AMMONITES OF THE LIASSIC FAMILY JURAPHYLLITIDAE IN BRITAIN

by M. K. HOWARTH and D. T. DONOVAN

ABSTRACT. The genus *Galaticeras* is recorded from the Lower Lias of Britain for the first time. The palaeontology and stratigraphy of *Tragophylloceras* are revised, ten out of fourteen previously described species being placed in synonymy, while one new one, *T. carinatum*, is described. Microconch–macroconch pairs are recognized in *Tragophylloceras* and formally described, this being the first full description of dimorphic pairs in Liassic ammonites.

THE Jurassic members of the ammonite superfamily Phylloceratáceae are well known to have been restricted in their geographical distribution. In Europe, they are abundant in the Mediterranean countries, and spasmodic in their occurrence further north. In the Lower and Middle Lias of north-western Europe they are represented by two genera of the family Juraphyllitidae. One of these, *Galaticeras*, was a straggler from the southern province. The other, *Tragophylloceras*, was peculiar to north-western Europe and is not recorded from the Mediterranean area.

Galaticeras is a new record for the British Lias. It was discovered by Mr. J. F. Jackson in the Flatstones of the Lower Lias near Charmouth, Dorset, and simultaneously recognized by one of us (D.T.D.) in borehole material in the Geological Survey collections. *Tragophylloceras* has been reviewed in the light of all relevant British collections and a systematic description of its species is given for the first time. In three of the five species described dimorphic pairs of microconchs and macroconchs have been found. The pairs are considered to be dimorphic forms of the same species for reasons discussed under the section on the genus *Tragophylloceras*. By referring them to the same species we do not mean to imply that the dimorphism is sexual; this could indeed be the case, but there is not sufficient material of *Tragophylloceras* to throw any light on the subject of sexual dimorphism in ammonites. Such dimorphism has only been recognized in Liassic ammonites in recent years, and this is the first formal description of any Liassic dimorphic pairs.

Acknowledgements. We wish to thank Dr. J. H. Callomon for the gift of two specimens from his collection, and Brigadier G. Bomford, Dr. J. C. W. Cope of Swansea University College, Dr. M. L. K. Curtis of Bristol City Museum, Mr. D. Emlyn Evans of the National Museum of Wales, and Dr. R. J. G. Savage of Bristol University for the loan of specimens under their care. Our thanks are also due to Mr. L. Bairstow for allowing us to quote determinations of ammonites in his collection from Robin Hood's Bay. Specimens in the British Museum (Natural History) are listed under the abbreviation BM, those in the Geological Survey and Museum, London, as GSM, those in the National Museum of Wales, Cardiff, as NMW, and those at the Sedgwick Museum, Cambridge, as SM. Whorl dimensions are quoted in millimetres in the following order: diameter: whorl height, whorl breadth, umbilical width.

SYSTEMATIC DESCRIPTIONS

Family JURAPHYLLITIDAE Arkell 1950

The family comprises eight genera (Arkell 1957, pp. L189–92) which have phylloceratid suture-lines, but which have shells with umbilici larger (commonly between 15 and

[Palaeontology, Vol. 7, Part 2, 1964, pp. 286–305, pls. 48–49.]

30 per cent. of the diameter) than in contemporary members of the family Phylloceratidae. Constrictions on the internal mould, due to thickenings of the shell-wall, are present, though sometimes on the inner whorls only. The shell is ornamented by sigmoidal growth-lines. Ribbing of the same form is often present, and is usually developed on the outer whorls only. Modification of the venter may occur, by a keel in *Harpophylloceras*, an interrupted keel in *Meneghiniceras*, or a groove in *Schistophylloceras*.

In Europe, juraphyllitids are common in Lower and Middle Liassic rocks south of the Alpine geosyncline, and they are also found in North Africa. *Galaticeras* is a typical southern genus which seems to have migrated north during the Obtusum Zone. *Tragophylloceras* is known only from north of the Alps, with the exception of records from Portugal (Arkell 1956, p. 242).

Genus *Galaticeras* Spath 1938

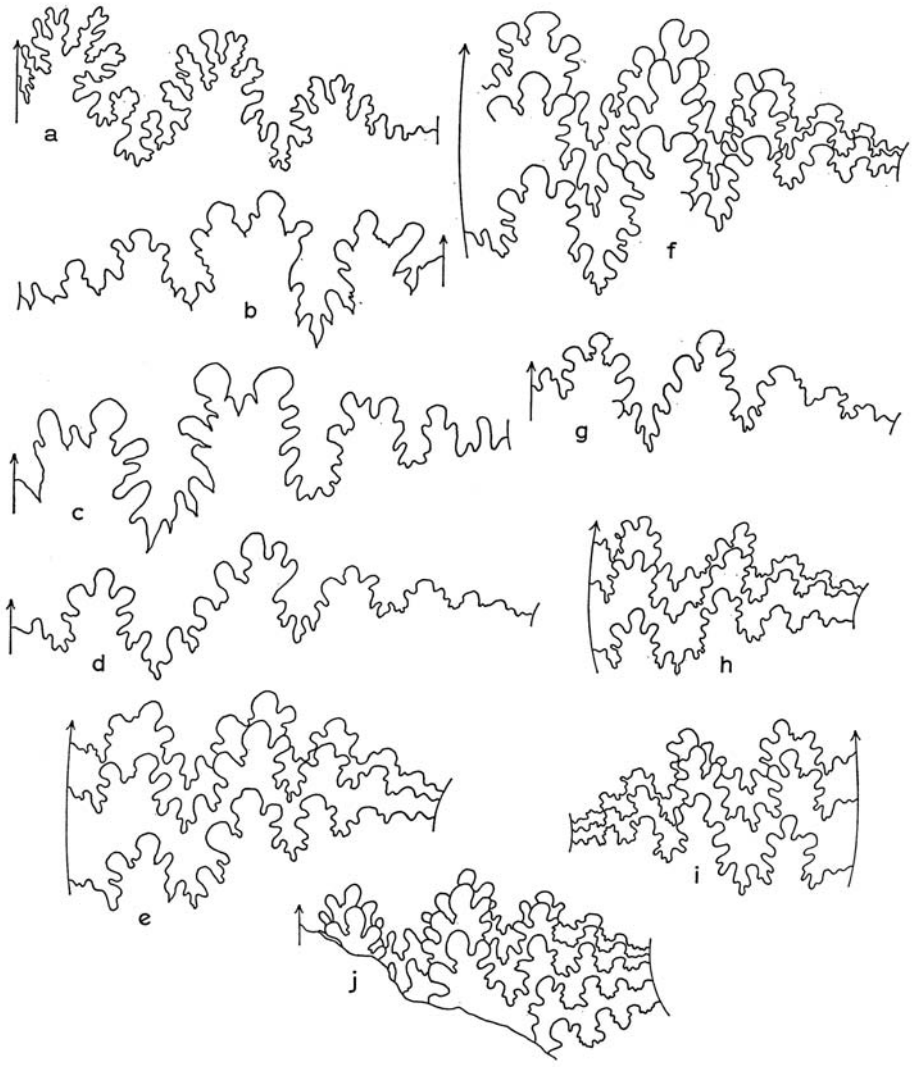
Type species. Amphiceras harpoceroides Gemmellaro 1884.

Synonym. Amphiceras Gemmellaro 1884, *non* Gray 1847.

This genus is known mainly from the '*Terebratula*' *aspasia* Beds at Rocche Rosse, near Galati, Sicily, which are of Jamesoni and Ibex Zone age. Five species were described by Gemmellaro (1884, pp. 192–8): *Galaticeras harpoceroides*, *G. aegoceroides*, *G. flexistriatum*, *G. propinquum* (doubtfully distinct from *G. harpoceroides*), and *G. mariani*. Outside Sicily the genus is rare. There are two specimens in the British Museum (Natural History) (C52815–6) from the High Atlas, Morocco, that can be identified with *G. aegoceroides* (Gemmellaro 1884, p. 192, pl. 4, figs. 28–33, *non* figs. 26, 27 = *G. harpoceroides*), and show the characteristic low radial folds on the dorsal half of the side of the whorl. The specimen figured as '*Amauroceras*? *sp.*' by Mouterde (1951, p. 187, pl. 2, fig. 6) from the Ibex Zone of San Pedro de Muel, Portugal, might be another species of *Galaticeras*. This was said by Howarth (1959, p. 27) to be a polymorphitid, possibly *Tropidoceras masseanum* (d'Orbigny) var. *mediterranea* (Gemmellaro 1884, p. 200, pl. 5, fig. 1), but reference to *Galaticeras* seems more likely from the type of ornament. The suture-line was not figured by Mouterde, but was obtained when the specimen was on loan and is now figured here (text-fig. 1*a*). Although the suture-lines of *T. masseanum* (d'Orbigny 1844, pl. 58, fig. 3; Gemmellaro 1884, pl. 5, fig. 4) and *Galaticeras* (Gemmellaro 1884, pl. 4, fig. 23) do not differ fundamentally, those of *Tropidoceras* have narrow-necked saddles with minor lobes penetrating deeply into the dorsal sides of the second lateral and first auxiliary saddles. Such features do not occur in the Portuguese specimen, which has a suture-line which does not differ significantly from *Galaticeras*. The evidence favours reference of this specimen to *Galaticeras*, but confirmation could only be obtained by sectioning it to reveal the presence or absence of a keel on the inner whorls, for the outer whorl is an internal mould with no keel.

The new species described below from the Obtusum Subzone of Dorset is referred to *Galaticeras*, rather than made the type of a new genus on account of its considerably lower horizon, because of its marked resemblance to *G. mariani* (Gemmellaro), from which it differs only in being more involute.

