N. Jb. Geol. Paläont. Abh.	124	3	289—312	Stuttgart, Mai 1966

Covariation and taxonomy of the Jurassic ammonite *Sonninia adicra* (WAAGEN)

by

G. E. G. Westermann

McMaster University, Hamilton, Ont., Canada

With 11 figures and 1 table in the text and on 3 folders

Abstract: — The rich *Sonninia* assemblage from the single bed of the *L. discites* Subzone (*S. sowerbyi* Zone, Bajocian) of Bradford Abbas in Dorset, England, was referred by S. S. BUCKMAN to 69 new species. Based on the redrawn photographs of all 83 median to large-sized type specimens which include 64 "species", semi-quantitative graphical methods give evidence of the complete morphologic intergradation of the whole "sample", ranging from subcircular, highly ornate to compressed smooth whorls. All 64 "species" are therefore considered to belong to a single palaeospecies and probably a single chronodeme of *Sonninia (Euhoploceras) adicra* (WAAGEN). The four or five small apparently mature "species" are provisionally retained as *S. subdecorata* BUCKM.

Covariation of measured characters is evident from scatters of individual allomorphosis. Of particular interest is the inter-correlation between costation, whorl section, and coiling which has been observed in different, unrelated ammonoid stocks and cannot be satisfactorily explained. This phenomenon is here named BUCKMAN's Law of Covariation.

At least nine other European "species" and five "subspecies" are placed in synonymy with *S. adicra* apparently the only European species of *S. (Euhoploceras)*. *S. subdecorata* BUCKM. is probably the corresponding microconch (male). Other species occur in Alaska, British Columbia, Oregon and California. The subgenus is an excellent marker for the lower part of the *Sonninia sowerbyi* Zone and can now be clearly distinguished from the slightly younger *S. (Papilliceras)*.

Zusammenfassung: Eine einzige fossilreiche Bank repräsentiert die *Ludwigia discites*-Subzone der *Sonninia sowerbyi*-Zone (Bajocium) bei Bradford Abbas in Dorset, England. Ihre *Sonninia*-Fauna wurde durch S. S. BUCKMAN in 69 neue Spezies gestellt. Semi-quantitative graphische Methoden für Messungen an allen 83 grösserern Typen von 64 „Spezies" veranschaulichen die morphologische Homogeneität dieses „samples"; stark skulptierte evolute und glatte involute Formen intergradieren. Alle 64 „Spezies" werden daher als zu einer einzigen Paläospezies und zu wahrscheinlich einem einzigen Chromodem gehörig angesehen, *Sonninia (Euhoploceras) adicra* (WAAGEN). Die vier oder fünf anscheinend ausgewachsenen kleinen „Spezies" werden vorläufig als *S. subdecorata* BUCKMAN unterschieden.

Kovariation der vermessenen Merkmale wird durch Diagramme (Individual-Allomorphosis) demonstriert. Besonders interessant ist die Interkorrelation zwischen Berippung, Windungsquerschnitt und Aufrollung, die bereits in mehreren, nicht näher verwandten Ammoniten-Gruppen beobachtet wurde, aber nicht genügend erklärt werden kann. Dieses Phänomen wird hier BUCKMAN's Kovariations-Gesetz genannt.

Mindestens neun andere europäische „Spezies" und fünf „Subspezies" werden in Synonymie mit *S. adicra* gestellt, anscheinend die einzige europäische Spezies von *S. (Euhoploceras)*. *S. subdecorata* BUCKMAN ist wahrscheinlich der entsprechende Microkonch (Männchen). Andere Spezies kommen in Alaska, Britisch Columbia, Oregon and Californien vor. Das Subgenus ist leitend für den unteren Teil der *S. sowerbyi*-Zone und kann jetzt klar von der etwas jüngeren *S. (Papilliceras)* unterschieden werden.

Introduction

From the *Sonninia sowerbyi* Zone, Bajocian, of NW and Central Europe approximately 120 "species" of the genus *Sonninia* were named. In the most recent literature this large number has been reduced by synonymy, although in very different and repeatedly disputed ways, to about 35 admittedly arbitrarily distinct "species". The large majority of the forms originated in the lower *S. sowerbyi* Zone, the *Ludwigia discites* Subzone. About 85 of the original and more than half of the "species" as currently understood belong to the subgenus *S. (Euhoploceras)*, which is restricted to the lower and middle part of the zone. It is here emphasized that most of these "species" are usually associated throughout their geographic range in Europe.

In his monograph of the Inferior Oolite ammonites, BUCKMAN (1892—94) attributed the extraordinary rich and morphologically varied *Sonninia* fauna from the "concava Zone" [recte *L. discites* Subzone of the *S. sowerbyi* Zone] of the Sherborne district, Dorset, to 70 "species", and all but one came from a single 0.18 m thick bed of Bradford Abbas. 110 specimens were profusely figured on about 47 large excellent plates, and external views or cross-sections given of most specimens. In addition to these "species" BUCKMAN distinguished "varieties" which fortunately were not formally named, but he nevertheless figured also several "intermediate forms".

BUCKMAN already realized that all these "species" may be mere morphotypes of a single biological species; he writes (1892, p. 287—288) "The series of specimens is generally so extraordinarily complete that division into species is often purely arbitrary. The species are simply different gradations in development. My object will be to show the gradual development of members of the different genera [of Sonniniidae]; and the word 'species', or so called 'specific names', will only be used as a means to attain that end, and as presenting after all the shortest method of nomenclature." It can therefore reasonably be assumed that this assemblage is derived from a single chronodeme, since only a single subzone is represented, with the possible exception of BUCKMAN's "dwarf *S. subdecorata* group" with 4 or 5 "species" which may represent the corresponding microconchiate dimorph.

