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Ammonites from the Middle Albian of Helgoland and Adjacent Regions with some Phylogenetic Observations

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Hoplitidae (Hoplitinae, Sonneratiinae), Albian, classification, phylogeny, sexual dimorphism, new taxon (*Hoplites strategus* n.sp.), taxonomy, biostratigraphy, correlation

Northwest German Lowlands, Helgoland, Schleswig-Holstein, North Sea, London Basin, East Anglia, southeast England

Abstract: The graue Minimus-Kreide is exposed in submarine outcrops off the coast of Düne. Loose blocks derived from the outcrop have been washed onto the beach and from these, eight ammonites all belonging to the genus *Hoplites*, have been collected. By comparison with the Lower Gault sequence in the Weald and East Anglia (United Kingdom), the ammonites from Helgoland indicate the presence of sediments of the uppermost part of the *Hoplites spathi* Subzone (*Hoplites dentatus* Zone, Middle Albian). There is some evidence, however, of the presence of other Albian horizons within the graue Minimus-Kreide.

The ammonites from Helgoland comprise three forms: *Hoplites* aff. *paronai* Spath, *H.* aff. *escragnollensis* Spath and *H. strategus* n. sp., the latter being the most common. A brief commentary is given on the state of taxonomy in the Hoplitinae.

[Ammoniten aus dem Mittel-Alb von Helgoland und Umgebung und einige phylogenetische Beobachtungen]

Kurzfassung: Die graue Minimus-Kreide streicht in submarinen Aufschlüssen vor der Helgoländer Düne aus. Aus angespülten Strandgeröllen dieses Vorkommens wurden acht Ammoniten geborgen, die sämtlich der Gattung *Hoplites* angehören. Nach Vergleichen mit der Unter-Gault-Folge im südostenglischen Weald-Gebiet und in East Anglia (Großbritannien) weisen die Helgoländer Ammoniten auf Ablagerungen des höchsten Teils der *Hoplites spathi*-Subzone (*Hoplites dentatus*-Zone), Mittel-Alb) hin. Allerdings existieren Anzeichen für die Ausbildung weiterer Horizonte der Alb-Stufe in der grauen Minimus-Kreide.

Die Helgoländer Ammoniten umfassen die drei Formen *Hoplites* aff. *paronai* Spath, *H.* aff. *escragnollensis* Spath und *H. strategus* n. sp., von denen die letztgenannte die häufigste ist.

Abschließend wird kurz der Stand der Taxonomie bei den Hoplitinae erörtert.

[Ammonites de l'Albien moyen de Helgoland et des régions limitrophes; quelques observation phylogénétiques]

Résumé: La craie grise à *Minimus* apparaît en affleurements sous marins au large de la Dune de Helgoland. Dans des galets de plage provenant de cette craie ont été récoltés huit ammonites qui appartiennent toutes au genre *Hoplites*. Après comparaison avec les successions du Weald (Angleterre du SE) et de l'East Anglia (Royaume Uni), il ressort que les ammonites de Helgoland indiquent des dépôts de la partie sommitale de la Sous-zone à *Hoplites spathi* (Zone à *Hoplites dentatus*, Albien moyen). En outre dans cette craie grise existent des indices d'autres horizons de l'Albien.

Les ammonites de Helgoland appartiennent à trois formes: *H.* aff. *paronai* Spath, *H.* aff. *escragnollensis* Spath et *H. strategus*, cette dernière étant l'espèce la plus abondante. En conclusion est brièvement rappelée l'état actuel de la taxonomie des Hoplitinae.

[Аммониты из среднего альба о-ва Гельголанда и смежных районов с некоторыми замечаниями о филогенезе]

Резюме: Graue Minimus-Kreide выходит в подводных обнажениях перед островком «Düne», расположенным в непосредственной близости от о-ва Гельголанда. Было собрано восемь аммонитов из намытых прибрежных галек этого проявления. Все эти аммониты принадлежат к роду *Hoplites*. На основе сравнений с нижнегольтской толщей в вельдском районе и Ист Англии (Великобритания) гельголандские аммониты указывают на

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отложения верхов подзоны *Hoplites Spathi* (зона *Hoplites dentatus*, средний альб). Однако существуют признаки образования дальнейших горизонтов альбского яруса в graue Minimus-Kreide.

Гельголандские аммониты охватывают следующие три формы: *Hoplites* aff. *paronai* SPATH, *H.* aff. *escragnollensis* SPATH и *H. Strategus* n. sp. Последняя форма встречается наиболее часто.

В заключение кратко обсуждается изученность таксономии у Hoplitinae.