Galaticeras has been recognized from two recent boreholes in the south of England. Two small specimens from the British Petroleum borehole at Brightling, Sussex (Falcon



TEXT-FIG. 1. Suture-lines of Juraphyllitidae. *a*, ? *Galaticeras sp.*, from the Ibex Zone at San Pedro de Muel, Portugal; final suture-line at 90 mm. diameter from specimen figured by Mouterde (1951, p. 17, pl. 2, fig. 6). *b*, *c*, *Galaticeras jacksoni* sp. nov., bed 83, Flatstones, Obtusum Subzone, Stonebarrow, Charmouth, Dorset; *b*, BM C50907, at 26 mm. diameter; *c*, BM C50904, holotype, at 30 mm. diameter. *d*, *e*, *Tragophylloceras undulatum* (Smith), Valdani or Jamesoni Limestones, Radstock, Somerset; *d*, GSM 24430, final suture-line at 34 mm. diameter before adult body-chamber; *e*, BM C49721, Kilmersdon Road, Radstock, final three suture-lines showing crowding at 25 mm. diameter. *f*, *g*,

and Kent 1960, pp. 10, 11), show the characteristic ornament and suture-line of the genus. They are GSM 102186, about 11 mm. in diameter and preserving the beginning of the body chamber, and GSM 102187, retaining one-quarter of a whorl of body chamber at a diameter of 9 mm., preceded by approximated suture-lines. They occurred 17 feet above an asteroceratid ammonite and are probably from the Obtusum Zone, but the upper limit of this zone was not determined, the next ammonite being a Raricostatum Zone form 65 feet higher up the borehole.

The second record is from near Highbridge, Somerset, where small (*c.* 20 mm.) pyritized ammonites with typical *Galaticeras* ornament were collected. Suture-lines are not seen. This occurrence is accurately dated by other ammonites as belonging to the Stellare Subzone of the Obtusum Zone.

Galaticeras is readily distinguished from *Juraphyllites*, which has stronger, straight ribs and is often constricted. *Tragophylloceras* is usually more involute and has phylloid endings to the long monophyllic endings of the suture-lines. The only other genus which can be compared with *Galaticeras*, and particularly the Dorset species described here, is *Bouhamidoceras* Dubar (1962, p. 320). This occurs in the Oxynotum Zone at Ziz, High Atlas, Morocco, and is a compressed, involute and feebly ribbed form with a highly characteristic suture-line, in which the ventral lobe is very shallow, the first lateral saddle asymmetrical, and the first lateral lobe wide and divided by large minor saddles. Another species which should probably be referred to this genus is *Amphiceras kammerkerense* Hahn (1910, p. 358, pl. 16, fig. 3; Lange 1952, p. 87, pl. 18, fig. 5), from the Hettangian (Liasicus or Angulata Zones) of the northern Alps. This species has a more evolute body chamber which shows adult characters near the aperture. Lange referred it to *Galaticeras*, and it shows some resemblance to *G. propinquum* (Gemmellaro 1884, pl. 6, figs. 10–12), but it is better placed in *Bouhamidoceras* on account of its suture-line. The Dorset species has stronger ribs than *Bouhamidoceras* and a different suture-line.

Galaticeras jacksoni sp. nov.

Plate 48, figs. 1–4; text-figs. 1*b*, *c*

Material. Nine specimens collected by Mr. J. F. Jackson.

Holotype. BM C50904 (Pl. 48, figs. 1*a*, *b*). *Paratypes.* BM C50905–6, BM C50907 (Pl. 48, fig. 2), BM C71099 (Pl. 48, fig. 3), BM C71100, NMW 60.510 G1714, G1887 (Pl. 48, fig. 4), G2202.

Horizon and locality. The Flatstones, bed 83h (possibly also bed 83d), Black Marl, of the Obtusum Subzone, Obtusum Zone. Stonebarrow cliff, Dorset (Lang 1926, p. 160).

Diagnosis. A relatively involute species, in which the sigmoidal striae increase in strength on the venter to form forwardly projected chevrons on the keel. The whorl section is

---

T. loscombi (J. Sowerby), Stokesi Subzone, Eype Nodule Bed, Dorset; *f*, SM J44818, Eype Mouth, Dorset, final three suture-lines showing crowding at 25 mm. diameter; *g*, GSM 102185, Golden Cap, Seatown, Dorset, final suture-line at 21 mm. diameter. *h–j*, *T. carinatum* sp. nov.; *h*, BM C56679, holotype, Ibex or Davoei Zone, Stonebarrow, Charmouth, Dorset, final three suture-lines showing crowding at 16 mm. diameter; *i*, BM C28222, Ibex Zone, Battledown brickworks, Cheltenham, final three suture-lines at 17 mm. diameter; *j*, BM C71121, Luridum Subzone, brickpit at Blockley Station, Gloucestershire, final five suture-lines showing crowding at 21 mm. diameter.
Fig. 1*a*, ×1·7; remainder ×5.

nearly flat sided, has a slightly differentiated ventral keel, and umbilical walls varying between gently sloping and near-vertical. The ornament consists of somewhat irregular striae or fine ribs which are highly sigmoidal or S-shaped on the side of the whorl; towards the venter they are inclined strongly forwards and increase in strength to form marked chevrons on the keel.

Description and remarks. The material consists of nine specimens in which the septate whorls are preserved as solid casts of calcite and have the shell intact in a few places, while the body chambers are crushed flat but retain good preservation of the ornament. The calcite casts have well-preserved suture-lines and these are spaced normally up to the body chamber with no signs of crowding. The body chambers show no adult characters, but all are less than half a whorl and incomplete, and the mouth border is unknown. Dimensions of the septate whorls of the two best-preserved specimens are as follows:

C50904—at 38·5 mm.: 19·8 (0·51), 9·4 (0·24), 7·5 (0·19).
C50907—at 35·0 mm.: 17·0 (0·49), 8·6 (0·25), 7·8 (0·22).

These measurements show the extent to which C50904 is more involute than C50907, a fact which can be readily seen in the figures (Pl. 48, figs. 1*a* and 2*b*). In much larger collections of similar-sized ammonites a difference of this order of magnitude in the size of the umbilicus (19 to 22 per cent. of the diameter) is often well within the variation of the species. C50904 and 50907 also differ in the steep umbilical wall and small chevrons on the venter of the former, compared with the gently sloping rounded umbilical wall and larger chevrons of the latter specimen. All the other specimens are intermediate between these two and form a continuous series; the specimen of Plate 48, fig. 4 has an umbilicus of similar size to that of C50904, but it has sloping umbilical walls and rather larger chevrons, while the example in Plate 48, fig. 3 has large chevrons and a wide umbilicus like C50907, but it has small, steep umbilical walls. To a large extent the size of the chevrons, the size of the umbilicus, and the type of umbilical walls vary independently of each other; this is the normal variation of the species and should not be made the basis of splitting into more than one species.

The suture-lines (text-fig. 1*b*, *c*) are characterized by bifid first and second lateral saddles, which have rounded, slightly phylloid endings. The first lateral lobe is much deeper than the external lobe and has a long pointed central ending. They agree in all respects with the suture-lines of the Sicilian population figured by Gemmellaro (1884, pl. 1, figs. 12, 17; pl. 4, figs. 23, 30, 38; pl. 6, fig. 12; pl. 7, fig. 23).

The closest comparison with the Sicilian species is to be made with *G. mariani* (Gemmellaro 1884, p. 197, pl. 1, figs. 13–17; pl. 4, figs. 34–39, pl. 7, fig. 23). The three medium-sized specimens figured by Gemmellaro differ somewhat amongst themselves, and the original of his pl. 4, fig. 34 is closest to the Dorset specimens. The only significant differences between this specimen and C50907 (Pl. 48, fig. 2) are the smaller umbilicus and lower horizon of the latter. In both the Dorset and Sicilian specimens the ribs are straight and inclined forwards at an angle of about 45° to the venter for some distance before they reach the keel on the mid-ventral line. As in the Dorset specimens the size of the chevrons varies in the three Sicilian examples. The sigmoidal shape of the striate ribs on the whorl side is exactly the same in the two populations. The four other species of *Galaticeras* figured by Gemmellaro (1884) have smooth venters with no chevrons.

Genus TRAGOPHYLLOCERAS Hyatt 1900, p. 568

Type species. The sole definition of the genus given by Hyatt was 'Type *T.* (*Phyl.*) *heterophyllus-numismalis*, Quenst. sp.' According to the International Code of Zoological Nomenclature (edition of 1961), Article 68 (a), this is the nominal type species by original designation. In the *Treatise*, Arkell (1957, p. L191) stated the type species to be so by subsequent designation by Buckman (1912, p. *viii*), but Buckman's designation was superfluous. In accordance with Article 45 (d) (i) of the Code, the name *numismalis* as originally cited by Quenstedt in the combination *Ammonites heterophyllus numismalis* is interpreted as a sub-specific name raised to specific rank by later authors. The type species of *Tragophylloceras* is therefore *A. numismalis* Quenstedt 1845.

Synonym. Phyllolobites Vadász 1907, p. 352. In proposing *Phyllolobites*, Vadász (1907, p. 402) said 'Nachdem wir als Typus des oberwähnten Phyllolobites *Ammonites loscombi* Sow. und *Amm. ibex* Quenst. betrachten, . . .' We therefore designate *Ammonites loscombi* J. Sowerby 1817, as the type species. We agree with all other workers in regarding this genus as a subjective synonym of *Tragophylloceras*.

Characters of genus. Tragophylloceras is a phylloceratid genus with open umbilicus. The whorl is strongly compressed, with parallel or convergent sides. The first whorl after the protoconch is always smooth. On the second or third whorl, constrictions appear on the internal mould due to thickening of the shell wall on its inner side; they are not seen in specimens with the shell preserved. The constrictions persist for one or two whorls only, except in *T. numismale*, in which they may continue up to a diameter of over 20 mm. Sigmoidal ornament is present throughout. This may remain as growth-lines or be developed as ribs. It is usually strongest over the venter, as in *Galaticeras* and *Juraphyllites*. The early sutural development has been worked out by Spath (1914) for *T. loscombi* and by Schindewolf (1961, pp. 711, 713) for *T. ibex* and *T. undulatum*. At an early stage (by 20 mm. diameter in *T. loscombi*) the saddles bear inflated folioles of typical phylloceratid type. The adult external suture-line has six or seven saddles; the first lateral saddle is monophyllic and roughly symmetrical. The second lateral saddle, however, changes during development from a monophyllic state to one described by Spath (1914, p. 346) as subdiphyllic, with two terminal leaflets, of which the one nearer the venter is usually slightly larger than the other.

