempt has been made to study the ontogeny of this species, but it presumably includes the gradual concentric accretion of normal rostral lamellae around the growing phragmocone.

Stratigraphical variation

The four specimens listed here, from the jamesoni Zone, beds 110 and 111b, and davoei Zone, beds 122a - c, are all of similar size and form.

Schumann's (1974, Taf. 4, fig. 9) similar but larger single specimen of Coeloteuthis excavata from Ostercappeln, North Germany, is from the ibex Zone (Lias gamma 2c, equivalent to bed 121 of the Belemnite Marls). This specimen is sectioned, and closely resembles the sectioned specimen, now lost, figured by Phillips (1866, pl. 2, fig. 4 S) upon which the genus was founded.

Distribution

Charmouth, Dorset: Belemnite Marls, *jamesoni* Zone, *polymorphus* and *brevispina* Subzones, beds 110 IV and 111b; Green Ammonite Beds, *davoei* Zone, *maculatum* Subzone, beds 122a - c.

Family HASTITIDAE Naef, 1922

Type genus Hastites Mayer-Eymar, 1883

Genus HASTITES Mayer-Eymar, 1883

Type species: Hastites clavatus(Stahl, 1824); Upper Pliensbachian.

Description

Rostra slender, clavate, often highly so. Apical furrows absent. Adoral part of the rostrum bears sharply incised paired lateral furrows. Transverse section rounded tetragonal to hexagonal in stem portion, oval to circular in inflated portion. Apical line tends to be cyrtolineate, strongly excentric along most of its length. Alveolar angle variable, 18 - 30°.

Epirostra unknown.

Discussion

The above description is slightly modified after Schumann (1974, p. 28), who describes the apical line as ortho- or cyrtolineate, due presumably to his inclusion in the genus of species allied to or conspecific with Belemnites charmouthensis and Belemnites longissimus (q.v.). The present author regards a cyrtolineate, excentric apical line as an identifying characteristic of Hastites.

Poor calcification of the alveolar part of the rostrum is a characteristic of the family Hastitidae as defined by Jeletzky (1966).

Stratigraphical range

Lower Pliensbachian, upper jamesoni Zone (?brevispina Subzone) - Toarcian.

Hastites microstylus (Phillips, 1867)

Pl.28, figs 1-3.

non 1824 *Belemnites clavatus* Schlotheim interpreted by Stahl, p.31, pl.1, fig.2.

1866 *Belemnites clavatus* Blainville (sic); Phillips, p.39, pl.3, fig.7.

1867 *Belemnites microstylus* sp.nov.; Phillips, p.66, pl.13, fig.31G (not fig.31 O).

1869 *Belemnites microstylus* Phillips; Dumortier, p.45, pl.4.

1876 *Belemnites microstylus* Phillips; Tate & Blake, p.321.

1883 *Belemnites microstylus* Phillips; Mayer-Eymar, p.642.

1925 *Hastites microstylus* (Phillips); Lissajous, p.110.

1928 *Hastites fustiformis* sp.nov.; Lang, p.218, pl.15, fig.6.

1928 *Hastites spadix-ari* (Simpson); Lang, pp.218-220, pl.15, fig.8.

1928 *Hastites microstylus* (Phillips); Lang, p.220.

1928 *Hastites stonebarroensis* sp.nov.; Lang, p.220, pl.15, fig.7.

?1974 *Hastites clavatus clavatus* (Stahl); Schumann, pp.30-32.

1974 *Hastites spadix-ari* (Simpson); Schumann, p.33, pl.6, figs 15, 17, 18; pl.7, figs 1-10.

p1974 *Hastites microstylus microstylus* (Phillips); Schumann, pp.34-35, pl.7, figs 12-21 (not fig.11); pl.8, fig.1, ?fig.2.

non 1974 *Hastites microstylus araris* (Dumortier); Schumann, pp.35-36, pl.8, figs 3-8.

Type material

GSM 94536 in the Geological Survey Museum was chosen as lectotype by Lang (1928, p.220) and is here retained. This was figured by Phillips (1867, pl.13, fig.31G) as Belemnites microstylus collected by Day "in a nodule from the Belemnite-bed of Lyme Regis" - probably the Belemnite Stone (bed 121) but possibly the Green Ammonite Beds overlying it.

Other material

Author's collection, Belemnite Marls, between Charmouth and Seatown, Dorset: 23 specimens.

bed 118a: TB993, TB994 (both fragmentary).

bed 119: TB1066-1069, TB1078-1084.

beds 120a-b: TB1108-1113.

beds 120d-e: D144, TB146, TB151.

bed 121: TB151.

Green Ammonite Beds, Golden Cap: 18 specimens.

beds 122a-c: D204, D205, TB563, TB582-587, TB1192-1200.

?ibex and davoei Zones, near Aselfingen, South West Germany: numerous uncatalogued specimens, mostly fragmentary.

BMNH, coll. and/or det. W.D.Lang, Belemnite Marls, near Golden Cap, unless otherwise stated: 4 specimens.

bed 119: (Hastites spadix-ari) C2899; (H. fustiformis) C29003 (holotype; from Green Pit Knap, north of Charmouth).

bed 121: (H. spadix-ari) C28997; (H. stonebarroensis) C11996.

Green Ammonite Beds, near Golden Cap: 27 specimens.

bed 122a: (H. spadix-ari) c29002.

bed 122b: (H. spadix-ari) C42175; (H. stonebarroensis) C42201.

bed 122c: (H. stonebarroensis) C28991 (holotype), C42000, C42205, C42206.

bed 122d: (H. spadix-ari) c28996.

bed 123: (H. stonebarroensis) C42184.

bed ?124: (H. fustiformis) C29005.

bed 124: (H. stonebarroensis) C42001.

bed 125: (H. stonebarroensis) C42003.

bed 127: (H. spadix-ari) C42009, C42039.

bed 129: (H. fustiformis) C42031, C42032; (H. spadix-ari) C29001, C42033; (H. stonebarroensis) C28992-28995, C42034-42036.

bed 131: (H. fustiformis) C42030.

bed 132: (H. fustiformis) C42022.

Description

Rostrum small to medium, strongly clavate, extremely slender in anterior portion. Transverse section nearly circular in post-alveolar portion, usually slightly compressed but sometimes slightly depressed. Sections of anterior portion sub-quadrate. Apical line cyrtolineate, apex of rostrum tending to migrate upwards relative to axis of phragmocone during growth, producing a somewhat curved profile. Apex acute to globular, depending on position of maximum diameter of inflated portion of rostrum.

Paired lateral furrows well developed. Apical furrows absent.

Alveolar portion of rostrum frequently poorly calcified and exfoliated. Alveolus very short, usually less than 10% of total rostral length.

Dimorphism not detected.

Epirostrum unknown.

Discussion

Hastites microstylus as here defined is based mainly on material from the ibex and davoei Zones, although it first appears in the upper jamesoni Zone and persists into at least the lower margaritatus Zone. It is clearly closely related to H. clavatus, the type material of which is Toarcian (Lang 1928, p.218) and it is quite possible that the two are conspecific, further research being required to test this. The long ranges of species of Hastites and species of its probable descendants Hibolithes and Belemnopsis were accepted by Jeletzky (1966, p.144), but actual ranges were not given.

The present research indicates that only one species of H. clavatus - like belemnite is present in the upper Belemnite Marls and Green Ammonite Beds of Dorset, the earliest valid type specimen being the lectotype of Hastites microstylus (Philips) detailed above.

The species is highly variable, a fact which Phillips (1866, p.39) encountered when he assigned to Belemnites clavatus several upper Lower Lias specimens from various English localities. This variability led Lang (1928) to describe four species (Hastites fustiformis sp. nov., H. spadix-ari (Simpson), H. microstylus (Phillips) and H. stonebarroensis sp. nov.) with the reservation that, "There is some grading between the forms; but, on the whole, the specimens group themselves in this way, and the arrangement, even if it should ultimately prove to be artificial, is provisionally convenient." (Lang 1928, p.217). Morphometric study does not support this division (figs.73-75).

Ontogeny

The ontogeny of this species was not examined in detail, but the section drawn in figure 76A reveals an early rostrum that, as might be expected, is more slender than in any of the species of Belemnites studied here. From the earliest stages, the alveolus is comparatively very short and the rostrum clavate, the postion of minimum diameter being just anterior to the protoconch; this suggests that the maximum efficiency of the rostrum as a counterbalance was important right from the earliest period of the animal's life, which in turn is possibly related to a greater degree of activity in young Hastites compared with Belemnites.

Stratigraphical variation

As well as showing wide variation in form at a single horizon, there is some slight shifting of morphology from bed to bed. At Charmouth, specimens from bed 119 tend to attain the largest size (compare figs.73 and 74), but samples from all beds seem to belong to one adult size group.

Specimens from the Green Ammonite Beds are generally less compressed than those from the Belemnite Marls (fig.75), and are often slightly depressed in the posterior inflated portion of the rostrum.

Histograms of clavateness were not constructed as the very high values found in many specimens would require more than 30 ranks on the scale used for other species, and, variation in this character being large, a correspondingly large sample would be required to produce useful comparative diagrams.

The material from North Germany described and figured by Schumann (1974) under several sub-species headings of Hastites clavatus and H. microstylus (see synonymy) reveals a range of form and stratigraphical distribution similar to that observed in Dorset.

Distribution

This species is widely distributed. Localities where its vertical range may be established include:

1. Charmouth, Dorset: Belemnite Marls, jamesoni Zone, jamesoni

Subzone, bed 118a (two fragmentary specimens in author's collection) to base of *margaritus* Zone (top of Green Ammonite Beds) and possibly above.

2. Rottorf and Ostercappeln, North Germany: *jamesoni* Zone, *jamesoni* Subzone to *davoei* Zone, *figulinum* Subzone (Schumann 1974).

3. Robin Hood's Bay and Huntcliff, Yorkshire: *ibex* and *davoei* Zones (Phillips 1866 (*Belemnites clavatus*) and personal observation).

FIG.73

<u>Hastites</u> <u>microstylus</u>

$D_{v.ant.}$:L
$D_{v.post.}$:L
beds 119–120a-b

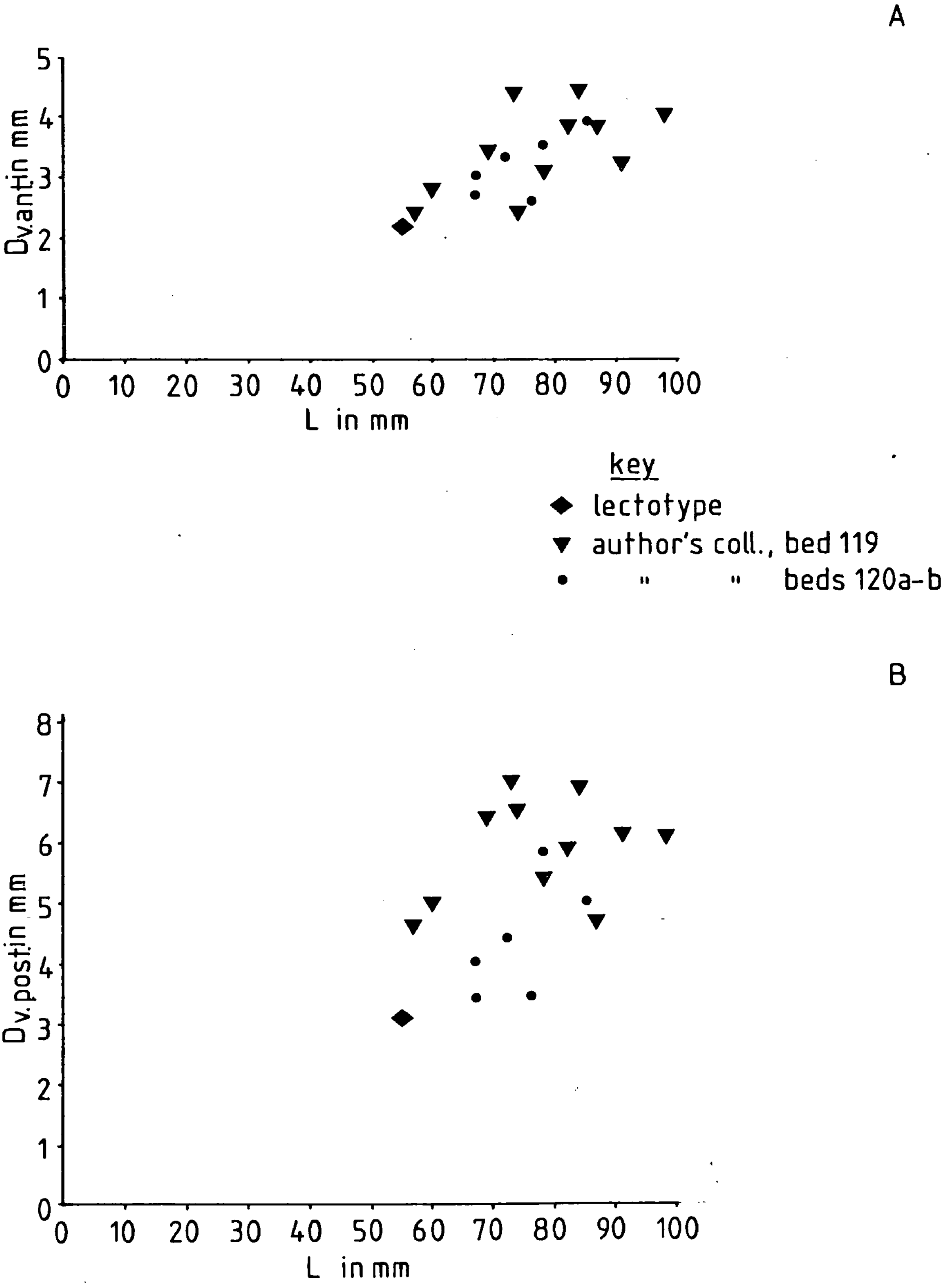


FIG.74

Hastites microstylus

$D_{v.ant.}:L$

$D_{v.post.}:L$

beds 122a-c

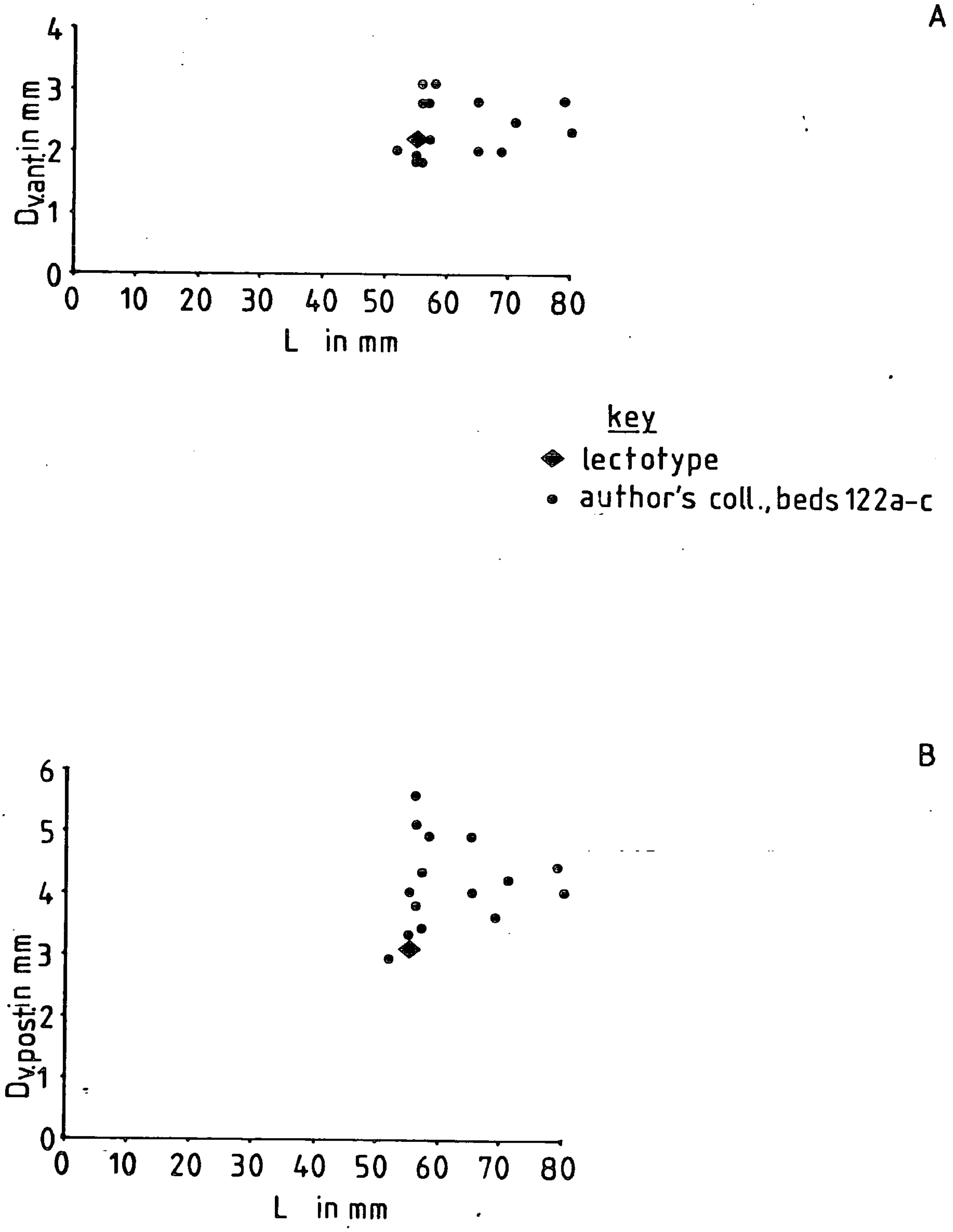


FIG. 75

Hastites microstylus
compression

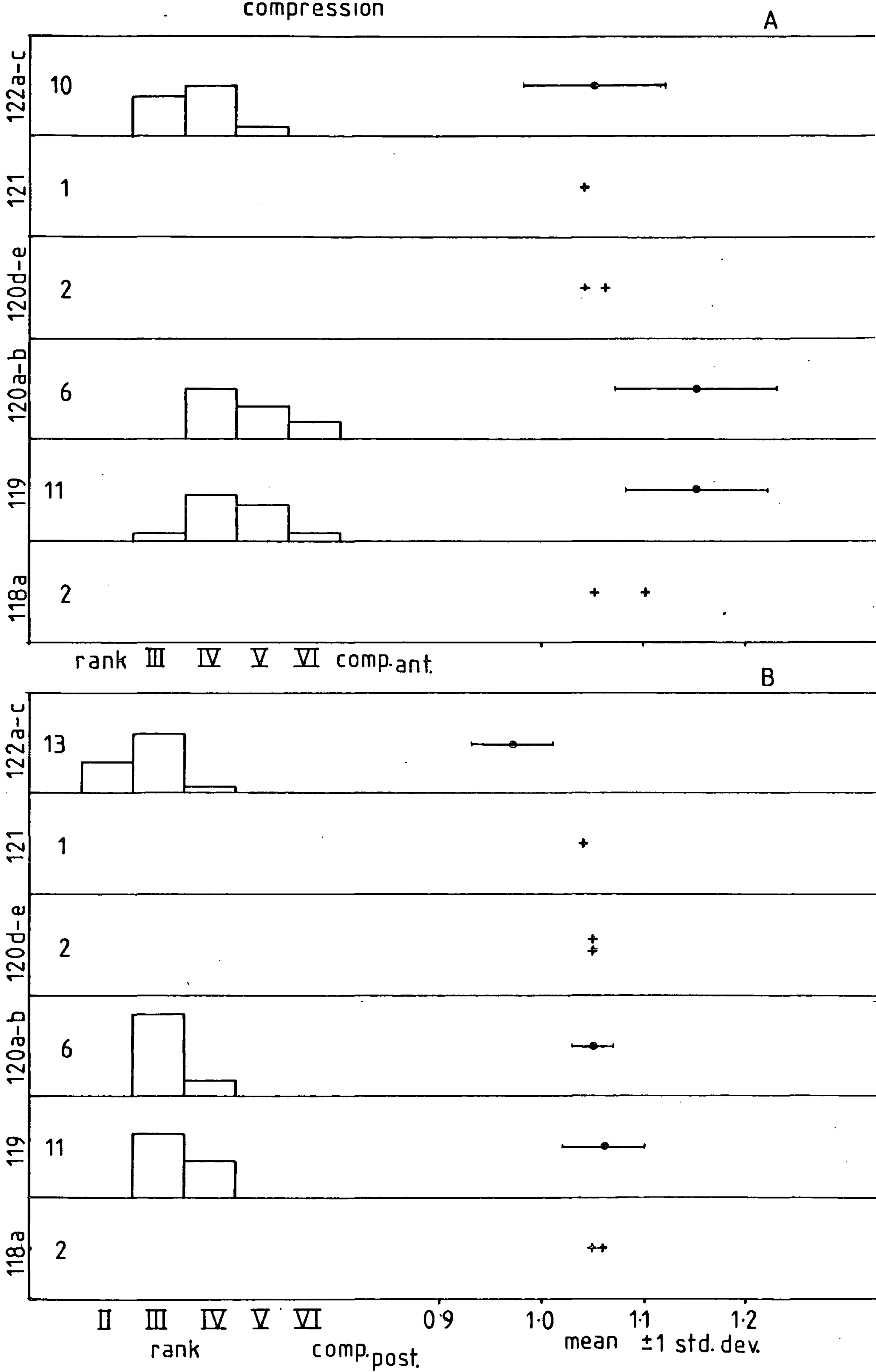


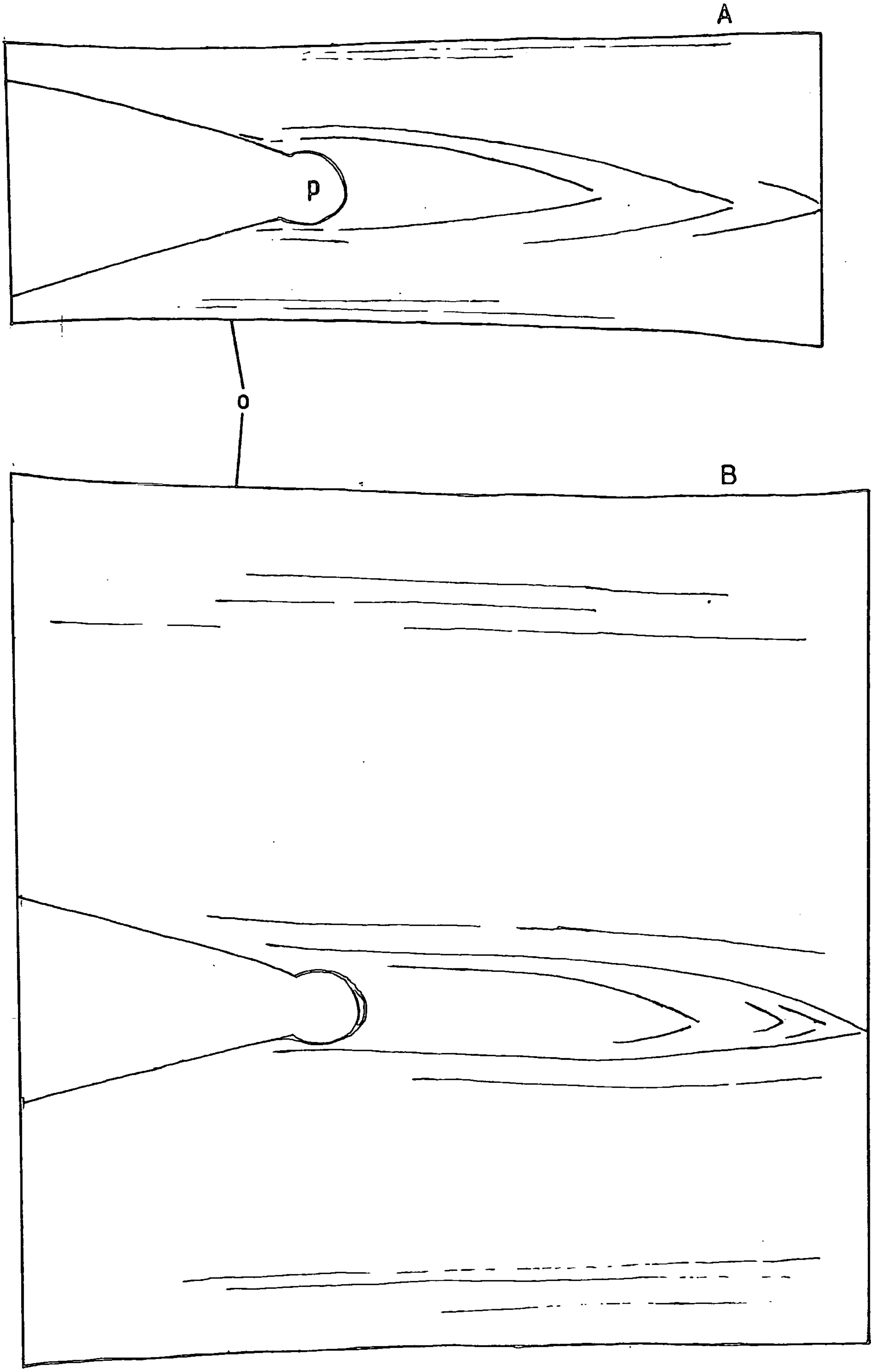
FIG.76 Camera lucida drawings of median longitudinal polished sections.

A: Hastites microstylus: TB1078 bed 119, x24

B: Hastites sp. nov.: TB152 bed 120d, x24

p - protoconch
o - outer surface of rostrum

FIG. 76



Hastites sp. nov.

Pl. 28 fig.4, Pl.29, fig.1

? 1864	*Belemnites charmouthensis* sp. nov.; Mayer, p. 364 (no figure), "*fimbriatus* beds", Saint Fortunat, Rhone.
non 1864	*Belemnites charmouthensis* sp. nov.; Mayer, p. 364 (no figure), *jamesoni* Zone, Charmouth.
? 1869	*Belemnites charmouthensis* Mayer; Dumortier, p. 50, pl. 5.
p 1974	*Hastites clavatus charmouthensis* (Mayer); Schumann, pp. 32 - 33, Taf. 6, fig. 10, 11 only.

Material

Author's collection, Belemnite Marls, foreshore below Golden Cap, near Charmouth, Dorset: 7 specimens

bed 120 d: TB129, TB131, TB140, TB145, TB150, TB152, TB153

Description

Rostrum fairly small, slender and markedly clavate. Section not more than slightly compressed, sometimes slightly depressed in posterior inflated portion of rostrum. Faint paired lateral furrows present, the lower ones tending to be stronger. Apical furrows absent.

Apical line curved upwards and excentric, especially anteriorly.

Alveolus fairly short, less than 25% of total rostral length.

Dimorphism not apparent.

Discussion

This rare belemnite, which is immediately distinguishable from its contemporaries by its strongly excentric apical line, was found in the Belemnite Marls only in bed 120d, but very similar material, probably of the same species, appears to occur more commonly at other European localities. It is possibly conspecific with Mayer's invalid paratype of Belemnites charmouthensis from the "fimbriatus beds" of Rhone (discussed on pp. 61 -63), and is almost certainly conspecific with material from the ibex Zone of Rottorf, North Germany, included by Schumann (1974) in Hastites clavatus charmouthensis. It differs from Belemnites charmouthensis as here defined in the excentricity and curvature of its apical line, its comparatively uncompressed section and lack of apical furrows. These characters, added to the clavateness of the rostrum, are here considered to warrant the inclusion of this species in the genus Hastites.

Ontogeny

As the species was only recognized at a late stage in the preparation of this report, its ontogeny has not been investigated in detail. The stem region of one specimen (TB152) was sectioned longitudinally (fig.76B), and this agrees with Schumann's single figured section from the ibex Zone, Lias gamma 2b (1974, Taf. 6, fig. 11), which reveals early growth stages (post-alveolar length 5 - 10 mm) to be slender and slightly clavate.

Distribution

1) Golden Cap, near Charmouth, Dorset: Belemnite Marls, ibex Zone, valdani Subzone, bed 120d.
2) Rottorf, North Germany: ibex Zone, valdani Subzone, Lias gamma 2b (Schumann 1974)
3) ? Saint Fortunat, Rhone, France: ibex Zone, ? davoei Zone, ("fimbriatus beds") (Mayer 1864).

?Hastites sp. nov.

Pl.29 fig.2

cf. 1974 Hastites compressoides sp. nov.; Schumann, pp. 37 - 39, Taf. 8, fig. 9 - 17

Material

Author's collection, Belemnite Marls, foreshore below Golden Cap, Dorset: ?3 specimens.

bed 120c: TB1135, also two uncatalogued specimens, probably of the same species, on the surface of a slab taken from bed 120c.

Description

Rostrum small, strongly clavate especially in horizontal plane due to strong degree of compression in anterior portion. Transverse section of inflated posterior portion sub-circular, only slightly compressed; anterior section sub-quadrate. Paired lateral furrows present, lower ones more strongly developed. Apical furrows absent. Apex rounded and sub-mucronate, faintly striated, symmetrical in vertical plane.

Dimensions of specimen TB1135 are (in mm): L46; $D_{v.post}$ 8.2; $D_{h.post.}$ 8.2; $D_{v.ant.}$ 7.1; $D_{h.ant.}$ 5.2. Derived indices are: comp.$_{ant.}$ 1.37; comp.$_{post.}$ 1.07; clav.$_{v.}$ 1.24; clav.$_{h.}$ 1.58.

Discussion

This species resembles H. compressoides Schumann in general appearance, and bed 120c in which it occurs is stratigraphically a very close equivalent of those beds in North Germany from which Schumann records H. compressoides ("Lias gamma 2b Mitte", which places it in the middle of the valdani Subzone; at Charmouth, this subzone includes beds 118d - 120e).

The species differs from H. compressoides in that the maximum compression in the latter is in the inflated posterior portion of the rostrum, rather than in the stem region.

Until more material is obtained, the status of this species must remain in question. It is provisionally assigned to Hastites on the grounds of its strong clavateness and absence of apical furrows. A re-examination of bed 120c in its exposures below Golden Cap may yield a few more specimens; unfortunately, the effective exposed area of the bed is rather small, much of it being covered by seaweed, and much of the material in it was crushed and fractured prior to lithification.

Ontogeny

This has not been investigated. In H. compressoides, juvenile rostra are slender and cylindrical, the club form developing only gradually (Schumann 1974, p. 38).

Distribution

Golden Cap, near Charmouth, Dorset: Belemnite Marls, ibex Zone, valdani Subzone, bed 120c.

Chapter 5

Aspects of palaeobiology

Assemblages and populations

It is well known that modern cephalopod schools or local populations are of very variable constitution in respect of age and sex of individuals and fossil cephalopod assemblages probably often reflect similar patterns.

Pelagic cephalopod schools may comprise (a) adults of one sex only, (b) adults of both sexes, (c) juveniles of both sexes, or (d) adults and juveniles of both sexes (Kennedy and Cobban 1976, p.5). Where fossil cephalopod assemblages represent local mortality patterns (as opposed to post mortem drifted remains) it may be possible to recognize such groupings, and they are indeed well established for ammonites (Kennedy and Cobban 1976, p.34). Large assemblages of adults may be due to mass mortality following spawning. Partial segregation of sexes in local populations (i.e. lack of a one to one ratio of adult males to females where both are present) is often found in modern cephalopod schools (Westermann in Westermann (ed.) 1969, p.19) and, again, is frequently encountered in ammonite assemblages. In modern cephalopods, this may be due either to the earlier migration of females to egg laying grounds or to sampling errors (Westermann op. cit., pp.19-20). In fossil assemblages, additional factors may contribute to apparent partial segregation, including (a) contamination of the local population with drifted material, (b) formation of the entire assemblage from drifted material or (c) formation of the assemblage from successive (e.g. seasonal) migrating populations of segregated sexes; at a given locality, if sedimentation had been slow enough, a collection made from a single bedding plane could easily represent several years accumulation of material. For a modern example of such behaviour, (in Octopus vulgaris (which, although largely benthonic in mode of life, is migratory), mature males are present the whole year round in the area of Banyuls-sur-Mer (France), whilst females with mature eggs are found from March to August and brooding females may remain until October (Mangold and Boletzky 1973).

Further complications in the interpretation of fossil assemblages are suggested by other studies on modern cephalopods, and four examples are given here:

(a) There may exist more than one morphological variety of a species within a restricted area, reproductively partially isolated by migratory behaviour and different maturation times. Thus in the Gulf of Arcachon (France) there are three varieties of Sepia officinalis. One of these inhabits shallow water in the summer months while sexually immature, and moves to deeper waters at the approach of winter to lay eggs. The other two varieties migrate from deeper to shallower water to spawn, one in early spring and the other in summer. Intermediate forms exist, due probably to occasional interbreeding made possible by some overlap in periods of sexual maturity (Tompsett 1939). The life span of Sepia is probably about one year (Packard 1972).

(b) Morphometric sexual dimorphism is not manifested in all cephalopod species. More importantly, where present in some it may not be evident in very closely related species. For example, in the squid *Illex*, three geographical subspecies, or possibly species, are recognized, only two of which are clearly dimorphic (the males being larger, which is a little unusual) (Mangold *et al* 1969, pp.1155-56).

(c) Rate of growth can be considerably affected by temperature and food supply, thus size may not always be closely related to age, and size at sexual maturity may vary considerably (see, for example, the laboratory studies on *Octopus vulgaris* by Mangold and Boletzky 1973). Cold water populations take longer to reach maturity: in the case of *Sepia officinalis*, which normally dies after spawning at the end of its first year, *two* year classes are found to enter the English Channel (Packard 1972, p.281) (Specimens in captivity have been reported as living for about two years, with one period of spawning eight to ten months, with the males especially tending to survive afterwards (Schroeder 1973). Perhaps this is related to artificial feeding or other factors of captivity. Temperature was constant at 20°C.)

(d) The interpretation of size classes in modern cephalopods is not straightforward, often relating to seasonal rather than yearly hatching. Simple year classes may exist, but it appears probable that most modern cephalopods have a life span of two years or less, mass mortality, at least of females, occurring after spawning (Packard 1972, p.281). Most growth occurs in the first few months: *Sepia officinalis* and the Japanese species of cuttlefish lay down one cuttlebone layer a day for the first few weeks or months of life and thereafter cease. *Sepia officinalis* has fast and slow growing classes of individuals, hatched respectively at the beginning and end of the growing season, and in Japanese squid two seasonal age classes occur, "probably representing populations with different reproductive cycles and migration patterns" (Packard 1972, p.280).

Whatever their origin, size classes (up to three or perhaps four) were found to be often present in samples of species of belemnites from the Dorset coast Lower Pliensbachian. Very similar groupings were found by Hewitt (1980) in assemblages of Belemnopsis and Cylindroteuthis from the Callovian of Brora, Sutherland. Three size groups were recognized in each genus, being particularly well defined in Belemnopsis. It was postulated that these represented year groups, the discrete mortality clusters being due to concentration of growth during summer and higher mortality in winter. Hewitt concluded that, "Size frequency distributions show that Jurassic belemnites were seldom if ever concentrated by localised post-spawning mortality" (Hewitt 1980, p.191), although he also suggested that, "It is probable that the third size group were adults that died a few days after spawning" (p.188). If this was so, then belemnites were different in this respect from most modern cephalopods as individuals of the third size group are much less abundant than the others, which would imply an unusually high mortality rate in the smaller, supposedly sexually immature specimens, with post-spawning mortality accounting for only a small percentage of total mortality. (Note that the element of mortality due to predation cannot be assessed; although whole rostra only are considered in the present work, it is conceivable that whole rostra were excreted or regurgitated by some predators which might significantly bias the samples.]