Contents

1 Introduction

Sediments of Albian age have been known to outcrop offshore of Helgoland since the early part of this century, but were first described in any detail by ERNST (1927:136). In more recent years, the submarine outcrop off the coast of Düne and the fauna obtained from loose blocks derived from it, have been mentioned by KEMPER, RAWSON, SCHMID & SPAETH (1974: 131–2). The sediment sequence consists essentially of grey-green sandy limestones, some 1.1 m to 1.4 m in thickness, called the graue Minimus-Kreide by ERNST (1927). Within this Member, ERNST recognized a reddish-grey sandy and marly basement bed some 10 cm thick resting non-sequentially upon the Ewaldi Kreide of Aptian age. Above this basement bed there occurs the principal bed of grey-green sandy limestone, 1 m to 1.3 m in thickness, in which ERNST recognized a number of distinct lithological subdivisions.

In his faunal list, ERNST (1927: 140) records *Inoceramus sulcatus* which, if correctly identified, would indicate the presence of the lower part of the Upper Albian (*Dipoloceras cristatum* and/or *Hysteroceras orbignyi* Subzones). The prolific belemnite fauna recorded by STOLLEY (1920) and ERNST (1927) suggests an Upper Albian age, but SPAETH (1971) has indicated that all the forms present belong to the Middle Albian.

In recent years, Herr H. H. STÜHMER and Herr H. KÜSTERMANN have discovered ammonites indicating the presence of the upper part of the *Hoplites spathi* Subzone of the *Hoplites dentatus* Zone, in loose blocks in beach debris derived from the submarine outcrop (KEMPER, RAWSON, SCHMID & SPAETH 1974: 132). Nine specimens, all species of *Hoplites*, have been obtained but the exact horizon of this fauna within the graue Minimus-Kreide is unknown. The description of these ammonites forms the nucleus of

Table 1. Zonal and subzonal scheme for the Lower, Middle and Upper Albian in the hoplitinid ammonite faunal province

Substage	Super-Zone	Zones	Subzones
Upper Albian		*Stoliczkaia dispar*	*Mortoniceras (Durnovarites) perinflatum* *Mortoniceras (Mortoniceras) rostratum*
		Mortoniceras (M.) inflatum	*Callihoplites auritus* *Hysteroceras varicosum* *Hysteroceras orbignyi* *Dipoloceras cristatum*
Middle Albian		*Euhoplites lautus*	*Anahoplites daviesi* *Euhoplites nitidus*
		Euhoplites loricatus	*Euhoplites meandrinus* *Mojsisovicsia subdelaruei* *Dimorphoplites niobe* *Anahoplites intermedius*
		Hoplites dentatus	*Hoplites spathi* *Lyelliceras lyelli*
Lower Albian	*Douvilleiceras mammillatum*	*Otohoplites auritiformis*	*Pseudosonneratia (Isohoplites) steinmanni* *Otohoplites bulliensis* *Protohoplites (Hemisonneratia) puzosianus* *Otohoplites raulinianus*
		Sonneratia chalensis	*Cleoniceras floridum* *Sonneratia kitchini* *Sonneratia (Globosonneratia) perinflatum*
		Leymeriella tardefurcata	*Leymeriella regularis* *Leymeriella acuticostata* (including *Hypacanthoplites milletioides* and *Farnhamia farnhamensis*) *Leymeriella schrammeni*

this paper. It must not be assumed, however, that the whole of the graue MinimusKreide is of *dentatus* Zone age and of *spathi* Subzone age. A similar thickness of pebbly sandy limestones at Hunstanton, Norfolk – the Hunstanton Red Rock Member of the Gault Formation – represents several Middle and Upper Albian horizons (Owen 1979: 580, Owen in preparation). Even in the case of this well known Norfolk locality collected from since the early decades of the 19th Century, the top beds of the Carstone formerly thought to be of Lower Albian or upper Aptian age, have yielded an ammonite of lower *spathi* Subzone age.

2 Systematic Palaeontology

The nine original specimens from Helgoland are in the private collection of Herr H. KÜSTERMANN and in the collection of Herr H. H. STÜHMER which forms the palaeontological nucleus of the new Helgoland Museum. Casts of eight of these specimens have been deposited in The Natural History Museum, London, signified in the text by the initials BMNH; in the British Geological Survey, Keyworth (BGS); Geologisch-Paläontologisches Institut, Universität Hamburg (GPIH) and the Niedersächsisches Landesamt für Bodenforschung/Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover (NLfB).