Three out of the five species show adult shells of two different sizes. These correspond to the microconchs and macroconchs recognized in Upper Jurassic ammonites by Callomon (1955, p. 238) in that the smaller forms have apertures with constrictions and lappets, while the larger have plain apertures. The observations may be tabulated as follows:

Species	*Approximate diameter of microconchs*	*Approximate diameter of macroconchs*
carinatum	3 cm. Rare.	Not known.
loscombi	3–4 cm. Common at two horizons only.	9–15 cm. Common.
undulatum	4–5 cm. Common.	Over 8 cm. A few.
ibex	5 cm. A few.	13–14 cm. Common.
numismale	Not known.	20–22 cm. Common.

We conclude that dimorphism existed in *Tragophylloceras*, but the material available does not add anything to our knowledge of this phenomenon. The disparity in relative abundance and in stratigraphic horizon between the microconchs and macroconchs of each species is no greater than in many other cases of dimorphism.

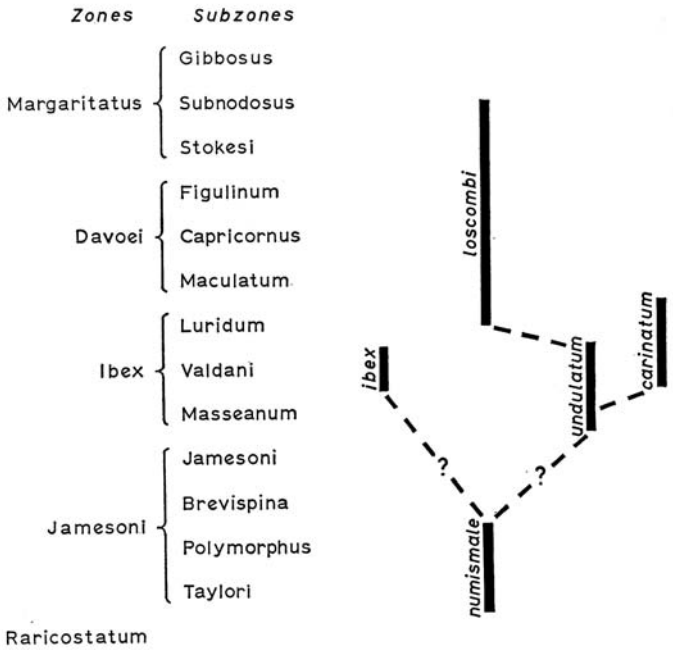
In each case the microconch differs from the macroconch only in those characters associated with the attainment of the complete adult microconch shell. At all growth stages before the final half whorl the microconch cannot be distinguished from similar-sized inner whorls of the macroconch. For this reason the two forms are referred to the same species. Other scales of classification which could have been adopted are the reference of the two forms to separate species, such as has been done in the case of large collections of closely associated large and small forms obtained in the Upper Lias by one of the authors (Howarth 1962*b*, pp. 412–13), or the reference of the two forms to separate subgenera, such as is commonly adopted in the Upper Jurassic. In the case of the Upper Lias species it has been found that similar-sized inner whorls of the large and small forms are separable by small but distinct differences (other than the adult features of the small forms), and reference to different species seems to be appropriate. On the other hand the large and small forms of *Tragophylloceras* are only separable when the small forms show their adult characters. The reference of many Upper Jurassic pairs to different subgenera follows the scaling down of the original morphological classification in which generic status was given to the small forms with lappets as distinct from the larger forms without lappets. But recent revival of interest into the possibility of sexual dimorphism in ammonites, as a result of careful and accurate collecting, may lead to the eventual adoption of an entirely different classification. *Tragophylloceras* does not add anything of significance to the theory of sexual dimorphism in ammonites. The small numbers and restricted distribution of the small forms found so far are undoubtedly due to the reluctance of collectors to collect what they considered to be inner whorls when larger outer whorls were available. The discovery during unbiased collecting of roughly similar numbers of large and small forms at all horizons and localities is necessary before any contribution can be made to the theory of sexual dimorphism.

Tragophylloceras is currently (e.g. by Arkell 1957, p. L191) placed in the family Juraphyllitidae, and it shows a general resemblance to other members of the family, and difference from the Phylloceratidae, in its open umbilicus and its tendency to have ornamented outer whorls. The Juraphyllitidae, like the Phylloceratidae, are overwhelmingly Tethyan in distribution, and *Tragophylloceras* is the only genus which is common in north-west Europe; it is, in fact, almost restricted to this area. The geographical distribution will be discussed further below.

It would be fruitless, at present, to seek to establish the immediate ancestors of *Tragophylloceras* among the numerous Tethyan phylloceratids and juraphyllitids, in view of the poor stratigraphical dating of many of these. The earliest British species, *T. numismale*, has the longest constricted stage. From purely morphological considerations *Tragophylloceras* could have evolved from *Juraphyllites*, or from one of the numerous constricted phylloceratids (Subfamily Calliphylloceratinae) which abounded in the Tethyan area from the Hettangian onwards.

Tragophylloceras numismale is found in the Inner Hebrides and the north of England, and rarely as far south as Somerset, but it is not known from the Dorset coast. This can hardly be due to collection failure, for the subzones in which it occurs are represented by over 20 feet of strata in Dorset. It is found in Europe, however, in Swabia and on the borders of the Massif Central. The only *Tragophylloceras* from the upper part of the Jamesoni Zone in Britain, from beds 115–118c on the Dorset coast, are not specifically identifiable. *T. ibex* and *T. undulatum*, the two most strongly ornamented species, appear

roughly simultaneously at the beginning of the Ibex Zone. They have a different distribution from *T. numismale*, being common in the south-west of England but absent from Yorkshire and the Hebrides. They do not form an obvious evolutionary development from *T. numismale*, and no transitional forms are known. The third ornamented species, *T. carinatum*, appears later in the Ibex Zone and could have evolved from *T. undulatum* by sharpening of the venter to form a keel.



TEXT-FIG. 2. Stratigraphical ranges and possible phylogeny of species of *Tragophylloceras*.

Tragophylloceras loscombi, which appears late in the Ibex Zone and has a long range, has a similar geographical distribution to *T. ibex* and *T. undulatum*, being common in the south of England and rare in Yorkshire. It could have evolved from *T. undulatum* by weakening of the ornament.

It is clear that the evolutionary history of *Tragophylloceras* is very imperfectly known. The most probable phylogeny is shown in text-fig. 2, but it must be regarded as very tentative.

Previous authors have described fifteen species which are now placed in *Tragophylloceras*. Fourteen of these were described from north-western Europe—France, Germany and Britain—and one (*T. vadaszi* Lóczy 1915) from Hungary. Our revision has reduced the fourteen north-west European species to four, and added one, the rare *T. carinatum*.

T. vadazsi has been recently redescribed by Géczy (1959), but its relationship to the north-west European species remains uncertain.

Stratigraphy of species of Tragophylloceras

The range of *Tragophylloceras* in Britain is from the lowest part of the Jamesoni Zone up to the base of the Subnodosus Subzone, Margaritatus Zone. The horizons of specimens collected from the outcrop between Gloucestershire and the Humber are rarely recorded more accurately than the nearest zone, and even the zone is often inferred from the species themselves. The main exception is in the case of *T. ibex*, which is found in association with *Acanthopleuroceras valdani* (d'Orbigny) at many localities and is therefore known to come from the Valdani Subzone. More accurate stratigraphy is available for the collections from Dorset, Radstock, Yorkshire and Pabay, Inner Hebrides, and it can be summarized here.

Dorset. Collections made by Lang (1928, pp. 189–95; 1936, pp. 431–5) from the Lower Lias and by Howarth (1957, pp. 188–94) from the Middle Lias give the following sequence of species:

		Bed		
Margaritatus Zone	Subnodosus Subzone	24	Margaritatus Stone	*Tragophylloceras loscombi*
	Stokesi Subzone	18	Eype Nodule Bed	
		11–16		
		6–10	Three Tiers	
		1–3		
Davoei Zone		122–130	Green Ammonite Beds	
Ibex Zone	Luridum Subzone	121	Belemnite Stone	
	Valdani Subzone	119	*T. ibex*, *T. undulatum*	
		118d	*T. undulatum*	
	Masseanum Subzone	118c		
Jamesoni Zone	Jamesoni Subzone	118b	*Tragophylloceras* sp. indet.	
	Brevispina Subzone	115		

Bed 121, the Belemnite Stone, is the most probable horizon of the holotype of *T. loscombi*.

Radstock, Somerset. Considerable numbers of well-preserved *Tragophylloceras undulatum* together with some *T. ibex* and *T. numismale* are known from the Radstock area. All are preserved in the same ironshot limestone matrix and Tutcher and Trueman's (1925) stratigraphical description of the Lower Lias in that area shows that this must represent both the Valdani and Jamesoni Limestones. *T. ibex* is recorded from the Valdani Limestone (Valdani Subzone) only, but *T. undulatum* is recorded (as *T. 'wechsleri'*) from both limestones (Tutcher and Trueman 1925, pp. 605, 616), while the horizon of *T. numismale* is not given. Ammonites recorded from the Jamesoni Limestone indicate the presence of the Polymorphus, Brevispina, Jamesoni, and Masseanum Subzones (Tutcher and Trueman 1925, pp. 601, 605) but the position of *T. undulatum* in this sequence is not known. It can only be inferred, therefore, that *T. undulatum* occurs in the Valdani and Masseanum Subzones of the Ibex Zone, with the possibility that it also occurs at lower horizons.