However, these size groups and those here identified from the Belemnite Marls and Green Ammonite Beds are consistent with the three or four year life span for most belemnites as suggested by Stevens [1965, p.65], based on observation of prominent growth lamellae. Depending largely on studies of Jurassic and Cretaceous belemnites from the Indo-Pacific region, he found that assemblages consisted mostly of the third and fourth growth stages, and attributed this to post-spawning mortality. He also pointed out that mass mortality may on occasion be due to catastrophes such as earthquakes or dinoflagellate blooming, and cites some modern examples.

The belemnite assemblages from each adopted unit of the Belemnite Marls and Green Ammonite Beds are shown in figures 78 to 103 in the form of envelopes that include all the measurable specimens collected. Figure 77, based mainly on "adult" & "adolescent" specimens [L greater than 40mm] gives an overall view of the species present in each unit, "slenderness" indicating the approximate rostral profile.

These assemblages include both of the mortality distribution types found by Stevens [1965] and Hewitt [1980], together with some others, and are consistent with what has been said of school compositions and migrations of modern cephalopods, although the relative contribution of these factors cannot be determined.

The species occur in the following types of size grouping:

1) Three or four groups, juvenile to adult sizes.
   e.g. beds 122 a-c *Belemnites aduncatus*
   beds 118a, 117, 111 b-d *B. nitidus*

2) Same size range as (1), but grouping weaker or not recognizable (may be two clear groups, the second corresponding to groups two and three (or four)).
   e.g. beds 112 d-f, 112 a-c, 110 V *B. nitidus*
   bed 110 V *B. longissimus*

3) Mostly adults only, broadly equivalent to size group three; this is of frequent occurrence.
   e.g. beds 122 a-c *Hastites microstylus*
   bed 119 *B. cricki*
   H. microstylus
   bed 110 V *B. abruptus*
   bed 110 IV *B. imus*
   B. charmouthensis
   B. longissimus

4) Mostly "adolescents" only, broadly equivalent to size group two.
   e.g. bed 122 a-c *B. nitidus*
   bed 118 b-d *B. nitidus*
   bed 108 I *B. charmouthensis*

5) "Juveniles" only, broadly equivalent to group one; this is rarely demonstrated due to difficulties in identification.
   e.g. bed 110 IV *B. nitidus*

In some samples, there is a tentative interspecific pattern of size distribution; when the normally large and abundant *B. nitidus* is restricted in size, other large species seem to be numerically well developed. Thus, in beds 122 a-c, *B. aduncatus* is numerically dominant, in beds 118 b-d, *B. cricki*, whilst in bed 110 IV *B. imus* and *B. charmouthensis* are the dominant large belemnites (also *B. longissimus*, which at other horizons is numerically co-dominant with *B. nitidus*).

These patterns are likely to be largely due to school compositions of local populations, although the cosmopolitan appearance of *B. aduncatus* in the *ibex* and *davoei* Zones and the general rarity of *B. nitidus* from the *davoei* Zones onwards suggests a more widespread reduction and perhaps extinction of the latter that may be related to competition from *B. aduncatus*.

Probable sexual dimorphism is also represented where possible on these diagrams, and is further discussed below.

Of course, one of the main problems in the interpretation of these assemblages is that each one was collected from a definite thickness of rock representing a fairly long period of time. (As a simplistic calculation, assuming an ammonite zone to represent 1,000,000 years, then the Belemnite Marls were deposited in 2,000,000 years; they are here represented by 29 belemnite assemblages (including bed 116 with a sample size of zero), so on average each assemblage covers about 35,000 years.) On the other hand, the assemblages are usually well defined, and appear to be uniform in profile throughout their range, thus it appears likely that a good proportion of them represent temporarily stable local populations (with or without regular migration patterns).

Changing local conditions would be likely to affect breeding areas and migration linked segregation patterns, and this could largely account for the varying distribution of size classes and sexes in individual species from successive beds. Size changes could also be due to direct environmental effects on growth, which were invoked by Hewitt and Hurst (1977) to explain the size changes in liperoceratid ammonites from the ibex and davoei Zones of Southern England.

The situation is further complicated by the shifting morphology displayed by various species (described in the previous chapter), but until a great deal more information is available concerning other localities it cannot be decided if this is due to overall fluctuations within species or to succession of facies controlled varieties.

As mentioned under "Stratigraphy", beds 110 and 108 of Lang (1928) are, for the purpose of this work, subdivided on the basis of belemnite assemblages; although there are corresponding lithological differences, these are not easily recognizable in the field. The assemblages are:

110 V: Belemnites abruptus (adult)
B. nitidus (juvenile-adult, some size grouping)
B. longissimus (juvenile-adult, dimorphic)

110 IV: B. abruptus very rare (one adult and one probable juvenile)
B. imus (adult only, dimorphic)

B. nitidus (juvenile only)
B. charmouthensis (adult, dimorphic)
B. longissimus (mostly adult, dimorphic)

110 III: *B. imus* (rare, two adult specimens)
B. nitidus (juvenile-small adult)
B. charmouthensis (mostly adult, dimorphism not evident)
B. longissimus (mostly adult, dimorphic)

110 II: *B. imus* (adult, dimorphism not evident)
B. nitidus (juvenile-small adult)
B. longissimus (adult, dimorphism not evident)

110 I: *B. charmouthensis* (mostly small adult, dimorphism not evident)

108 II: *B. imus* (rare, two adult specimens)
B. nitidus (rare, two juvenile specimens)
B. charmouthensis (juvenile-adult, dimorphism possibly present; larger sample required)

108 I: *B. imus* (adult)
B. nitidus (juvenile-adult)
B. charmouthensis (juvenile-adult, dimorphism not evident)

These assemblages are shown in figures 81 to 88.

Slenderness

FIG. 77

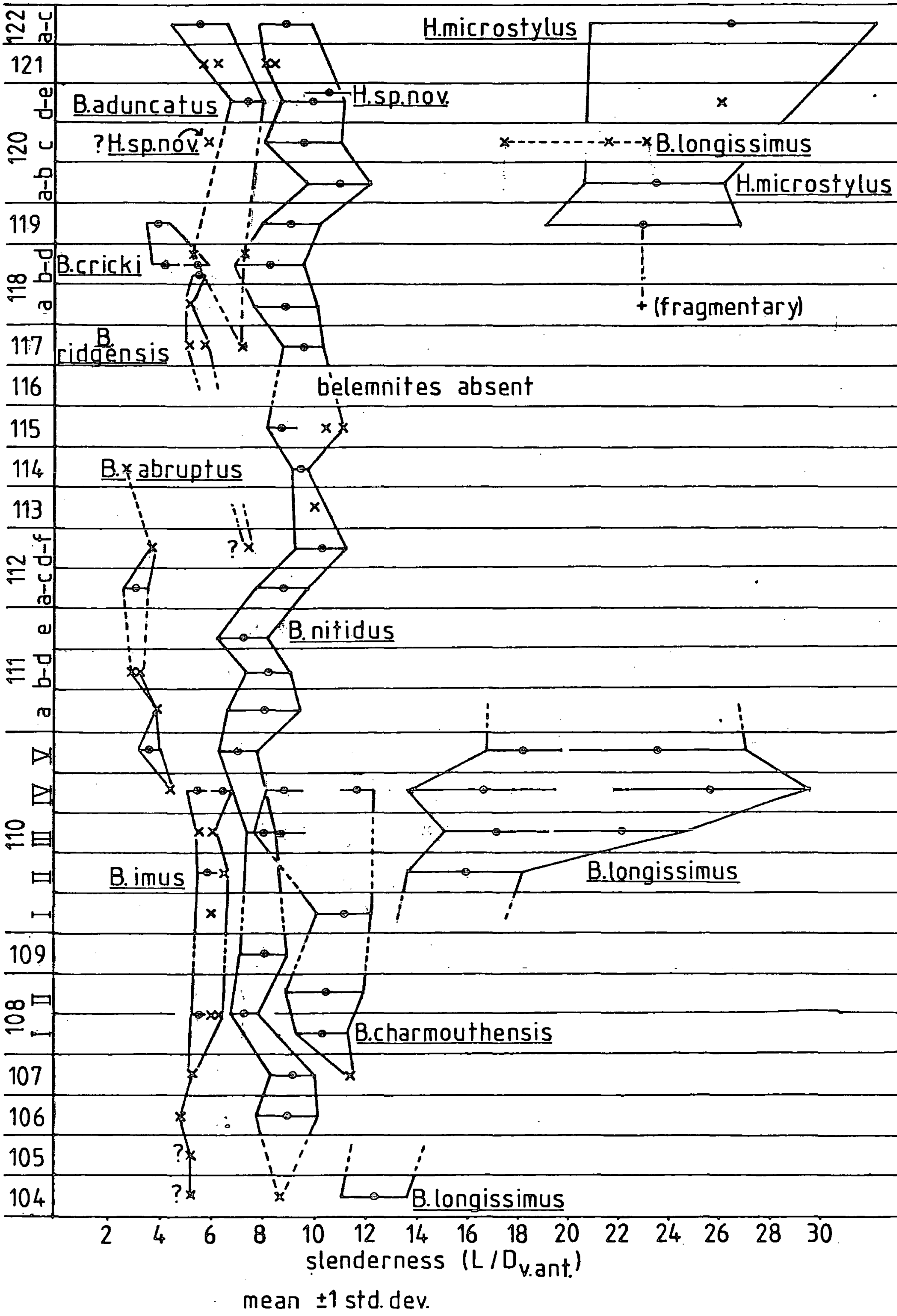


FIG. 78

$D_{v.ant.}$:L   Bed 104

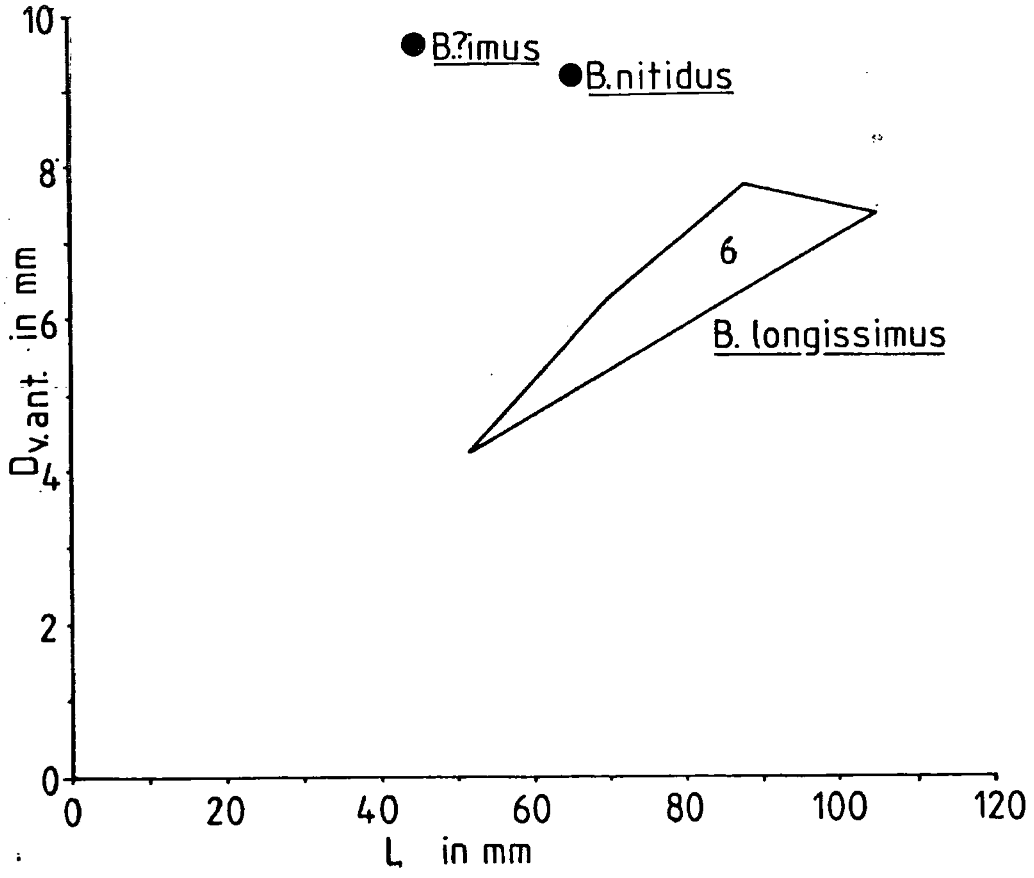
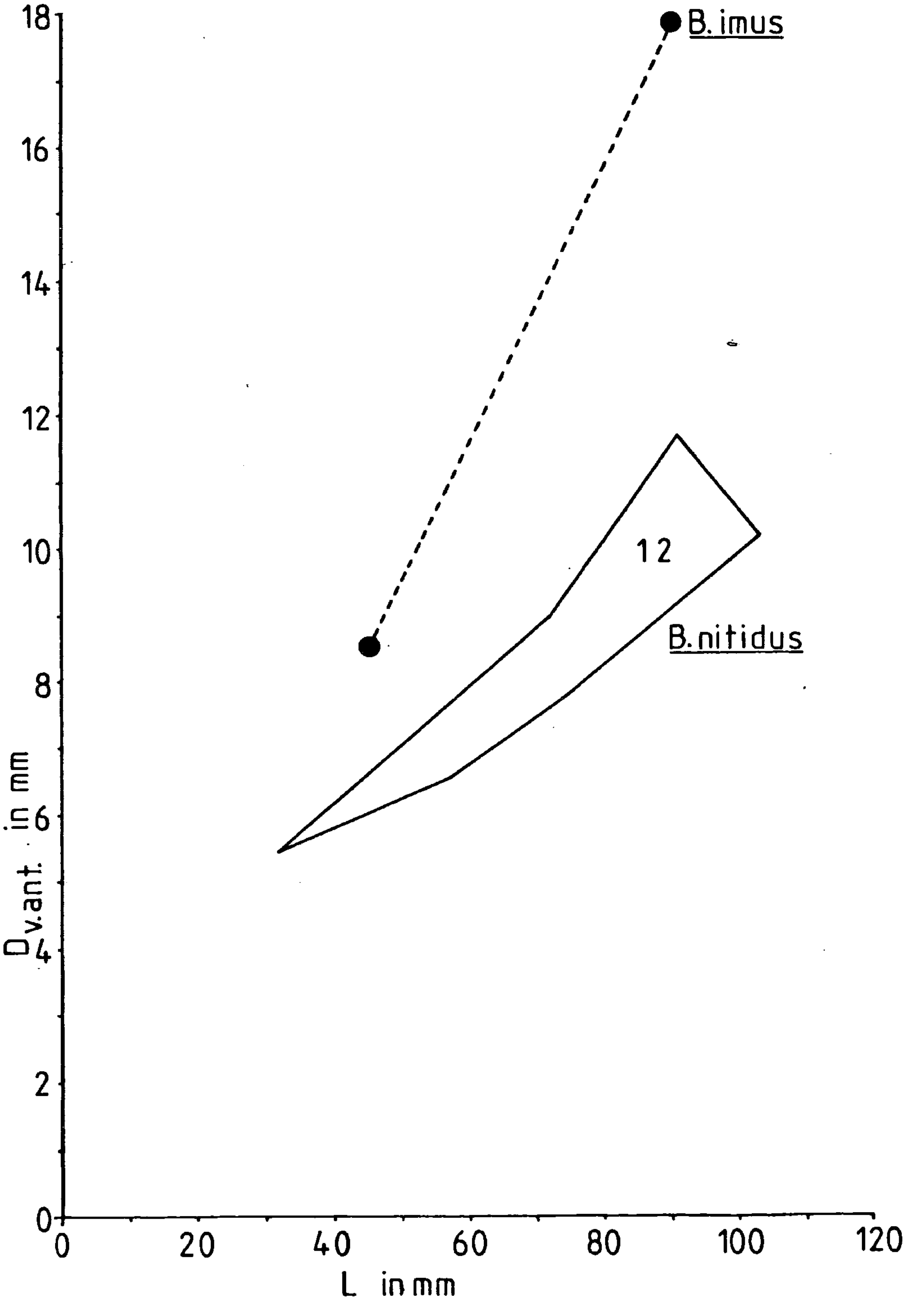
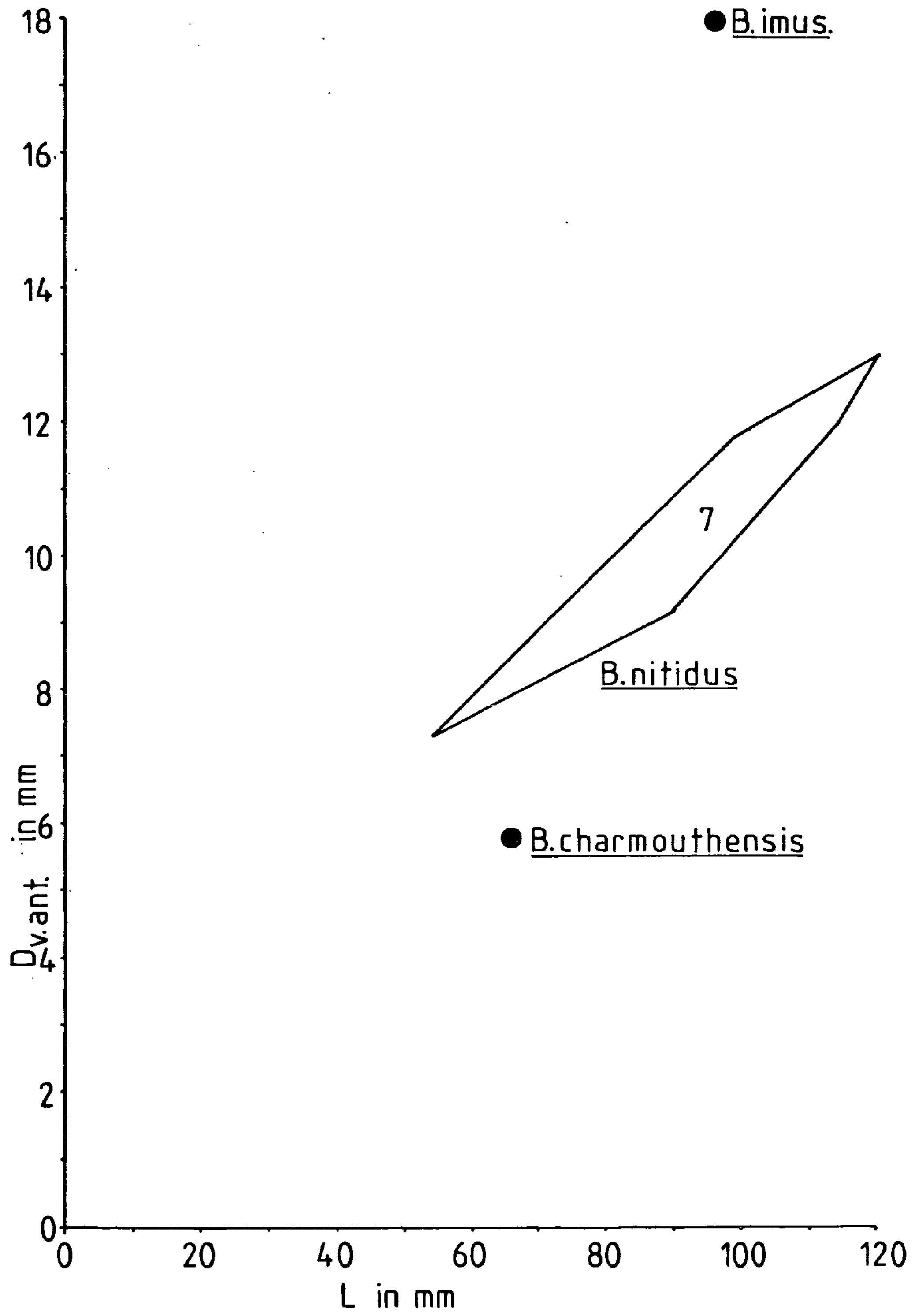