2.1 Description of the Helgoland Ammonite Fauna

The supraspecific classification of the Albian ammonites from Helgoland described here is as follows.

Superfamily: Hoplitaceae H. DOUVILLÉ 1890
Family: Hoplitidae H. DOUVILLÉ 1890
Subfamily: Hoplitinae H. DOUVILLÉ 1890
Genus: *Hoplites* NEUMAYR 1875
validated I.C.Z.N Opinion 353, 1955

Type Species: *Ammonites dentatus* J. SOWERBY 1821
validated I.C.Z.N Opinion 353, 1955

2.1.1 *Hoplites* aff. *paronai* SPATH

Plate 1 Figs 2a, b

aff. 1897 *Hoplites benettianus* SOWERBY. PARONA & BONARELLI: p. 91, Pl. 12, Figs 11a, b
aff. 1925 *Hoplites paronai* SPATH. SPATH: p. 107.
aff. 1925 *Hoplites paronai* SPATH. SPATH.: p. 114 Pl. 9, Figs. 2a, b.
1974 *Hoplites (H.)* aff. *paronai* SPATH. KEMPER, RAWSON, SCHMID & SPAETH: p. 132.
1979 *Hoplites (H.)* aff. *paronai* SPATH. OWEN: p. 571.

Material: One specimen in the KÜSTERMANN collection, a cast of which is deposited in the collections of The Natural History Museum, London (BMNH C78508), from beach debris derived from the graue Minimus-Kreide, Düne, Helgoland.

Discussion: SPATH (1925: 114) cited as holotype of *H. paronai* the specimen BMNH C862d figured by him in Plate IX, Figs. 2a, b. However, on page 107 of his Monograph of the Ammonoidea of the Gault, he cites the ammonite figured by PARONA & BONARELLI (1897) in their Plate XII, Figs. 11a, b. At this date (1925) such a citation was sufficient to validate the species and, therefore, the holotype of the species *Hoplites paronai* SPATH is, by precedence, the original of PARONA & BONARELLI's figure which is preserved in the collections of the Museo Geologico in Turin, Italy, and is from the condensed late Lower Albian and Middle Albian sequence at Escragnolles, Alpes Maritime, France.

Until now, *Hoplites paronai* has been interpreted in accordance with BMNH C862d, a specimen more robust than the holotype and closely comparable to the original of PARONA & BONARELLI's Plate XII, Figs. 10a, b. All three specimens, however, lie well within the morphological range of variation to be seen in a single species of *Hoplites*.

H. paronai SPATH is a relatively uncommon species of the *spathi* Subzone. It originates in the late Lower Albian, *Otohoplites auritiformis* Zone, *Pseudosonneratia steinmanni* Subzone (OWEN 1988), in an inflated species of *Pseudosonneratia (Iso-*

hoplites). In the basal Middle Albian, *Lyelliceras lyelli* Subzone it is represented by the form known as *Hoplites baylei* SPATH (1925: 107, 118–119, Text-Fig. 29, Plate XI, Fig. 5) in which the ribbing arises in pairs from comma-shaped umbilical bullae projected high onto the whorl flank and is straighter than in *H. paronai*, with ventro-lateral rib endings well rounded into low clavi. The intercostal areas merge into the siphonal line without the more marked ventro-lateral shoulders seen in later forms. The only essential difference between this *lyelli* Subzone form and its late *auritiformis* Subzone ancestor is that the rib endings are isometric across the venter in the latter form and are arranged en echelon in its descendant. In the lower part of the *spathi* Subzone, the ribbing projects forward onto the venter, ending in pronounced, but still rounded, ventro-lateral clavi. The intercostal areas now terminate at the venter with a distinct lateral shoulder. This is the stage reached by BMNH C862d figured by SPATH (1925: Plate IX, Fig. 2a, b). The early upper *spathi* Subzone form, demonstrated by the holotype, has sharp ribs arising in pairs and triplets from high sharp bullae and are projected well forward on the whorl flank, terminating in platy ventro-lateral clavi. A tendency for ribs to join up in the lautiform manner is apparent and the venter is now distinctly sulcate.

The slightly worn specimen from Helgoland differs from the holotype of *H. paronai* in possessing more pronounced umbilical bullae each giving rise to three ribs, the centre one of which tends to join up with the posterior rib of the same triplet. This tendency to lautiform ribbing is common among all species of *Hoplites* in the higher part of the *spathi* Subzone and the Helgoland specimen can be considered a late mutation of *H. paronai.* In England, this form occurs in the lower part of division 4 (iii), upper *spathi* Subzone, at the Horton Clay Pit, Small Dole, Sussex (OWEN 1971: 34–41).