Yorkshire. Detailed collecting at Robin Hood's Bay by Mr. L. Bairstow has yielded the following sequence of species:

Bed	
	Ibex Zone, ? Luridum Subzone
569	*Tragophylloceras loscombi*
	Jamesoni Zone, Taylori Subzone (beds 501–30)
521	*Tragophylloceras* sp. indet.
520.5 520.35 520.2 517.73	*T. numismale*
515.5 506	*Tragophylloceras* sp. indet.
505.2	*T. numismale*

Bed 569 could be the horizon from which the holotype of *Ammonites ambiguus* Simpson (= *T. loscombi*) was obtained, and it may also have been the horizon of the holotype of *A. robinsoni* Simpson. The holotype of *A. nanus* Simpson and the paratype of *A. huntoni* Simpson figured by Buckman (1921, pl. 219) (both are synonyms of *T. numismale*) came from beds 517 or 520.

Pabay, Inner Hebrides. *Tragophylloceras numismale* was obtained by Spath (1922, p. 550) in association with *Platypleuroceras caprarium* (Quenstedt) and *Radstockiceras* ('*Metoxynoticeras*') in beds just below the lowest *Platypleuroceras brevispina* (J. de C. Sowerby) at Pabay. The horizon can be fixed accurately as the upper part of the Polymorphus Subzone, Jamesoni Zone.

Tragophylloceras numismale (Quenstedt)

Plate 48, fig. 5

? *Ammonites huntoni* Simpson 1843, p. 41.
Ammonites heterophyllus numismalis Quenstedt 1845, p. 100, pl. 6, figs. 4*a*, *b*, 5*a*, *b*, *non* figs. 3*a*, *b*, 5*c*.
Ammonites nanus Simpson 1855, p. 38.
? *Ammonites huntoni* Simpson 1855, p. 83.
? *Ammonites heterophyllus numismalis* Quenstedt 1856, p. 119, pl. 14, fig. 3.
Ammonites heterophyllus numismalis Quenstedt 1885, p. 291, pl. 37, figs. 8–11, 21.
Phylloceras numismale (Quenstedt); Pompeckj 1893, p. 14, pl. 3, figs. 4–7.
Phylloceras elteni Pompeckj 1893, p. 18, pl. 3, fig. 3.
Phylloceras paucicostatum Pompeckj 1893, p. 20, pl. 3, fig. 2.
Tragophylloceras typicum Buckman 1912, p. *viii* (holotype, Quenstedt 1885, pl. 37, fig. 11).
Tragophylloceras huntoni (Simpson); Buckman 1921, pl. 219.
Tragophylloceras numismale (Quenstedt); Buckman 1921, pl. 233.
Tragophylloceras nanus (Simpson); Buckman 1926, pl. 679.
Tragophylloceras loscombi (J. Sowerby); Maubeuge 1951, p. 1, pl. 1, fig. 1.

Type specimen. The specimen from Ofterdingen figured by Quenstedt (1845, pl. 6, figs. 5*a*, 5*b*) was selected lectotype by Buckman (1912, p. *viii*).

Description and remarks. The available material of *T. numismale* consists of the Swabian examples figured by Quenstedt and Pompeckj, stated to come from the Jamesoni Zone, and the small collections from various British localities. In Britain it occurs most

commonly in Yorkshire; specimens obtained from Robin Hood's Bay consist almost entirely of small pyritized inner whorls, and Mr. L. Bairstow's careful collecting has shown that these come from beds containing species of *Phricodoceras* and referable to the Taylori Subzone of the Jamesoni Zone (see stratigraphical section above). Similar small inner whorls were obtained from material excavated from the railway tunnel one mile south-east of Old Dalby, Leicestershire (Woodward 1893, pp. 170–1), in beds presumed to belong to the Jamesoni Zone. The species may occur rarely in beds of Jamesoni Zone age in Gloucestershire, and a few medium to large specimens are known from the Radstock area, Somerset. No specimens are known from Dorset. The age of the species is again known accurately from its occurrence in beds at Pabay, Inner Hebrides (Spath 1922, p. 550), that are referable to the Polymorphus Subzone, Jamesoni Zone. Thus the stratigraphical range of *T. numismale* known so far embraces the Taylori and Polymorphus Subzones.

The complicated ontogeny of *T. numismale*, in which several of the growth stages have different features, and the considerable amount of variation within each growth stage, has led to the proposal of the six specific names listed in the synonymy. The first whorl after the protoconch is smooth, and constrictions commence on the second whorl at about 1·5 mm. diameter. Deeply incised constrictions occur on the second and most of the third whorls, numbering six to seven per whorl, up to a diameter of 5 to 6 mm. The holotype of *Ammonites nanus* Simpson 1855, figured by Buckman (1926, pl. 679), is an example of small inner whorls at this stage of growth. From a diameter of 6 mm. onwards the whorl section becomes rapidly more compressed, and the constrictions remain as prominent, slightly curved bands, numbering six to eight per whorl, though not so deeply incised as at the smaller sizes. The strength of the constrictions varies, but in only a few individuals are they difficult to detect, and in most examples irregular low ribs appear between the constrictions. Several Swabian specimens in this stage of growth have been figured (Quenstedt 1845, pl. 6, fig. 4; 1885, pl. 37, fig. 21; Pompeckj 1893, pl. 3, figs. 4–7), and almost all the material from the Yorkshire coast and Old Dalby, Leicestershire, consists of inner whorls of this size. One of these is the paratype of *Ammonites huntoni* Simpson 1843, from Robin Hood's Bay, figured by Buckman (1921, pl. 219). This specimen is probably not the holotype of Simpson's species (see Howarth 1962*a*, p. 98), and as it cannot now be determined whether Simpson's description refers to the same species, *Ammonites huntoni* is best regarded as a *nomen dubium*. Acceptance of *A. huntoni* on the basis of the paratype of 10·5 mm. diameter not known to belong definitely to the species Simpson described, would relegate Quenstedt's much better defined species to its synonymy. The characteristic constrictions of this stage, which

EXPLANATION OF PLATE 48

All figures natural size, except fig. 5, ×1·6. Specimens coated with ammonium chloride.

Figs. 1*a*, *b*; 2*a*, *b*, *c*; 3; 4. *Galaticeras jacksoni* sp. nov. Bed 83, Flatstones, Obtusum Subzone, Stonebarrow, Charmouth, Dorset. 1*a*, *b*, Holotype, BM C50904. 2*a*, *b*, *c*, Paratype, BM C50907. 3, Paratype, BM C71099. 4, Paratype, NMW 60.510 G1887.

Figs. 5*a*, *b*. *Tragophylloceras numismale* (Quenstedt). Jamesoni Zone, Robin Hood's Bay, Yorkshire. BM C67766, ×1·6, maximum diameter 17·5 mm.

Figs. 6*a*, *b*; 7*a*, *b*; 8*a*, *b*; 9*a*, *b*. *Tragophylloceras undulatum* (Smith). 6*a*, *b*, Microconch, BM C49721, Kilmersdon Road, Radstock, Somerset. 7*a*, *b*, GSM 24441, Radstock. 8*a*, *b*, Macroconch, BM C50451, Radstock. 9*a*, *b*, Microconch, GSM 24430, Radstock.

occur on the inner, and not on the outer surface of the shell, continue up to 15–23 mm. diameter, when they die out. A well-preserved Yorkshire example with constrictions up to 17·5 mm. diameter is figured in Plate 48, fig. 5.

The specimens from Old Dalby, Leicestershire, were described in some detail by Trueman (1916). The range of variation between examples with constrictions up to 23 mm. diameter, through others with less marked constrictions, to rare examples with no constrictions and rather more involute whorls, led Trueman to believe that both *T. numismale* and *T. loscombi* were present together with a whole series of intermediate forms, and that the evolution of the latter species from the former could be traced through the intermediates according to recapitulation theory. There is no reason to believe, however, that anything younger than Jamesoni Zone was present in the tunnel heaps at Old Dalby, and the whole fauna probably came from one restricted part of the Jamesoni Zone. The variation found and described by Trueman is that of immature forms of *T. numismale*, and it is no greater than the variation commonly found in the young whorls of other ammonite species that can be proved to be strictly contemporaneous.

At sizes larger than 25 mm. diameter there is considerable variation in the presence or absence of ornament. The lectotype (Quenstedt 1845, pl. 6, figs. 5*a*, *b*) and another Swabian example (Quenstedt 1885, pl. 37, fig. 8) are figured as entirely smooth. In others, ribs form chevrons of varying strength on the venter—Quenstedt 1885, pl. 37, fig. 10, and the Radstock specimen figured by Buckman (1921, pl. 233) have rudimentary chevrons; Quenstedt 1885, pl. 37, fig. 11, which is the holotype of *Tragophylloceras typicum* Buckman (1912, p. *viii*), Quenstedt 1856, pl. 14, fig. 3, and the holotype of *Phylloceras elteni* Pompeckj (1893, pl. 3, fig. 3), have larger chevrons on the venter. Still other specimens have chevrons on the venter combined with very irregular, low ribs—such are the holotype of *P. paucicostatum* Pompeckj (1893, pl. 3, fig. 2) and the only large specimen (BM C18115, 80 mm. diameter) found so far at Robin Hood's Bay, Yorkshire. Specimens at this stage are readily distinguishable from similar-sized specimens of *T. loscombi* by their thicker whorls and larger umbilici, and the variation in the presence and strength of their ornament is not markedly greater than the variation of the ornament in *T. loscombi*.

Larger examples are rare; they are smooth and have the typical trapezoidal whorl section seen in the specimen figured by Quenstedt (1885, pl. 37, fig. 9). The largest known specimens are two body chambers found by Spath in the Polymorphus Subzone of Pabay. Both appear to be smooth except for growth-lines, and the whorl sections are trapezoidal. The larger body chamber is incomplete at its maximum size of 200 mm. diameter, but it has a small part of an apparently plain mouth border near the umbilicus at a size which would indicate about 220 mm. diameter. The smaller specimen is nearly, if not quite complete at 200 mm. diameter; the mouth border, if present, is plain; and it has typical inner whorls. No evidence of the existence of smaller adults has been found.

Tragophylloceras undulatum (Smith)

Plate 48, figs. 6–9; Plate 49, fig. 1; text-fig. 1*d*, *e*

Ammonites undulatus Smith 1817, p. 114.
Ammonites heterophyllus numismalis Quenstedt 1845, p. 100, pl. 6, fig. 5*c*.
Ammonites ibex-heterophyllus Quenstedt 1856, p. 119, pl. 14, fig. 2.