FIG. 79

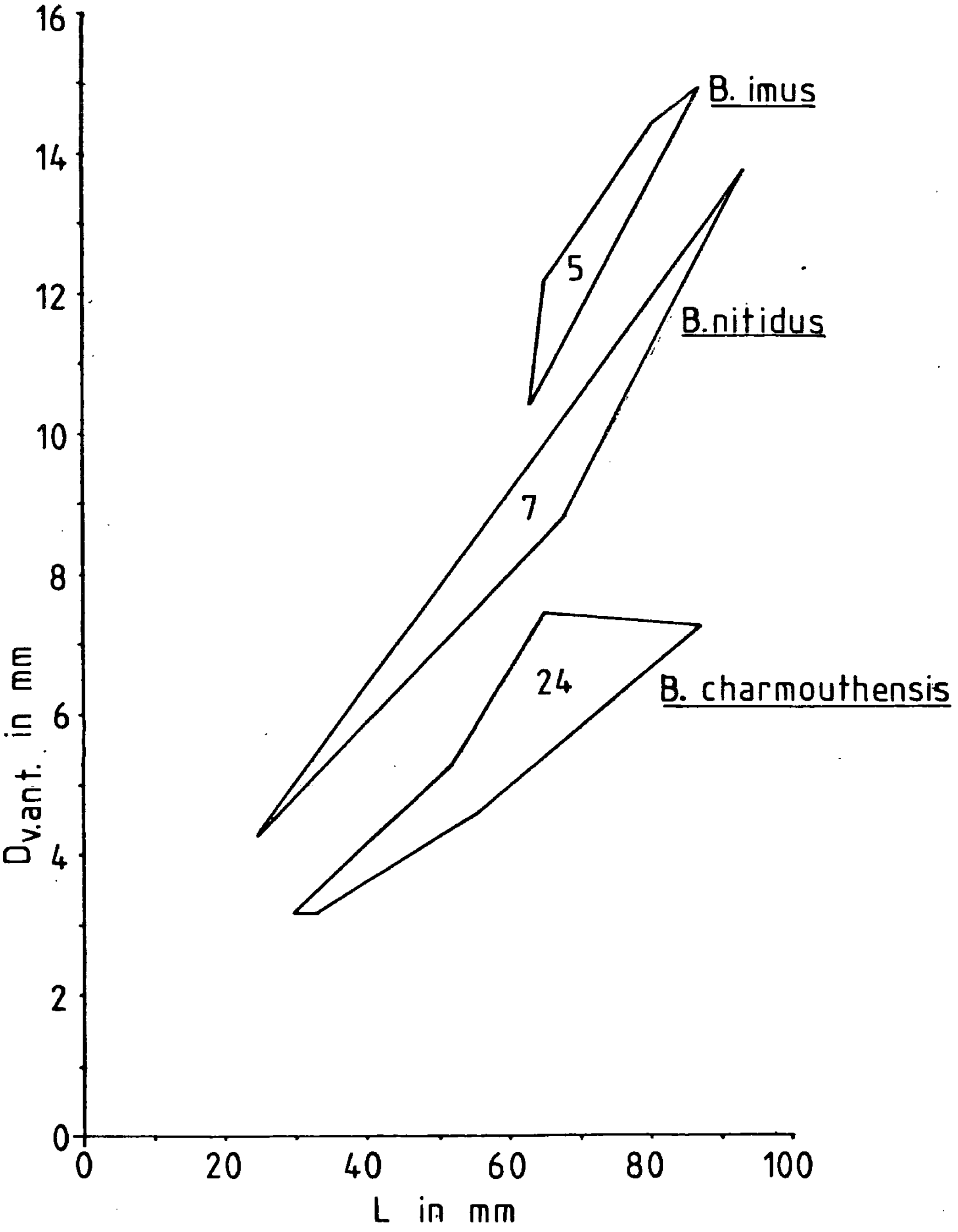
$D_{v.ant.}$:L Bed 106



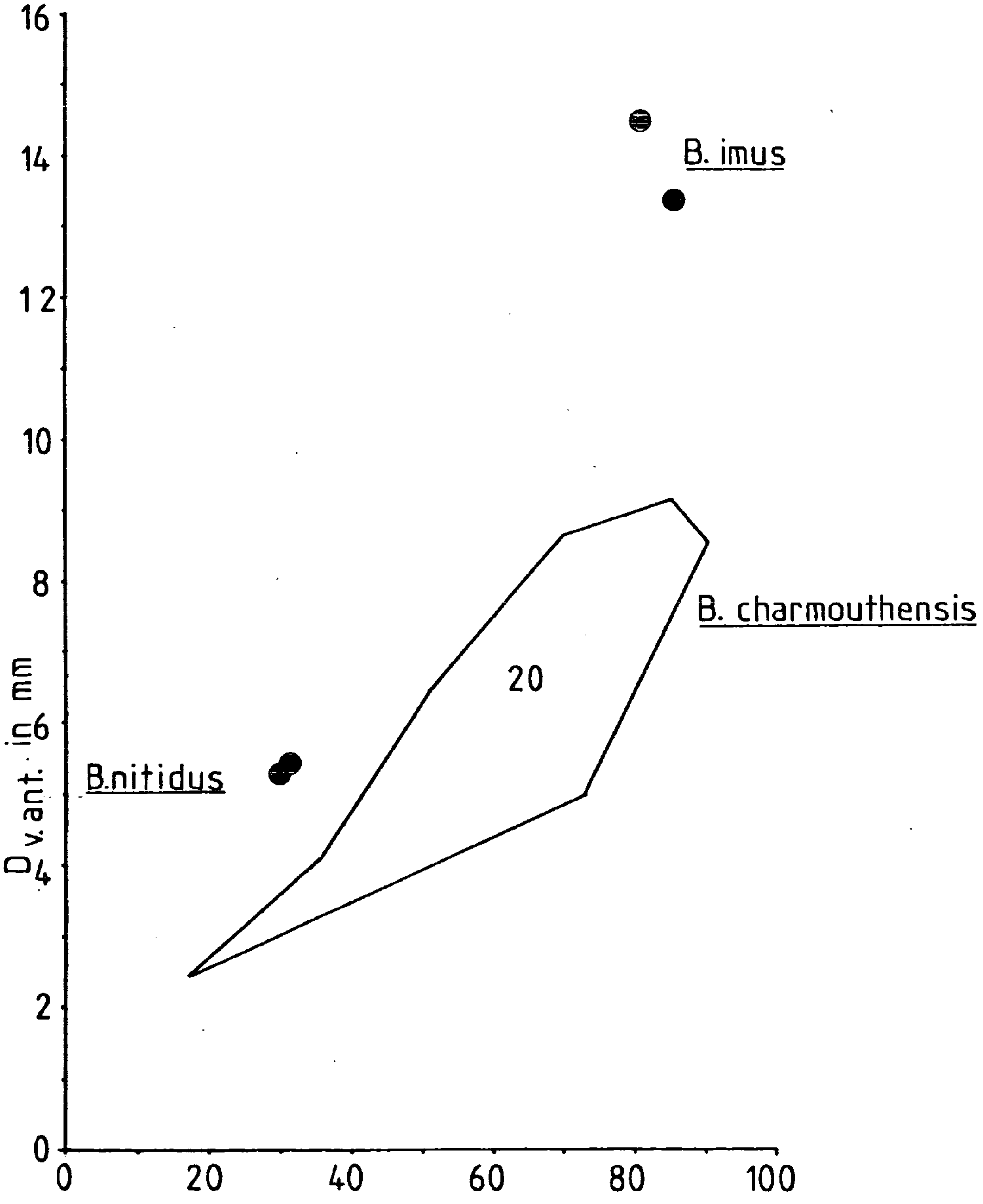
$D_{v.\,ant.}$:L Bed 107



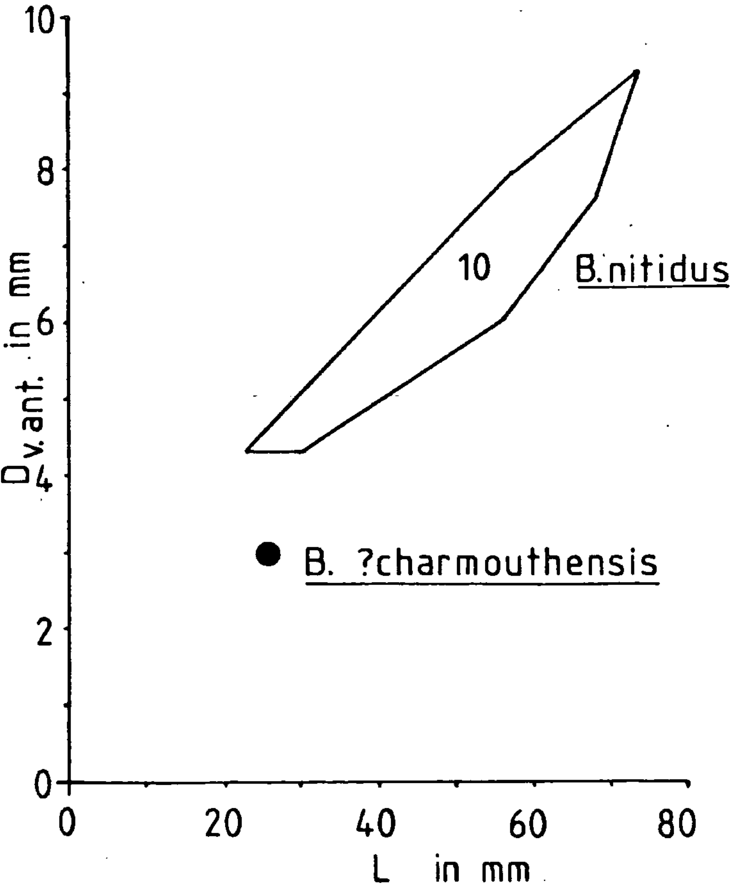
$D_{v.ant.}$: L Bed 108 I



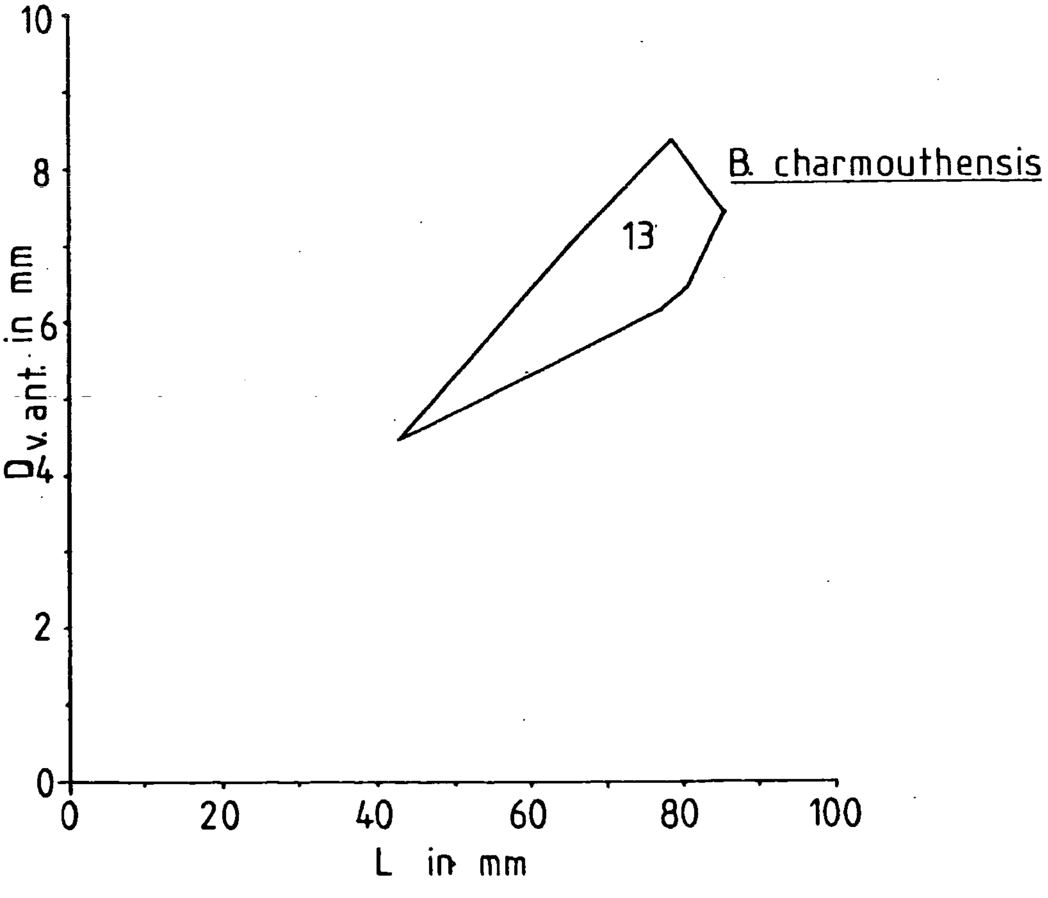
$D_{v.ant.}$: L Bed 108 II



$D_{v.\,ant.}$:L Bed 109



$D_{v.ant.}$:L Bed 110 I



$D_{v.ant.}$: L Bed 110 II

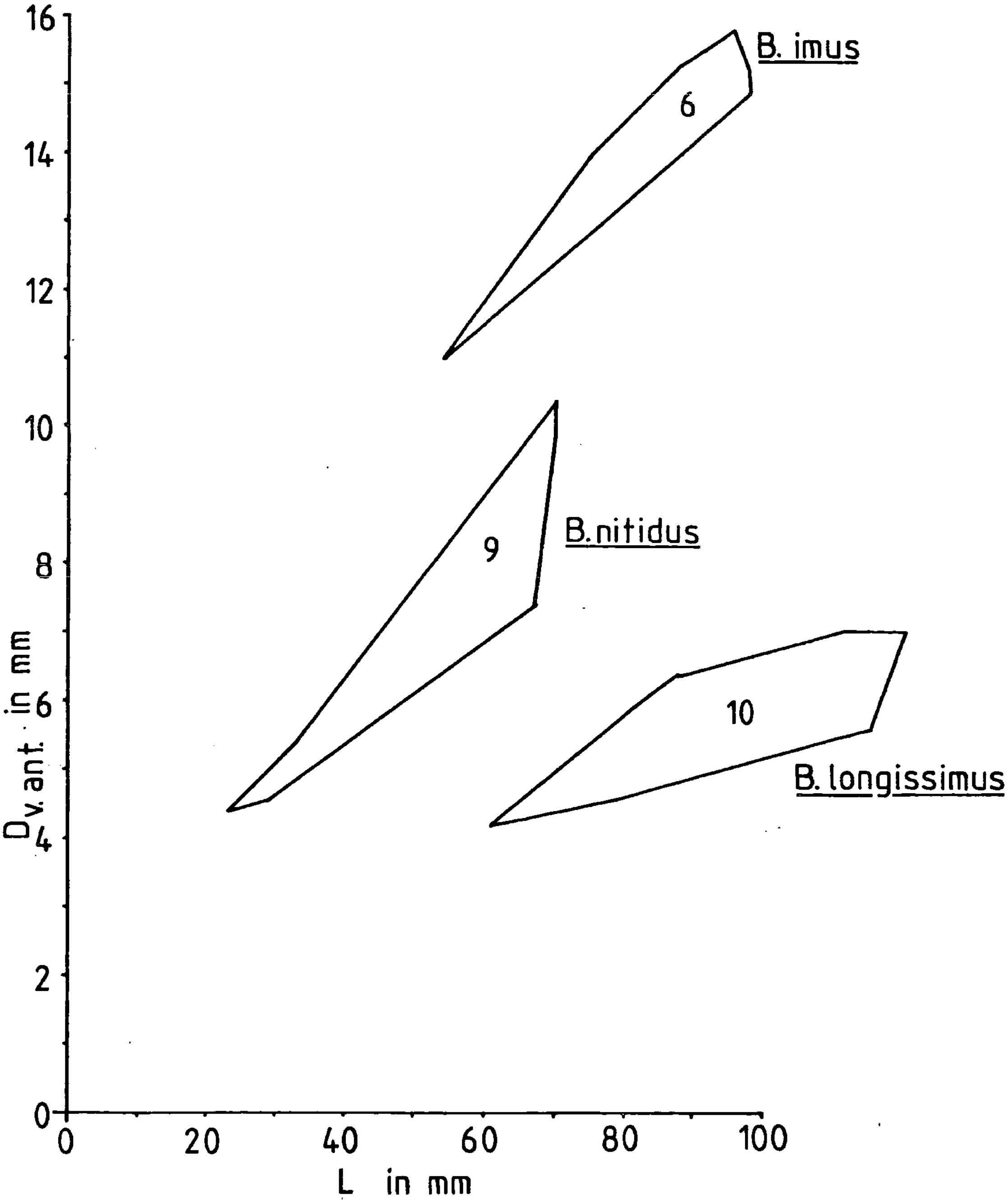


FIG. 86

$D_{v.\,ant.}$: L Bed 110 III

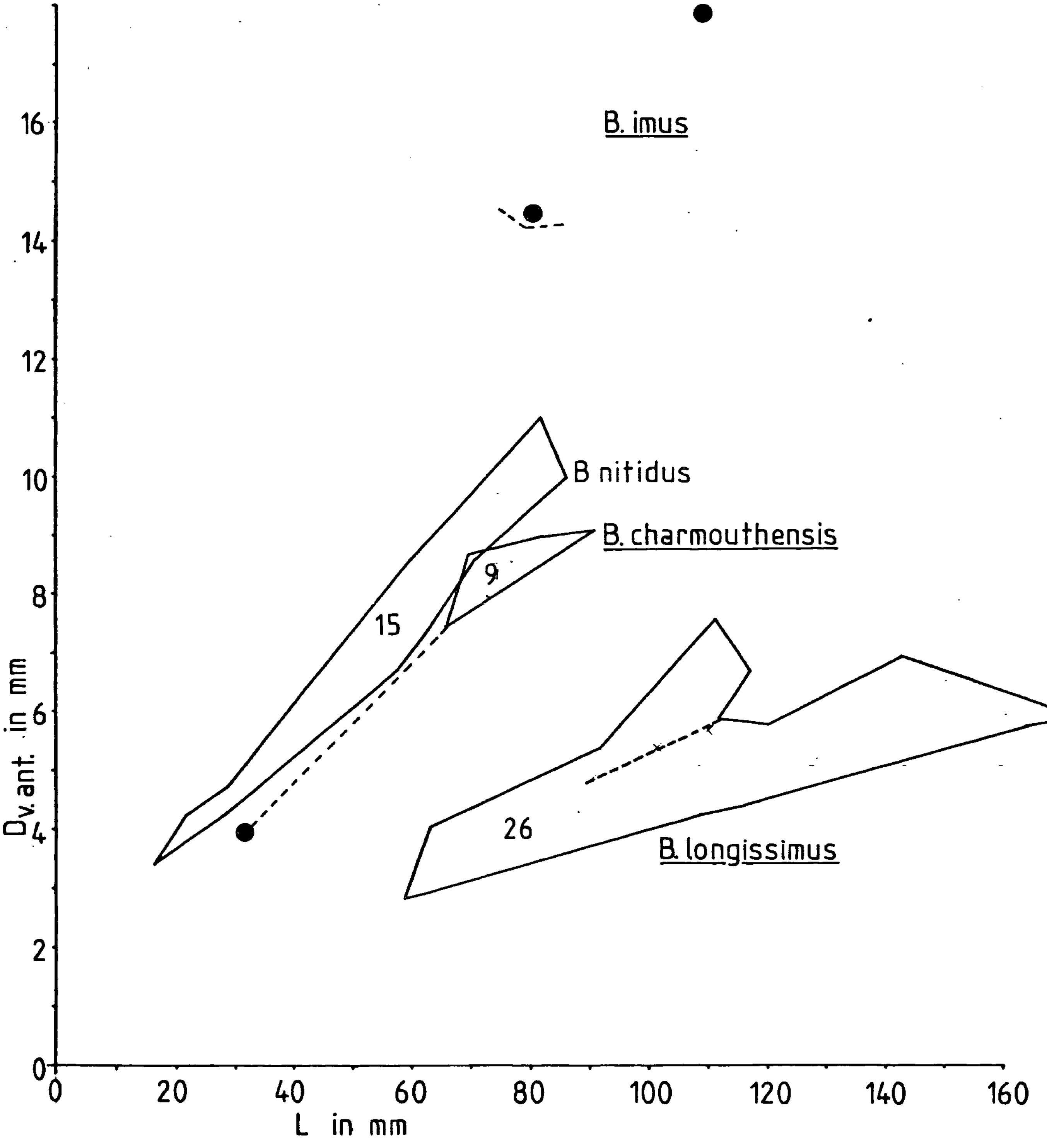


FIG. 87

$D_{v.ant.}$:L Bed 110 IV

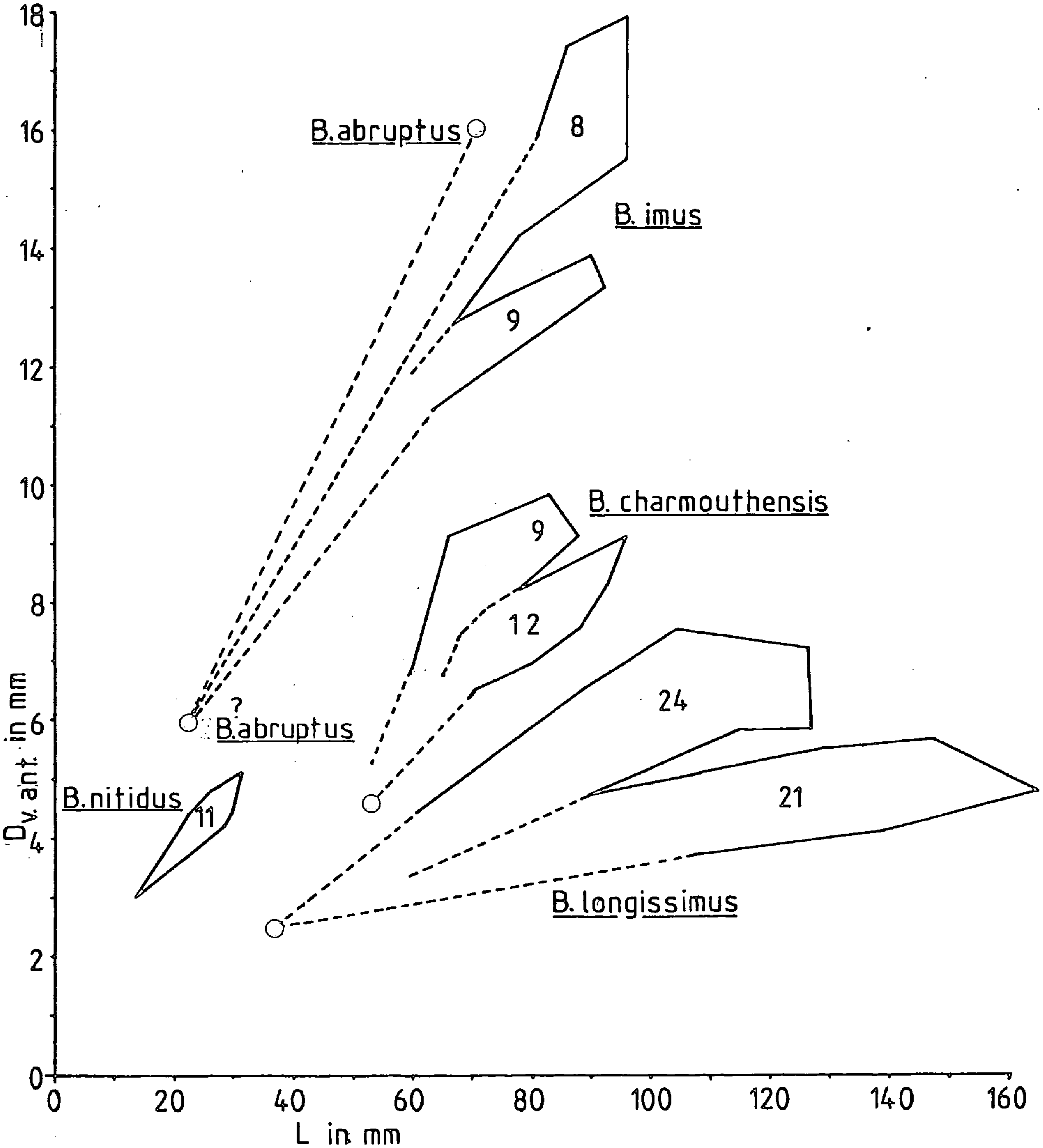
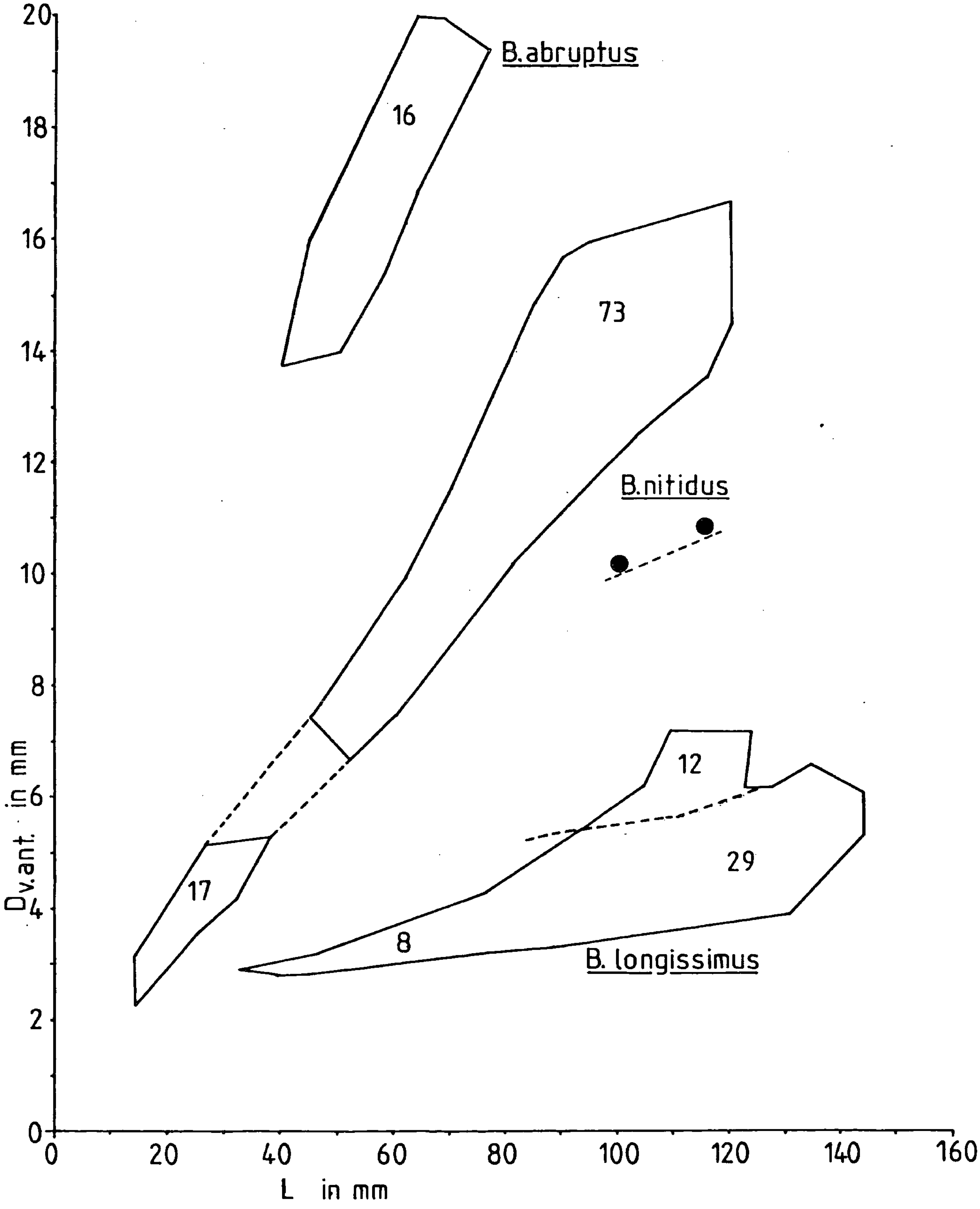


FIG. 88

$D_{v.\,ant.}$: L   Bed 110 V



$D_{v.ant.}:L$ Bed 111 a

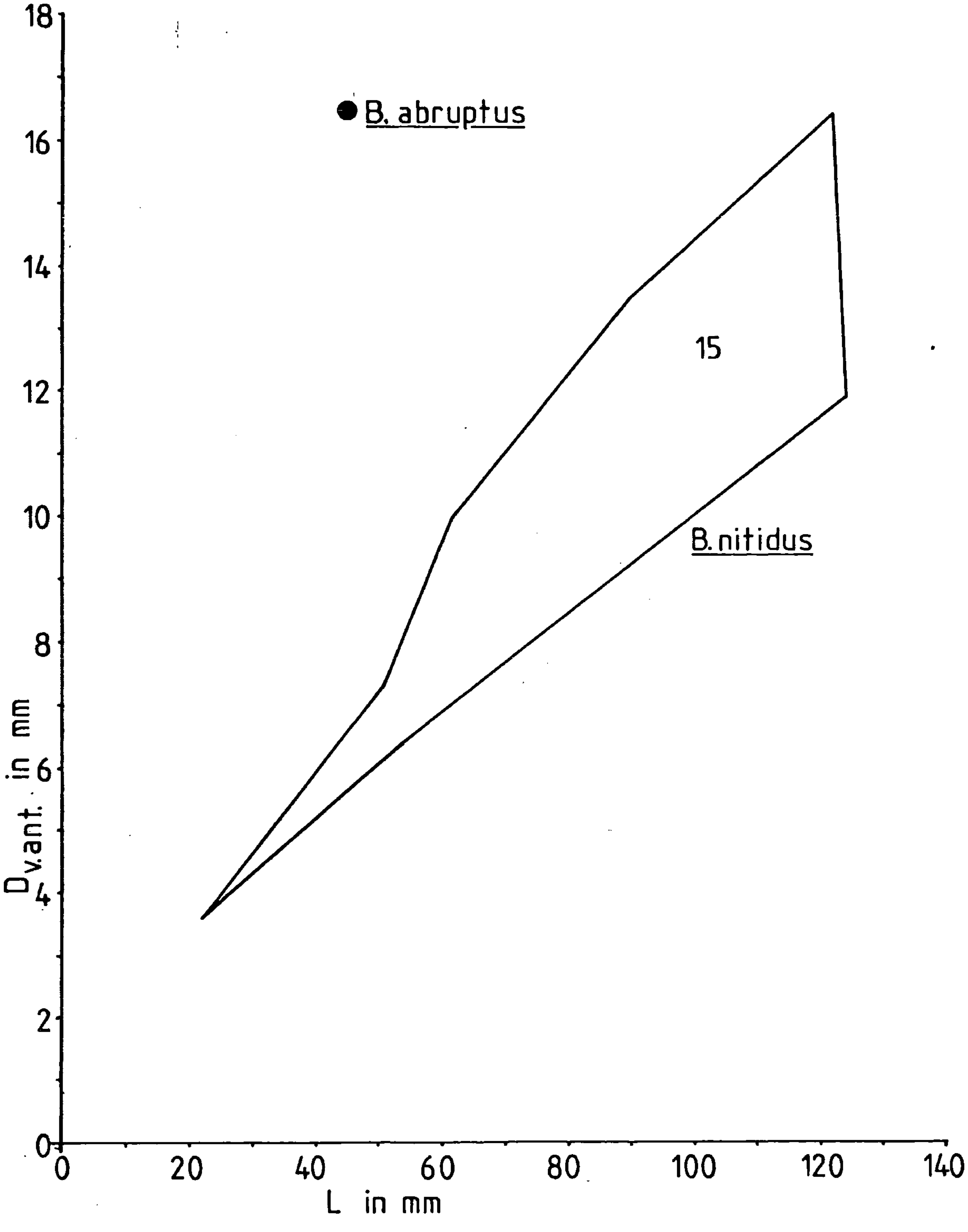
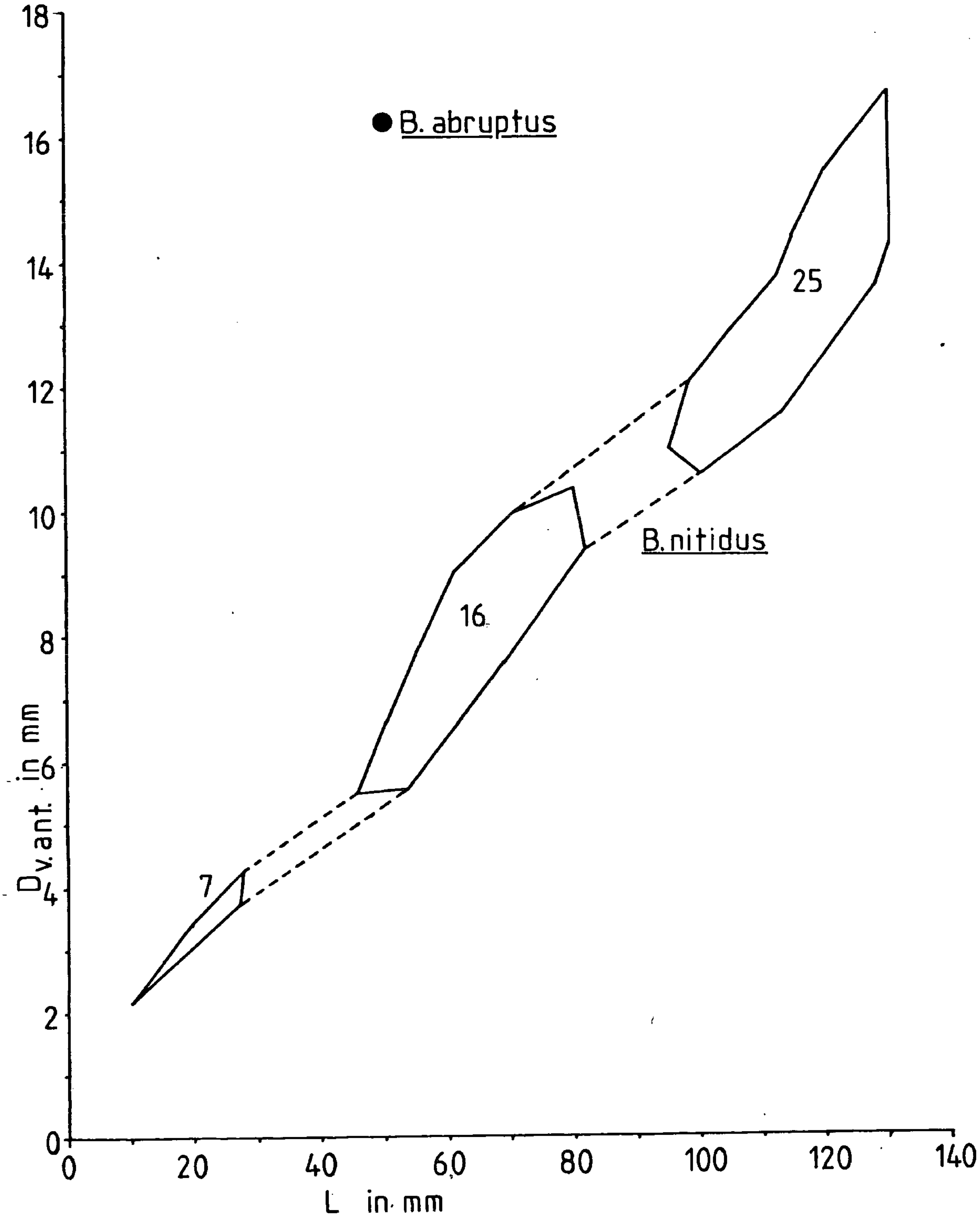
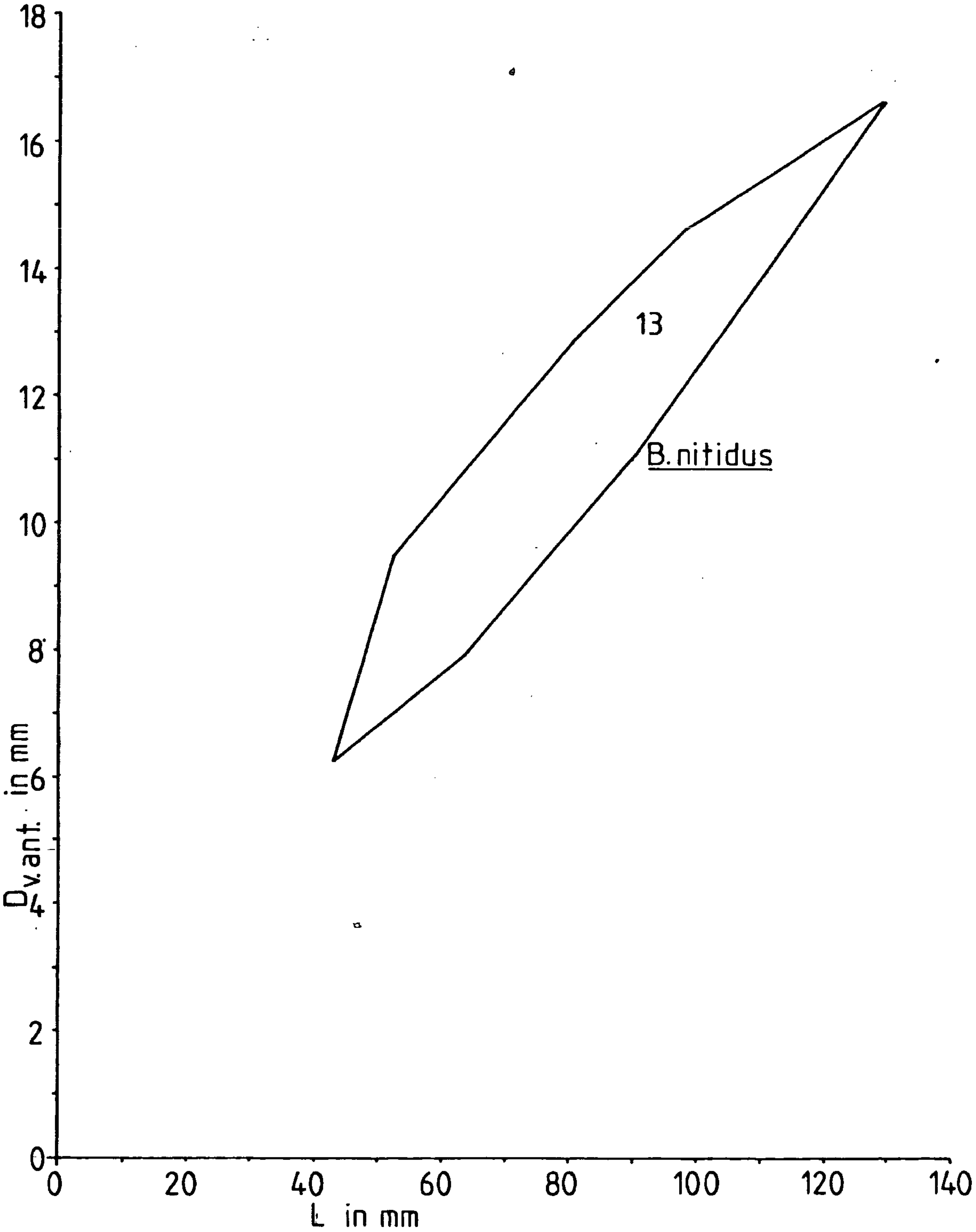


FIG. 90

$D_{v.ant.}$ L Beds 111 b-d



$D_{v.ant}$:L Bed 111e



$D_{v.ant.}$:L Beds 112 a-c

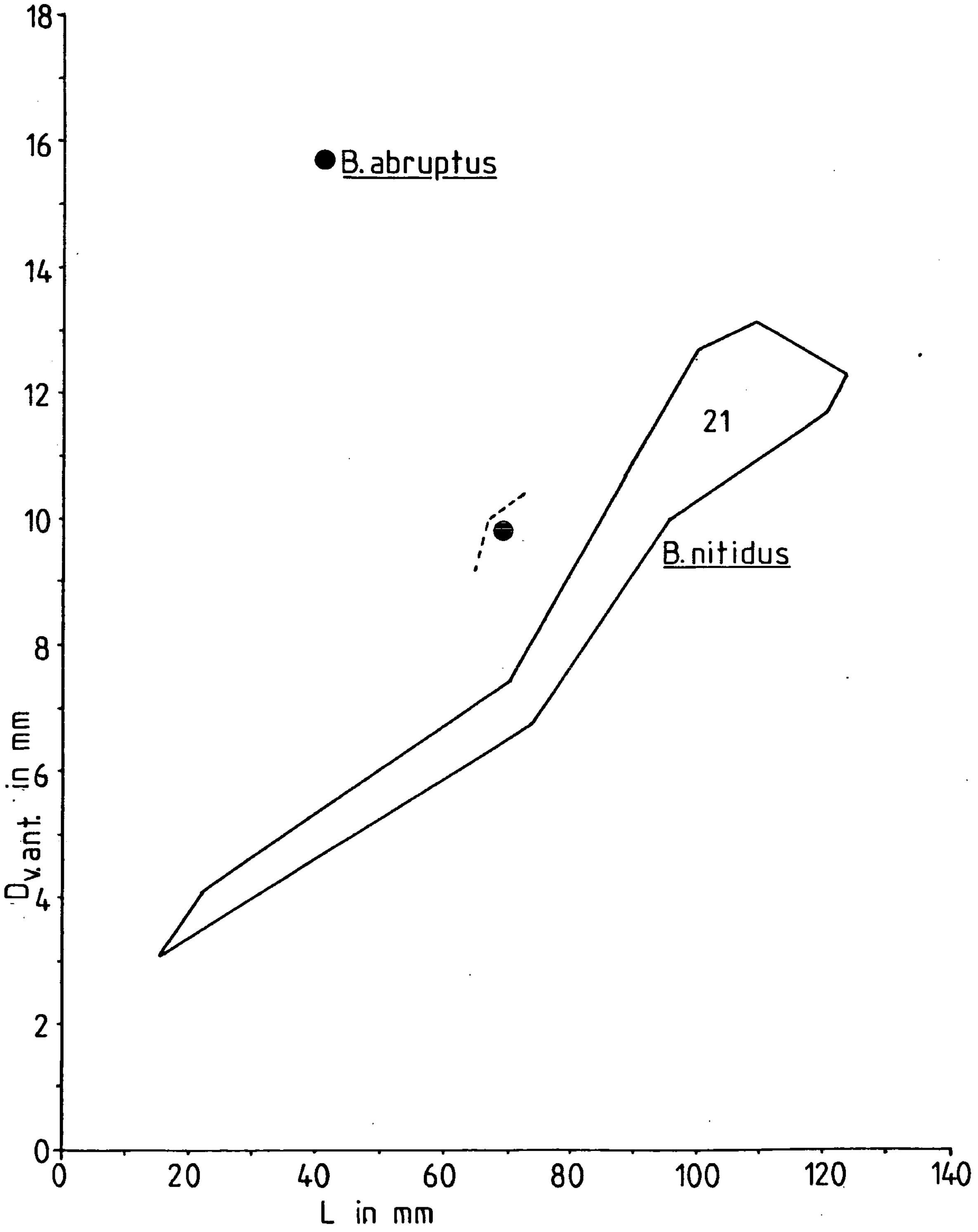
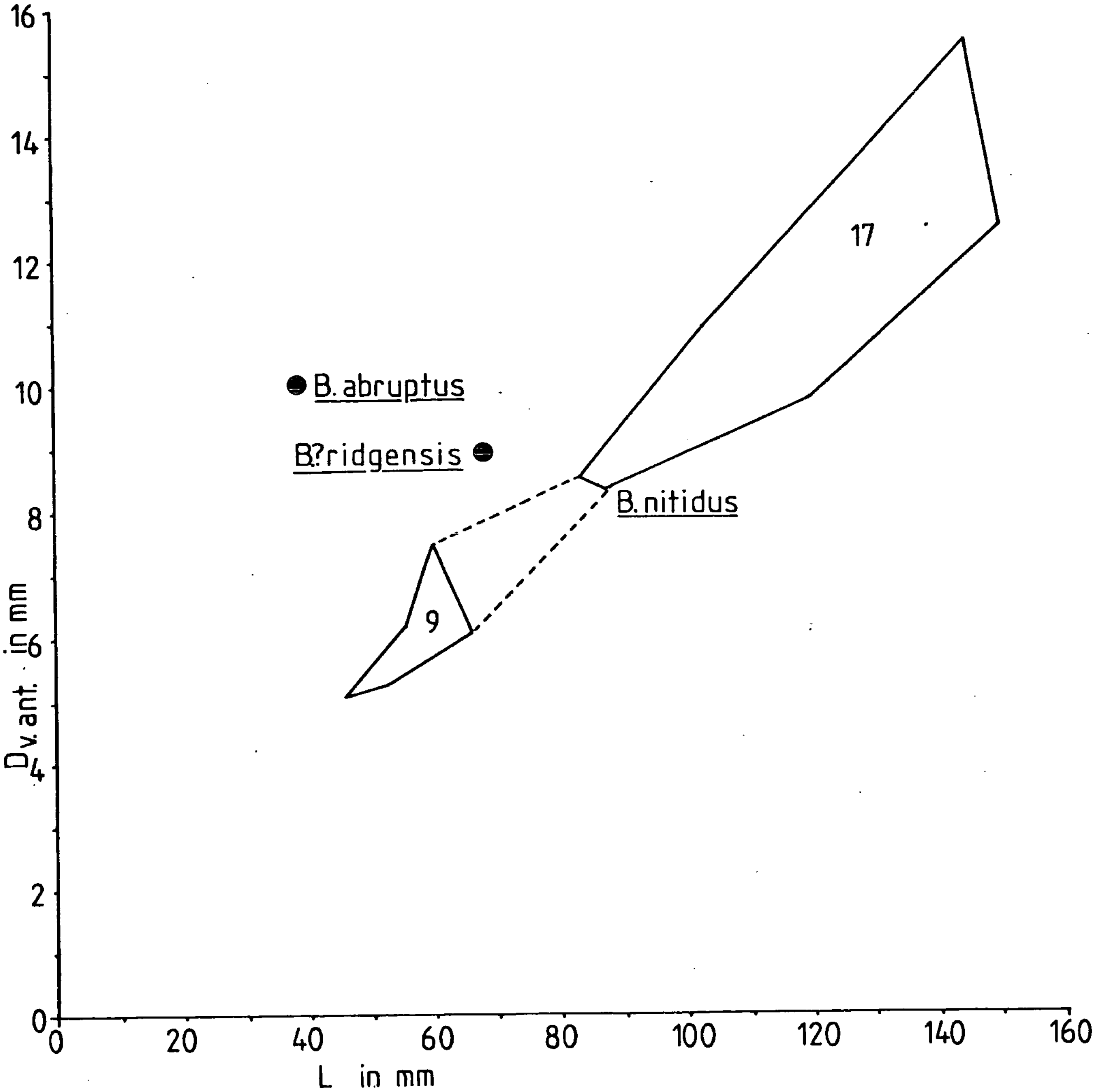
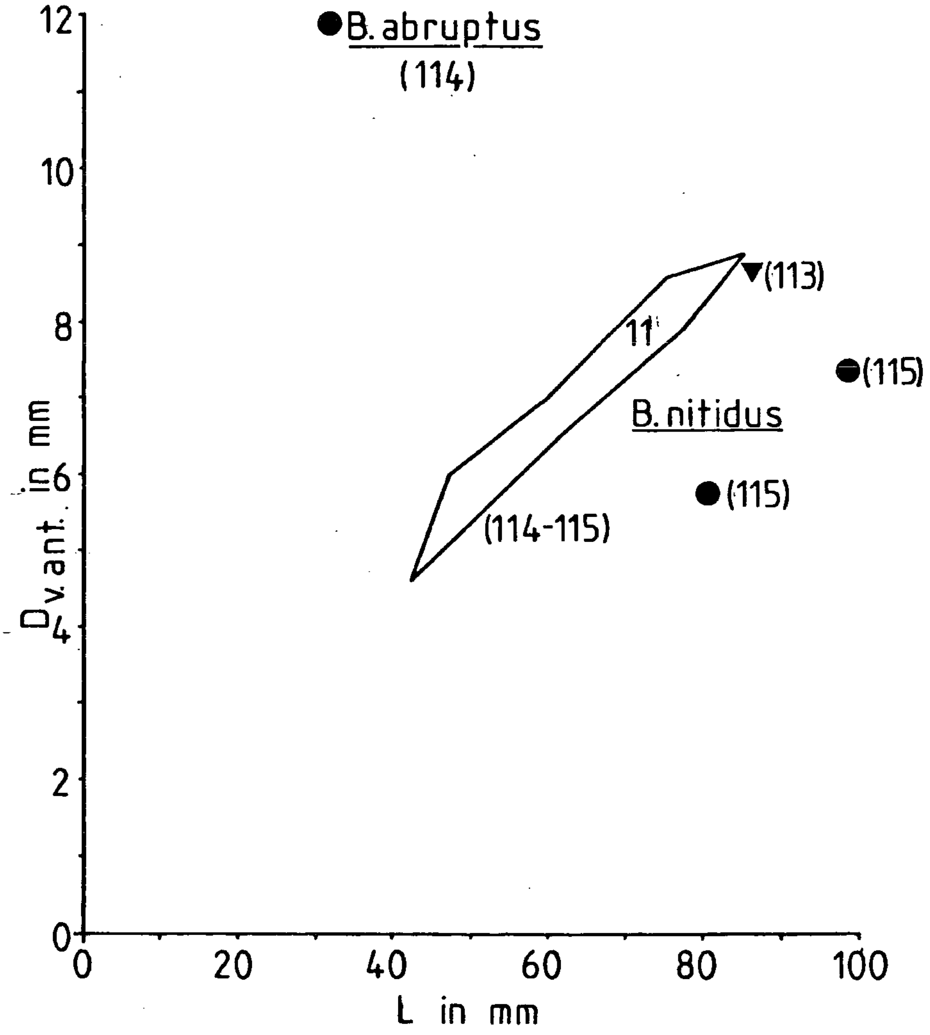