2.1.2 *Hoplites strategus* n. sp.

Plate 1 Figs. 1a, b; Plate 2 Figs. 1–5

1974 *Hoplites* sp. KEMPER, RAWSON, SCHMID & SPAETH: p. 132.
1979 *Hoplites (H.)* sp. transitional to *Dimorphoplites* OWEN: p. 571.
1982 *Dimorphoplites hilli* SPATH. STÜHMER, H. H., SPAETH, CHR., & SCHMID, F.: Colour pls 15, 16, pl. 60, Figs. 1, 1a.

Derivation of name: Greek ὁπλιτας heavily armoured soldier; στρατηγος army commander.

Holotype: A specimen in the Helgoland Museum, STÜHMER collection No. 1111 of which casts are in the Natural History Museum, London – BMNH C83411 and the British Geological Survey, Keyworth-BGS FOR 4054, from beach debris derived from the graue Minimus-Kreide, Helgoland.

Paratypes: Five specimens in the STÜHMER collection (Nos. 1436–1439, unnumbered) of which casts of the first four numbered are in The Natural History Museum, London (BMNH C83412–C83415), all from blocks derived from the graue Minimus-Kreide found on the beach at Düne and which are figured here in Plate 2. One poorly preserved fragment, not figured here, is the specimen in the KÜSTERMANN collection recorded as *Hoplites* sp. by KEMPER, RAWSON, SCHMID & SPAETH (1974: 132) and as *Hoplites (H.)* sp. transitional to *Dimorphoplites* by OWEN (1979: 571). A cast of this specimen is in The Natural History Museum, London (BMNH C78509).

Diagnosis: *Hoplites*, shell discoidal, evolute, with quadrate whorl section; umbilical wall rounded with slender comma-shaped bullae, about 18–20 per whorl, projecting high on the umbilical margin and each buttressed by a weak umbilical rib arising from the umbilical suture. In the inner whorls, each bulla gives rise to three ribs which are straight on the whorl flank initially and then project forward strongly towards the

ventro-lateral shoulder. Ribbing is distinctly lautiform; the leading and centre ribs of each triplet uniting into a single ventro-lateral clavus, the trailing rib remaining separate and terminating also in a ventro-lateral clavus. Approaching the adult body chamber, the umbilical bullae give rise to pairs of ribs in which the leading rib of each pair unites with the trailing rib of the next formed pair. Clavi are arranged en echelon each side of a shallow sulcate venter with marked forward projection towards the siphuncular line. Suture line unknown.

Dimensions: Holotype (Plate 1 Figs 1 a, b)

diameter (mm)	74
whorl height (30 mm)	0.45
whorl width (30 mm)	0.45
umbilical width (22 mm)	0.35

Discussion: When poorly preserved and seen in lateral aspect only, this species resembles a coarse-ribbed *Dimorphoplites* of the *pinax* group from the *Euhoplites loricatus* Zone (for example the cast BMNH C78509 of the specimen in the KÜSTERMANN collection). The ventral aspect of this species is, however, distinctly that of *Hoplites*. Morphologically, *H. strategus* lies mid-way between the simple ribbed *H. escragnollensis* SPATH (1925: 128, Fig. 34) of earlier upper *spathi* Subzone age and the later, *intermedius* Subzone species *Euhoplites microceras* SPATH (1928: 266; 1930: 267–283, Plate XXVI, Figs. 2 a, b).

In England, fragmentary examples of this species have been discovered in the upper part of the *spathi* Subzone above the level of the condensed upper *spathi* nodule bed (division 2 and equivalents of the Lower Gault Member OWEN 1971) in north Kent and Surrey. In the relatively little condensed sequence of *spathi* Subzone sediments at the Horton Clay Pit, Small Dole, Sussex (OWEN 1971: 34–41, Fig. 15), *H. strategus* occurs in the lower part of division 4 (iii). A typical crushed specimen from a well section in *Lower Gault* at the Cottenham Waterworks, Cambrigdeshire (BGS ED 2585) is figured here in Plate 2 Fig. 5.

2.1.3 *Hoplites aff. escragnollensis* SPATH

Plate 1 Figs 3 a, b;

aff. 1925 *Hoplites escragnollensis* SPATH. SPATH: p. 128 Fig. 34.
1974 *Hoplites (H.)* aff. *escragnollensis* SPATH. KEMPER, RAWSON, SCHMID & SPAETH: p. 132.
1979 *Hoplites (H).* aff. *escragnollensis* SPATH. OWEN: p. 571.
1982 *Dimorphoplites* cf. *hilli* SPATH. STÜHMER, SPAETH & SCHMID: Taf. 37 Fig. 3.