Ammonites wechsleri Oppel 1862, p. 135, pl. 43, fig. 1*a*, *b*.
Phylloceras loscombi (Sowerby); Wright 1883, p. 419, pl. 39, figs. 1–3.
Ammonites heterophyllus intracrustatus Quenstedt 1885, p. 293, pl. 37, figs. 12, 13.
Ammonites ibex-heterophyllus Quenstedt 1885, p. 293, pl. 37, figs. 14, 18.
Phylloceras wechsleri (Oppel); Pompeckj 1893, p. 19.
Tragophylloceras radstockense Spath 1923, p. 293.
Tragophylloceras undulatum (Smith); Cox 1930, p. 303, pl. 12, fig. 5*a*, *b*.

Type specimen. The caption 'Fig. 3, Marlstone Plate' in Smith's (1817, p. 114) original description refers to a projected plate which was never prepared or published. BM C33499 was designated lectotype and figured for the first time by Cox (1930, p. 303, pl. 12, fig. 5); this specimen bears Smith's number 'C 3', which denotes the third species of the genus *Ammonites* described by Smith in his Marlstone section. There is a second specimen in Smith's collection (BM C721) bearing his number 'E 6', which differs in no way from the lectotype. 'E 6' does not coincide with any of his descriptions, so the number of specimens from which Smith described *A. undulatus* remains unknown.

The locality of the lectotype was given as 'Coal Canal', and the possible localities can be narrowed down greatly by considering where the Somerset Coal Canal, the construction of which William Smith supervised during 1794–9, crossed the outcrop of the upper part of the Lower Lias. This canal ran in two branches from Midford, 3 miles south-south-east of Bath. The northern branch ran west up the valley of the Cam brook to end at a point just short of Paulton, while the southern branch, which was partly constructed but never completed, was to have run south-west up the valley of the Wellow Brook to Radstock. After a century of use the northern branch was drained and replaced by a railway, which has recently been removed. The northern branch of the canal crossed the top of the Lower Lias one mile south-west of Dunkerton, where quarries and cuttings exposing the Jamesoni Limestone have been described by Tutcher and Trueman (1925, pp. 622–4, text-figs. 8, 9). Excavations on the uncompleted southern branch of the canal crossed this horizon between Wellow and Stoney Littleton, and the Jamesoni Limestone occurs in a quarry near the latter locality (Tutcher and Trueman 1925, p. 614). Smith's type specimen could only have been obtained from one of these two localities, which are 2 miles apart.

Description and remarks. In Britain *T. undulatum* is best known from the Radstock area of Somerset. In addition to Smith's originals there are forty-five specimens of this species in the British Museum, Geological Survey and Bristol University collections, and associated with them are several examples of *T. ibex* and a few of *T. numismale*. The horizons of these three species are discussed in the stratigraphical section above, and it can be deduced that *T. undulatum* occurs in the Masseanum and Valdani Subzones of the Ibex Zone, and possibly occurs also in the Jamesoni Zone below.

Some of the Radstock specimens show clear adult features: a prominent constriction at the mouth border, diminution of the whorl height on the last quarter whorl, modification of the ribs at the end of the body chamber, and crowding and some modification of the last two or three suture-lines. The type specimen (Cox 1930, pl. 12, fig. 5) is one such adult, and another specimen with more marked adult features is figured in Plate 48, fig. 9. These two have adult mouth borders at 49 mm. diameter and final suture-lines at 33–34 mm. Ten other specimens have adult mouth borders at sizes between 42 and 49 mm. diameter, and there is one smaller specimen with an incomplete body chamber that has adult suture-lines at 25 mm. diameter (Pl. 48, fig. 6; text-fig. 1*e*), which indicates a mouth border at about 38 mm. There are a few considerably larger specimens which are not adult and have maximum sizes between 60 and 80 mm. diameter and are septate up to 53 mm. (Pl. 48, fig. 8). There is a possibility that adults of two distinct sizes are represented here, the smaller series being complete at diameters between 38 and 50 mm. and having a constricted mouth border, the larger series being complete at sizes greater than 65 mm. and of which the mouth border characters are not yet known.

The Radstock population shows a certain amount of variation in ornament. From the normal type as exhibited by the type specimen and the example of Plate 48, fig. 9, there is a continuous series leading to a rather more coarsely ribbed form as in the specimens figured in Plate 48, fig. 7, and Plate 49, fig. 1. Two examples of unspecified locality, but almost certainly from Radstock, were figured by Wright (1883, pl. 39, figs. 1–3). Neither has been found, but assuming the drawings to be accurate, the original of Wright's figs. 1 and 2 is one of the more coarsely ribbed Radstock examples; it has a constricted mouth border and appears to be adult, but its maximum size is not known. [As drawn, the specimen is 83 mm. diameter, but the drawing has some features which suggest that it might be magnified. The size is not stated in the plate explanation; on the same plate, fig. 5, also of unstated size, is magnified $\times 2$, while fig. 4, said to be magnified, is in fact natural size. Wright was careless in this respect throughout his monograph.] Spath (1923, p. 293) renamed Wright's figs. 1 and 2 *T. radstockense*. In view of the complete series of transitions between the normal type and this slightly more coarse-ribbed form, and the fact that none of the coarse-ribbed forms approach the style of ribbing in *T. ibex*, *T. radstockense* is considered to be a synonym of *T. undulatum*. The specimen of Wright's fig. 3 is a more finely ribbed example and is close to the normal *T. undulatum*.

In Dorset a few crushed specimens are known from beds 118d and 119 of Lang (1928, pp. 191–2), which are referable to the Valdani Subzone. The best preserved example is from bed 119 and matches the type specimen of *T. undulatum* exactly; it shows distinct traces of a constriction at its mouth border at 47 mm. diameter. Another fragment from the same bed has a similar constriction at roughly the same size. A few specimens have been found in excavations near Kilsby, Northamptonshire, at an horizon low in the Valdani Subzone and a few feet below the lowest *T. ibex*.

T. undulatum is widely known in Germany from the descriptions and figures of Quenstedt and Oppel. One of Quenstedt's earliest figures (1845, pl. 6, fig. 5*c*) agrees with *T. undulatum* in ornament, and his later figures of this species (1856, pl. 14, fig. 2; 1885, pl. 37, figs. 14, 18) carried the name *Ammonites ibex-heterophyllus*, denoting a transitionary form. Two specimens figured as *A. heterophyllus intracrustatus* (Quenstedt 1885, pl. 37, figs. 12, 13) also agree closely with *T. undulatum*. Meanwhile Oppel (1862, p. 293, pl. 43, fig. 1) had proposed the name *A. wechsleri* for a large and typical example of *T. undulatum* from the Ibex Zone of the Swabian Alb in Württemberg. Oppel's figure is probably idealized, but the drawing matches the larger Radstock specimens exactly (Pl. 48, fig. 8) and the relegation of *A. wechsleri* to the synonymy of *T. undulatum* cannot be doubted. A specimen figured more recently by Gerth (1956, pl. 1, fig. 7) might also be a *T. undulatum*.

Tragophylloceras ibex (Quenstedt)

Plate 49, figs. 2, 3

Ammonites ibex Quenstedt 1843, p. 179.
Ammonites boblayei d'Orbigny 1844, p. 251, pl. 69.
Ammonites boblayei d'Orbigny; Buckman 1845, p. 89, pl. 12, fig. 1*a*, *b*.
Ammonites ibex Quenstedt 1845, p. 101, pl. 6, fig. 6*a–d*.
Ammonites ibex Quenstedt; Oppel 1853, p. 87, pl. 2, figs. 7, ?8.
Ammonites ibex Quenstedt 1856, p. 119, pl. 14, figs. ?4, 5.
Amaltheus ibex (Quenstedt); Wright 1882, p. 395, pl. 39, figs. 4, 5.

Ammonites ibex Quenstedt 1885, p. 293, pl. 37, figs. 15–17, 19, 20.
Phylloceras ibex (Quenstedt); Pompeckj 1893, pp. 21–24.
Tragophylloceras ibex (Quenstedt); Dean, Donovan and Howarth 1961, pl. 69, fig. 4.

Type specimens. The two syntypes from Reutlingen, Swabia, were figured by Quenstedt (1845, pl. 6, figs. 6*a*, *b*, and 6*c*, *d*).

Description and remarks. Further Swabian specimens from Hinterweiler were figured by Oppel (1853, pl. 2, figs. 7, ?8) and Quenstedt (1856, pl. 14, figs. ?4, 5; 1885, pl. 37, figs. 15–17, 19, 20), and this fauna was described in more detail by Pompeckj (1893, pp. 21–24). *T. ibex* is a highly distinctive species and can be accurately interpreted even though no Swabian specimen has been figured photographically. *Ammonites boblayei* d'Orbigny (1844, p. 251, pl. 69) is clearly synonymous with Quenstedt's species. Four British specimens from Gloucestershire have been figured by Buckman (1845, pl. 12, fig. 1*a*, *b*) and Wright (1882, pl. 39, figs. 4, 5), and a Northamptonshire specimen was figured by Dean, Donovan and Howarth (1961, pl. 69, fig. 4).

The stratigraphical range of *T. ibex* is confined to the zone of which it is the index species. In Swabia, where its zonal value was first recognized, it is particularly common in the Valdani Subzone. In Britain it occurs widely in the Ibex Zone from Somerset to Warwickshire, often in association with *Acanthopleuroceras valdani* (d'Orbigny), and in Dorset the only definitely identifiable specimens occur in bed 119, which also belongs to the Valdani Subzone. No specimens have yet been found in the Lower Lias of the Yorkshire coast. *T. ibex* has not been found in the Luridum Subzone, the uppermost subzone of the Ibex Zone, where it appears to be replaced by *T. loscombi*, nor in the Masseanum Subzone at the base of the Ibex Zone. According to the accurately dated records available at present, *T. ibex* is confined, therefore, to the Valdani Subzone.