FIG. 93

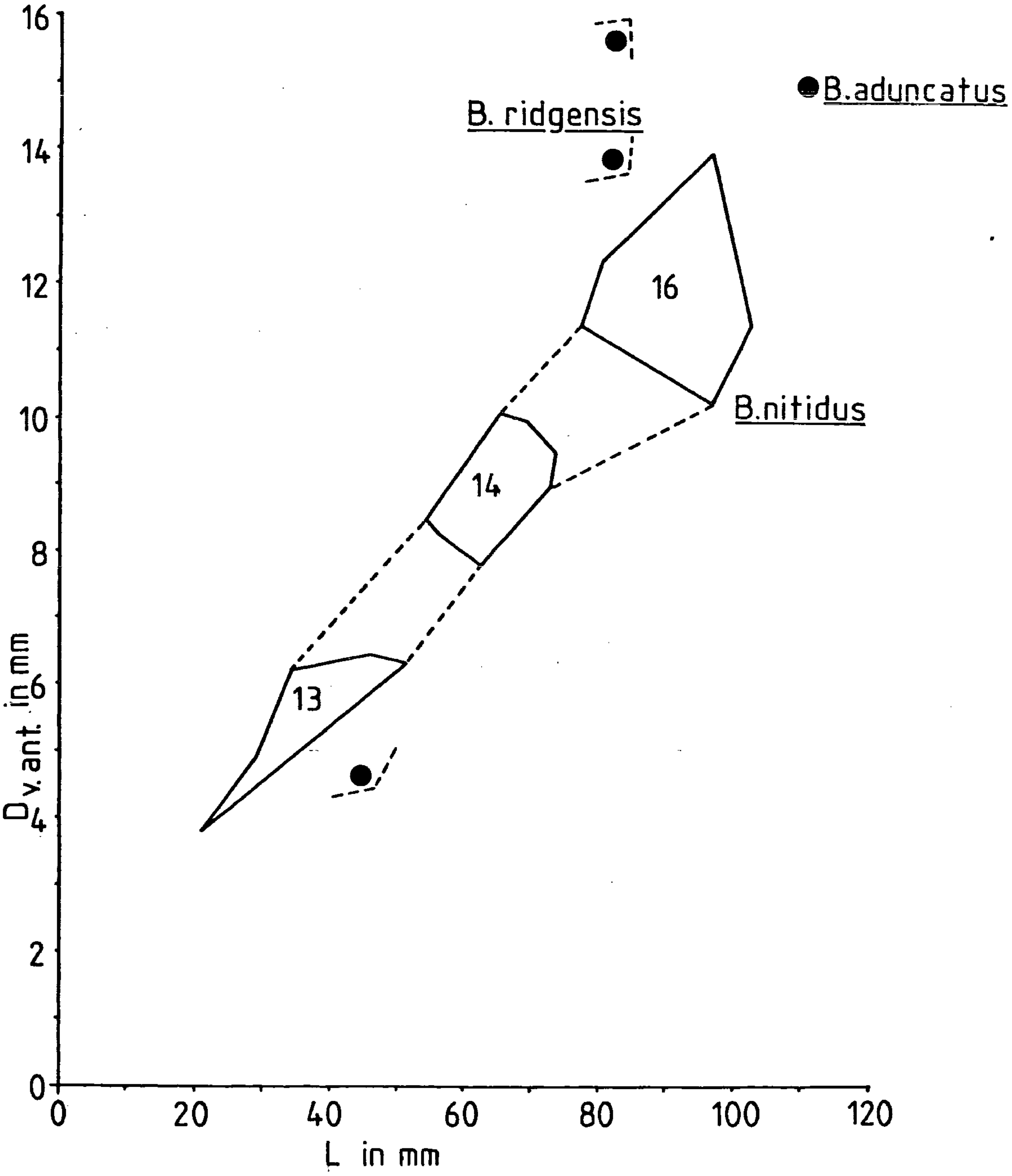
$D_{v.\,ant.} : L$ Beds 112 d–f



$D_{v.ant.}$:L Beds 113-115



$D_{v.ant.}:L$ Bed 117



$D_{v.ant.}$:L Bed 118 a

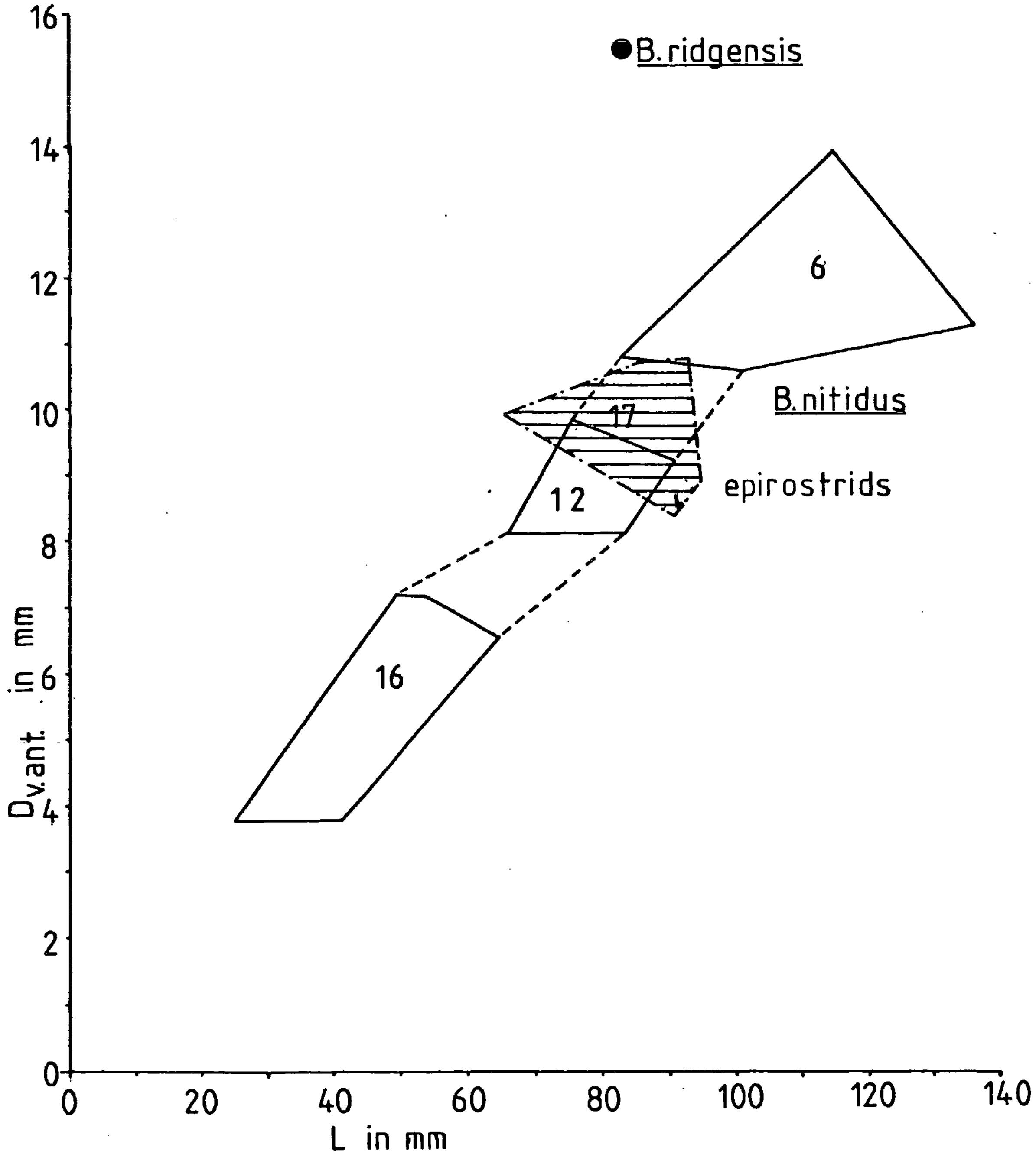


FIG.97

$D_{v.ant.}$:L Beds 118 b–d

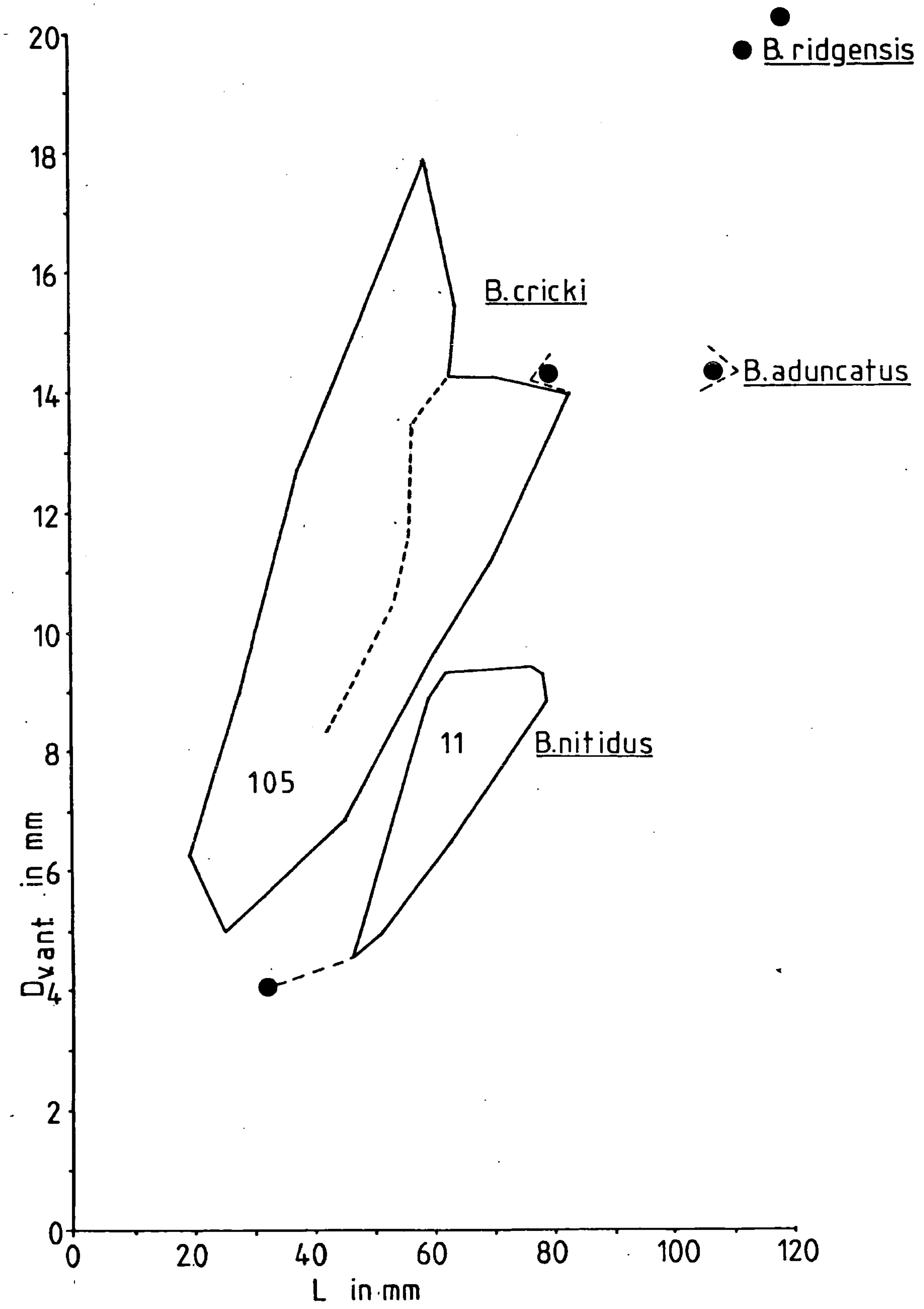
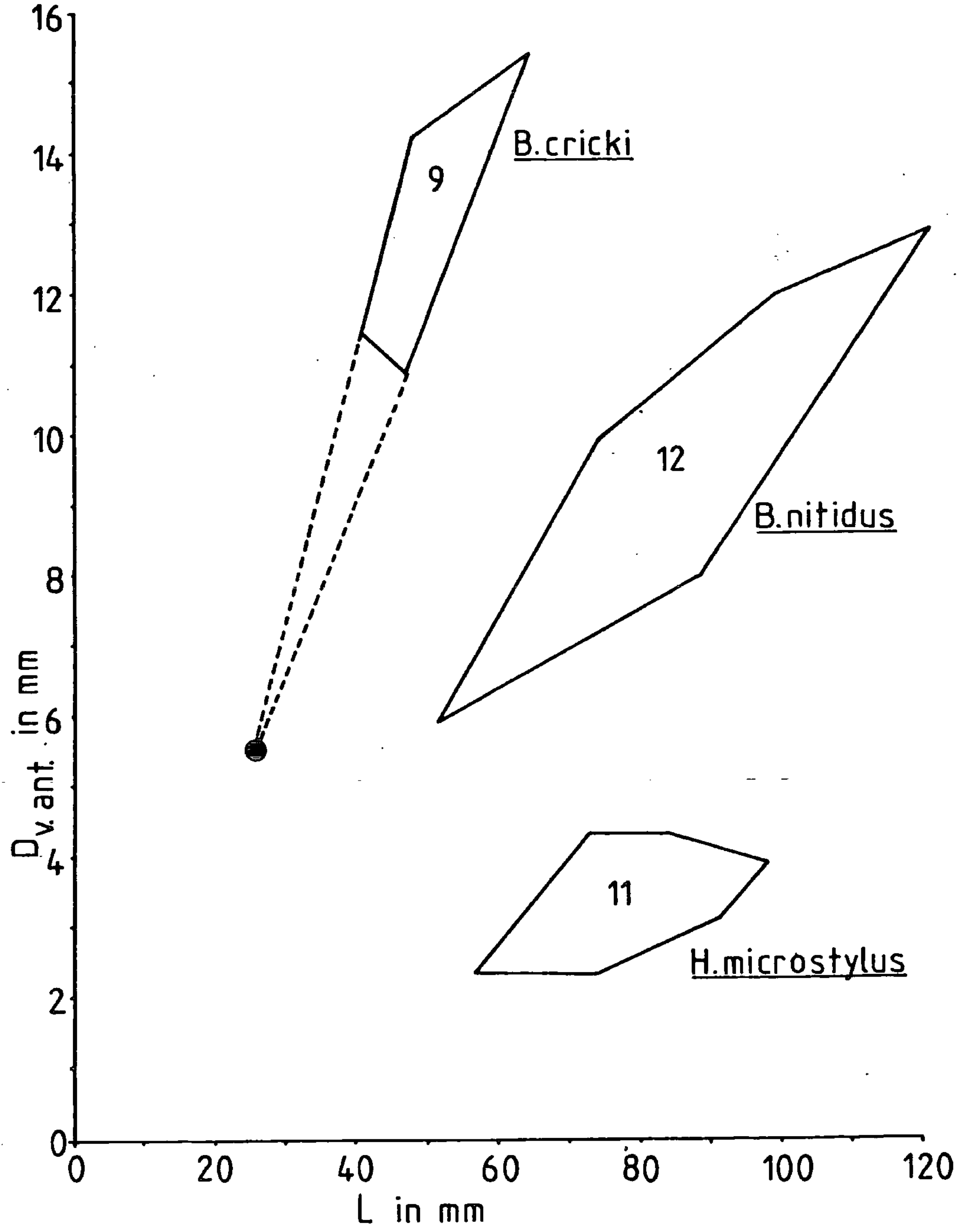


FIG. 98

$D_{v.ant.}$:L Bed 119



$D_{v.ant.}:L$ Beds 120 a-b

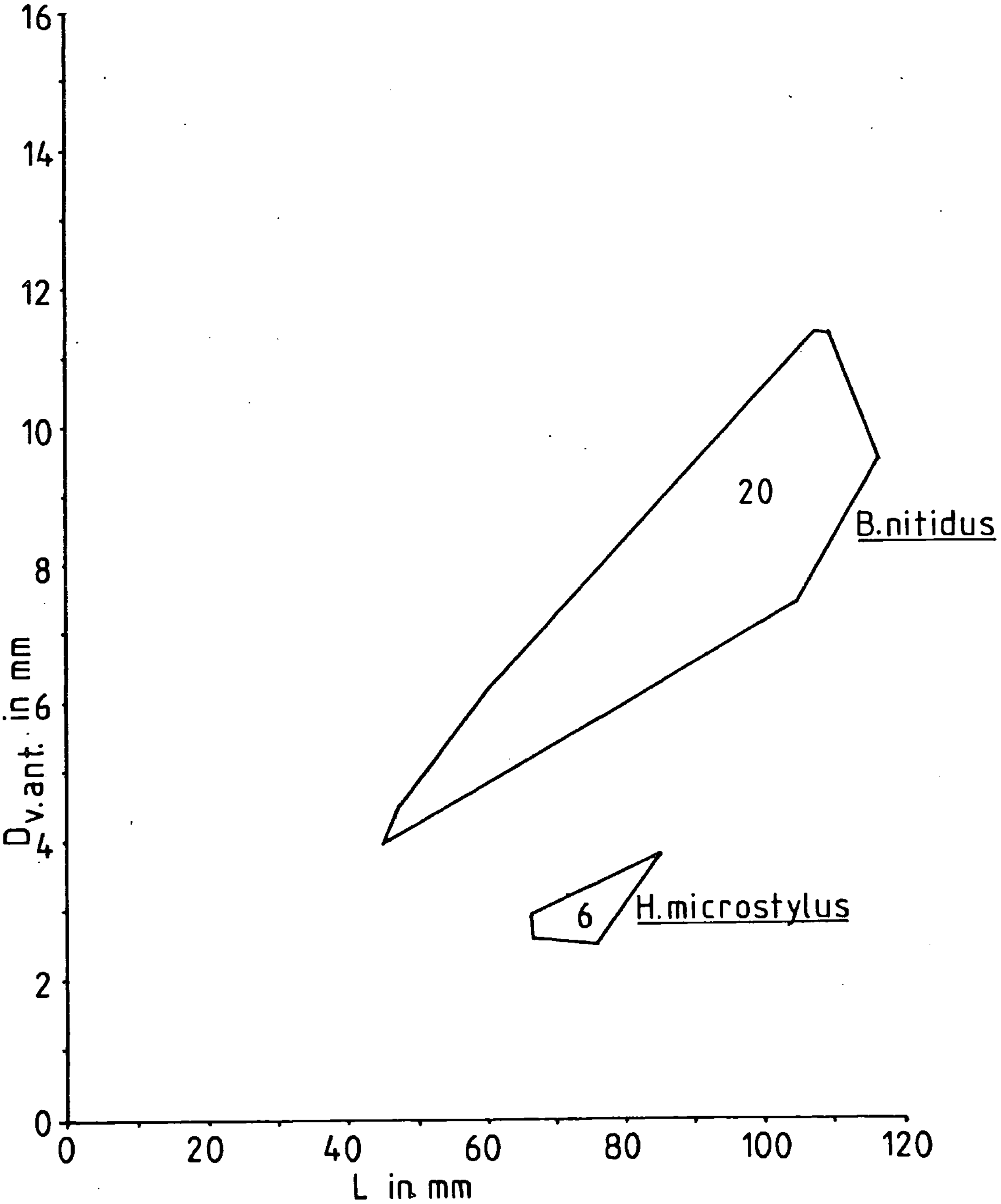
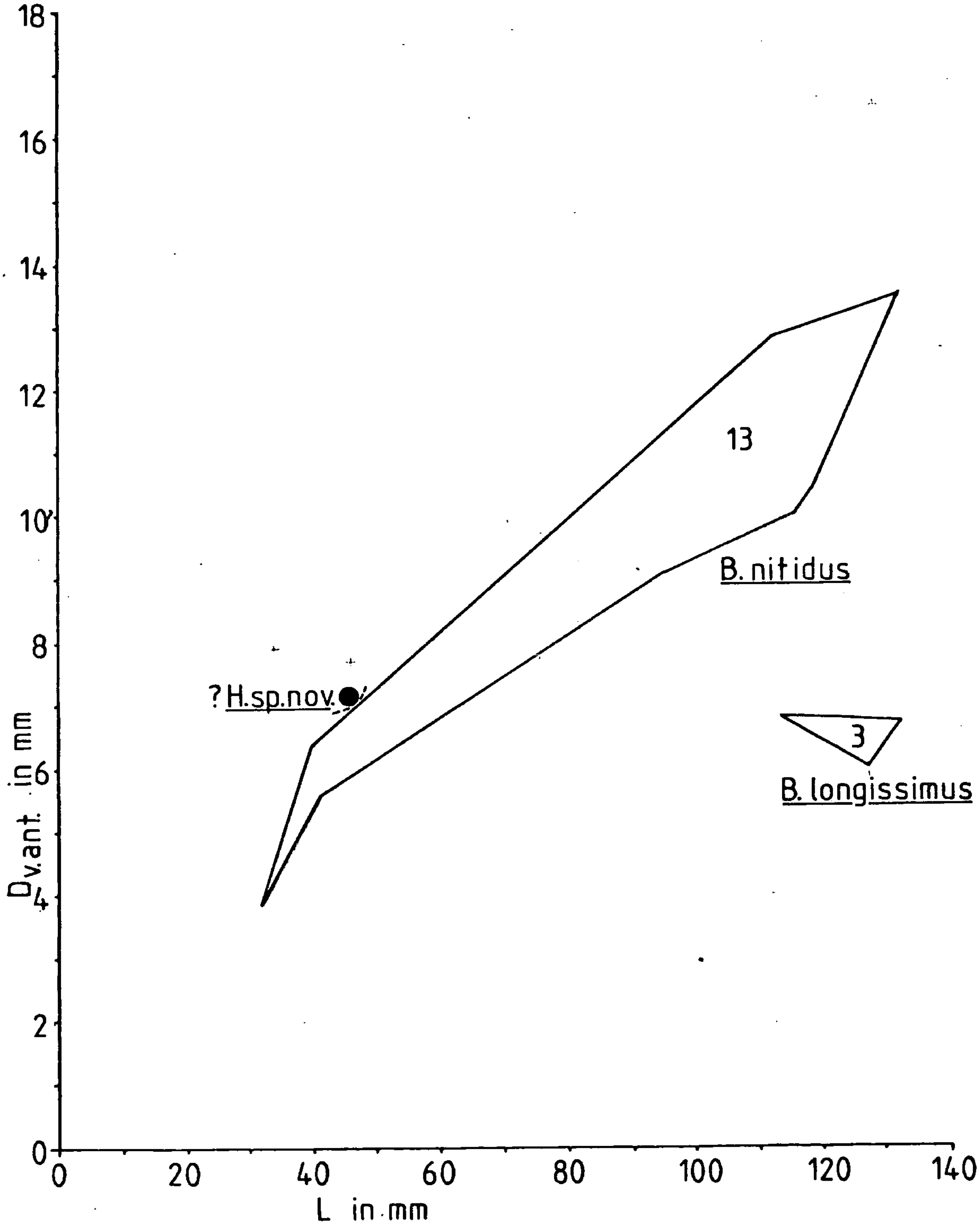
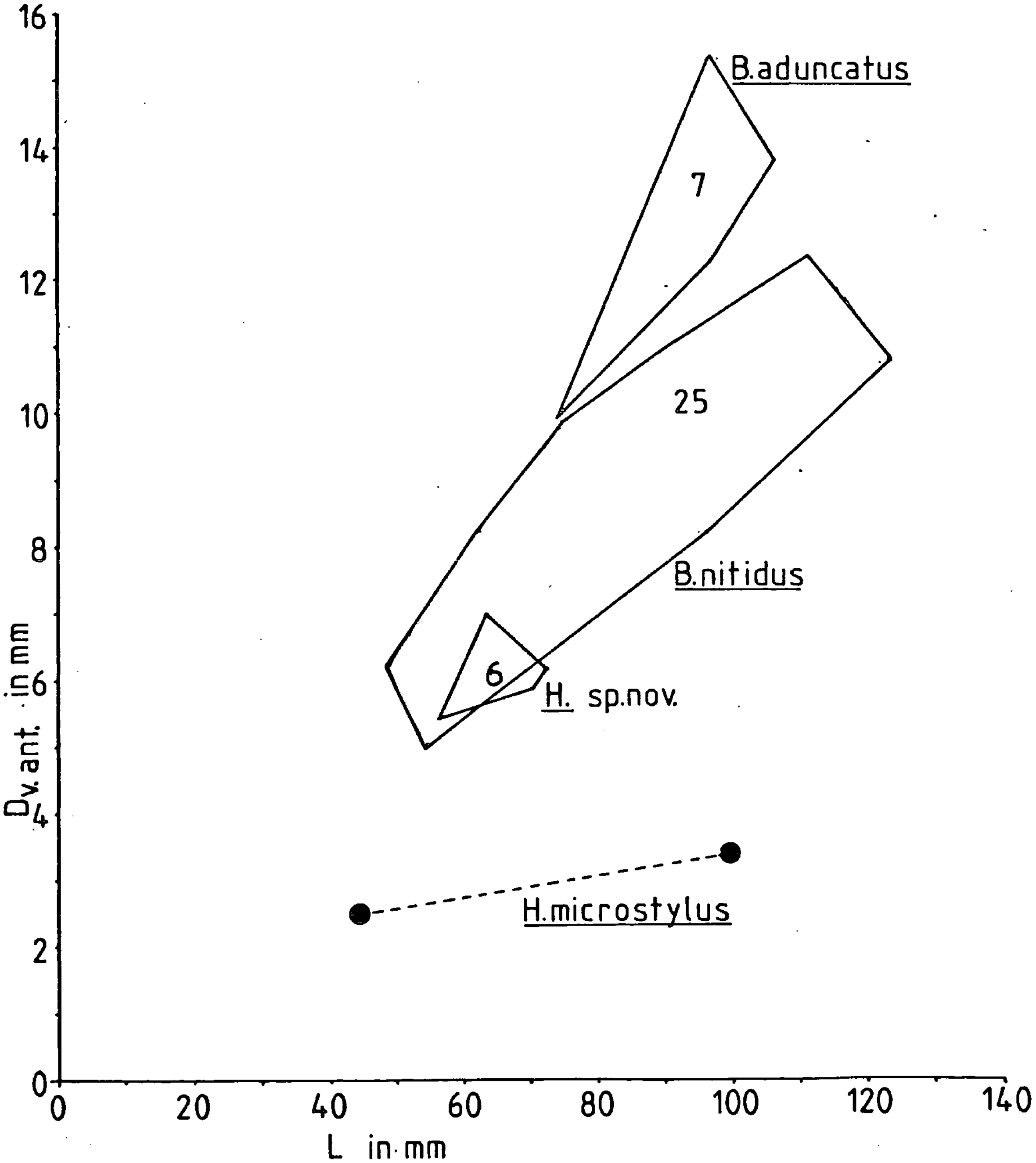


FIG.100

$D_{v.ant.}:L$ Bed 120c



$D_{v.ant.}$:L Beds 120 d–e



$D_{v.ant.}$:L Bed 121

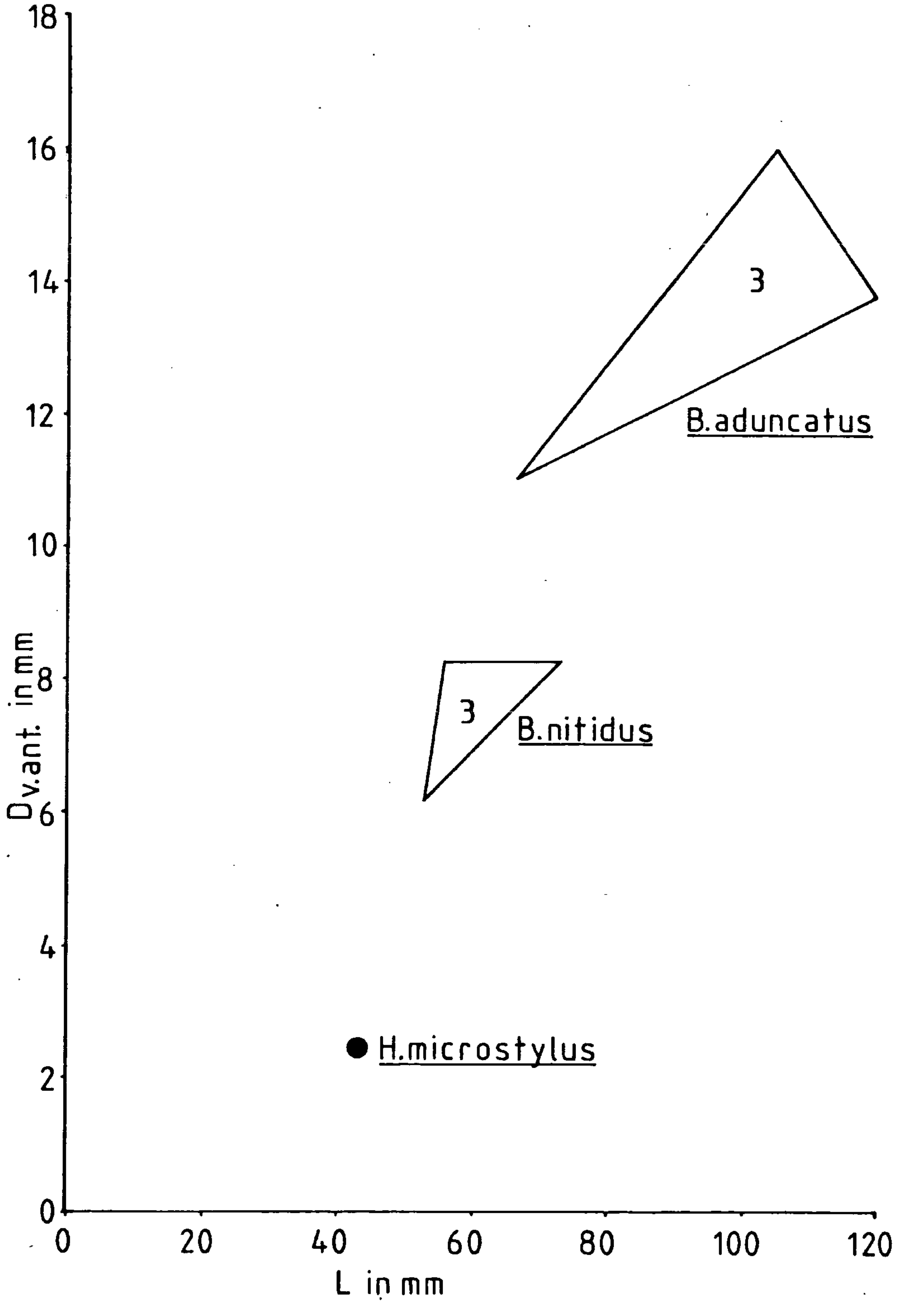
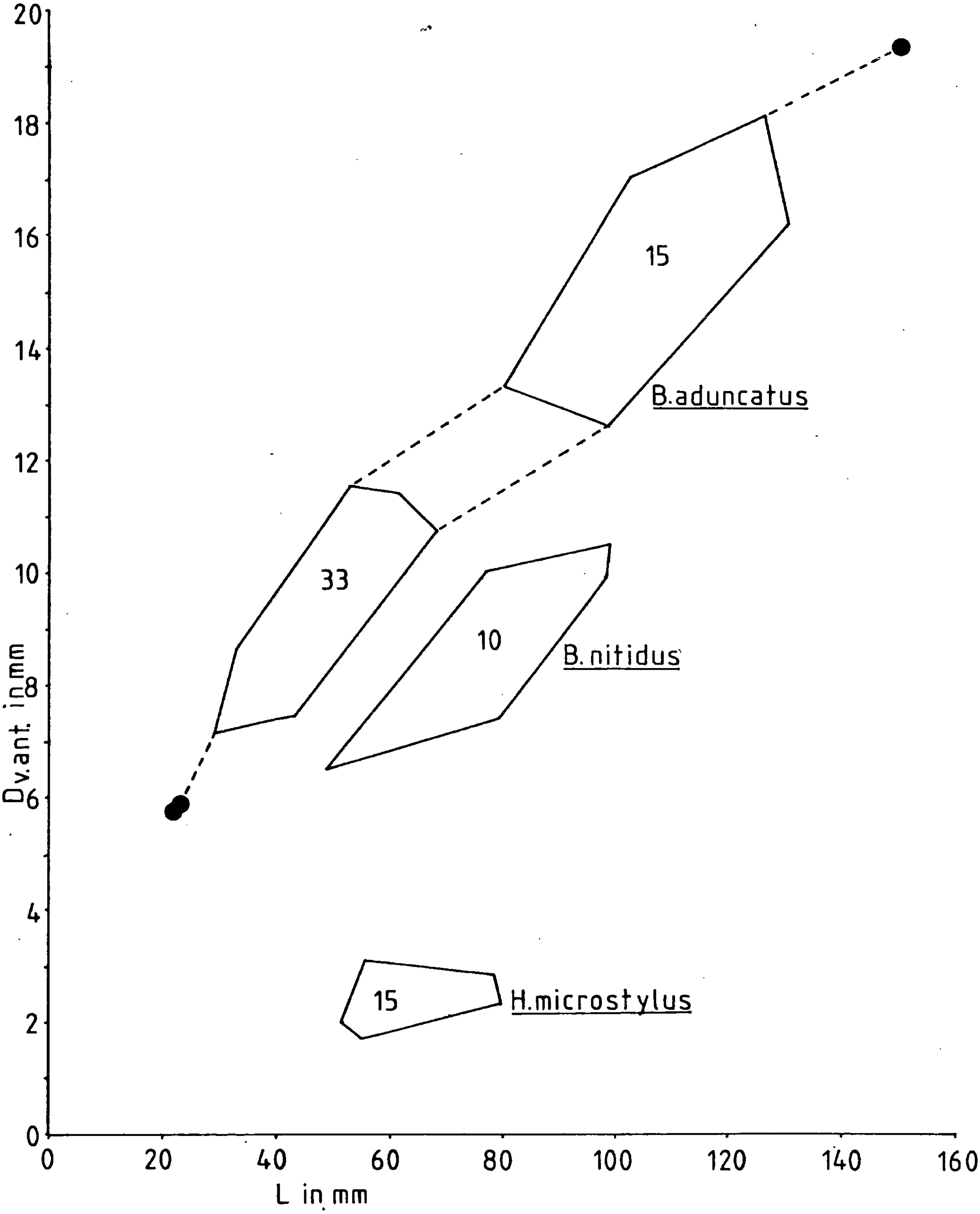


FIG.103

Dv.ant.:L Beds 122 a-c



Sexual dimorphism

Attempts have been made for well over a century (starting with d'Orbigny 1840-42) to recognize sexual dimorphism in belemnites, usually by analogy with body and shell dimensions in modern dibranchiates. Some authors (e.g. Lissajous 1925, pp.43-44), whilst accepting the possibility of dimorphism in principle, have concluded that its recognition in rostra is difficult if not impossible, and it has been pointed out that the anterior parts of the shell, particularly the pro-ostracum, are more likely to be affected by differences in gonads or body shape (e.g. Stevens 1965, p.54; Pinckney 1975, p.83). Where definite rostral dimorphism has been claimed (e.g. Delattre 1956), it has been regarded by other workers as possibly due to intraspecific variation and inadequate sampling. Varyingly tentative degrees of rostral dimorphism are commonly reported (e.g. Phillips 1870; Lissajous 1925; Challinor 1975; Pinckney 1975; Hewitt 1980), mostly hinging on different degrees of slenderness.