Material: One specimen in the Helgoland Museum, STÜHMER collection No. 1056 of which a cast is deposited in The Natural History Museum, London (BMNH C78510) from the beach debris derived from the graue Minimus-Kreide, Düne, Helgoland.

Discussion: The specimen is worn but sufficient of it is preserved to show that it differs from the typical *H. escragnollensis* SPATH only in the presence of irregular lautiform ribbing. The specimen differs from the contemporary *H. strategus* n. sp. by possessing the more slender and rounded whorl-section convergent towards the venter characteristic of *H. escragnollensis* and the lack of regular lautiform ribbing.

3 Observations on Taxonomy within the Subfamily Hoplitinae

The present paper is concerned primarily with the systematic description of the Albian ammonites collected so far on the islands of Helgoland. It is worth reviewing briefly, the state of taxonomy within the Hoplitinae, particularly in respect of changes introduced during recent years. The Subfamily Hoplitinae originated in the subgenus *Pseudosonneratia (Isohoplites)* in the late *mammillatum* Super-Zone, *Pseudosonneratia (Isohoplites) steinmanni* Subzone (a detailed discussion of the biostratigraphy and ammonite faunas of the european *mammillatum* Super-Zone is given by OWEN 1988). In *Pseudosonneratia* SPATH (1925 with type species *Pseudosonneratia typica* SPATH) simple sonneratiinid branched ribbing stems from umbilical bullae to sweep across the venter with a distinct forward projection but without break along the siphonal line. In its subgenus *Isohoplites* CASEY (1954 with type species *Parahoplites steinmanni* JACOB of which *Hoplites (Isohoplites) eodentatus* CASEY 1961A: 599, Pl. 83, Figs. 4a, b. 1965: 538, Text-Fig. 202 is a subjective synonym), the ribbing along the siphonal line becomes progressively effaced with time until it foreshadows the subsulcate aspect of early *Hoplites*. In the *steinmanni* Subzone, *P. (Isohoplites)* shows ventro-lateral rib terminations similar to *Hoplites*, but these are opposite each other across the venter. At the end of the Subzone, many specimens show a marked tendency towards the en-echelon arrangement of the ventro-lateral rib terminations characteristic of *Hoplites* and the Hoplitinae of which this genus is the earliest member. This instability in shell accretion affects individual specimens which can show both opposite and en-echelon rib terminations at different stages of ontogeny. The earlier genera *Otohoplites* and *Protohoplites* included within the Sonneratiinae, while foreshadowing the morphology seen in the Hoplitinae, spring from a different stock and there are other good reasons for separating the *mammillatum* Super-Zone Subfamily Sonneratiinae from the Middle Albian to Cenomanian Subfamily Hoplitinae (OWEN 1988). Both subfamilies are monophylectic as now defined.

The present grouping of ammonites of the genus *Hoplites* into species is not particulary satisfactory. SPATH in his Monograph of the Ammonoidea of the Gault (1923–1943) worked essentially with English specimens collected from condensed phosphatic nodule beds, or indigenous material collected from isolated sequences of which the exact stratigraphical relationships were unknown. This was all that was available to him at that time, but the end product has proved to be an almost meaningless systematic jumble. The relationships of the stratigraphic sequences one to another has been determined (eg. OWEN 1971) but it is the systematic relationships of the ammonites which now require to be studied.

Phosphatic nodule beds represent the pebble debris derived from sequences of clays or loams which have subsequently undergone submarine current winnow. The accumulation of a pebble fauna may be derived from various horizons within one Subzone, as in the case of the dentatus nodule bed (Bed I v) at Folkestone, Kent (eg. OWEN 1971), or from various horizons within several Subzones or even Zones (eg. Escragnolles, Alpes Maritimes, France). Such a derived accumulation assemblage can provide and does in the case of *Hoplites*, a bewildering plexus of morphotypes transitional between arbitrarily selected "species". SPATH recognized this feature in the hoplitinids as a group (eg. 1942: 691) and it is well known to all who have collected from such condensed stratigraphical sequences. However, when there is a relatively little condensed sequence of sediments of *dentatus* Zone age, as in Sussex, England and the Aube, France (eg. DESTOMBES 1979), bedding planes show individuals of the same species with relatively little morphological variation between them. In this latter category falls the group of specimens of *Hoplites strategus* from Helgoland described in this paper. Although the *spathi* Subzone appears to be far from completely represented by sediments in the outcrop off Düne, by chance, those that have been preserved were deposited during a short period of time within the upper part of the Subzone and there is little variation between the individual specimens of *H. strategus*.