The ontogeny of *T. ibex* is seen in a series of specimens, from the area around Cheltenham, in which the inner whorls can be exposed back to the protoconch. The first two whorls after the protoconch up to a diameter of 2 mm. are smooth. The third whorl and early part of the fourth whorl from 2 to 6 mm. diameter contain constrictions of varying

EXPLANATION OF PLATE 49

All figures natural size. Specimens coated with ammonium chloride.

Figs. 1*a*, *b*. *Tragophylloceras undulatum* (Smith). GSM 24439, Radstock, Somerset.

Figs. 2*a*, *b*, 3. *Tragophylloceras ibex* (Quenstedt); microconchs. 2*a*, *b*, GSM 24443, Radstock, Somerset; complete specimen with constriction at aperture mostly concealed by shell. 3, Bristol University, 13148–1, North Wick, Dundry, Bristol; shows part of constricted aperture.

Figs. 4*a*, *b*, *c*; 5*a*, *b*; 6*a*, *b*; 7*a*, *b*. *Tragophylloceras loscombi* (J. Sowerby); microconchs. Eype Nodule Bed, Margaritatus Zone, Dorset. 4*a*, *b*, *c*, BM C36719, Eype Mouth, Dorset; opposite sides show constriction at aperture on internal mould, but unconstricted and striate external surface of shell. 5*a*, *b*, BM C49765, Doghouse Hill, Seatown, Dorset. 6*a*, *b*, BM C70873, Ridge Cliff, 400 yards east of Seatown, Dorset. 7*a*, *b*, SM J44818, Eype Mouth, Dorset; constriction at aperture concealed by shell.

Figs. 8*a*, *b*; 9*a*, *b*; 10*a*, *b*; 11*a*, *b*, *c*, *d*; 12*a*, *b*, *c*. *Tragophylloceras carinatum* sp. nov. 8*a*, *b*; 9*a*, *b*, Paratypes, BM C71121 and C71122, Luridum Subzone, brickpit at Blockley Station, Gloucestershire. 10*a*, *b*, Paratype, BM C28222, Ibex Zone, Battledown brickpit, Cheltenham. 11*a*, *b*, *c*, *d*, Holotype, BM C56679, Stonebarrow, Charmouth, Dorset; 11*a* shows constriction and rudimentary lappet; 11*d* shows completely preserved rostrum. 12*a*, *b*, *c*, Paratype, BM C28226, Ibex Zone, Battledown brickpit, Cheltenham; opposite sides show constricted internal mould and unconstricted external surface of shell.

strength. In the majority of examples the constrictions are only moderately marked, but a few show three or four deep constrictions at 3·0 to 3·5 mm. diameter; in a few others, however, the constrictions are so weak as to be barely detectable. As in all constrictions in *Tragophylloceras*, these occur on the inner surface of the shell and not on the outer surface. From a diameter of 6 mm. the shell is smooth until fine ribs appear at about 10 mm.; these increase rapidly in strength and the characteristic ribbing of *T. ibex* is attained at diameters varying between 13 and 20 mm. The ribs on the venter forming the forwardly pointing chevrons are not connected with the ribs on the side of the whorl, but each commences between two of the latter ribs near the edge of the venter. This alternating character of ribs and chevrons makes *T. ibex* readily separable from more coarsely ribbed examples of *T. undulatum*.

In most examples the bold ribs persist to approximately the beginning of the adult body-chamber at diameters varying between 80 and 100 mm. The ribs on the side of the whorl then quickly disappear and are replaced by falciform striae; the chevrons persist for up to one-eighth of a whorl longer and then disappear to leave the venter rounded-tabulate. The adult body-chamber is smooth for nearly half a whorl, then broad folds appear on the side of the whorl just before the adult mouth border which occurs at 130 to 140 mm. diameter. Only a few complete adults of this sort are known and it is probable that the size range of adults is much greater.

A few much smaller adults are known. The smaller of the two specimens figured by Wright (1882, pl. 39, fig. 5—twice natural size) is from Cheltenham, and has a widening umbilicus and sharpening of the chevrons on the venter as if close to the adult state at its maximum diameter of 42 mm. Three similar specimens are known from Northamptonshire which appear to be nearly adult at 40–45 mm. diameter, but there are two specimens from the Valdani Limestone at Radstock which show clear adult features. Both are 49 mm. in diameter at a constricted mouth border which has a small rostrum and a slight lateral lappet. The ribs remain bold up to the mouth border but they become somewhat sharper. The umbilicus widens towards the end of the body-chamber and the final suture-lines are approximated. The best preserved specimen is figured in Plate 49, fig. 2. A third complete adult with a constricted mouth border at 48 mm. diameter and crowded final suture-lines is known from North Wick, Dundry (Plate 49, fig. 3). Another specimen showing similar adult features and a mouth border at 48 mm. diameter is from an unknown locality. Septate whorls of these specimens cannot be distinguished from similar-sized specimens of the much larger adults.

Tragophylloceras loscombi (J. Sowerby)

Plate 49, figs. 4–7; text-fig. 1*f*, *g*

Ammonites loscombi J. Sowerby 1817, p. 185, pl. 183.
Ammonites ambiguus Simpson 1843, p. 8.
? *Ammonites robinsoni* Simpson 1843, p. 42.
Ammonites loscombi Sowerby; d'Orbigny 1844, p. 262, pl. 75, figs. 1–3.
Phylloceras loscombi (Sowerby); Wright 1883, p. 419, pl. 40, figs. 4, 5.
Rhacoceras ambiguum (Simpson); Buckman 1910, pl. 16.
Tragophylloceras loscombi (Sowerby); Spath 1914, pp. 336–62, pls. 48, 49.
? *Tragophylloceras robinsoni* (Simpson); Buckman 1921, pl. 220.
Tragophylloceras loscombi (J. Sowerby); Spath 1936, pp. 439–41, pl. 33, figs. 2–5.
Tragophylloceras loscombi (J. Sowerby); Howarth 1957, p. 194, pl. 17, fig. 7.

The stratigraphical range of *T. loscombi* is best known from its development in Dorset, where it occurs in considerable numbers at many horizons from the Belemnite Stone of the Luridum Subzone, Ibex Zone, up to the Margaritatus Zone. The horizon of the holotype (Sowerby 1817, pl. 183; Spath 1914, pl. 49, fig. 1) is not known accurately, but by comparing matrixes Spath (1914, p. 337) surmised that it came from either the Upper or Lower Limestone (bed 129 or 123a) of the Green Ammonite Beds (Davoei Zone) near Charmouth. Comparison with the extensive Dorset coast collection made by Lang suggests, however, that the nearest matrix match is with the Belemnite Stone. In inland areas of Britain the species occurs in most exposures of the Davoei Zone and Stokesi Subzone, Margaritatus Zone, but precise stratigraphical details are lacking in most cases. In Yorkshire the species was described by Simpson (1843, p. 8; holotype figured by Buckman 1910, pl. 16) as *Ammonites ambiguus*, and Spath (1914, p. 347) first pointed out that this was a synonym of *T. loscombi*. It is apparently rather rare at Robin Hood's Bay, for Mr. L. Bairstow has found only one specimen *in situ*, in bed 569 at the base of the Luridum Subzone, a specimen which matches the Dorset fauna exactly. *A. robinsoni* Simpson (1843, p. 42) might also be a synonym of *T. loscombi*; a paratype from Robin Hood's Bay figured by Buckman (1921, p. 220; see Howarth 1962*a*, p. 98) may or may not be the same as the lost holotype. It agrees well with the inner whorls of *T. loscombi* at the same size, and it has the characteristic suture-line of this species.

The development of *T. loscombi* from the protoconch to the adult was described in great detail by Spath (1914). Constrictions are present only at very small growth stages and never occur beyond 3·5 mm. diameter. This is the most important feature for separating small inner whorls from those of *T. numismale* (Quenstedt), where marked constrictions occur up to about 23 mm. diameter. At larger sizes *T. numismale* has considerably more evolute and thicker whorls. A large Dorset specimen was figured by Wright (1883, pl. 40, figs. 4, 5), and further medium-sized and small specimens from the same area were figured by Spath (1936, pl. 33, figs. 2–5) and Howarth (1957, pl. 17, fig. 7). In relative whorl dimensions, variation in *T. loscombi* is small, but considerable variations occur in ornament, the radial ribbing varying from striae to bold folds on the side of the whorl which form ribs and crenulations on the venter.

The only feature of significance which was not dealt with in these previous descriptions concerns the characters and size variations of adult specimens. Body-chambers at or near the adult stage in the Davoei and Margaritatus Zones in Dorset and Gloucestershire vary in size between about 90 and 150 mm. diameter at the mouth border. This adult mouth border has the same slightly sinuous curve as the growth lines, and there are no traces of lappets or of a constriction immediately before the aperture. The adult body-chamber occupies two-thirds of a whorl and in some cases the final approximated suture-lines can be seen.

A series of much smaller adult specimens occurs at two horizons in Dorset. Nine examples are known from the Eype Nodule Bed (Stokesi Subzone) near Seatown and Eype Mouth, and one example is known from the Lower Limestone (bed 123a, Davoei Zone) of Black Ven, Charmouth. The Eype Nodule Bed examples (one was figured by Spath 1936, pl. 33, fig. 5) vary from 30 to 41 mm. diameter at the mouth border and the Lower Limestone example is 37 mm. diameter. All are characterized by a marked constriction immediately preceding the mouth border, a small lappet in the mouth border in the middle of the side of the whorl, a small rostrum on the venter, and the appearance of

prominent crenulations on the venter of the final quarter whorl (Pl. 49, figs. 4–7). The constriction at the mouth border occurs only on the internal surface of the shell, the outer surface is not constricted, and consequently the shell thickness is greatly increased at the constriction (Pl. 49, fig. 4*a*, *b*). The body-chamber occupies two-thirds of a whorl and in each case where the final suture-lines are visible they are markedly approximated. The suture-lines (text-fig. 1*f*, *g*) agree exactly with those of the large form at a similar size (cf. Spath 1914, p. 341, fig. 1*m*). A considerable number of inner whorls of the large form have been examined at the same size as the small forms, but no traces of any of the adult characters of the small forms have been detected on these inner whorls. It is concluded that the small forms are truly adult, and they are classified here as a small form of *T. loscombi* because they show no morphological differences from the large forms, other than those directly connected with the attainment of the adult stage (i.e. crowded suture-lines, constrictions, lappets, and venter crenulations).