Detailed numerical analyses are sparse; as an example Delattre (1956) provided data, but no diagrams, for supposed dimorphism in Aalenian _Acrocoelites_ and _Brachybelus_ from Mamers, France. He utilized the same parameters as the present work and data for two pairs are plotted in figure 104. He described three pairs of dimorphs, members of a pair being termed types 'A' and 'B'. Type A forms had a shallower alveolus, more slender rostrum and more tapering apex than type B. (Note that, where phragmocones are similar, rostra with a greater diameter in the alveolar region necessarily have deeper alveoli.) This style of dimorphism is very similar to that described here in species from the Belemnite Marls. Unfortunately, as the figure shows, there is little sign of bimodality and, as Stevens (1965, p.54) suggested, normal intraspecific variation would account for the observed differences in morphology. It is possible that a larger sample would vindicate Delattre; in particular, the range of variation in the Acrocoelites triscissus and A. conoideus pair is similar to that observed in some of the clearly dimorphic pairs described here (e.g. Belemnites imus). (Delattre did not formalize his taxonomy, retaining two specific names for one supposed dimorphic species.)

The equivocal nature of most reported instances of dimorphism is due largely to reliance on observations of only the final growth stage of each rostrum (i.e. the whole specimen). As with ammonites, ontogenetic studies are required to identify juvenile similarity and subsequent separation of dimorphs. For the present research, specimens were chosen at random from whole assemblages and were longitudinally sectioned. The clusters of growth curves derived from these specimens, as well as clearly defining morphospecies, often show a subsidiary more or well developed bifurcation within single species. Data from suitably fractured unsectioned rostra plot very well onto the growth curve clusters (e.g. fig.105).

The dimorphism resulting from this bifurcation, where present, is detailed for each species in the previous chapter. The terms "robust" and "gracile" have been adopted to describe dimorphic rostra. Different styles of dimorphism may be recognized, depending on which growth curves (Dp:Lp) change slope to produce the bifurcation. In the Belemnite Marls, the following patterns were observed:

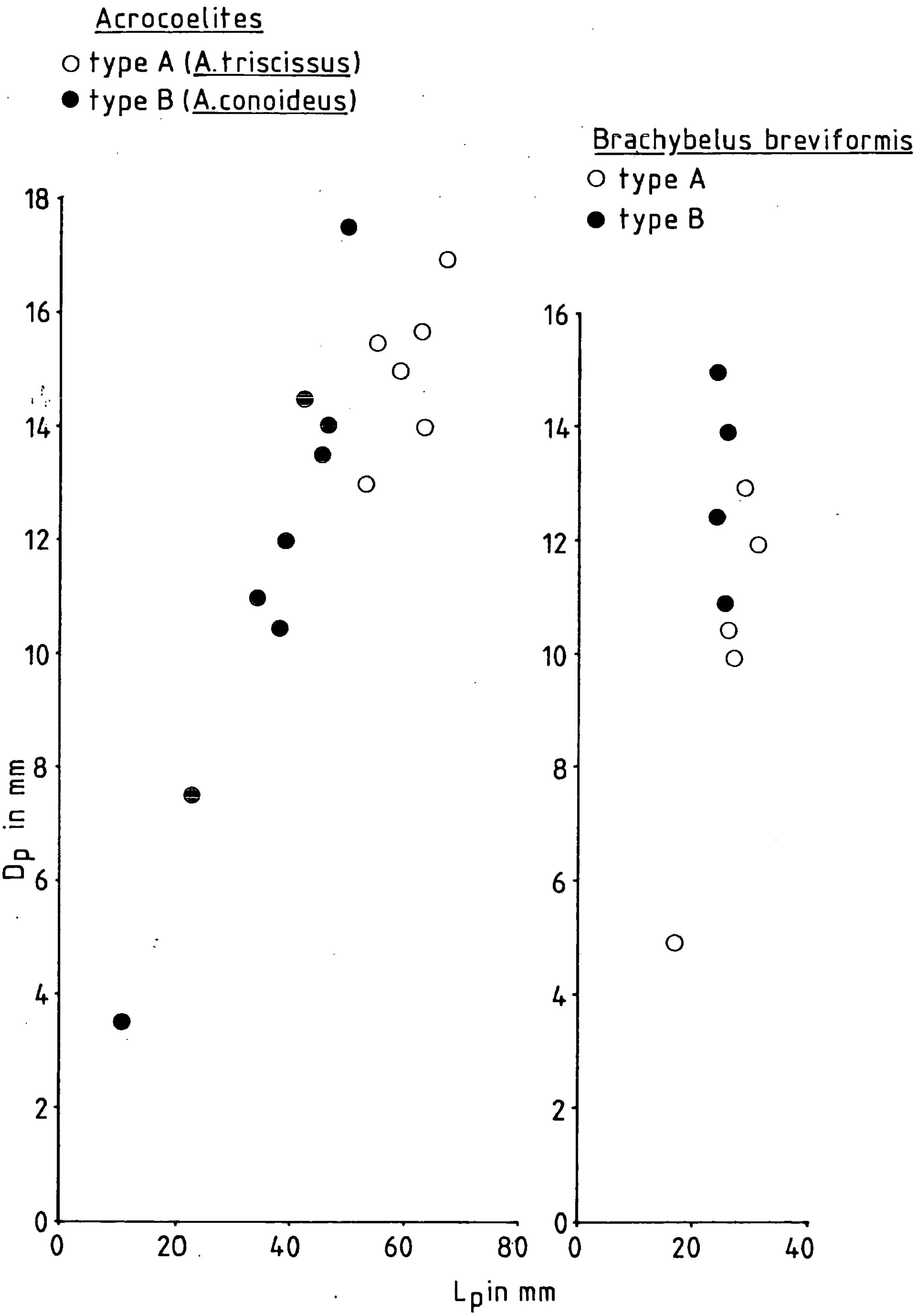
1) Gracile lines decrease slope, robust lines remain nearly constant: Belemnites imus.
2) Robust lines increase slope, gracile lines remain nearly constant: B. charmouthensis, B. longissimus and possibly B. nitidus.
3) Both sets of lines increase slope, robust more so: B. cricki.

In some other instances (e.g. B. nitidus in beds 111 b-d and 112, see figs. 31 and 32), although dimorphism is not apparent, the degree of variation in specimens above a certain size noticeably increases, and it is possible that there is here a "concealed" dimorphism. Statistical analysis of a larger sample might reveal a degree of bimodality in some such cases.

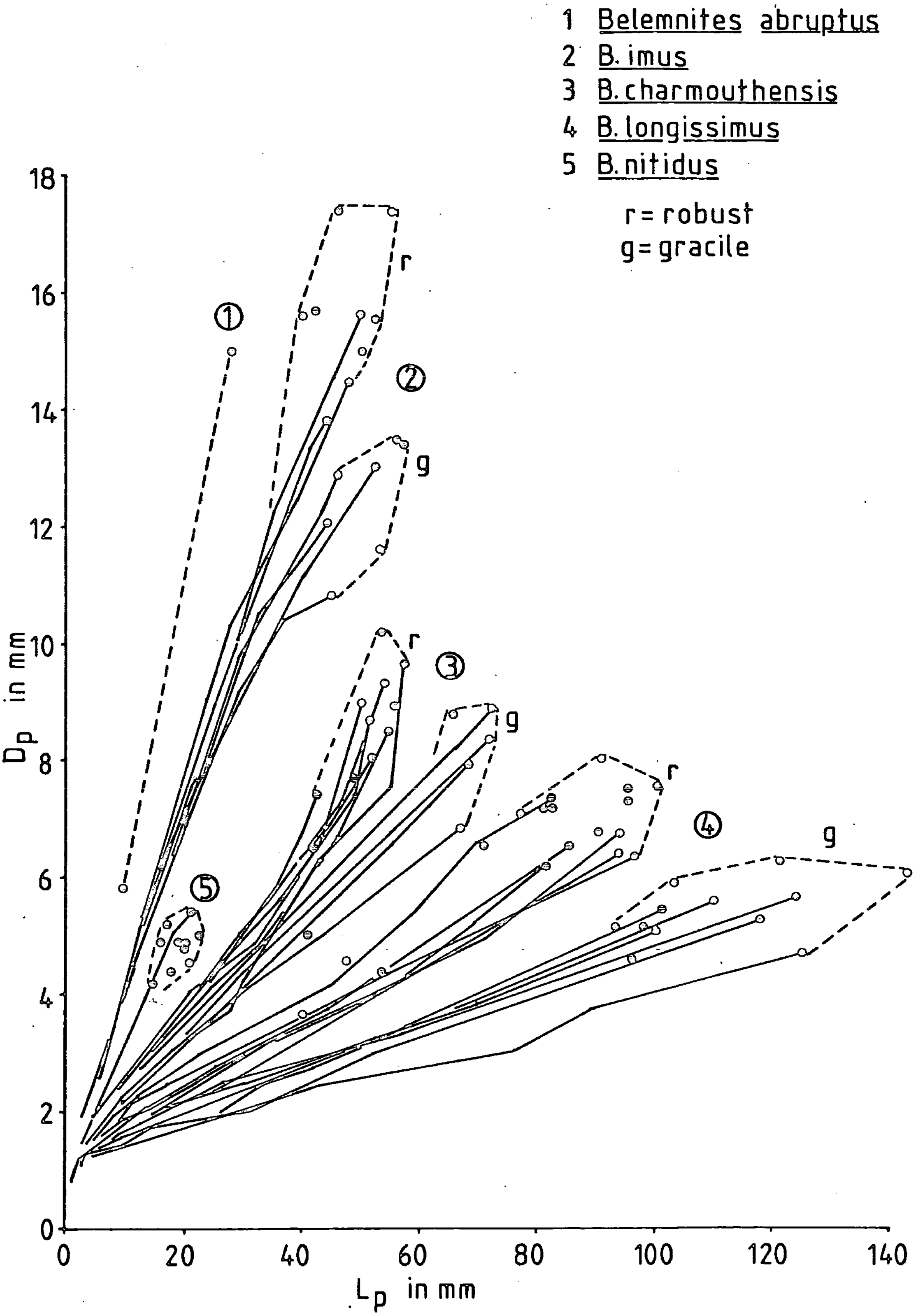
Assuming that it is sexual in origin, the actual function (if any) of rostral dimorphism is obscure. The most obvious suggestion would be that the male and female anatomies require slightly different counterbalances once a certain degree of maturity is reached, possibly related to egg mass or brood pouch development in the females. It is not at present possible to identify the sex of each dimorph; it may be that a better knowledge of variation in pro-ostraca would throw more light on the nature of belemnite dimorphism.

FIG.104

Supposed dimorphism in Aalenian belemnites
(after Delattre 1956)



Bed 110 IV $D_p : L_p$



Early ontogeny

Various interpretations of the structural components and ontogeny of the belemnitid skeleton have been proposed (e.g. Huxley 1864; Naef 1922; Müller-Stoll 1936; Mutvei 1964; Jeletzky, 1966) with a general lack of agreement between authors that is probably due mainly to differences in preservation and preparation of material and reliance on conventional light microscopes. However, use of the scanning electron microscope has clarified some of the more contentious details of structure, and in particular work by Barskov 1973 (a, b) on Upper Jurassic Pachyteuthis and Lower Cretaceous Conobelus and Mesohibolites has done much to elucidate early ontogeny.

The present research, while dependent on light microscope, in general supports Barskov's model of early ontogeny. This model is augmented by the observation in many Belemnite Marl specimens of opaque spherulitic calcite structures, with a diameter of the order of 0.1mm, posterior to the protoconch. In a number of instances (e.g. fig.9), rostral lamellae are clearly seen to be convoluted concentrically with these spherules which are thus regarded as being of primary origin, and are here termed "primary spherules". They were probably initial loci of rostral calcite growth, deposited within the elongating mantle epithelium to provide a framework for the deposition of normal rostral lamellae. Although most commonly observed within the area bounded by the earliest clear lamellae, they may occur at any point along the apical line where they were probably rapidly secreted within the soft growing apex of the mantle before being surrounded by lamellar material. Primary spherules were not observed in all specimens and are not regarded as obligatory skeletal elements; this mode of calcite deposition is appropriate where rapid elongation of the mantle occurs, and would probably have been largely dependent on external conditions (e.g. temperature, salinity, food supply). Spherules are most common in the more slender species, particularly *B. longissimus*.

The structural elements of the protoconch and early phragmocone and the ontogenetic interpretation of the early belemnitid shell are shown in figure 106. The growth stages shown are as follows:

1) Skeleton external, formed by initial inner prismatic layer of protoconch.

2) Mantle extruded, secreting outer prismatic layer of protoconch so that the skeleton is now internal.

3) Protoconch sealed off by closing membrane (an extension of the prismatic layers) to form a buoyancy chamber.

4) Deposition of nacreous layer around protoconch and commencement of phragmocone wall consisting of one inner prismatic layer and the outer nacreous layer. The nacreous layer frequently, if not always, encloses a boss-shaped void on the posterior face of the protoconch which, being filled with diagenetic sparry calcite, has been misinterpreted as a skeletal element (see below). Barskov, (1973b, p.221) by analogy with the ammonites, associates the deposition of the nacreous layer with a differentiation of the shell epithelium accompanying metamorphosis from a larval form.

5) Formation of first rostral layers as boss on the posterior face of the nacreous layer of the protoconch, with subsequent elongation of the mantle and deposition of primary spherules. Continued growth of phragmocone, with formation of septa and siphuncle (only one septum and connecting ring of the siphuncle are shown).

6) Deposition of convoluted rostral lamellae around primary spherules and subsequent smoothing out of rostral profile. Rostral lamellae probably consisted of alternations of prismatic calcite and nacreous aragonite with some degree of primary porosity. (Barskov 1973b; Spaeth 1971; Spaeth 1975).

Note that rostral growth cannot be correlated with phragmocone growth, so the relative timing suggested above cannot be proven. The initial elongation of the rostrum is assumed to correspond approximately to the initial development of camerae in the phragmocone.

The void formed by the nacreous layer on the posterior face of the protoconch was not recognized as such by Jeletzky (1966), although it is often filled with secondary sparry calcite identical to that usually occupying the protoconch (e.g. Jeletzky 1966, pl.11, fig.1). He included it in a structure that he termed the "primordial guard" (1966, p.129), appearing in the suborder Belemnitina as a saucer adhering directly to the outer wall of the protoconch and restricted to its apical part. Although the bulk of this structure consists of secondary calcite, a few lamellae external and concentric to the apical part of the nacreous layer can sometimes be seen, but, like the primary spherules, they were probably not obligatory features of rostral development but depended rather on the rate of elongation of the posterior mantle.

Subsequent development of the rostrum has been described for each species under the relevant headings; early profiles of various species from the Belemnite Marls are shown in figures 107 and 108. These different forms presumably provided appropriate counterbalancing for different shapes of young animal. Although the form of the rostrum at this stage more or less prefigures that of the adult, it is invariably more stout and has a deeper alveolus; this may partly have been to protect the fragile protoconch and early phragmocone during the animal's juvenile stages.

FIG.106

A: structure of the protoconch and first phragmocone chamber
(after Barskov 1973a)

B: early ontogeny; see text for details
(1-4 after Barskov 1973b; 5-6 after Barskov 1973b and pers. obs.)

FIG. 106

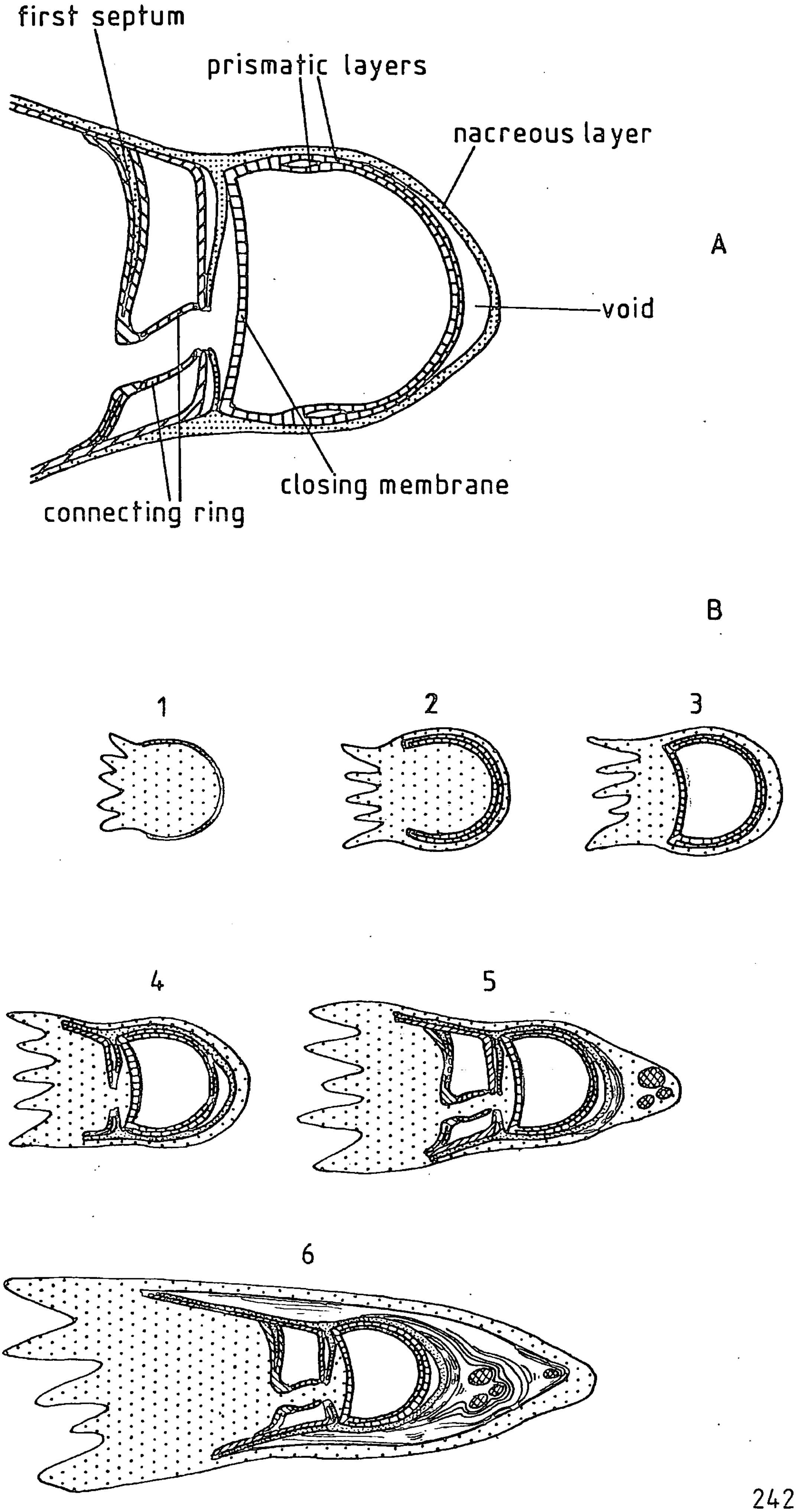
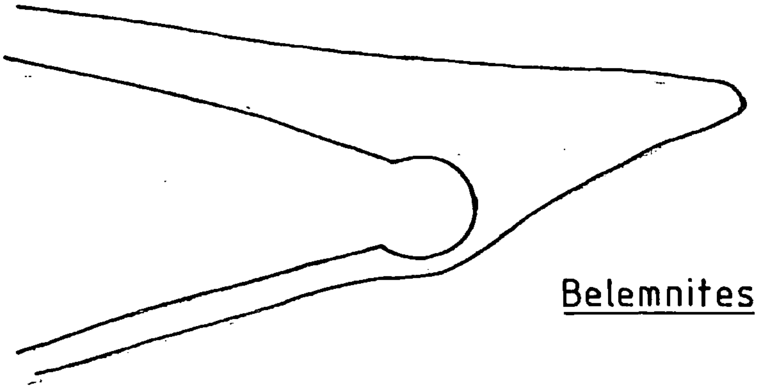
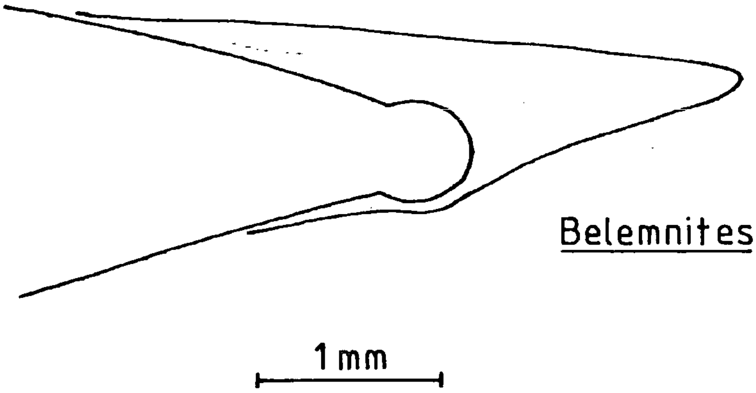

first septum
prismatic layers
nacreous layer
A
void
closing membrane
connecting ring
B
1
2
3
4
5
6

FIG. 107

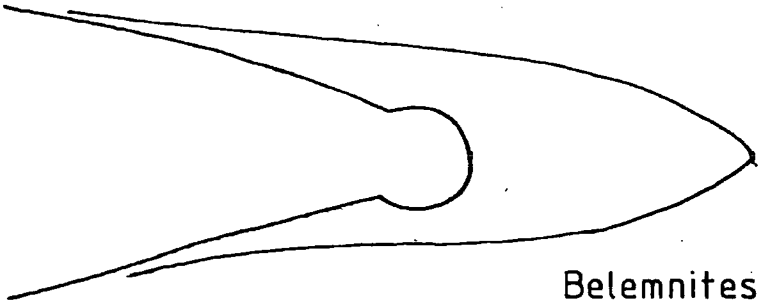
Typical early rostral profiles



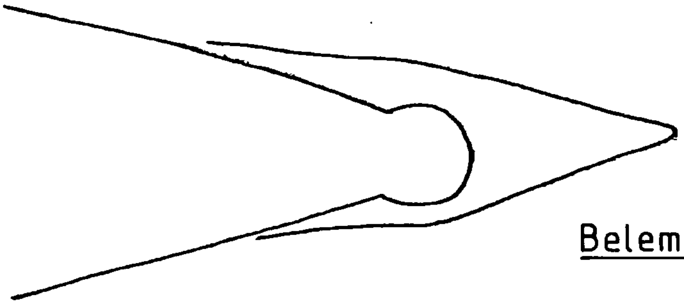
Belemnites abruptus



Belemnites imus



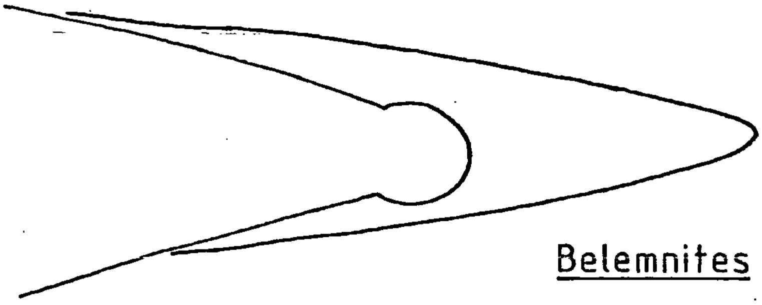
Belemnites cricki



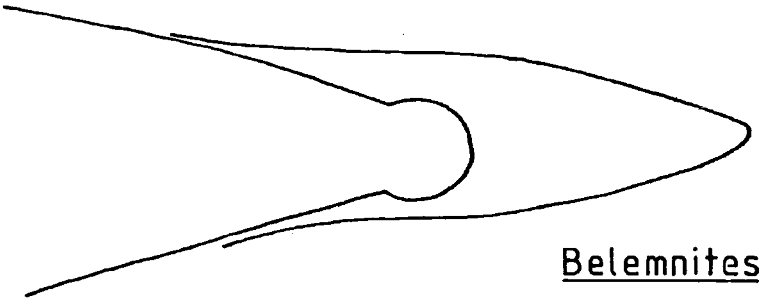
Belemnites nitidus

FIG.108

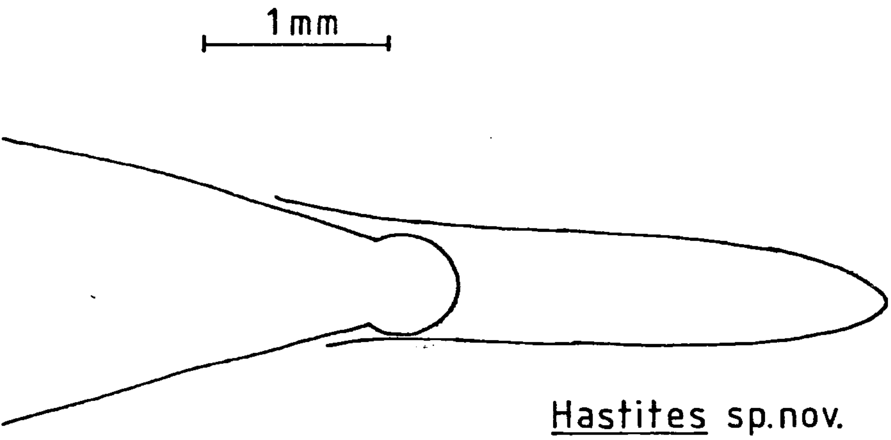
Typical early rostral profiles



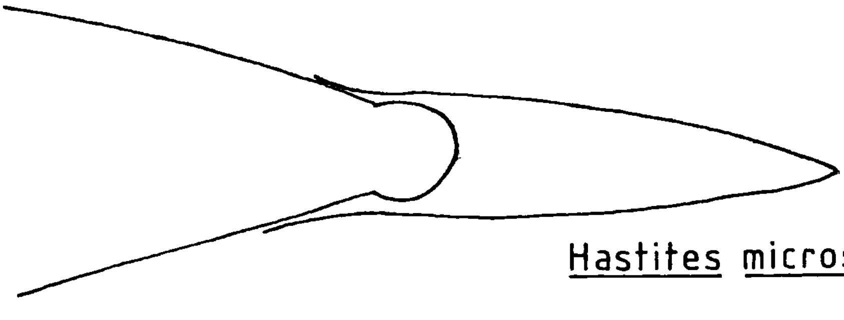
Belemnites charmouthensis



Belemnites longissimus



Hastites sp.nov.



Hastites microstylus

Rostral form and function

It is generally accepted (e.g. Stevens 1965, p.49) that the belemnite rostrum functioned principally as a counterweight, while its development as a protection for the phragmocone was usually of secondary importance.

The variation in shape of the rostrum encountered in the Lower Pliensbachien is considerable, ranging from short obtuse cones (?Coeloteuthis sp., Belemnites abruptus) where phragmocone protection may be an important function, to highly slender elongate forms, often strongly clavate (B. longissimus, Hastites spp.). If the entire belemnite fauna of the Belemnite Marls is considered, then every degree of slenderness between these extremes is present.

It is reasonable to suppose that this variation is to some degree related to variation in form in the rest of the animal; however, the only other structure whose form can be deduced - the phragmocone - was found to be remarkably similar, at least in its alveolar portion, in all of the species studied (fig.109). There is almost certainly a wide variation in the size attained by phragmocones of various species; from the few reasonably well preserved specimens found, it appears that the phragmocones of the slenderest species (B. longissimus) are much shorter than in stouter species of comparable rostral length (B. aduncatus) (fig.112).

Usually, the rostrum is the only structure available from which to deduce its own significance, but, despite this, some useful speculation is possible. Firstly, it is likely that much rostral variation, particularly intra-specific variation, was not closely related to function.

As Schumann (1974, p.14) pointed out, belemnite taxonomy is "upheld by features which formerly played only a minor role in the life of the animal. Such is the case, for instance, with the cross section (in so far as its shape is not determined by the impressions of the furrows). It is especially true of the shape of the apex; whether it was more or less acute or obtuse was in general completely insignificant to the organism" (my transl.). He is in effect stating that much rostral variation is due to low selection pressure. This is also borne out by the surprisingly common occurrences of deformed or damaged and regenerated rostra that manage to have reached full size subsequent to initial deformation or fracture, suggesting that a deformed rostrum was not particularly disadvantageous to the animal.

One aspect of rostral form whose function can be recognized is that which results in a more effective use of available skeletal material as a counterbalance. Obviously, the effective turning moment of a given mars of rostral material is maximised by placing as much of it as possible as far away as possible from the centre of buoyancy of the animal. Forms with long, slender rostra (including epirostra - see below) and/or clavate rostra may be explained in this way. There may also be streamlining advantages. These characters are found separately or in combination in many Jurassic and Cretaceous belemnites; of interest here is the lineage that commenced with Hastites, which first appears in the jamesoni Zone. The Hastitidae, and, later, the Belemnopseidae (see Jeletzky 1966) developed characters that show them to have differed significantly in organization from the Belemnitidae. In addition to possessing a clavate rostrum that is often extremely slender in the alveolar portion, the Hastitidae show a "strong tendency toward development of shallow ventro- and dorsoalveolar furrows and toward partial to complete destruction of apparently poorly calcified alveolar part of guard, commonly resulting in Actinocamax - like appearance at alveolar end." (Jeletzky 1966, p.143). In, for example, Hastites microstylus, the extraordinarily thin alveolar part of the rostrum and the additional fragility conferred by its poor calcification suggest that it was supported by more soft tissue than in other belemnites; at least some belemnite rostra are supposed to have been only thinly covered by mantle tissue (Seilacher 1968).

Increased internalization of the rostrum in the Hastitidae may be reflected in ventral and dorsal alveolar furrows, not found in the Belemnitidae, which may indicate an increased vascular supply to this part of the animal.

The paired lateral furrows or lines are similar to those found in many of the Belemnitidae, but are nearly always well developed whereas in the Belemnitidae they are of very variable depth even within single species. On the other hand, the dorsoventral apical furrows that are nearly always present in the Belemnitidae as posterior extensions of the upper lateral furrows are invariably absent in the Hastitidae. The furrow patterns observed in the species dealt with here are shown in figs. 110 and 111. As discussed by Stevens (1965, pp.49-50), lateral furrows probably represent "the points of termination (against the flanks of the guard) of lateral structures such as fins".

The transverse section of the rostrum often varies much within and between species, and is only occasionally of practical taxonomic value (e.g. in B. imus). Most belemnite rostra are more or less compressed along the whole length. In Lower Pliensbachian species in which some depression occurs, it is usually most marked in the posterior portion of the rostrum (e.g. B. ridgensis). The shape of the section is partly determined by the rostral furrows and facets; representative sections (taken across the apex of the alveolus) are shown in figs. 110 and 111).

FIG. 109 Drawings traced from photographs of median longitudinal sections to show alveolar profile.
All x2.

A: Belemnites longissimus: 147 (robust) bed 110

B: B. nitidus: D121 bed 110 V

C: B. imus: D87 (robust) bed 110 II

D: B. abruptus: D175 bed 110 V

E: B. cricki: D139 (robust) beds 118b-c

F: B. nitidus: TB117 beds 120a-b

FIG. 109

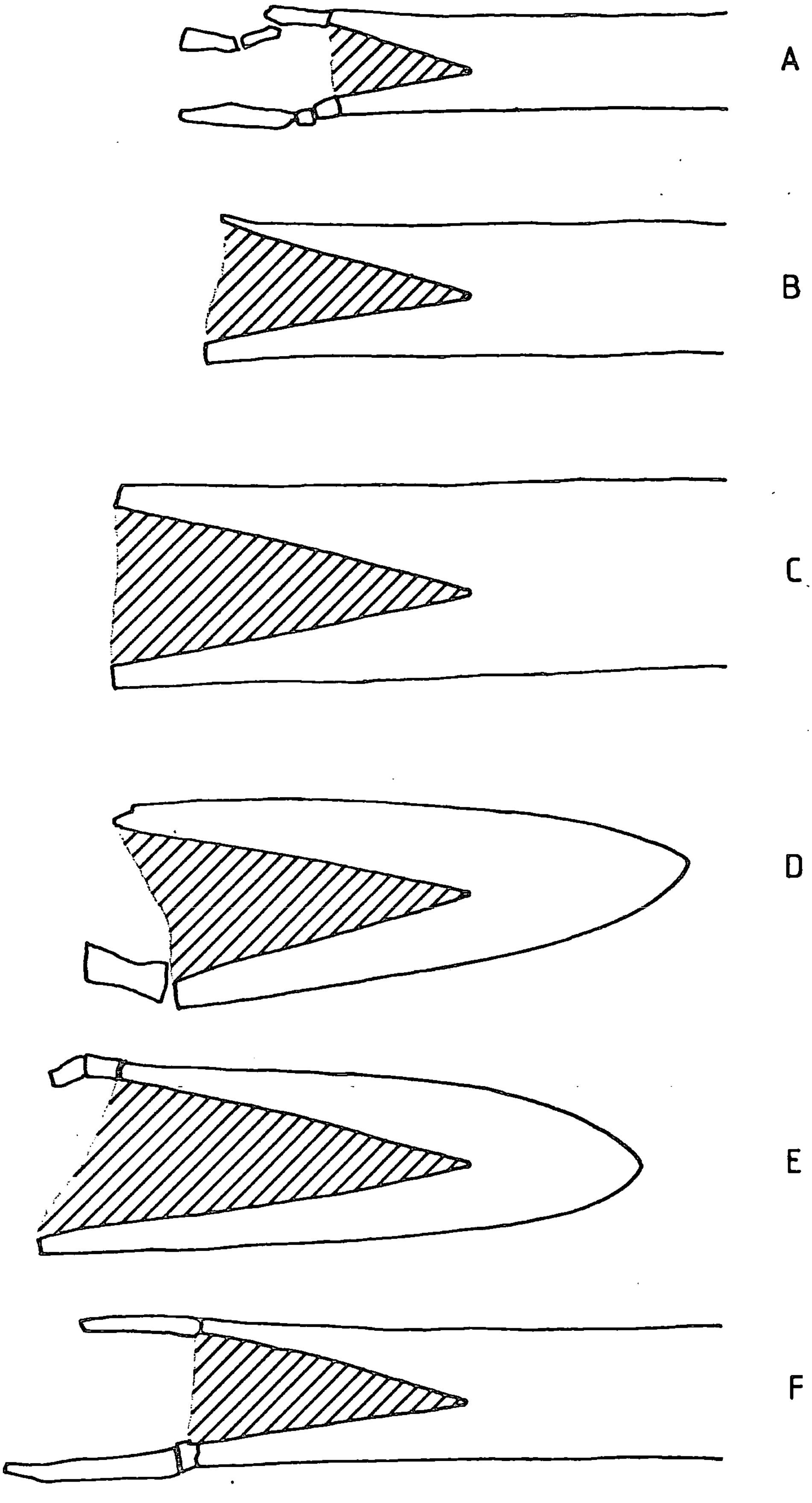


FIG.110

A: _Belemnites cricki_

B: ?_Coeloteuthis_ sp.

C: _B_. _ridgensis_

D: _B_. _aduncatus_

E: _Hastites microstylus_

F: _H_. sp. nov.

G: ?_H_. sp. nov.

Dashed lines indicate course of furrows; hatched areas represent facets or very wide, shallow furrows.