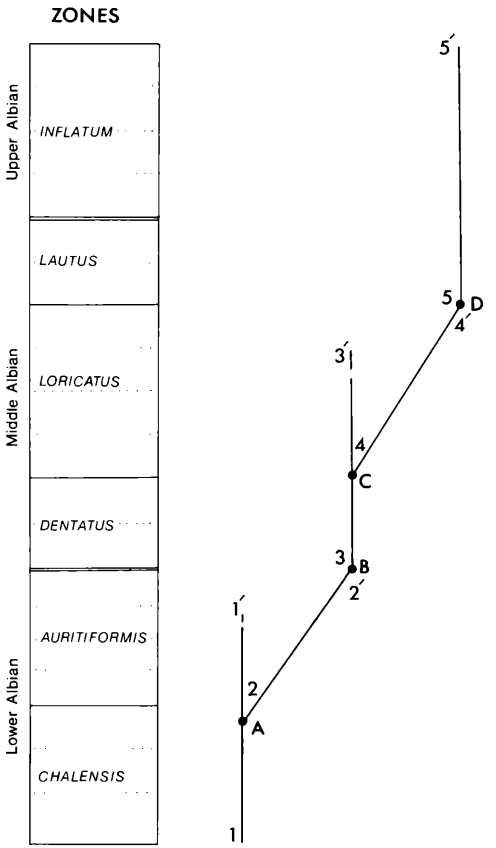

Fig. 1. A projected phylogeny of the lineage *Sonneratia* – *Euhoplites* (Sonneratiinae-Hoplitinae) to illustrate fundamental points of change in morphology and its reflection in the nomenclature. 1–1′ range of *Sonneratia* spp. 2–2′ range of *Pseudosonneratia* and *P. (Isohoplites)* spp. 3–3′ range of *Hoplites* spp. 4–4′ range of *Euhoplites* spp. *"loricatus* group". 5–5′ range of *Euhoplites* spp. *"lautus* group". A – development of discoidal shells with ribs continuous across the venter and projected forward along the siphonal line with effacement progressively in *Isohoplites*. B – development of sulcate venter with interrupted ventro – lateral rib endings changing from being opposite each other across the venter to an en-echelon arrangement. C – development of regular lautiform ribbing at an early stage in ontogeny and a distinctly U-shaped venter. D – rapid change from a simple U-shaped venter to a distinctly channelled venter.

It is now possible to discern certain natural lineages within *Hoplites*, each of which can be regarded as a species rather than a series of named morphotypes. These lineages originate in late forms of the subgenus *P. (Isohoplites)* and, in turn, proceed forward in time into *Euhoplites* by changes in ornament pattern which affect each lineage more or less simultaneously. For long periods of time, the changes in morphology are gradual but at intervals, sudden changes affect the population of species as a whole. To illustrate this point, one of these lineages at generic rank is illustrated in Fig. 1. Each straight line in Fig. 1 represents a group of shells of similar morphological and structural characteristics, divided arbitrarily into species and collected into a "subgenus" or "genus". The labelled connecting points indicate a distinct morphological change undergone by the bulk of the

known population. Exactly the same diagram can be constructed at species level. For example *Sonneratia dutempleana* (D'ORBIGNY) changes at point A into *Pseudosonneratia (I.) preadentata* CASEY, at point B via the short-lived stage called *P. (Isohoplites) steinmanni* (JACOB) into *Hoplites dentatus* (J. SOWERBY), at point C into *Euhoplites aspasia* SPATH and at point D to *Euhoplites lautus* (J. SOWERBY). Why these sudden changes indicated in the caption to Fig. 1 should occur, is unknown but might bear comparison with species changes in other invertebrate phyla through time, termed punctuated equilibria. Associated with the natural lineages are some morphological transitions which in all probability represent cross-breeding. However, the fuller stratigraphic record suggests that these mongrels are the exception, rather than the rule evinced by condensed pebble faunas.

In terms of artificial classifications based upon certain morphological characteristics, such as the presence or absence of lautiform ribbing, like that proposed for the Hoplitinae by DESTOMBES, JUIGNET & RIOULT (1973: 70), the natural lineage given in Fig. 1 would be split between different groups of hoplitinids in a total arbitrary manner.