Tragophylloceras carinatum sp. nov.

Plate 49, figs. 8–12; text-figs. 1*h–j*.

Material. Eight specimens: BM C56679 from Stonebarrow, Charmouth, Dorset; BM C28216, 28222, 28225 and 28226 from Battledown Brickworks, Cheltenham; BM C71121–2 from Blockley Station brickpit, Gloucestershire; and GSM 102184 from Wyboston borehole, Cambridgeshire.

Holotype. BM C56679 (Pl. 49, fig. 11*a–d*); its dimensions are: at 26·0 mm.: 12·8, 6·0, 4·5; at 20·0 mm.: 10·2, 4·5, 3·2. *Paratypes.* The other seven specimens listed above.

Diagnosis. A small species of *Tragophylloceras* in which a ventral keel is developed on the adult body-chamber. Fine sigmoidal ribs on the sides of the whorl end in small tubercles on the middle of the venter, and the partial amalgamation of these tubercles forms the crenulated keel. The adult mouth border is slightly flared and is preceded by a constriction, and there is a rudimentary lateral lappet and a small rostrum. Maximum size varies between about 23 and 32 mm. diameter.

Description and remarks. Only eight specimens of this species have been found so far. Six are complete adults with mouth borders at diameters of 32 mm. (C71121–2), *c.* 30 mm. (C28216), 26·5 mm. (C56679, the holotype), 26·5 mm. (C28222), and 23·5 mm. (C28226). The remaining two specimens are incomplete; C28225 has half a whorl of nearly adult body-chamber ending at 23 mm. diameter, and GSM 102184 has a complete body-chamber with mouth border at 24·0 mm. diameter, but it is not quite adult. The ventral keel in this species is unique in the genus *Tragophylloceras*, but the species is included in this genus because the characters of the whorls before the body-chamber and the suture-lines are clearly those of *Tragophylloceras*. The venter becomes sharpened on the last half whorl before the body-chamber, then distinct tubercles appear at the ends of the ribs at about the beginning of the adult body-chamber, and these partly join to form a well-marked crenulated keel on the final half whorl. A constriction occurs immediately before the mouth border, on the inside surface of the shell and not on the outer surface, so that the shell thickness is greatly increased at the constriction. The rudimentary lateral lappet is only a slight prolongation in the mouth border, while the rostrum on the venter is better developed. Only one specimen could be developed back to the inner whorls and this has four well-marked constrictions in the larger half of the second whorl ending at 2·5 mm. diameter. The fine sigmoidal ribs appear at about

10 mm. diameter. The only significant variation in the six specimens is in the size of the crenulations on the keel. In the holotype and C71122 (Pl. 49, figs. 9, 11) they are relatively large and widely spaced, but in the Cheltenham specimens and C71121 (Pl. 49, figs. 8, 10, 12) they are smaller. All six specimens show considerable variation in this respect and it does not appear to be of significance. The suture-lines (text-fig. 1*h–j*) are characteristic of *Tragophylloceras* and compare well with those of *T. loscombi* at a similar size (Spath 1914, p. 341, fig. 1*l*, *m*). A particularly fine example of approximated suture-lines is figured in text-fig. 1*j*.

The four specimens from Cheltenham were collected by L. Richardson and were recorded by him as from the Ibex Zone. The Wyboston specimen is also from the Ibex Zone, either the Valdani or Luridum Subzone. The specimens from Blockley station are from the Luridum Subzone. The zonal position of the Dorset holotype is not known, but it is preserved in a grey limestone matrix suggestive of the Belemnite Stone (Luridum Subzone) or possibly higher beds of the Davoei Zone, and it is most unlikely to have come from a lower horizon. If *T. carinatum* is the small form of a species which also has a large form, then the large form has not yet been found. There is nothing to suggest that it could be the small form of *T. undulatum*, for none have been found amongst the extensive Radstock collections, and *T. undulatum* has no trace of a keel at any growth stage.

REFERENCES

ARKELL, W. J. 1956. *Jurassic Geology of the World.* Edinburgh and London.

—— 1957. *In* R. C. MOORE (editor), *Treatise on Invertebrate Paleontology*. Part L, Mollusca 4, Cephalopoda, Ammonoidea. *Geol. Soc. Amer.*

BUCKMAN, J. 1845. *In* R. I. MURCHISON, *Outline of the Geology of the neighbourhood of Cheltenham.* 2nd ed. Cheltenham.

BUCKMAN, S. S. 1909–30. *Yorkshire Type Ammonites*, **1, 2,** and *Type Ammonites*, **3–7.** London.

CALLOMON, J. C. 1955. The ammonite succession in the Lower Oxford Clay and Kellaways Beds at Kidlington, Oxfordshire, and the zones of the Callovian Stage. *Phil. Trans.*, ser. B, **239,** 215–64, pl. 2, 3.

COX, L. R. 1930. On British fossils named by William Smith. *Ann. Mag. nat. Hist.* (10), **6,** 287–304, pl. 12.

DUBAR, G. 1962. Sur quelques ammonites du Lias inférieur du Haut-Atlas marocain. *Bull. Soc. géol. Fr.* (7), **3,** 320–3, pl. 10.

DEAN, W. T., DONOVAN, D. T. and HOWARTH, M. K. 1961. The Liassic ammonite zones and subzones of the North-west European Province. *Bull. Brit. Mus.* (*Nat. Hist.*), Geol. **4,** 435–505, pl. 63–75.

FALCON, N. L. and KENT, P. E. 1960. Geological results of petroleum exploration in Britain. *Mem. geol. Soc. Lond.* **2.**

GÉCZY, B. 1959. *Tragophylloceras vadaszi* (Lóczy, 1915) emend. nov. aus der Klippenzone der NW Karpaten. *Geol. Pracé, Bratislava*, **16,** 183–6, pl. 14.

GEMMELLARO, G. G. 1884. Sui fossili degli strati a *Terebratula aspasia* della contrada Rocche Rosse presso Galati (Provincia di Messina). *Giorn. Sci. Nat. Econ. Palermo*, **16,** 167–218, pl. 1–7.

GERTH, H. 1956. Die Fossilführung des Jura in den Bohrungen der 'Rijksopsporing van Delfstoffen' bei Winterswijk und ihre stratigraphische Bedeutung. *Meded. geol. Sticht.*, N.S., **9,** 45–54, 1 pl.

HAHN, F. F. 1910. Geologie der Kammerker-Sonntagshorngruppe. *Jb. geol. Reichsanst.* (*Bundesanst.*), *Wien*, **60,** 311–420, pl. 16, 17.

HOWARTH, M. K. 1957. The Middle Lias of the Dorset coast. *Quart. J. geol. Soc. Lond.* **113,** 185–204, pl. 17.

—— 1958–9. The ammonites of the Liassic family Amaltheidae in Britain. *Palaeontogr. Soc.* (*Monogr.*).

—— 1962*a*. The Yorkshire type ammonites and nautiloids of Young and Bird, Phillips, and Martin Simpson. *Palaeontology*, **5,** 93–136, pl. 13–19.

HOWARTH, M. K. 1962*b*. The Jet Rock Series and the Alum Shale Series of the Yorkshire coast. *Proc. Yorks. geol. Soc.* **33,** 381–422, pl. 24–28.

HYATT, A. 1900. *In* K. A. ZITTEL, *Textbook of Palaeontology*, 1st English ed., transl. C. R. EASTMAN, Cephalopoda, pp. 502–92.

LANG, W. D. 1926. The Black Marl of Black Ven and Stonebarrow in the Lias of the Dorset coast. *Quart. J. geol. Soc. Lond.* **82,** 144–87, pl. 8.

—— 1928. The Belemnite Marls of Charmouth, a series in the Lias of the Dorset coast. Ibid. **84,** 179–257, pl. 13–15.

—— 1936. The Green Ammonite Beds of the Dorset Lias. Ibid. **92,** 423–37, pl. 32.

LANGE, W. 1952. Der Untere Lias von Fonsjoch (östl. Karwendelgebirge) und seine Ammonitenfauna. *Palaeontographica* (A), **102,** 49–162, pl. 8–18.

LÓCZY, L. 1915. Die geologischen Verhältnisse der Gegenden zwischen Vágujhely, Ószombat und Jablánc in den Nordwest-Karpathen. *Jb. geol. Reichanst.* (*Bundesanst.*), Jahrg. 1914, 157–234.

MAUBEUGE, P. L. 1951. Sur quelques ammonites rares ou nouvelles du Lias moyen de Belgique. *Bull. Inst. roy. Sci. nat. Belg.* **27** (55), 6 pp., 1 pl.

MOUTERDE, R. 1951. Ammonites du Lias moyen Portugais. *Bol. Soc. geol. Portug.* **9,** 175–90, pl. 1, 2.

OPPEL, A. 1853. Der mittlere Lias Schwabens. *Jh. Ver. vaterl. Naturk. Württemberg*, **10,** 39–136, pl. 1–4.

—— 1862–63. *Paläontologische Mittheilungen aus dem Museum des Königl. Bayer. Staates*, **1.** Stuttgart.

ORBIGNY, A. D'. 1842–51. *Paléontologie française. Terrains jurassiques*, **1,** *Céphalopodes.* Paris.

POMPECKJ, J. F. 1893. Beiträge zu einer Revision der Ammoniten des Schwäbischen Jura. *Jh. Ver. vaterl. Naturk. Württemberg*, **49,** 151–248, pl. 2–8.

QUENSTEDT, F. A. 1843. *Das Flözgebirge Württembergs.* Tübingen.

—— 1845–9. *Petrefactenkunde Deutschlands.* Tübingen.

—— 1856–8. *Der Jura.* Tübingen.