FIG. 110

Furrow patterns and transverse sections
(sections at alveolar apices)

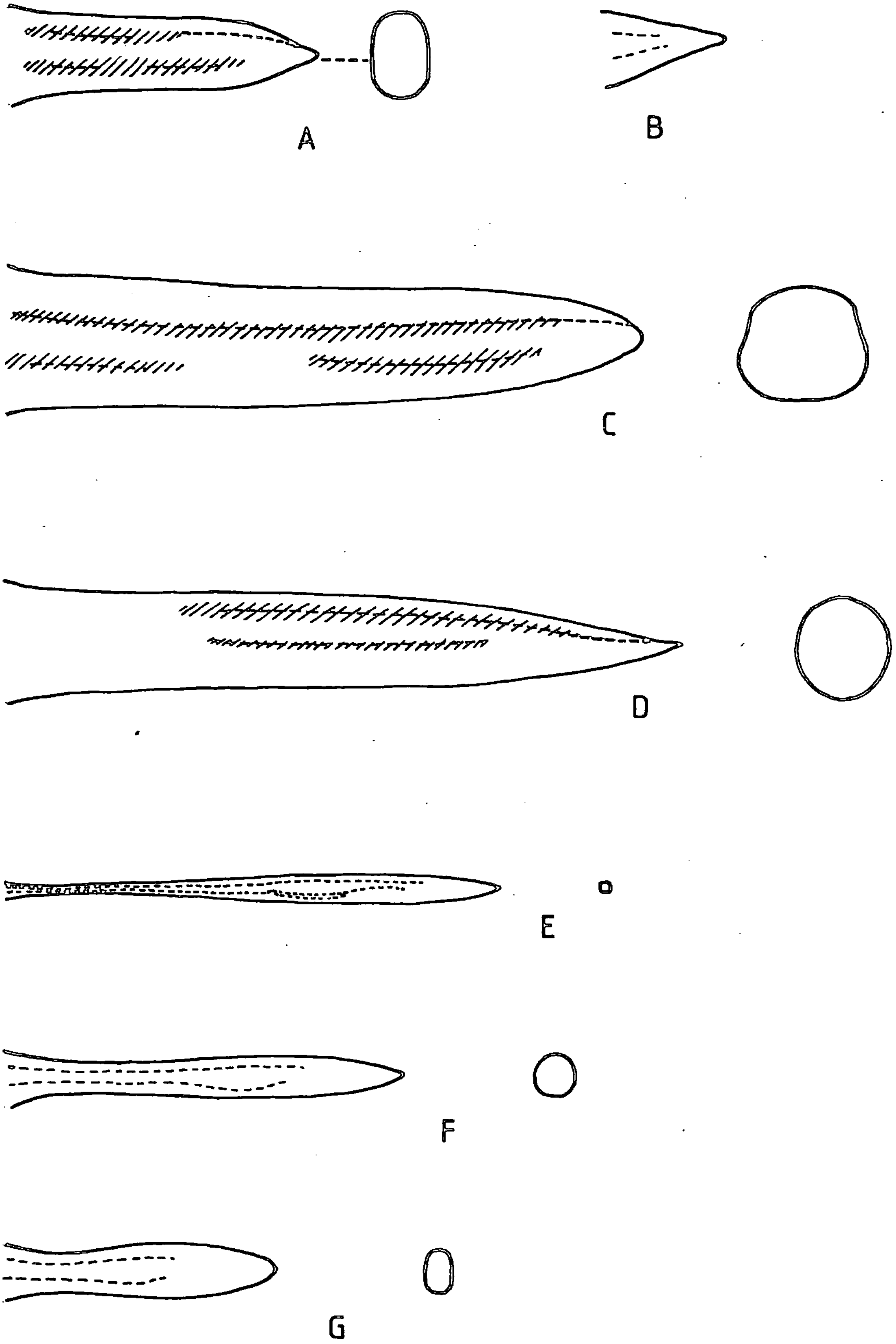


FIG.111

A: Belemnites longissimus

B: B. charmouthensis

C: B. nitidus

D: B. imus

E: B. abruptus

Dashed lines indicate course of furrows; hatched areas represent facets or very wide, shallow furrows.

FIG.111

Furrow patterns and transverse sections
(sections at alveolar apices)

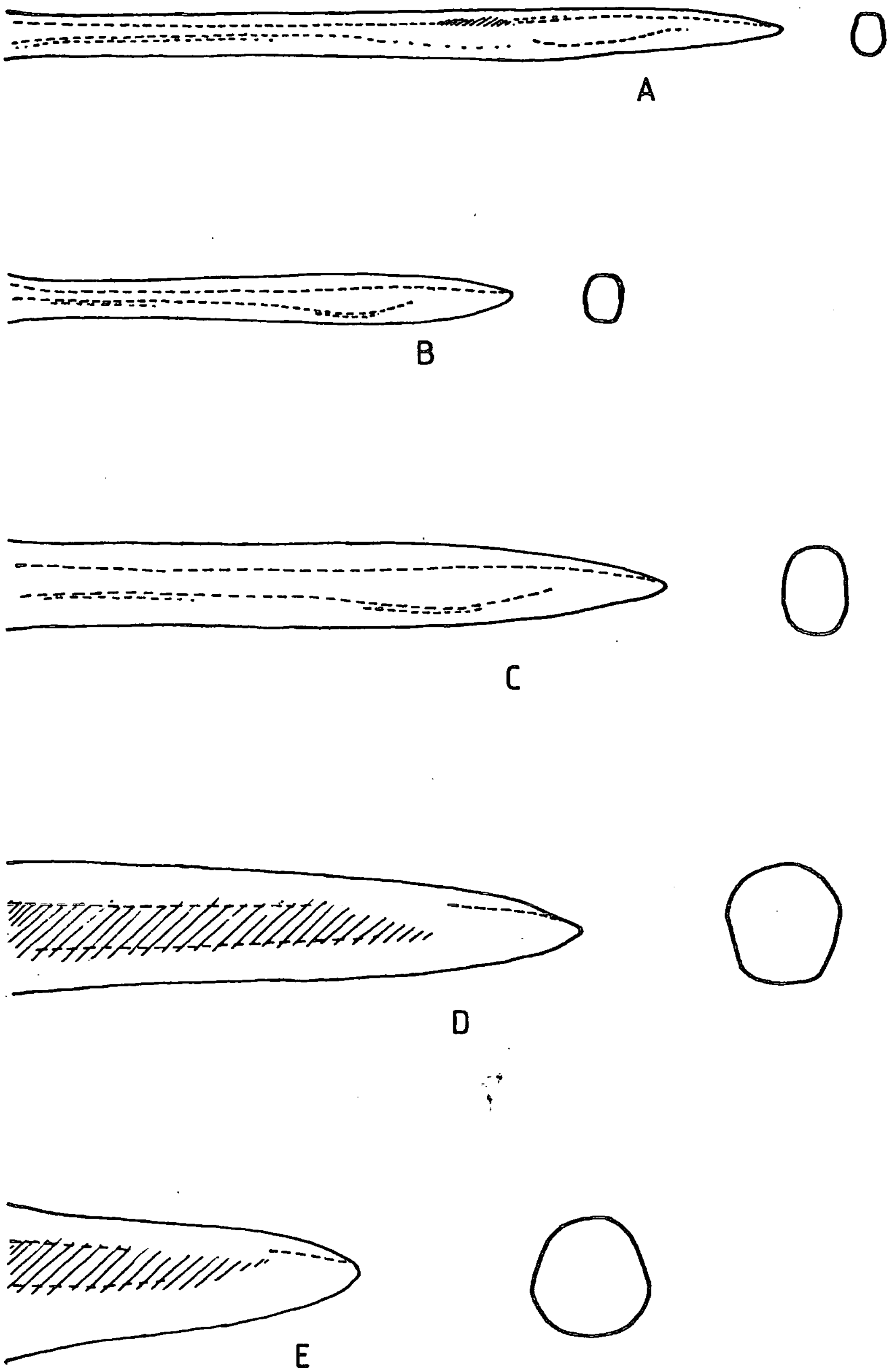
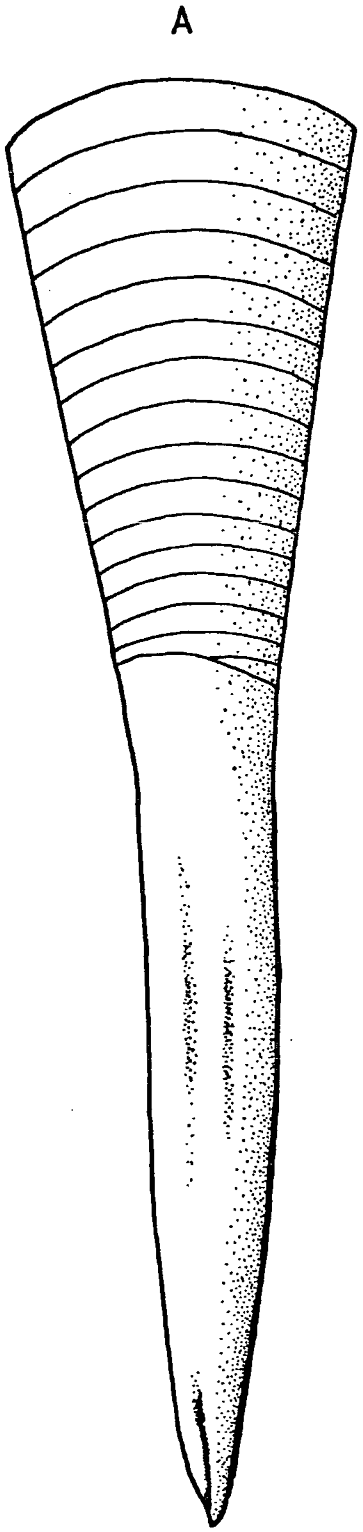


FIG.112 Reconstructions of Belemnites aduncatus and B. longissimus to show probable sizes of phragmocones.

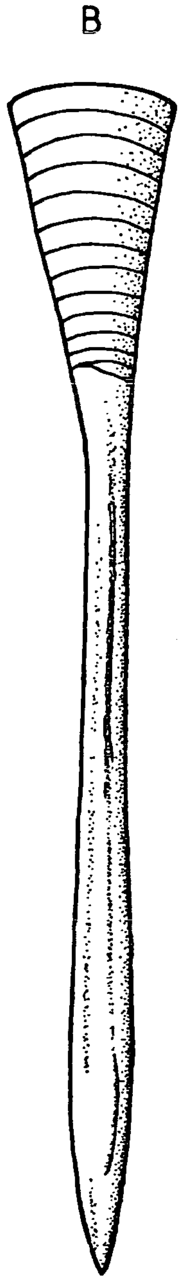
A: based on three specimens in the author's collection from unknown horizons (loose blocks) in the Green Ammonite Beds.

B: based on TB178 and TB369, bed 110 IV (see also pl. 2, fig. 7).

FIG. 112



Belemnites aduncatus



Belemnites longissimus

Epirostra

Occurrences of belemnites with posterior tubular extensions to the rostrum are well known and poorly understood. These epirostra have a simple structure, consisting of an outer wall of normal rostral lamellae enclosing a hollow filled with an ill-sorted mixture of organic material and calcite, sometimes showing a crude lamination in well preserved specimens. The epirostrum is often markedly narrower than the rostrum, which produces a distinctive profile in uncrushed specimens (fig. 113A); the majority of epirostra are preserved in a crushed state.

As suggested by Krymgol'ts (1958, p.150 (p.240 of translation)), the epirostrum probably arises due to a rapid elongation of the mantle and temporary cessation of normal lamellar deposition, producing the poorly structured core before normal deposition recommences to form the outer tube. Müller-Stoll (1936) attempted to show that the epirostrum could be resorbed, leaving a scarred umbilicate apex to the rostrum, and he figured an impressive series of sections of uncrushed specimens in support of this idea (Müller-Stoll 1936, pls.1-8). This is an attractive hypothesis that merits further investigation; if vindicated, it would imply that epirostra were more commonly developed than is realised. Unfortunately, the material from the Belemnite Marls is of little use in this respect as the epirostra are almost invariably badly crushed and show little internal detail. They are also rare at most horizons.

Various functions have been proposed for the epirostrum, commonly invoking sexual dimorphism (e.g. d'Orbigny 1840-42;

Lissajous 1925); others include: an additional balancing organ (not sex linked), a protection for the rostrum and a regulator of rostral development, but, as Roger (1952 pp.700-701) concludes, none of these can be proven.

In the Belemnite Marls, specimens with epirostra occur sporadically in various beds. Short examples are sometimes observed in *Belemnites longissimus* (bed 110) and *B. cricki* (bed 118 b-c) and better developed but poorly preserved specimens of at least two species (*B. longissimus* and *B. nitidus*) occur in bed 120 c. The best and most consistent development of epirostra was found in *B. nitidus* in bed 118 a (although with occasional examples from beds 115, 117 and 120d) where, as described on p.81 approximately half of the "adult" rostra bear epirostra, which is suggestive of sexual dimorphism. The other interesting point arising from this assemblage is that the epirostra all appear to have initially developed in size group 2 specimens (fig.96) (L is measured to the point of commencement of the epirostrum). The combined rostrum and epirostrum (not measured, as these epirostra were usually broken prior to fossilization) matches or exceeds the rostral length of group 3 specimens, while remaining more slender.

As with other occurrences (e.g. *Cuspiteuthis tubularis* from the Jet Rock of the Yorkshire Coast), these epirostrid specimens often bear an irregular, longitudinally ridged surface pattern, developed particularly on the dorsal surface of the rostral portion (pl.14, fig.4). This feature is not invariably present within a single species; it may have some function as an improved attachment area for the extended mantle, or it may simply be a localised depletion of skeletal material due to the sudden requirements of epirostrum formation.

It is likely that the key to an understanding of the epirostrum lies in regarding it not as a distinct structure that is either present or absent but as a more or less occasional response of essentially normal rostral growth to some as yet unidentified change of conditions within the animal. This view is supported by the occurrence in other contexts of loosely organized material resembling the epirostrum core material, in each case probably corresponding to a period of rapid mantle growth. Observed instances include:

1) The material observed within the apical region of early growth laminae of *B. abruptus*, and also reported in *Megateuthis* (which often has an epirostrum as well) (see p.135). In *B. abruptus* at this stage, the rostral profile is somewhat irregular, recalling the inflected profile seen in epirostrid specimens of other species.

2) Smaller volumes of similar material along the apical line, between the well developed lamellae, in many specimens of most of the species examined. Poor calcification along the apical line (corresponding perhaps to the rapidly dividing cells of the mantle at its apex) is probably responsible for the weathered umbilicus seen in many belemnite species.

3) Material associated with regeneration (of damaged rostra or with pathological growth. Abel (1916, pp.215-216, figs. 83-85) figures an impressive series of sections of Cretaceous *Hibolites* and *Duvalia* in which the clearly

visible broken rostrum is surrounded first by undifferentiated material (especially in the apical region, where the shell epithelium may have been more active) and then by normal laminae (the eventual rostral profile being much deformed). A comparable deformed specimen of ?Acrocoelites sp. from an unspecified horizon in the Upper Lias of the Yorkshire Coast is shown in figure 113B, showing poorly organized material with some crude lamination around the apical region and following the direction of regenerated growth. The original rostrum in this case does not seem to have been fractured, and the condition may have been due to localized mantle damage, for example by the bite of a fish or reptile.

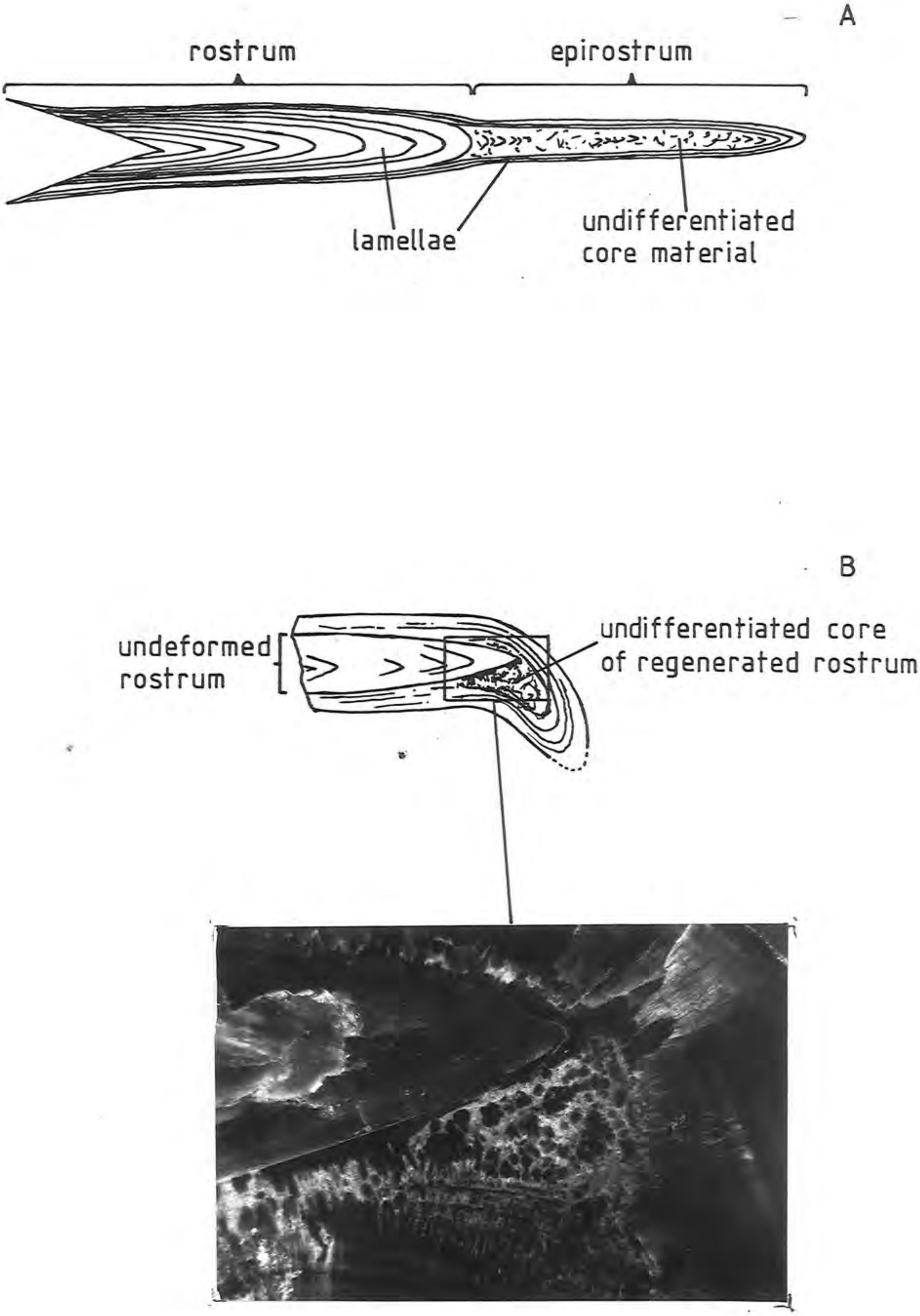
It is reasonable to suppose that the epirostrum was developed as a counterbalance to some alteration (probably a decrease) in the buoyancy of the anterior part of the animal, that moved the centre of buoyancy backwards. Net alterations in buoyancy could probably be compensated for by active control of phragmocone fluids, as in the modern cuttlefish (Denton and Gilpin-Brown 1973). Conceivable causes of imbalance include the development of egg masses or brood pouches in the female or a reduction in tissue buoyancy due to fat loss in both sexes at the onset of spawning. The major objection to such reasoning is the general rarity of epirostra. However, if resorption could be shown to have occurred, this objection would largely vanish and the occasional local abundance of epirostra would be explained.

FIG.113

A: Diagram showing relationship between rostrum and epirostrum.

B: Sketch x1 of section through a deformed rostrum of ?Acrocoelites sp. (alveolar portion missing), U. Lias, N. Yorkshire coast, with photograph x6 of the regenerated apex (coll. J. R. Senior).

FIG. 113


A
rostrum
epirostrum
lamellae
undifferentiated core material
B
undeformed rostrum
undifferentiated core of regenerated rostrum

Ornamentation

Apart from the furrows and apical striae, the majority of rostra studied were devoid of ornamentation. Two notable exceptions were observed: 1) the irregular ridged pattern occuring on the dorsal surface of the majority of specimens of Belemnites nitidus that bear epirostra (pl.14) and 2) the raised linear, reticulated and punctate patterns of variable extent on the surface of several of the larger specimens of B. aduncatus from the Green Ammonite Beds (pl.26, fig.1; pl.27, fig.2).

As previously mentioned, epirostrid specimens of various species bear the type of surface pattern shown by B. nitidus, and striated ornamentation on B. aduncatus has been noted in the past (e.g. Phillips 1866, p.49).

The primary nature of such patterns is demonstrated by one specimen of B. aduncatus (pl.26, fig.3) which shows that each raised element of the ornament is built up of concentric lamellae that abut on the earlier smooth surface, rather than being due to weathering along the radiating prismatic crystal faces of the rostrum.

It is feasible that the ornamentation in both species is a consequence of a reduction in the activity of the shell secreting epithelium, in the first case locally as a result of the requirements of epirostrum formation and in the second case more generally, perhaps as a result of old age. Due to its sporadic occurrence in these species, such ornamentation is not considered to have any taxonomic value.

Coleoid beaks

Two isolated beak elements were found, one from bed 110 V and one from a fallen block of the Green Ammonite Beds, probably beds 122 a-c (pl.29, figs. 3-4). Both are calcareous, and the one from bed 110 V is surrounded by a fragile carbonaceous structure that presumably represents its original support. As yet, no comparative study has been made of these specimens, and their affinities are uncertain although both are probably belemnitid. The one from the Green Ammonite Beds occurred in association with several specimens of Belemnites aduncatus.

Appendix

Belemnites nitidus: list of material. Author's collection, Belemnite Marls and Green Ammnonite Beds between Charmouth and Seatown, Dorset: 572 specimens

bed 104: TB1039, ?TB1042 (fragment)

bed 105: uncatalogued fragmentary material, probably this species.

bed 106: TB29 - 32, TB34 - 37, TB844 - 847, TB849

bed 107: D74, TB38 - 42, TB214, TB850, TB851

bed 108: TB218, TB594, TB595, TB600, TB612, TB626, TB634, TB635, TB856

bed 109: TB637 - 646

bed 110 II: TB270, TB281, TB283, TB285, TB295, TB296, TB302, TB304, TB305

bed 110 III: D98, TB314, TB318 - 321, TB323, TB325, TB326, TB337, TB338, TB343, TB344, TB345, TB349

bed 110 IV: TB224, TB228, TB231, TB355, TB386, TB387, TB388, TB403, TB403a, TB404

bed 110 V (lwr.): D107 - 110, TB233 - 238, TB416, TB421, TB517, TB518, TB519

bed 110 V (upr.):

L less than 40 mm: D126, TB46, TB241, TB439, TB440, TB473 - 476, TB486, TB493, TB513, TB535

L = 40 - 80 mm: D116, D117, D120 - 123, TB240, TB400, TB430, TB435, TB462 - 472, TB482 - 485, TB491, TB492, TB527, TB528, TB529, TB534, TB541, TB544

L greater than 80 mm: D113, D114, D119, D129, TB47 - 50, TB52, TB53, TB54, TB60, TB431 - 434, TB458 - 461, TB478 - 481, TB487 - 490, TB494, TB499,TB500, TB507, TB508, TB525, TB526, TB531, TB532, TB533, TB537 -

540, TB543, ?TB511, 512 (?gracile)

bed 111a: D130, D131, D132, TB61, TB63, TB510, TB647 - 653, TB767

bed 111b: D134, TB64, TB655 - 664, TB798 - 805, TB807

bed 111c: D135, TB68 - 73, TB665 - 671, TB806

bed 111d: TB74 - 84, TB243, TB672, TB673, TB674, TB807, TB808, TB809

bed 111e: TB85 - 92, TB675, TB810

beds 112a - c: TB93 - 105, TB676 - 693, TB811 - 827

beds 112d - f: TB244 - 247, TB694 - 702, TB704 - 709,TB830 - 838

bed 113: TB840 (pathological).

bed 114: TB841, TB842, TB843, TB1052, TB1053

bed 115: TB1054 - 1062

bed 117: TB710 - 748, TB859 - 873

bed 118a: TB863, TB929 - 984

beds 118b - d: TB757, TB759, TB761, TB764, TB783, TB784, TB876, TB897, TB926, TB927, TB928, TB1025 - 1029

bed 119: TB107, TB1063, TB1064, TB1065, TB1070 - 1077, TB1091

beds 120a - b: TB109, TB110, TB112, TB113, TB115 - 119, TB133, TB1093 - 1106

bed 120c: D146, TB120 - 123, TB126, TB1114 - 1121, ?TB124, ?TB1128, ?TB1130 - 1133

beds 120d - e: D141 - 143, TB128, TB130, TB131, TB134 - 141, TB143, TB144, TB155, TB156, TB1140, TB1142 - 1155

bed 121: TB158, TB1215, TB1216

Green Ammonite Beds, below Golden Cap: 10 specimens

beds 122a - c: D208, D209, TB568 - 570, TB589, TB1173, TB1174, TB1212, TB1213

Belemnitiferous Marls, road cutting on A303, near Tintinhull, Dorset.

OS ref. SY497205: uncatalogued fragmentary material. ?jamesoni to davoei Zones, Wutach valley, near Aselfingen, South West Germany: uncatalogued fragmentary material.

BMNH, coll. and/or det. W.D. Lang, Belemnite Marls, Charmouth and surrounding area: 85 specimens

bed 110a: (Passaloteuthis argillarum) C28870 - 28878, C28881, C43814; C28883 - 28887, C28889 (holotype), C28890 - 28892, C43801, C57216 - 57218

bed 110b: (P. argillarum) C28879, C28880 (holotype), C43813, C43815; (P. stonebarroensis) C28882

bed 111b: (P. elongata) C28990, C28991, C289903 - 289906, C29507

bed 111c: (P. elongata) C28902 (neotype)

bed 111d: (P. elongata) C29506

bed 112b: (P. westhaiensis) C28896

bed 112d: (P. westhaiensis) C28898, C28899, C43757, C43759

bed 112e: (P. westhaiensis) C28895, C28912 - 28917, C43771

bed 112f: (P. westhaiensis) C28893, C43782

bed 112 "about the middle": (P. westhaiensis) C28894 (holotype)

bed 115: (P. woottonensis) C28919, C43767

bed 117 or 118a: (P. woottonensis) C28918 (holotype)

bed 118a: (P. woottonensis) C28920, C29509, C29510

bed 119: (P. dayi) C29242

beds 120a - b: (P. dayi) C29168, C29171, C29173, C29183, C29235; (P. seatownensis) C29238, C29516

bed 120c: (P. apicicurvata) C 29195, C29202, C29225; (P. cf. apicicurvata) C29519; (P. dayi) C29520; (P. seatownensis) C29206, C29514, C29517

?bed 120c: (P. dayi) C11350, C11385, C11387, C11407 (holotype); (P. seatownensis) C6742, C11414 (holotype)

(Page 263 omitted from pagination)

bed 120d: (P. seatownensis) C29148, C29201, C29518

Staatl. Mus. Nat., Stuttgart: 4specimens

One specimen labelled "Belemnites virgatus Mayer", figured in Werner (1912), pl. 11, fig. 4. Lias gamma, Dürnau.

Three specimens, coll. Schlatter, no identification, from Lias gamma, Nurtingen.

Bibliography

References marked * are quoted from de Blainville (1827) pp.2-25.

Abel, O., 1916. Paläobiologie der Cephalopoden aus der Gruppe der Dibranchiaten. Fischer, Jena.

Arkell, W.J., 1933. The Jurassic System in Great Britain. Oxford University Press.

Arkell, W.J., 1956. The Jurassic Geology of the World. Oliver and Boyd, Edinburgh.

Bairstow, L., 1950. Coeloteuthis and synonymous homonymy at generic level. Correspondence, *Geol. Mag.* (87), 226-227.

Barker, R.M., 1964. Microtextural variation in pelecypod shells. *Malacologia* (2), 69-86.

Barskov, I.S., 1973a. Microstructure of the skeletal layers of belemnites compared with the external shell layers of other molluscs. *Palaeontol. J.* (6), 492-500.

Barskov, I.S., 1973b. Structure of the protoconch and ontogeny of the belemnites (Coleoidea, Cephalopoda). *Doklady* (*Proc.*) *Acad. Sci. U.S.S.R.* (*Earth Sci*) (208), 218-221.

*Belon, Pierre, 1553. Les observations de plusieurs singularités et choses mémorables trouvées en Grèce etc. Paris.

Blainville, M.H.D. de, 1827. Mémoire sur les bélemnites considérées zoologiquement et géologiquement. Levrault, Paris.

Boletzky, S. von, 1974. Effets de la sous-nutrition prolongée sur le développement de la coquille de *Sepia officinalis* Lamarck (Mollusca, Cephalopoda). *Bull. Soc. Zool. France* (99), 667-673, 4pl.

*Boodt, Boetius de, 1609. Gemmarum lapidium historia. Hannover.

*Brander, G., 1754. A Dissertation on the belemnites. *Philos. Trans. Roy. Soc.* (48), 803.

*Breynius, Johannes Phillippus, 1732. Dissertatio physica de polythamiis etc.

Buckland, W., 1837. Geology and Mineralogy considered with reference to natural theology. 2nd ed. W. Pickering, London.

Caley, E.R. and Richards, J.F.C., 1956. Theophrastus on stones. *Graduate School Monographs, Contributions in Physical Science* (1). Columbus, Ohio.

*Cesalpin (Caesalpinus, Andraeas), 1596. De metallicus, lib.III, Rome.

Challinor, A.B., 1975. Variation in *Hibolithes arkelli arkelli* - I. *New Zealand J. Geol. and Geophys.* (18) no.6, 803-835.

Challinor, A.B. and Turner, J.C. 1975. Variation in *Hibolithes arkelli arkelli* - 2. *New Zealand J. Geol. and Geophys.* (18) no.6, 837-848.

Christinsen, E., 1925. Neue Beiträge zum Bau der Belemniten. *Neues Jahrb. Mineral. Geol. Paläont.*, Beil. (51), 118-158. pls 4-6.

Cope, J.C.W., Getty, T.A., Howarth, M.K., Morton, N. and Torrens, H.S., 1980. A correlation of Jurassic Rocks of the British Isles. Part One. Geol. Soc. London (Special Report No.14).

Day, E.C.H., 1863. On the Middle and Upper Lias of the Dorsetshire coast. *Q. J. Geol. Soc.* (19), 278-297.

Dean, W.T., Donovan, D.T. and Howarth, M.K., 1961. The Liassic Ammonite Zones and Subzones of the North-west European Province. Bull. Br. Mus. (Nat. Hist.) (Geol.), (4), 437-505, pls 63-75.

Delattre, M., 1956. Les Bélemnites de l'Aalenien de Mamers. Ann. Cent. Docum. palaeont. (16), 35-43.

Denton, E.J. and Gilpin-Brown, J.B., 1973. Floatation mechanisms in modern and fossil cephalopods. Adv. Mar. Biol. (11), 197-268.

Dietl, G., Rieber, H. and Schlatter, R., 1977. Unpublished excursion notes.

*Dioscorides, Pedacius. De Materia medica. Transl. Ruellio, J., Paris, 1549.

Donovan, D.T. and Jones, E.J.W., 1979. Causes of world-wide changes in sea level. J. geol. Soc. (136), 187-192.

Donovan, D.T., Horton, A. and Ivemey-Cook, H.C., 1979. The transgression of the Lower Lias over the northern flank of the London Platform. J. geol. Soc. (136), 165-173.

Douville, M., 1892. Considerations sur la classification des Bélemnites. Bull. Soc. Geol. Fr. 3rd Ser. (20), 25-26.

Dumortier, E., 1869. Etudes Paléontologiques sur les Dépôts Jurassiques du Bassin de Rhône, pt.3. Paris.

Edwards, W.N., 1967. The early history of palaeontology. British Museum (Natural History).

Eichholz, D.E., 1962. Plinius Secundus, C. Natural History, Vol.10. Books 36-37. Heinemann, London.

Eichholz, D.E., 1965. Theophrastus. De Lapidibus. Clarendon Press, Oxford.

*Elsholtius, Johannes Sigismundus, 1678-79. De succino fossili et lapide belemnite.

*Encelius, Christophorus, 1557. De re metallica, lib.III. Frankfurt.

Epstein, S., Buchsbaum, R., Lowenstam, H.A. and Urey, H.C., 1953. Revised carbonate-water isotopic temperature scale. Geol. Soc. Amer. Bull. (64), 1315-1326.

*Erhartus, Johannes Balthazar, 1724. De belemnitis suevicis Dissertatio. Lyons.

Fire, J. and Erdoes, R., 1972. Lame Deer, Sioux Medicine Man. Davis-Poynter, London.

Gould, S.J. and Eldredge, N., 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Palaeobiology (3), 115-151.

Hallam, A., 1961. Cyclothems, Transgressions and Faunal Change in the Lias of North-West Europe. Trans. Edinburgh Geol. Soc. (18), 124-174.

Hallam, A., 1969. Tectonism and eustasy in the Jurassic. Earth Sci. Rev. (5), 45-68.

Hallam, A., 1975. Jurassic Environments. Cambridge University Press.

Hallam, A., 1978. Eustatic cycles in the Jurassic. Palaeogeogr. Palaeoclimatol. Palaeoecol. (23), 1-32.

Hanai, T., 1953. Lower Cretaceous Belemnites from Miyaker District, Japan. Japanese J. Geol. Geogr. (23), 63-80, pls 5-7.

*Helwing (Helwingius, Georgius Andraeas), 1717-20. Lithographia angerburgica etc. Leipzig.

Hewitt, R.A. and Hurst, J.M., 1978. Size changes in Jurassic liperoceratid ammonites and their stratigraphical and ecological significance. Lethaia (10), 287-301.

Hewitt, R.A., 1980. Quantitative studies of some Jurassic belemnite assemblages. Geobios (13), 173-197, 2pls.

Hinte, J.E. van, 1976. A Jurassic time scale. Bull. Am. Assoc. Pet. Geol. (60), 489-497.

Howarth, M.K., 1973. The stratigraphy and ammonite fauna of the Upper Liassic Grey Shales of the Yorkshire coast. Bull Br. Mus. (Nat. Hist.) (Geol.) (24), 237-277, pls 1-9.

Huxley, T.H., 1864. On the structure of the Belemnitidae. Mem. Geol. Surv. U.K. Figures and Descr. British Organic Remains, Mon.2.

*Isidore of Seville. De Originibus.

*Jacobaeus, Oligerus, 1696. Musaeum regium, etc.

Jeletzky, J.A., 1966. Comparative Morphology, Phylogeny and Classification of Fossil Coleoidea. Univ. Kansas Palaeont. Contrib. Mollusca, Art.7.

Jordan, R., Scheuermann, L. and Spaeth, C., 1975. Farbmuster auf jurassischen Belemniten-Rostren. Paläont. Z. (49), 332-343.

Kennedy, W.J. and Cobban, W.A., 1976. Aspects of ammonite biology, biogeography and biostratigraphy. Spec. Pap. Palaeontol., no.17.

*Klein, Jacobus Theodorus, 1731. Descriptiones tubulorum marinorum.

*Klein, J.T., 1740. Sciagraphica lithologica curiosa.