A distinct dimorphism is common among hoplitinid ammonites which has been given expression in the systematic nomenclature. Forms with closely comparable ornament are separable on account of a marked difference in whorl thickness. For example, the robust form of *Hoplites dentatus* (J. SOWERBY) was named "var". *robusta* by SPATH (1925: 103). *Euhoplites lautus* "var". *duntonensis* SPATH and *E. truncatus* "var". *quadrata* SPATH are similar robust forms of *E. lautus* (J. SOWERBY) and *E. truncatus* SPATH respectively. These quadrate forms appear often to grow to larger diameters than their more slender contemporaries and it is possible that this dimorphism is sexual in nature. A similar relationship is to be seen among the Middle Albian lyelliceratids; for example the basal *lyelli* Subzone forms *Lyelliceras hirsutum* (PARONA & BONARELLI) and *L. huberianum* (PICTET) and within *Lyelliceras lyelli* (LEYMERIE) itself. However, the marked dimorphism seen in Jurassic ammonites is not a feature of the Lower Cretaceous ammonite stocks.

4 Summary

The ammonites collected from the graue Minimus-Kreide of Helgoland, described here, all belong to the Subzone of *Hoplites spathi* and to the uppermost part of that Subzone according to the occurence of these forms in the more complete sequences seen elsewhere in Europe. They comprise *Hoplites* aff. *paronai* SPATH, a new species *Hoplites strategus* OWEN and *Hoplites* aff. *escragnollensis* SPATH. Although there is some palaeontological evidence of higher Albian horizons within the graue Minimus-Kreide, ammonites have not yet been found at these levels.

The state of taxonomy within the Hoplitinae is discussed briefly. The Subfamily originated in the late *mammillatum* Super-Zone subgenus *Pseudosonneratia (Isohoplites)* (Subfamily Sonneratiinae) in the *Pseudosonneratia (Isohoplites) steinmanni* Subzone (Lower Albian). There are discernible natural lineages within *Hoplites* each of which can be regarded as a distinct species, although nomenclatorially these lineages are superficially obscured by the arbitrary erection of names for random morphotypes. At the end of the *Hoplites spathi* Subzone (Middle Albian), the pattern of lautiform ribbing has become general within the bulk of the lineages within *Hoplites* and the *Euhoplites* condition is achieved. This relatively rapid change at the base of the *Anahoplites intermedius* Subzone and a similar rapid change from a sulcate venter characteristic of early *Euhoplites* to a channelled venter characteristic of later species of *Euhoplites* at the base of the *Euhoplites lautus* Zone (Middle Albian), may be a form of punctuated equilibria. There is little doubt that some cross-breeding occurs, but these might prove to be the exception rather than the rule. The nomenclature within the Hoplitinae also obscures the occurrence of a regular dimorphism with robust macroconchs and slender microconchs.

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Plate 1

Fig. 1. *Hoplites strategus* n. sp. Holotype Helgoland Museum H. H. STÜHMER colln. No. 1111. Loose block of graue Minimus-Kreide in beach debris, Düne, Helgoland. ×1. (H. TAYLOR photo).

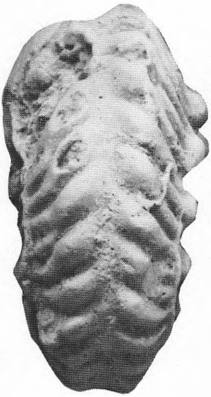
Fig. 2. *Hoplites* aff. *paronai* SPATH. H. KÜSTERMANN colln. graue Minimus Kreide beach debris, Düne, Helgoland. × 1. (H. TAYLOR photo.)

Fig. 3. *Hoplites* aff. *escragnollensis* SPATH. Helgoland Museum H. H. STÜHMER colln. No. 1056. Loose block of graue Minimus-Kreide in beach debris, Düne, Helgoland. ×1 (H. TAYLOR photo.)