—— 1882–5. *Die Ammoniten des Schwäbischen Jura.* **1,** *Der Schwarze Jura* (*Lias*). Tübingen.

SCHINDEWOLF, O. H. 1961. Studien zur Stammesgeschichte der Ammoniten; Lief. 1. *Abh. Akad. Wiss. Lit. Mainz*, Jahrg. 1960, no. 10, 635–744, 2 pl.

SIMPSON, M. 1843. *A Monograph of the Ammonites of the Yorkshire Lias.* London.

—— 1855. *The Fossils of the Yorkshire Lias; described from nature.* London and Whitby.

SMITH, W. 1817. *Stratigraphical System of Organized Fossils.* London.

SOWERBY, J. 1812–22. *The Mineral Conchology of Great Britain.* London.

SPATH, L. F. 1914. The development of *Tragophylloceras loscombi* (J. Sowerby). *Quart. J. geol. Soc. Lond.* **70,** 336–62, pl. 48–50.

—— 1922. On the Liassic succession of Pabay, Inner Hebrides. *Geol. Mag.* **59,** 548–51.

—— 1923. On ammonites from New Zealand. *Quart. J. geol. Soc. Lond.* **79,** 286–312, pl. 12–18.

—— 1936. The ammonites of the Green Ammonite Beds of Dorset. Ibid. **92,** 438–55, pl. 33.

—— 1938. *A Catalogue of the Ammonites of the Liassic Family Liparoceratidae in the British Museum* (*Natural History*). London.

TRUEMAN, A. E. 1916. The lineage of *Tragophylloceras loscombi* (J. Sow.). *Naturalist, Lond.* 220–4.

TUTCHER, J. W. and TRUEMAN, A. E. 1925. The Liassic rocks of the Radstock district, Somerset. *Quart. J. geol. Soc. Lond.* **81,** 595–666, pl. 38–41.

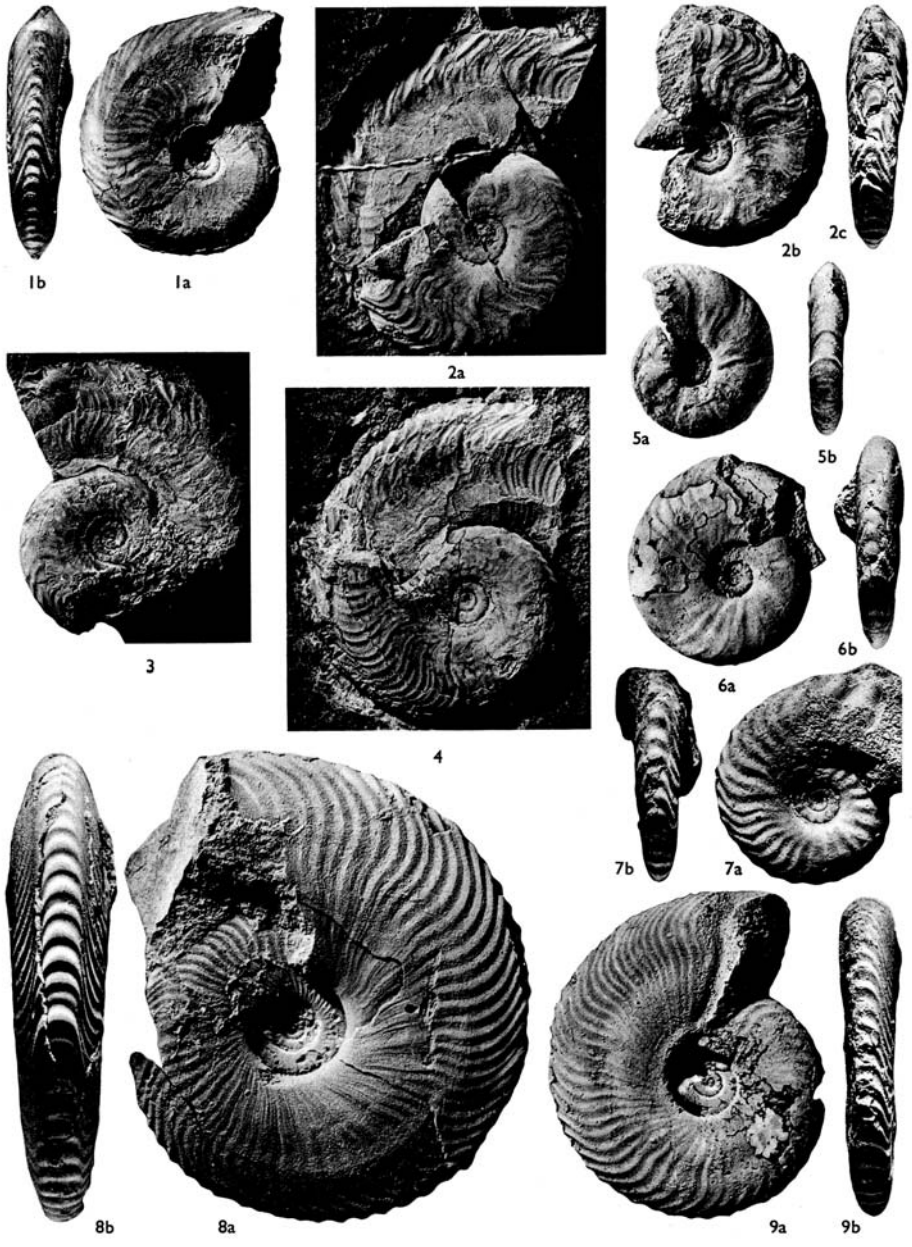
VADÁSZ, M. E. 1907. Fejlödésbeli elkülönülések a Phyllocerasok családjában. *Földtani Közlöny*, **37,** 349–55. (Same paper in German, ibid., pp. 399–405.)

WOODWARD, H. B. 1893. The Jurassic rocks of Britain. **3,** The Lias of England and Wales (Yorkshire excepted). *Mem. geol. Surv. Engld & Wales.*

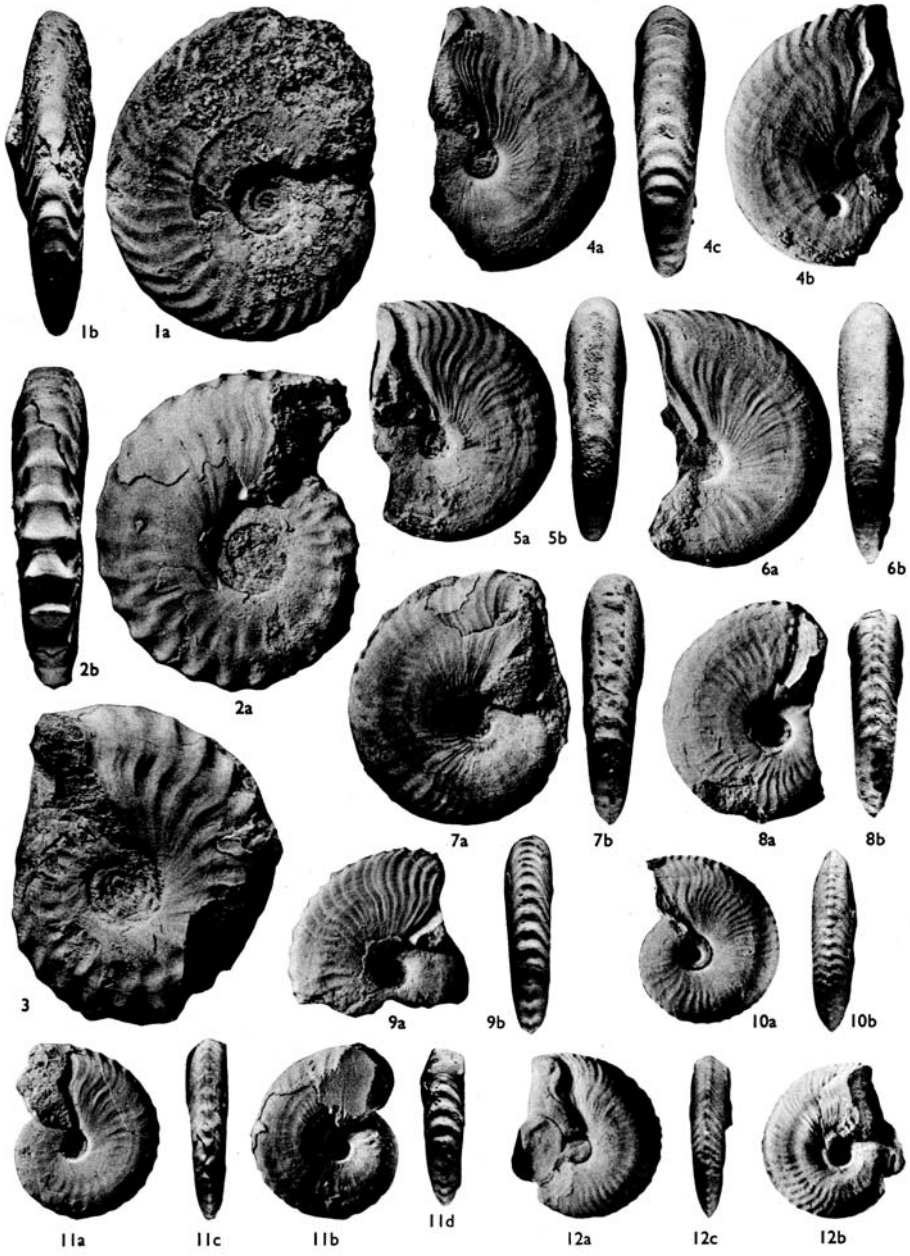
WRIGHT, T. 1878–86. Monograph on the Lias ammonites of the British Islands. *Palaeontogr. Soc.* (*Monogr.*).

M. K. HOWARTH
British Museum (Natural History),
Cromwell Road,
London S.W. 7
D. T. DONOVAN
Department of Geology,
University of Hull

Manuscript received 10 September 1963



HOWARTH and DONOVAN, Liassic ammonites



HOWARTH and DONOVAN, Liassic ammonites