Krymgol'ts, G.Ya., 1958. Subclass endocochlia. In: Fundamentals of Palaeontology (6), Mollusca - Cephalopoda II. Ed. Luppov, N.P. and Drushchits, R. Israel Program for Scientific Translations, Keter Publishing House, Jerusalem 1976.

Lamarck, J.B., 1799. Prodrome d'une nouvelle classification des coquilles. Soc. Hist. Nat. Paris. Mem. 63-91.

Lamarck, J.B., 1801. Systéme des animaux sans vertebrès. Paris.

Lang, W.D., 1913. The Lower Pliensbachian - 'Carixian' - of Charmouth. Geol. Mag. (10), 401-412.

Lang, W.D., 1914. The Geology of the Charmouth Cliffs, Beach and Foreshore. Proc. Geol. Assoc. (25), 293-360, pls 39, 40, maps 1-3, coloured section.

Lang, W.D., 1917. The ibex Zone at Charmouth and its relation to the zones near it. Proc. Geol. Assoc. (28), 31-36.

Lang, W.D., 1928. The Belemnite Marls of Charmouth. In Lang et al, The Belemnite Marls of Charmouth, a series in the Lias of the Dorset coast. Q. J. Geol. Soc. (84), 179-222, pls 13-15.

Lang, W.D., 1932. The Lower Lias of Charmouth and the Vale of Marshwood. Proc. Geol. Assoc. (43), 97-126, pl.6.

Lang, W.D., 1936. The Green Ammonite Beds of the Dorset Lias. Q. J. Geol. Soc. (92), 423-437, pl.32.

Lang, W.D., Spath, L.F., Cox, L.R. and Muir-Wood, H.M. 1926. The Black Marl of Black Ven and Stonebarrow, in the Lias of the Dorset coast. Q. J. Geol. Soc. (82), 144-187, pls 8-11.

Lang, W.D., Spath, L.F., Cox, L.R. and Muir-Wood, H.M., 1928. The Belemnite Marls of Charmouth, a series in the Lias of the Dorset coast. Q. J. Geol. Soc. (84), 179-257, pls 13-18.

*Lhwyd (Lhuydius, Edwardus), 1699. Lithophylaci Britannici ichonographia etc. London.

*Libavius, Andraeas, 1601. Singularium pars tertia, continens octo libros, bituminum et affinium etc. Frankfurt.

*Linnaeus, Carl von, 1747. Systema naturae.

Lissajous, M., 1907. Jurassique Maconnais. Description des fossiles caractéristiques et des espèces les plus communes. Bull. Soc. Hist. nat. Macon.

Lissajous, M., 1925. Repertoire Alphabetique des Bélemnites Jurassiques. Trav. Lab. Geol. Univ. Lyon.

Lissajous, M., 1927. Description de quelques nouvelles espèces de bélemnites jurassiques (Roman, F., (Ed.)). Trav. Lab. Geol. fac. sci. Lyon, part 10, mem.7 (suppl.).

Longinelli, A., 1969. Oxygen - 18 variations in Belemnite Guards. Earth Planet. Sci. Lett. (7), 209-212.

Mangold, K., Lu, C.C. and Aldrich, F.A., 1969. A reconsideration of forms of squid of the genus Illex (Illicinae, Ommastrephidae). II. Sexual dimorphism. Can. J. Zool. (47), 1153-1156.

Mangold, K. and Boletzky, S. von, 1973. New Data on Reproductive Biology and Growth of Octopus vulgaris. Mar. Biol. (19), 7-12.

Mantell, G.A., 1848. Observations on some belemnites and other fossil remains of Cephalopoda, discovered by Mr. Reginald Neville Mantell, C.E. in the Oxford Clay near Trowbridge, in Wiltshire. Philos. Trans. Roy. Soc. (138), 171-181, pls 13-15.

Matthews, S.C., 1973. Notes on open nomenclature and on synonymy lists. Palaeontology (16), 713-719.

Mayer, C., 1863. Liste, par ordre systématique, des Bélemnites des terrains jurassiques, et diagnoses des espèces nouvelles. J. Conchyliol., ser.3, tome 3, vol.II.

Mayer, C., 1964. Diagnoses de deux Bélemnites nouvelles. J. Conchyliol. ser.3, tome 4, vol.12.

Mayer, C., 1866. Diagnoses de Bélemnites nouvelles. J. Conchyliol. ser.3, tome 6, vol.14.

Mayer-Eymar, K., 1883. Grundzüge der Classification der Belemniten. Z. Dtschl. geol. Ges. (35), no.3.

*Mercati, Michael, 1717, 1719. Metallotheca et Appendix ad metallothecam Vaticanam etc. Rome.

Miller, J.S., 1826. Observations on Belemnites. Trans. Geol. Soc. (2), 45-62.

Müller-Stoll, H., 1936. Beiträge zur Anatomie der Belemnoidea. Nova Acta Leopold. new ser. (4), 159-226, pls 1-14.

Mutvei, H., 1964. Remarks on the anatomy of Recent and fossil Cephalopoda; with description of the minute shell structure of belemnoids. Stockholm Contrib. Geol. (11), 79-102.

Naef, A., 1922. Die fossilen Tintenfische. Fischer, Jena.

d'Orbigny, A., 1840-2. Paléontologie française. Terrains jurassiques, Vol.1 Céphalopodes. Paris.

Ovid. Metamorphoses. Transl. Innes, M.M. 1955. Penguin.

Owen, R., 1844. A description of certain Belemnites, preserved with a great proportion of their soft parts, in the Oxford Clay, at Christian-Malford, Wilts. Philos. Trans. Roy. Soc. (134), 65-85, pls 2-8.

Packard, A., 1972. Cephalopods and fish: the limits of convergence. Biol. Rev. (47), 241-307.

Palmer, C.P., 1972. A revision of the zonal classification of the Lower Lias of the Dorset Coast in S.W. England. Newsl. Stratigr. (2), 45-54.

Pavlow, A.P., 1913. Les céphalopodes du Jura et du Crétacé inférieur de la Sibérie septentrionare. Mem. Acad. Imp. Sci. St. Petersbourg, (21), no.4, pp.1-68.

Phillips, J., 1865-70. A monograph of British Belemnitidae: Jurassic. Palaeontogr. Soc. Mon.

Pinckney, G., 1975. The belemnite genus Acroteuthis in the late Jurassic and early Lower Cretaceous of N.W. Europe. Ph.D. thesis, Queen Mary College, University of London.

Platt, J., 1764. An Attempt to Account for the Origin and the Formation of the Extraneous Fossil commonly called the Belemnite. Philos. Trans. Roy. Soc. [54], 38-52.

Pliny the Elder [Plinius Secundus, Caius]. Natural History, vol.10, Books 36-37, Transl. Eichholz, D.E. 1962, Heinemann, London.

Quenstedt, F.A., 1846-9. Petrefactenkunde Deutschlands. Die Cephalopoden. Fues, Tubingen.

Quenstedt, F.A., 1852. Handbuch der Petrefactenkunde. 2nd ed. Laupp, Tubingen.

Quenstedt, F.A., 1858. Der Jura. Laupp, Tubingen.

Roger, J., 1952. Sous-classe des dibranchiata. In Piveteau, T. [Ed.], Traité de Paléontologie. Tome II. Masson, Paris.

Schlatter, R., 1977. The Biostratigraphy of the Lower Pliensbachian at the Type Locality [Pliensbach, Württemberg, S.W. Germany]. Stuttgarter Beitr. Naturkd. ser.B, no.27.

Schlotheim, J.F. von, 1820. Nachtrage zur Petrefactenkunde. Goettingen.

Schroeder, W., 1973. Cuttlefish. Mar. Aquarist [4], 22-27.

Schumann, H.O., 1974. Die Belemniten des norddeutschen Lias gamma. Geol. Jahrb. ser.A, no.12, 1-69, pls 1-8.

Schwegler, E., 1961. Revision der Belemniten des Schwäbischen Jura: 1. Palaeontographica A [116], 59-103.

Schwelger, E., 1962a. Revision der Belemniten des Schwäbischen Jura: 2. Palaeontographica A [118], 47-68.

Schwegler, E., 1962b. Revision der Belemniten des Schwäbischen Jura: 3. Palaeontographica A [120], 121-164.

Schwegler, E., 1965. Revision der Belemniten des Schwäbischen Jura: 4. Palaeontographica A [124], 113-153.

Seilacher, A., 1968. Swimming habits of belemnites - recorded by boring barnacles. Palaeogeogr., Palaeoclimatol. Palaeoecol. [4], 279-285.

Seilacher, A., 1969. Paleoecology of Boring Barnacles. Am. Zool. [9], 705-719.

Sellwood, B.W., 1970. The relation of trace fossils to small-scale sedimentary cycles in the British Lias. In: Crimes, T.P. and Harper, J.C. [Eds], Trace Fossils. Geol. J. Spec. Issue [3], 489-504.

Sellwood, B.W., 1972. Regional environmental changes across a Lower Jurassic stage-boundary in Britain. Palaeontology [15], 125-157, pls 28, 29.

Simpson, M., 1855. The Fossils of the Yorkshire Lias described from Nature. 1st ed. London.

Simpson, M., 1884. The Fossils of the Yorkshire Lias described from Nature. 2nd ed. London.

Simpson, M., 1942. The Fossils of the Yorkshire Lias described from Nature. 3rd ed. A. Brown & Sons Ltd., Hull.

*Solinus, Cajus Julius. Polyhistoria. Paris, 1629.

Sowerby, J.D.C., 1829. The Mineral Conchology of Great Britain Vol.6. London.

Spaeth, C., 1971. Aragonitische und calcitische Primärstrukturen im Schalenbau eines Belemniten aus der englischen Unterkreide. Palaont. Z. [45], 1/2, 33-40, pls 2-4.

Spaeth, C., 1975. Zur Frage der Schwimmverhältnisse bei Belemniten in Abhängigkeit vom Primärgefuge der Hartteile. Paläont. Z. [49] 3, 321-331.

Spaeth, C., Hoeffs, J. and Vetter, U., 1971. Some Aspects of Isotopic Composition of Belemnites and Related Palaeotemperatures. *Bull. Geol. Soc. Am.* (82), 3139-3150.

Spath, L.F., 1928. The Ammonites from the Belemnite Marls. *In*: Lang *et al*, The Belemnite Marls of Charmouth, a series in the Lias of the Dorset coast. *Q. J. Geol. Soc.* (84), 222-232, pls 16, 17.

Stahl, 1824. Uebersicht über die Versteinerungen Wurtembergs. *Correspondenzblatt des Würtembergischen Landwirthscheftlichen Vereins*. (6).

Stevens, G.R., 1965. The Jurassic and Cretaceous Belemnites of New Zealand and a review of the Jurassic and Cretaceous Belemnites of the Indo-Pacific Region. *N.Z. Geol. Surv. Palaeont. Bull* (36).

Stevens, G.R., 1973. Jurassic Belemnites. *In*: Hallam, A. (Ed.), Atlas of Palaeobiogeography, Elsevier.

Stolley, E., 1919. Die Systematik der Belemniten. *Niedersächs. Geol. Verein*, Jahresber. 11.

Tate, R. and Blake, J.F., 1876. The Yorkshire Lias. John van Voorst, London.

Taylor, J.E., 1885. Our Common British Fossils. Chatto & Windus, London.

Theophrastus. De lapidibus. Transl. Eichholz, D.E. 1965. Clarendon Press, Oxford.

Thompson, C., 1910. The Belemnites of the Yorkshire Lias. *Trans. Hull Geol. Soc.* (6), 99-102.

Tompsett, D.H., 1939. Sepia. *L.M.B.C. Mem.* (32). University Press of Liverpool.

Urey, H.C., 1947. The thermodynamic properties of isotopic substances. *J. Chem. Soc.*, 562-581.

Urey, H.C., Lowenstam, H.A., Epstein, S. and McKinney, C.R., 1951. Measurements of palaeotemperatures of the upper Cretaceous of England, Denmark and the south eastern United States. *Geol. Soc. Amer. Bull.* (62), 399-416.

Veizer, J., 1974. Chemical Diagenesis of Belemnite Shells and Possible Consequences for Palaeotemperature Determinations. *Neues Jahrb. Geol. Paläontol. Abh.* (147), 91-111.

*Volkman (Volkmannus, Georgius Antonius), 1720. Silesia subterranea. Leipzig.

Voltz, M., 1830. Observations sur les belemnites. *Soc. Mus. Hist. Nat., Strasbourg*, (1).

Werner, E., 1912. Uber die Belemniten des Schwäbischen Lias und die mit ihnen verwandren Formen des Braunen Jura (Acoeli). *Palaeontographica* (59), 103-146, pls 10-13.

Westermann, G.E.G. (Ed.), 1969. Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications. E. Schweizerbart'sche Verlagsbuchhändlung, Stuttgart.

Wilson, V., Welch, F.B.A., Robbie, J.A. and Green, G.W., 1958. Geology of the Country around Bridport and Yeovil. *Mem. Geol. Surv. G.B.*, H.M.S.O., London.

Woodward, H.B. and Ussher, W.A.E., 1911. The Geology of the Country near Sidmouth and Lyme Regis. 2nd ed. *Mem. Geol. Surv.*

Zieten, C.H. von, 1830. Versteinerungen Württembergs. Stuttgart.

PLATE 1

Belemnites longissimus Miller

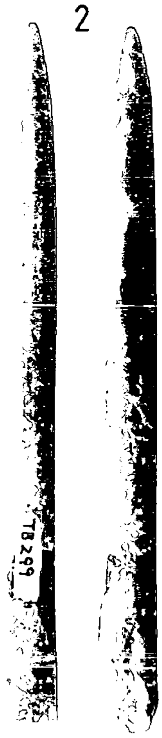
All specimens shown in right-lateral and dorsal views. All x1.

Fig. 1. TB297 (robust), bed 110 II.
Fig. 2. TB299 (robust), bed 110 II.
Fig. 3. TB303 (robust), bed 110 II.
Fig. 4. TB331 (robust), bed 110 III.
Fig. 5. TB161 (robust), bed 110 III.
Fig. 6. TB163 (gracile), bed 110 III.
Fig. 7. D83 (gracile), bed 110 III.

PLATE 1

1

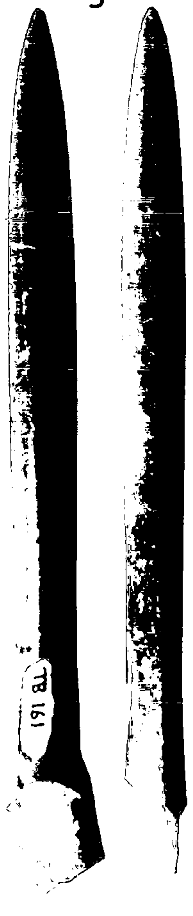
2



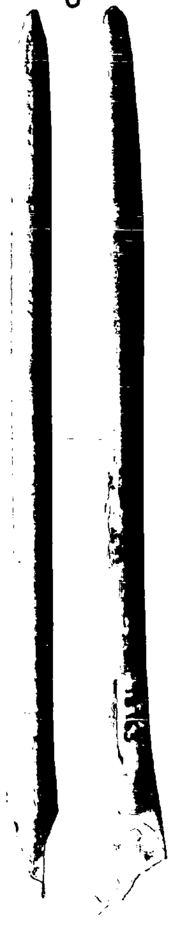
3

4

5



6



7

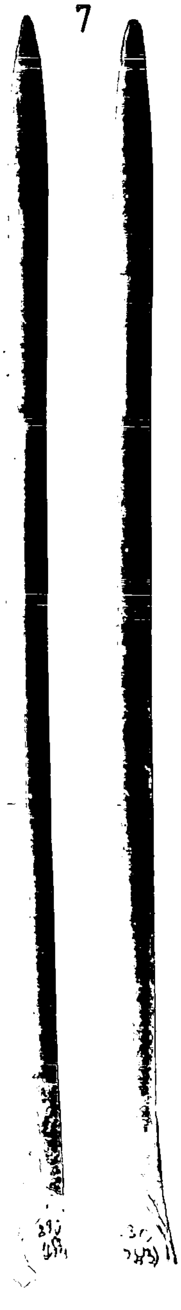


PLATE 2

Belemnites longissimus Miller

All specimens from bed 110 IV. All x1.

Fig. 1. TB358 (gracile), right-lateral and dorsal views.

Fig. 2. TB370 (gracile), right lateral and dorsal views; note short epirostrum.

Fig. 3. TB178 (gracile), left-lateral view.

Fig. 4. TB411 (robust), right-lateral and dorsal views.

Fig. 5. TB187 (gracile), dorsal view.

Fig. 6. TB426 (robust), right-lateral and dorsal views.

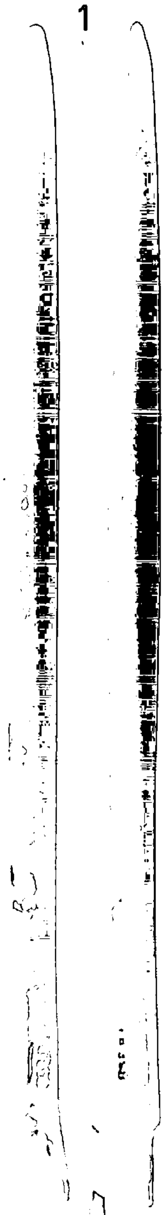
Fig. 7. TB372 (juvenile), right-lateral view.

Fig. 8. TB428 (juvenile), right-lateral view.

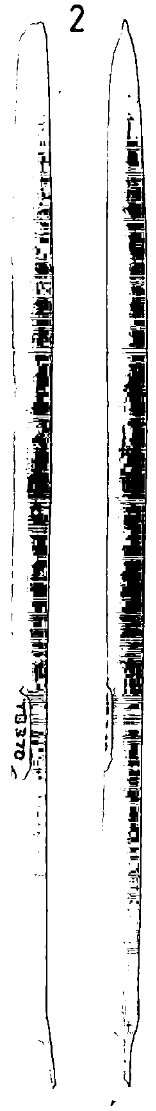
Fig. 9. TB371 (?robust, pathological), right-lateral and dorsal views.

PLATE 2

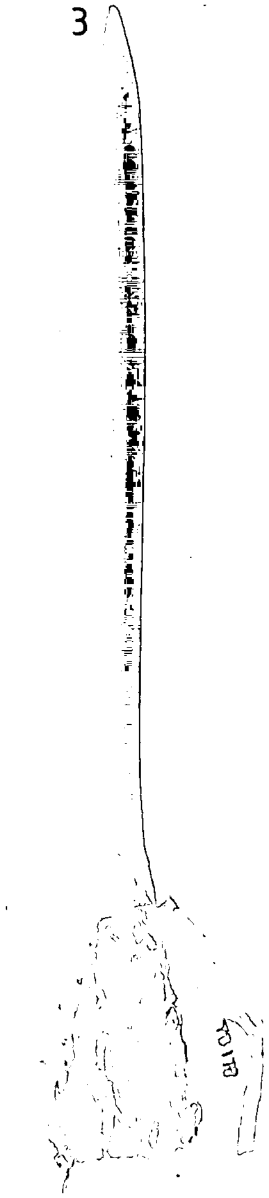
1



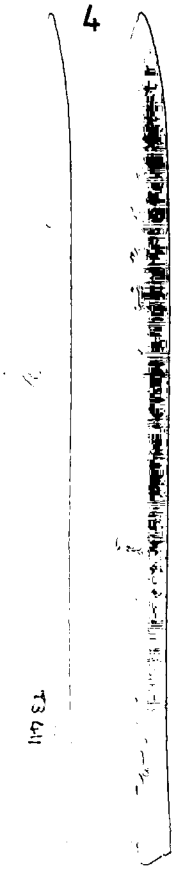
2



3

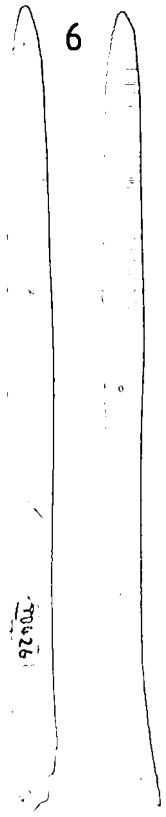


4



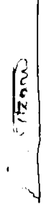
5

6



7

8



9

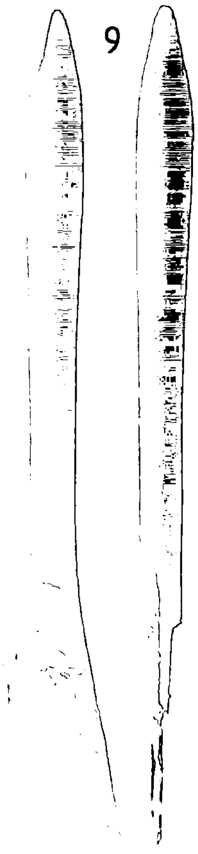


PLATE 3

Belemnites longissimus Miller

Figs. 1-11. Series illustrating dimorphism; all right-lateral views; all specimens from bed 110 V; all x1.

Figs. 1-3. Juvenile, TB167, TB166, TB1046.
Figs. 4-7. Gracile, D112, TB502, TB498, TB448.
Figs. 8-11. Robust, TB521, D100, TB451, TB524.

Fig. 12. TB455, deformed gracile rostrum, bed 110 V, right-lateral view.

Fig. 13. TB1122, diagenetically deformed rostrum, bed 120c, right lateral and dorsal views.

PLATE 3

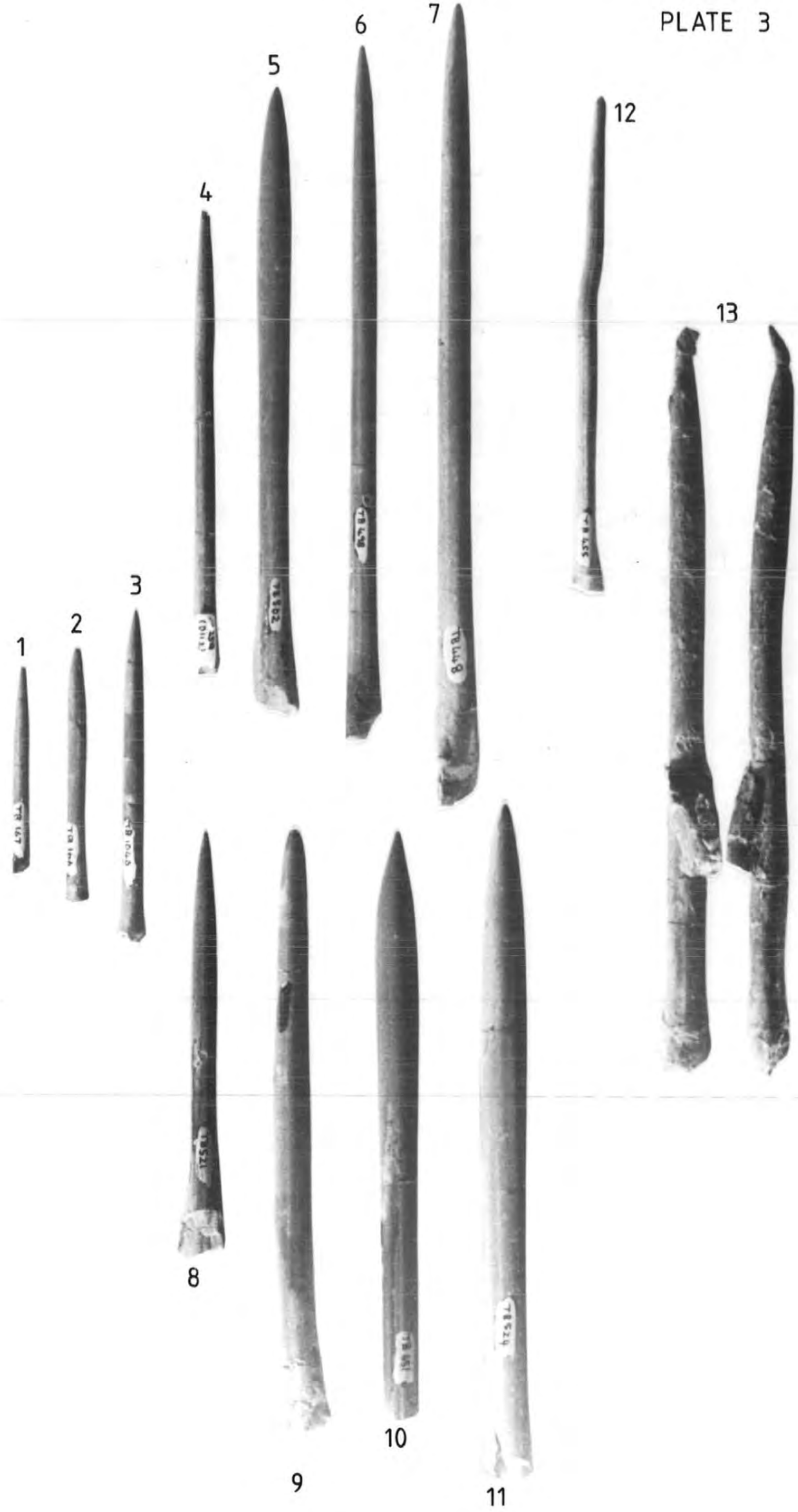


PLATE 4

Figs. 1-5. Belemnites charmouthensis Mayer All specimens shown in left-lateral, dorsal and ventral views. All x1. Dimorphism not clear due to small size of rostra.

Fig. 1. TB618, bed 108 II.
Fig. 2. TB633, bed 108 II, deformed rostrum.
Fig. 3. TB622, bed 108 II.
Fig. 4. D85, bed 110 I.
Fig. 5. 138, bed 110 I.

Figs. 6, 7. Belemnites longissimus Miller Both specimens shown in left-lateral and dorsal views. Both from bed 104. Both x1.

Fig. 6. TB1036 (juvenile).
Fig. 7. TB1032 (?robust).

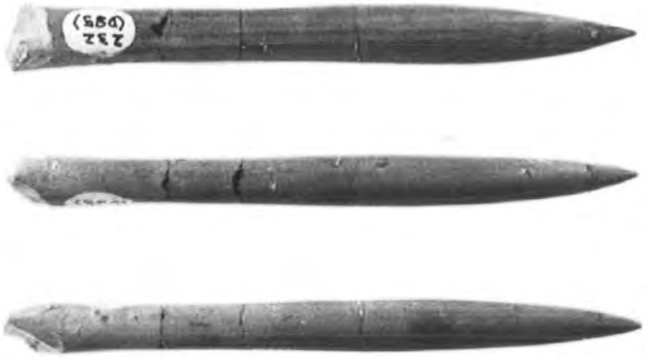
PLATE 4

1

2

3

4



5

6

7

PLATE 5

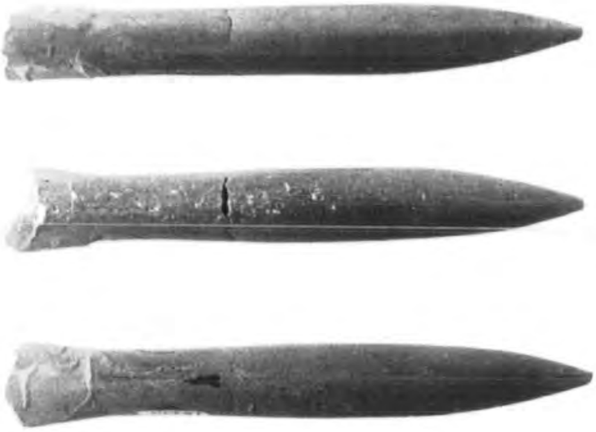
Belemnites charmouthensis Mayer

All specimens shown in left-lateral, dorsal and ventral views. All from bed 110 IV. All x1.

Fig. 1. TB398 (robust).
Fig. 2. TB402 (robust).
Fig. 3. TB378 (robust).
Fig. 4. TB373 (gracile).
Fig. 5. TB516 (gracile).
Fig. 6. TB180 (gracile).

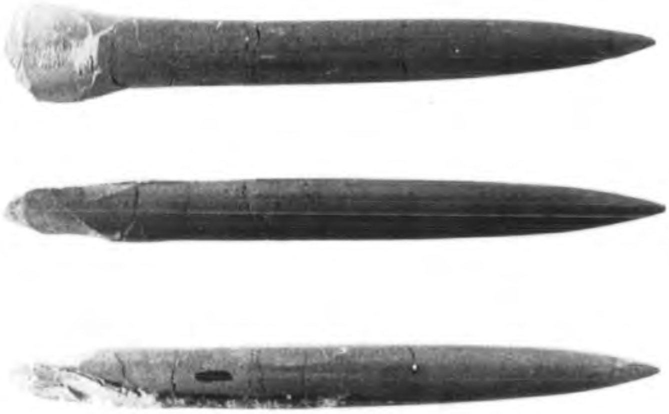
PLATE 5

1



2

3



4

5

6

PLATE 6

Belemnites nitidus Phillips

All x1.

Fig. 1. TB845, bed 106, left-lateral and dorsal views.

Fig. 2. D74, bed 107, left-lateral and dorsal views.

Fig. 3. TB595, bed 108 I, left-lateral, dorsal and ventral views.

PLATE 6

1

2

3

PLATE 7

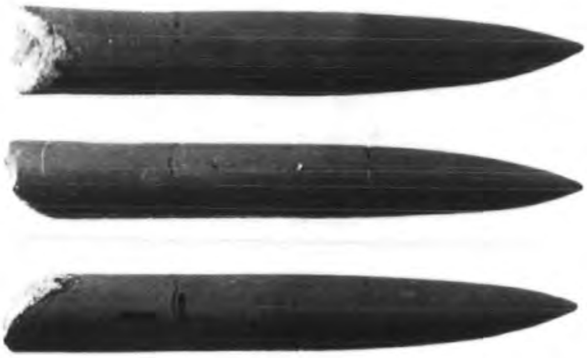
Belemnites nitidus Phillips

Figs. 1-7, specimens shown in left-lateral, dorsal and ventral views. Figs. 8-10, specimens shown in left-lateral view. All from bed 110 V. All x1.

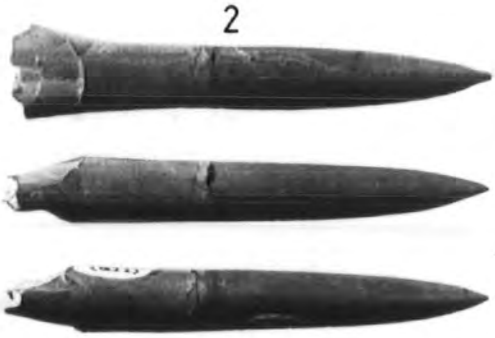
Fig. 1. TB491.
Fig. 2. D122.
Fig. 3. TB482.
Fig. 4. TB484.
Fig. 5. TB468.
Fig. 6. D123.
Fig. 7. TB473.
Fig. 8. TB241.
Fig. 9. D126.
Fig. 10. TB 476.

PLATE 7

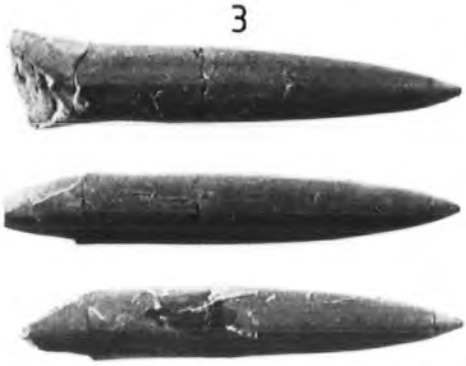
1



2



3



4

5

6

7

8

9

10

PLATE 8

Belemnites nitidus Phillips

All specimens shown in left-lateral, dorsal and ventral views. All from bed 110 IV. All x1.

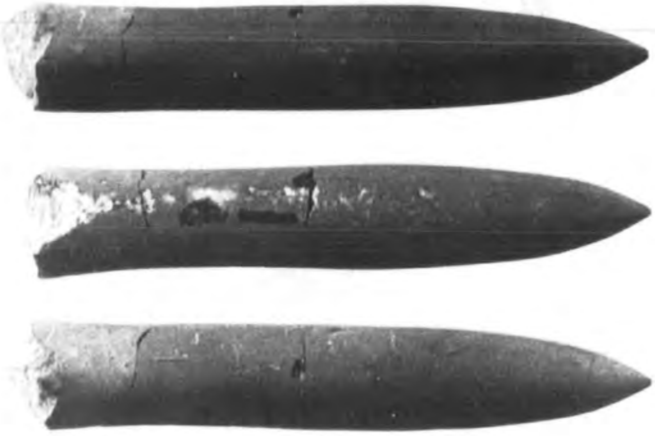
Fig. 1. TB537.
Fig. 2. TB490.
Fig. 3. TB481.
Fig. 4. TB529.

PLATE 8

1

2

3



4

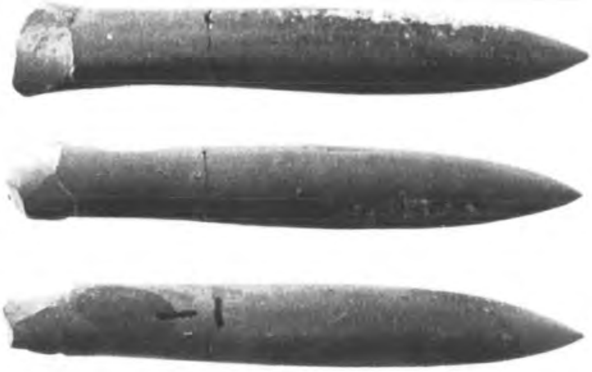


PLATE 9

Belemnites nitidus Phillips

All x1.

Fig. 1. TB799, bed 111b, left-lateral, dorsal and ventral views.

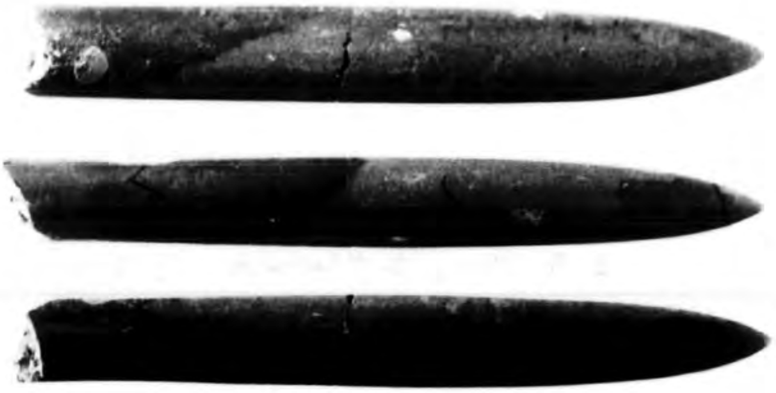
Fig. 2. TB72, bed 111c, left-lateral, dorsal and ventral views.

Fig. 3. TB672, bed 111d, left-lateral, dorsal and ventral views.

Fig. 4. TB84, bed 111d, left-lateral and dorsal views.

Fig. 5. TB75, bed 111d, left-lateral and dorsal views.

PLATE 9



1

2

3

4

5

PLATE 10

Belemnites nitidus Phillips

All x1.

Fig. 1. D135, bed 111e, left-lateral and dorsal views.

Fig. 2. TB677, beds 112a-c, left-lateral, dorsal and ventral views.