1a

1b

2a



2b

3a

3b

Plate 2

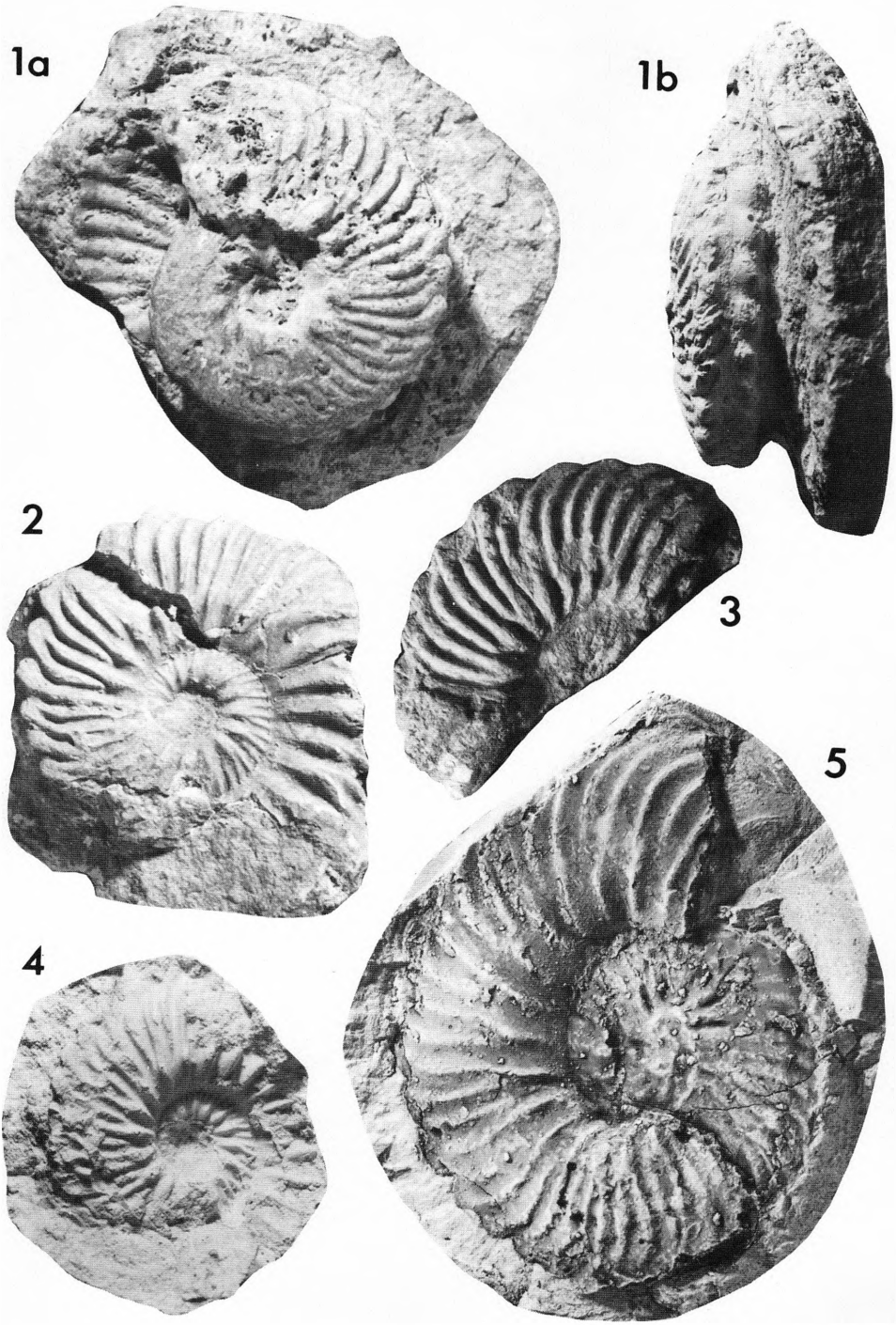
Fig. 1. *Hoplites strategus* n. sp. Paratype Helgoland Museum H. H. STÜHMER colln. No. 1437. Loose block of graue Minimus-Kreide in beach debris, Düne, Helgoland (H. TAYLOR photo.) ×1.

Fig. 2. *Hoplites strategus* n. sp. Paratype Helgoland Museum H. H. STÜHMER colln. No. 1436. Loose block of graue Minimus-Kreide in beach debris, Düne, Helgoland. ×1 (H. H. STÜHMER photo).

Fig. 3. *Hoplites strategus* n. sp. Paratype Helgoland Museum H. H. STÜHMER colln. No. 1439. Loose block of graue Minimus-Kreide in beach debris, Düne, Helgoland. ×1 (H. H. STÜHMER photo).

Fig. 4. *Hoplites strategus* n. sp. Paratype Helgoland Museum H. H. STÜHMER colln. No. 1438. Silicone rubber cast (BMNH C83415) from an external mould. Loose block of graue Minimus-Kreide in beach debris, Düne, Helgoland. ×1 (H. H. STÜHMER photo).

Fig. 5. *Hoplites* cf. *strategus* n. sp. crushed specimen from clays of the uppermost *spathi* Subzone, Lower Gault, in a well section at the Cottenham Waterworks, Cambridgeshire, England (BGS ED 2585) ×1. (H. TAYLOR photo.)


1a
1b
2
3
4
5