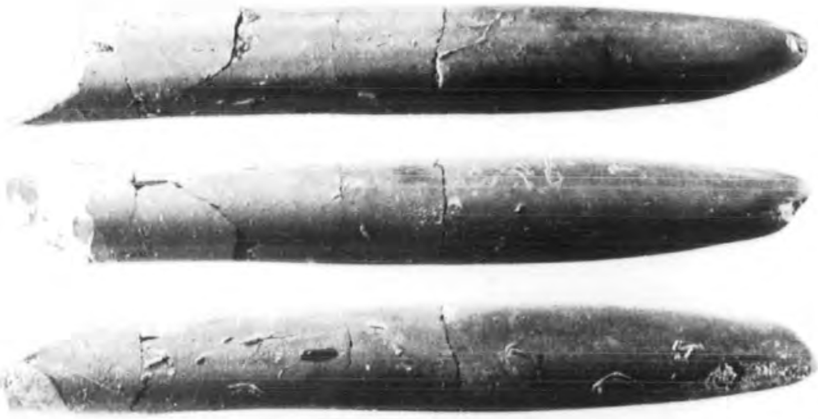
Fig. 3. TB185, beds 112a-c, left-lateral, dorsal and ventral views.

Fig. 4. TB825, beds 112a-c, left-lateral and dorsal views.

Fig. 5. TB682, beds 112a-c, left-lateral, dorsal and ventral views.

PLATE 10


1


2


3


4


5

PLATE 11

Belemnites nitidus Phillips

All specimens from beds 112d-f. All x1.

Fig. 1. TB245, left-lateral and ventral views.

Figs. 2-7. All specimens shown in left-lateral and dorsal views.

Fig. 2. TB705.
Fig. 3. TB833.
Fig. 4. TB698.
Fig. 5. TB835.
Fig. 6. TB699.
Fig. 7. TB701.

PLATE 11


1


2


3


4


5


6


7

PLATE 12

Belemnites nitidus Phillips

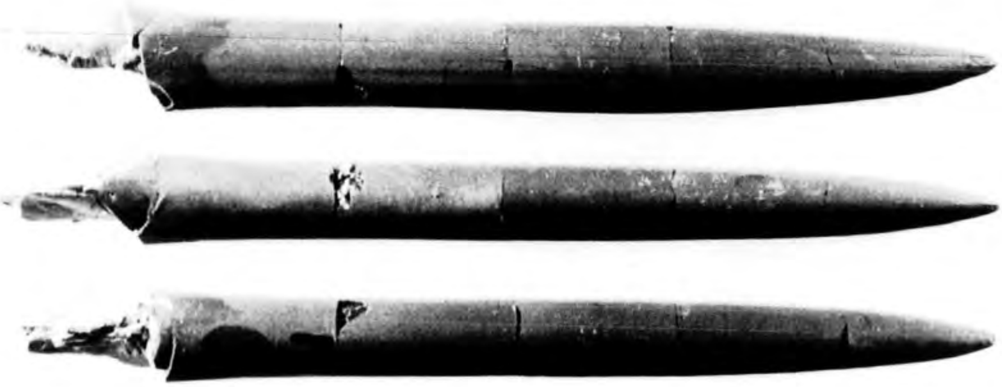
All specimens shown in left-lateral, dorsal and ventral views. All from beds 112d-f. All x1.

Fig. 1. TB830.
Fig. 2. TB704.
Fig. 3. TB696.

PLATE 12

1

2



3

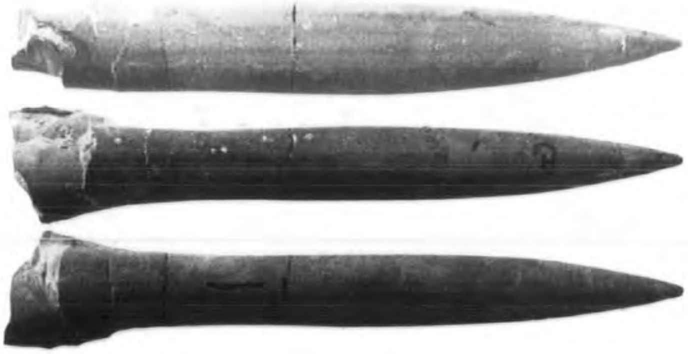
PLATE 13

Belemnites nitidus Phillips

All specimens shown in left-lateral, dorsal and ventral views. All x1.

Fig. 1. TB713, bed 117.
Fig. 2. TB932, bed 118a.
Fig. 3. TB929, bed 118a.
Fig. 4. TB966, bed 118a; with epirostrum.

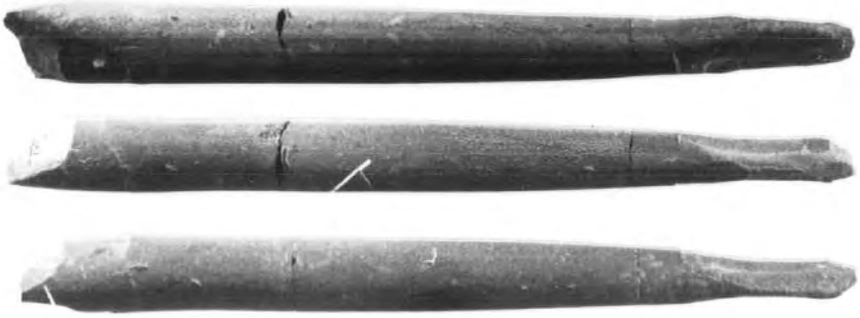
PLATE 13



1

2

3



4

PLATE 14

Belemnites nitidus Phillips

All specimens from bed 118a.

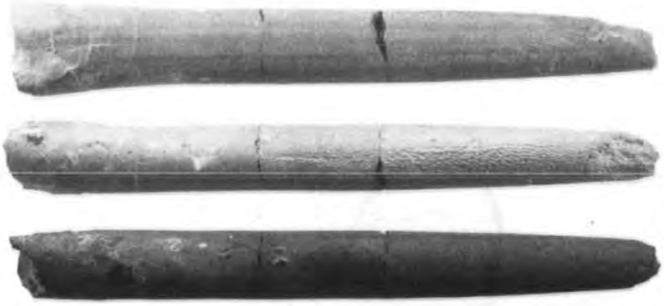
Fig. 1. TB968, left-lateral, dorsal and ventral views; specimen from which the epirostrum was broken prior to burial. x1.

Fig. 2. TB983, left-lateral, dorsal and ventral views; with epirostrum. x1.

Fig. 3. TB974, left-lateral, dorsal and ventral views; with epirostrum. x1.

Fig. 4. TB974, dorsal view showing epirostrum and wrinkled ornamentation on rostrum. x2.

PLATE 14


1


2


3


4

PLATE 15

Belemnites nitidus Phillips

All x1.

Fig. 1. TB783, beds 118b-c, left-lateral, dorsal and ventral views.

Fig. 2. TB1132, bed 120c, left-lateral and dorsal views; with epirostrum.

Fig. 3. TB1070, bed 119, left-lateral, dorsal and ventral views.

Fig. 4. TB115, beds 120a-b, left-lateral, dorsal and ventral views.

PLATE 15

1

2

3

4

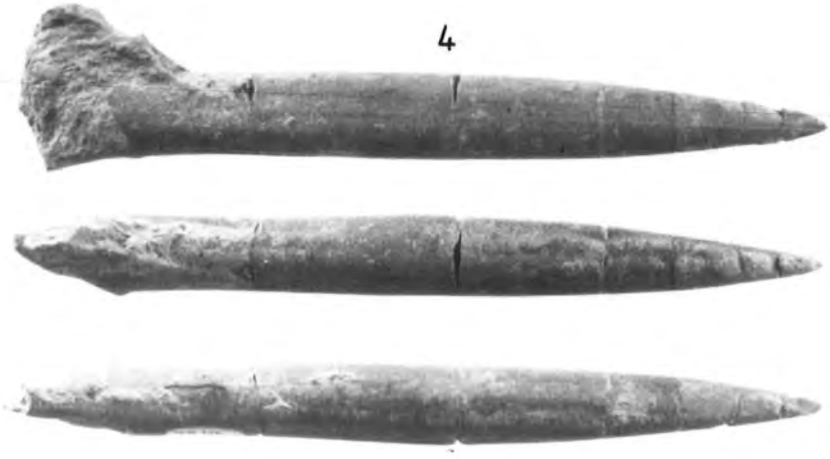


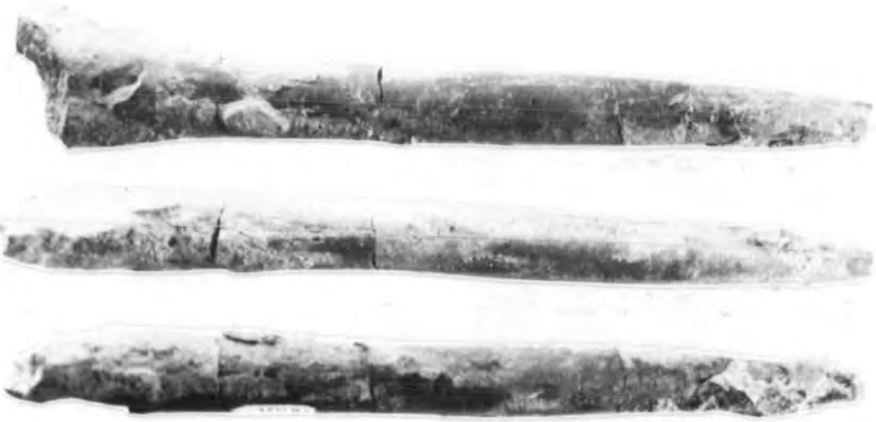
PLATE 16

<u>Belemnites nitidus</u> Phillips

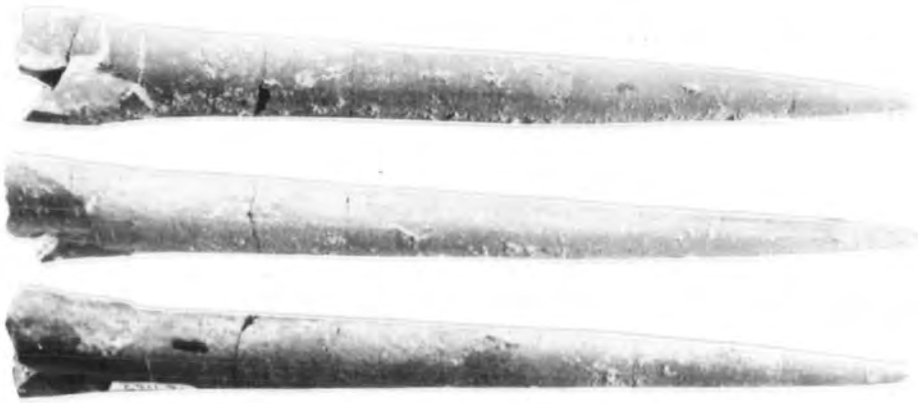
All specimens shown in left-lateral, dorsal and ventral views. All x1.

Fig. 1. TB1119, bed 120c.
Fig. 2. TB1142, bed 120d.
Fig. 3. TB568, beds 122a-c.

PLATE 16



1



2

3

PLATE 17

Belemnites imus (Lang)

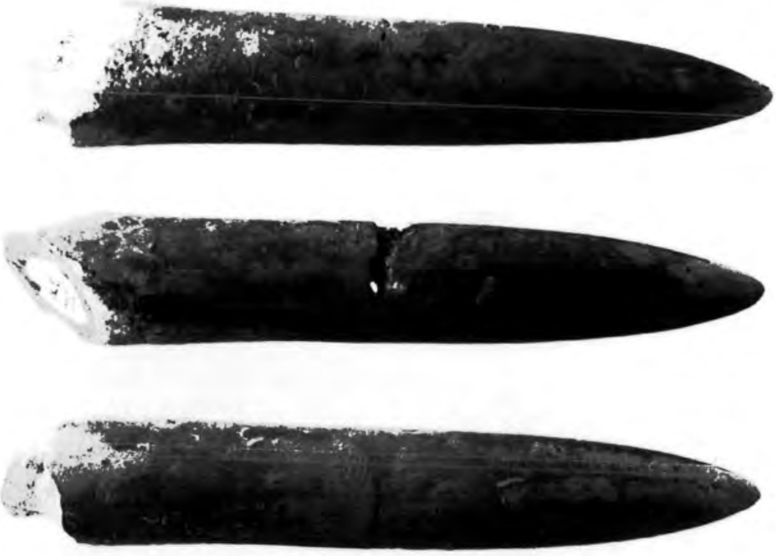
All x1.

Fig. 1. D75 (robust), bed 107, left-lateral, dorsal and ventral views.

Fig. 2. TB353 (gracile), bed 110 IV, left-lateral and dorsal views.

Fig. 3. TB361 (gracile), bed 110 IV, left-lateral and dorsal views.

PLATE 17



1

2

3

PLATE 18

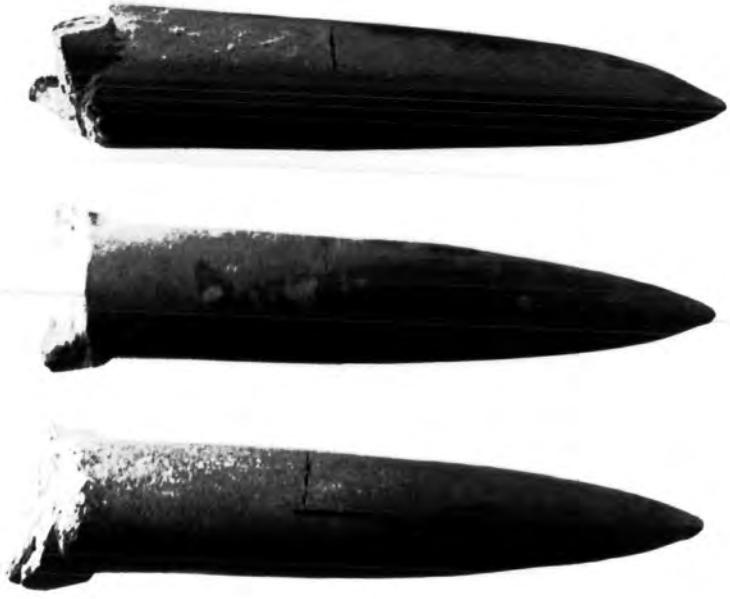
Belemnites imus (Lang)

Fig. 1. TB223 (robust), bed 110 IV, left-lateral, dorsal and ventral views. x1.

Fig. 2. TB229 (robust), bed 110 IV, left-lateral, dorsal and ventral views. x1.

PLATE 18

1



2

PLATE 19

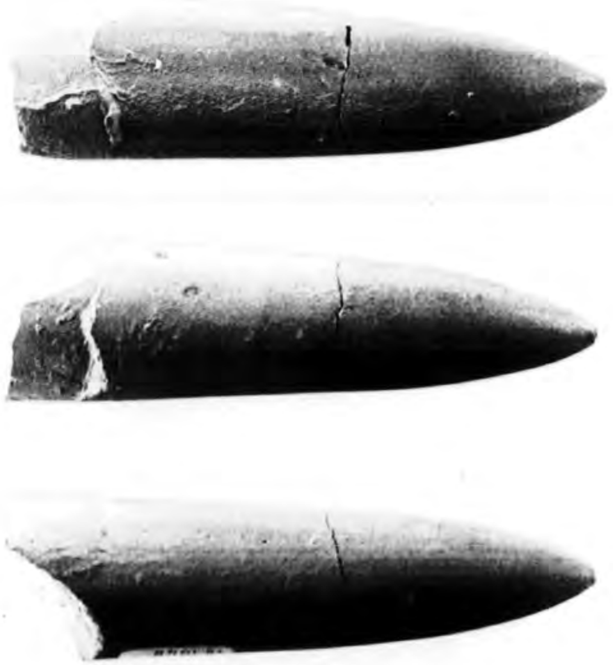
Belemnites abruptus (Lang)

All specimens shown in left-lateral, dorsal and ventral views. All from bed 110 V. All x1.

Fig. 1. TB1048.
Fig. 2. TB44.
Fig. 3. TB520.
Fig. 4. TB1049.

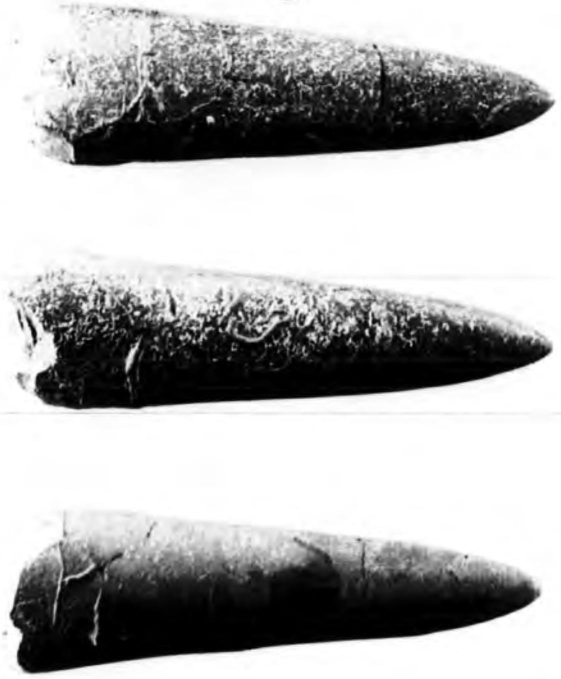
PLATE 19

1



2

3



4

PLATE 20

All specimens x1.

Figs. 1-4. Belemnites abruptus (Lang) All specimens shown in left-lateral, dorsal and ventral views. All from bed 110 V.

Fig. 1. TB51.
Fig. 2. D128.
Fig. 3. TB530.
Fig. 4. TB509.

Fig. 5. ?Coeloteuthis sp., TB389, bed 110 V, ?left-lateral and ?dorsal views.

Fig. 6. Belemnites ?abruptus, TB542, bed 110 V, left-lateral and dorsal views.

PLATE 20

1

2

3

4

5

6

PLATE 21

All specimens x1.

Figs. 1-4. Belemnites abruptus (Lang) All specimens shown in left-lateral, dorsal and ventral views.

Fig. 1. D133, bed 111b.
Fig. 2. TB703, beds 112d-f.
Fig. 3. TB1051, bed 114.
Fig. 4. TB828, beds 112a-c.

Fig. 5. Belemnites ?abruptus, TB67, bed 111b, left-lateral and dorsal views.

Figs. 6, 7. ?Coeloteuthis sp.

Fig. 6. TB805, bed 111b, ?left-lateral and ?dorsal views.

Fig. 7. TB562, beds 122a-c, ?left-lateral view.

PLATE 21


1


2


3


4

5


6


7


PLATE 22

Belemnites cricki (Lissajous)

All x1.

Fig. 1. TB758 (?gracile), beds 118b-c, left-lateral, dorsal and ventral views.

Fig. 2. TB775 (gracile), beds 118b-c, left-lateral, dorsal and ventral views; with epirostrum.

Fig. 3. TB921 (juvenile), bed 118c (top), left-lateral and dorsal views.

Fig. 4. TB767 (?robust), beds 118b-c, left-lateral, dorsal and ventral views.

Fig. 5. TB1023 (juvenile), beds 118b-c, left-lateral and dorsal views.

Fig. 6. TB925 (juvenile), bed 118c (top), left-lateral and dorsal views.

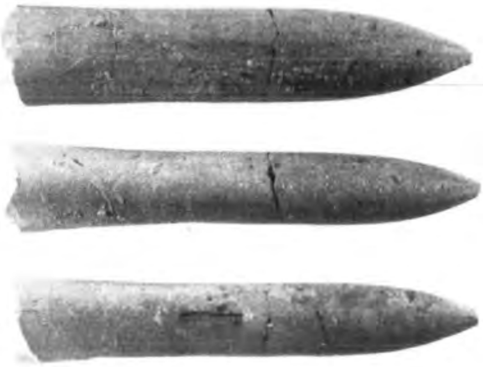
PLATE 22

1

2

3

4



5

6

PLATE 23

Belemnites cricki (Lissajous)

All specimens shown in left-lateral, dorsal and ventral views. All x1.

Fig. 1. TB898 (robust), bed 118c(top).

Fig. 2. TB915 (?robust), bed 118c(top).

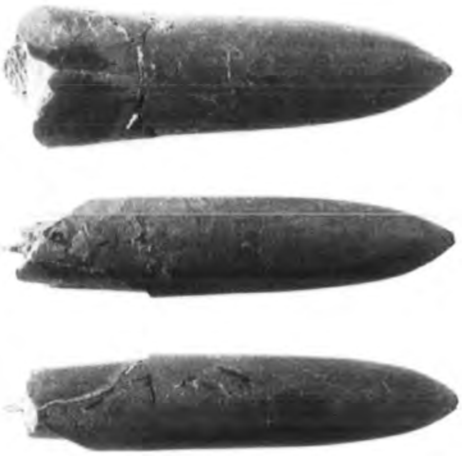
Fig. 3. D137 (?robust), bed 119; note weathered and striated apex.

Fig. 4. TB917 (?robust), bed 118c(top).

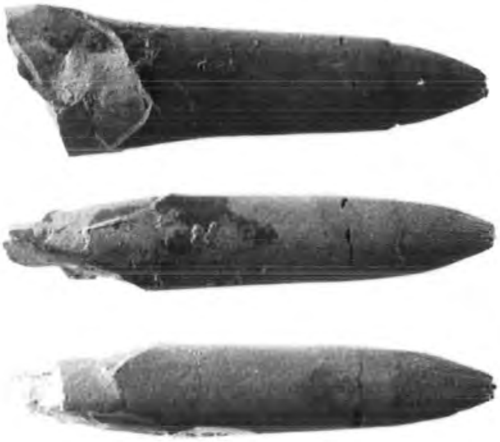
Fig. 5. TB1088 (?robust), bed 119.

Fig. 6. TB1087 (?robust), bed 119.

PLATE 23


1


2


3


4


5


6

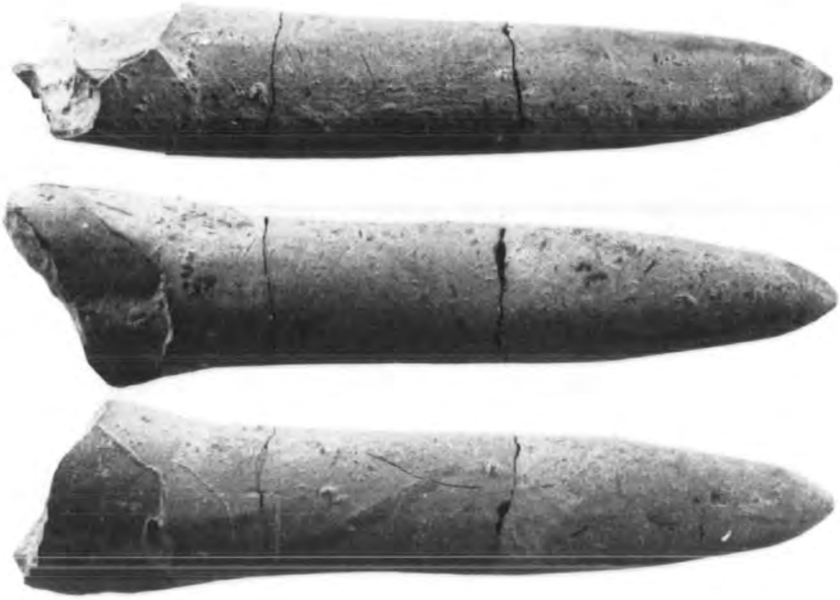
PLATE 24

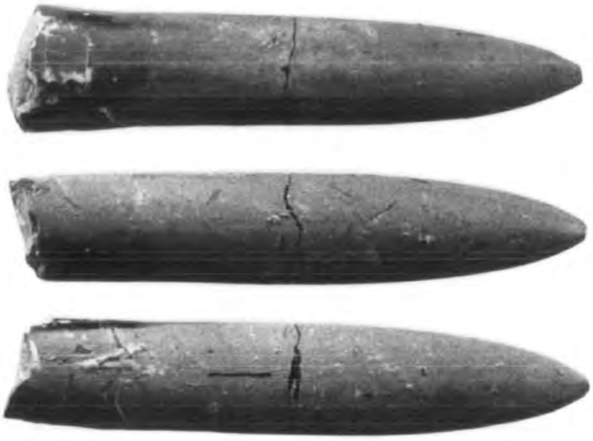
Belemnites ridgensis (Lang)

All specimens shown in left-lateral, dorsal and ventral views. All x1.

Fig. 1. TB1030, bed 118c.
Fig. 2. TB750, bed 117.
Fig. 3. Belemnites ?ridgensis, TB702, beds 112d-f.

PLATE 24


1


2


3

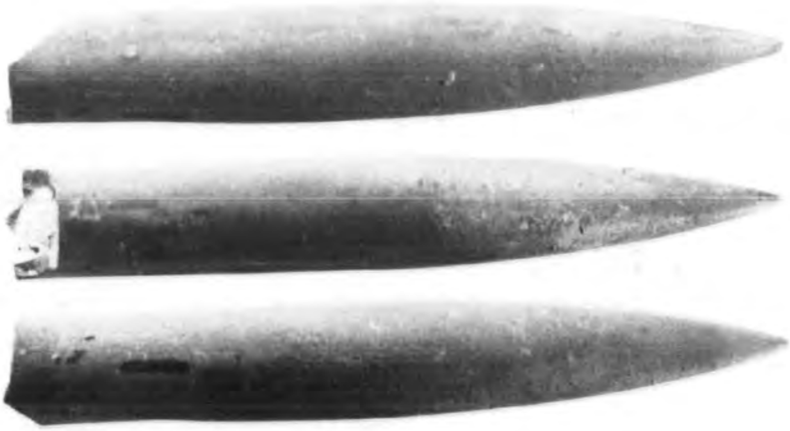
PLATE 25

Belemnites aduncatus Miller

All specimens shown in left-lateral, dorsal and ventral views. All x1.

Fig. 1. TB858, bed 117.
Fig. 2. TB147, bed 120d.
Fig. 3. TB549, beds 122a-c; note hooked apex.

PLATE 25


1


2

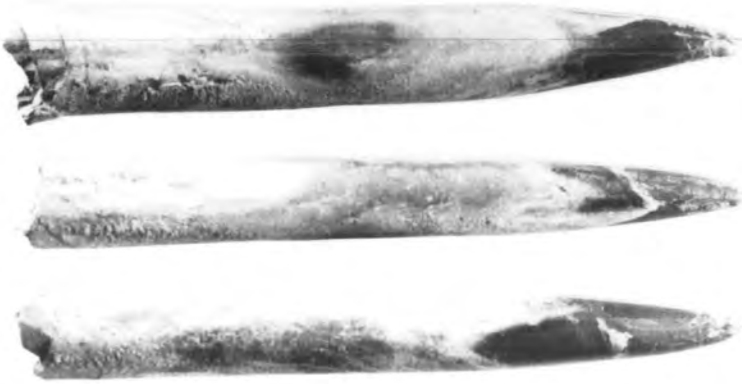

3

PLATE 26

Belemnites aduncatus Miller

All specimens from beds 122a-c.

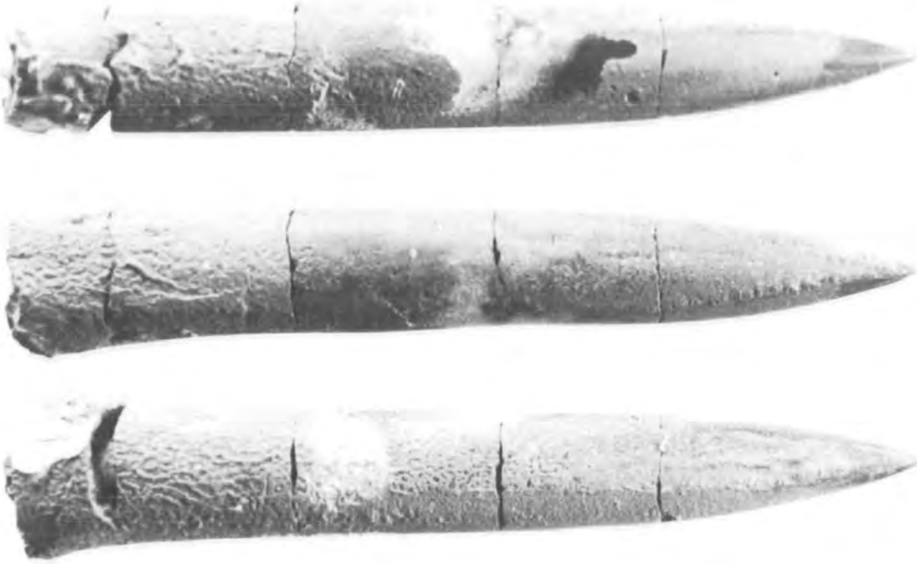
Fig. 1. TB547, left-lateral, dorsal and ventral views. x1.

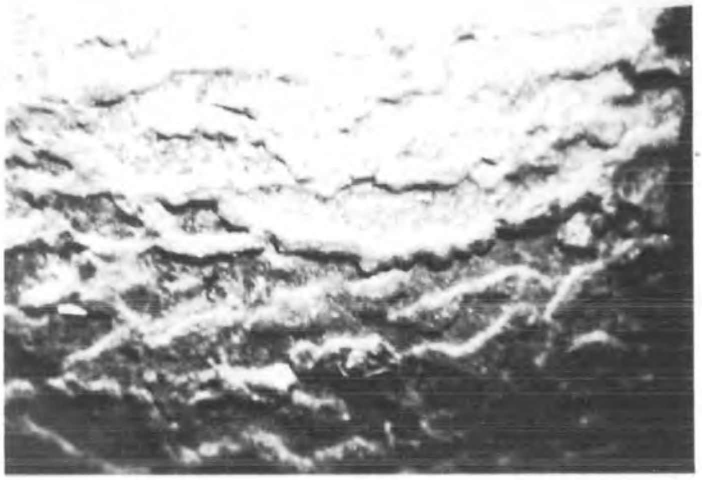
Fig. 2. TB547, part of anterior ventral surface showing ornament. x6. (The surface is covered with a thin layer of cemented matrix.)

Fig. 3. TB547, TS through part of anterior ventral surface of rostrum, showing concentric laminations of ornament. x25.

Fig. 4. TB554, left-lateral, dorsal and ventral views. x1.

Fig. 5. TB561, left-lateral, dorsal and ventral views. x1.


1


2


3


4


5

PLATE 27

Belemnites aduncatus Miller

All specimens from beds 122a-c.

Fig. 1. TB1156, right-lateral view. x1.

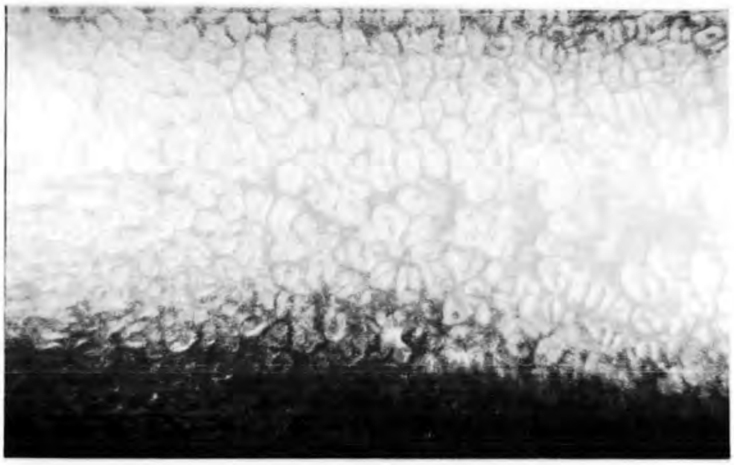
Fig. 2. TB1157, part of posterior lateral surface showing ornament. x6.

Fig. 3. TB1157, left-lateral, dorsal and ventral views. x1.

PLATE 27

1

2



3

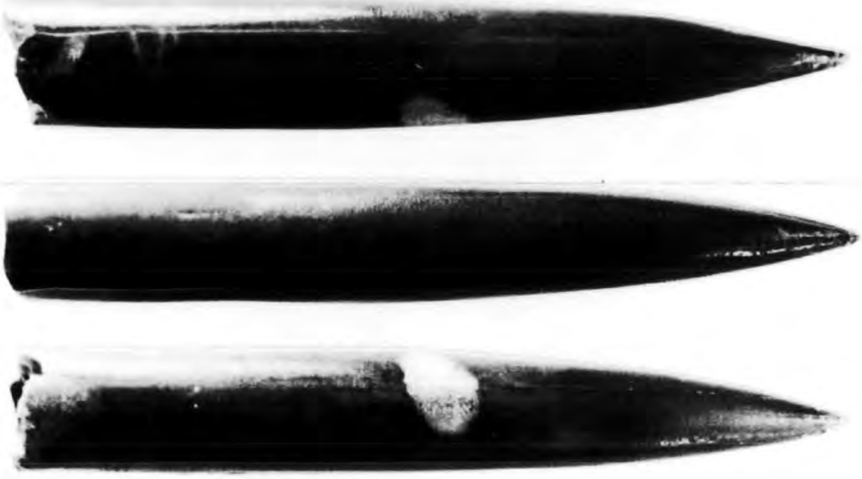


PLATE 28

Figs. 1-3. Hastites microstylus Phillips All specimens shown in left-lateral, dorsal and ventral views. All x1.

Fig. 1. TB1079, bed 119.
Fig. 2. TB1082, bed 119.
Fig. 3. TB1195, beds 122a-c.

Fig. 4. Hastites sp. nov., TB131, bed 120d, left-lateral, dorsal and ventral views. x1.

PLATE 28

1

2

3

4

PLATE 29

Fig. 1. Hastites sp. nov., TB140, bed 120d, left-lateral, dorsal and ventral views. x1.

Fig. 2. ?Hastites sp. nov., TB1153, bed 120c, left-lateral, dorsal and ventral views. x1.

Fig. 3. ?Belemnitid beak element, bed 110V. x6.

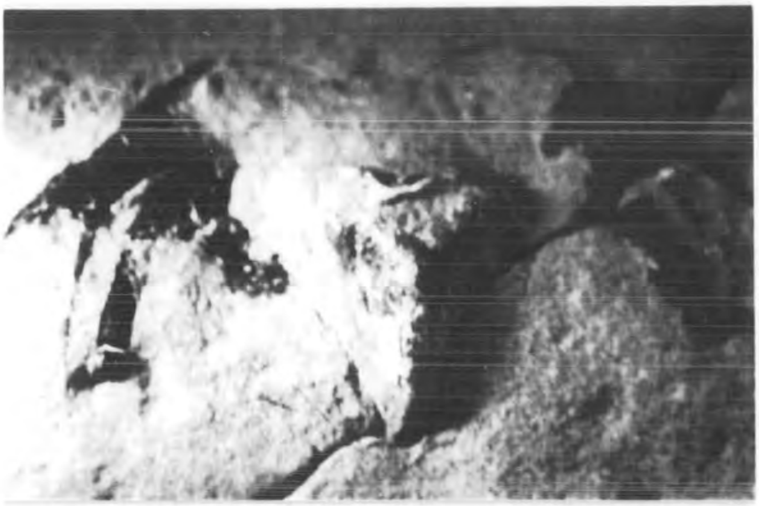
Fig. 4. ?Belemnitid beak element, beds ?122a-c, anterior and posterior views. x6.

PLATE 29


1


2

3



4