This "sample" is probably the most profusely figured and most elaborately described ammonite species, and although even more complete and less biased samples of ammonite species have been attained since BUCKMAN (as for example, REESIDE & COBBAN, 1960), none has necessitated nomenclatorial "lumping" on such a scale as *Sonninia adicra* (WAAGEN) which is here shown to include at least 70 and possibly as many as 85 synonyms.

The Section at Bradford Abbas, Dorset

The "East Hill Quarry" section was described by BUCKMAN (1893 a) as follows (altered to metrical scale and N.W. European standard zones):

Bajocian:	
Garantiana garantiana Zone:	0.05 m "dirt bed/Marl bed"
	0.10 m bluish white limestone
(Bajocian or Vesulian transgression)	
Otoites sauzei Zone :	0.10 m "Irony bed", bluish limestone, ironoolitic, with *Sonninia (Papilliceras) mesacantha* (WAAGEN), "*Witchellia*" sp.
Sonninia sowerbyi Zone	
Ludwigia discites Subzone :	0.18 m yellowish-blue ironshot limestone, with *Sonninia* and *Ludwigia (Hyperlioceras)*
Aalelian:	
Graphoceras concavum Zone	0.40 m light yellowish-blue ironshot limestone, with abundant *Graphoceras* ex. gr. *concavum*, *L. cornu*.
Ludwigia murchisonae Zone	
L. bradfordensis Subzone :	0.025 m soft yellow marl. *L. bradfordensis*, *L. v-scriptum*
L. murchisonae zone s. s. :	0.125 m "paving bed", yellow and blue shelly limestone, with *L. murchisonae*.

Sonninia (Shirbuirnia) and typical *Witchellia*, respectively representative for the middle and upper *S. sowerbyi* Zone are absent from the "discites bed" of Bradford Abbas, but present in the thicker and more complete Sandford Lane section, 5 km to the northeast, in the lower part of the superposed "Fossil bed". Thus the Bradford Abbas "discites bed" is not a "condensed" deposit but represents only a single subzone (see also ARKELL, 1933, p. 194). However, at Sandford Lane *S. (Euhoploceras)* (cf.) *adicra* supposedly is missing in the *L. discites* Subzone but occurs rarely in the underlying *L. concava* Zone ("*Sonninia crassispinata*" and "*S. palmata*") as well as in the middle *S. sowerby)* Zone of the "Fossil bed" ("*Sonninia adicra*" and "*Sherbornites projectifer*") (BUCKMAN, 1923 and 1923a), just above *Witchellia (Zugophorites) gelasinus* (BU.).

The fact that BUCKMAN (1892—94) throughout his Inferior Oolite monograph consistantly dated the Bradford Abbas "discites bed" as "Concava-Zone" is based on his arbitrary inclusion of the "discites hemera" in the upper *G. concavum*, instead of the lower *S. sowerbyi* Zone as recently defined.

The "Sample" and Statistics

The Bradford Abbas "sample" of *Sonninia (Euhoploceras)* consists of redrawn photographs, many drawn cross-sections, and measurements given by BUCKMAN (1892—94, pl. 50, 57—103) of all 86 median sized to large specimens, which besides 69 of BUCKMAN's "species" include several "inter-

mediate forms". The following measurements were taken and, if necessary, recalculated to scale:

Db = ultimate diameter of body chamber (usually incomplete and often missing)

Dph = diameter of phragmocone, mostly but not necessarily towards the end.

H = whorl height, without keel.

W = whorl width, between costae.

U = umbilical width

Dsp = (terminal) diameter of typical spinose stage. Recorded as interval if not accurately determinable because of gradation into mixed costate-spinose stage; the arithmetic mean is plotted in the graphs. If clearly determinable but followed by a stage still bearing some irregular spines on a costa base and alternating with groups of costae, the suffix + is added; in the plot 10 % is then added to the value. If a spinose stage is absent, O is recorded.

P = number of primaries per halfwhorl (terminating at D). However, because of strong irregularity and fasciculate secondaries this value can often only be roughly estimated. Absence of costae (smooth shell) is recorded as O, and very weak to obsolete costation noted.

Obviously, this "sample" of type-specimens is strongly biased towards unusually well preserved and probably also toward large specimens, and especially toward frequency increase of rare morphotypes since all "species" were figured in only one to three specimens. The only statistics that can be applied therefore are semi-quantitative methods. Certain arbitrary but reasonable weighted frequency values are therefore assumed for BUCKMAN's "species" based on his statements of relative abundance:

"very common" (cc)	12
"common" (c)	6
"moderately common" (m)	3
"rare" (r)	1
"very rare" (rr)/"single" (sg)	0.5

In the histograms for estimated frequency these values for "species" are divided by the number of measured specimens. The assumed scale of frequencies is probably still too low; however, the resulting histograms will be effected significantly only in regards to their kurtosis.

In scatters for bivariate distributions, in particular for studies of allomorphosis ("growth curves" or "mass curves"), dispersions will be much stronger and correlation weaker than for a random sample of comparative size; the distributions will still be reliable indicators of relative growth. The same holds for studies of individual allomorphosis, i.e. covariation between "adult" characters. However, in sonniniids criteria for adulthood are poorly developed. In *Sonninia* (usually reserved for the macroconchs) growth appears to be "unlimited", i.e. far beyond the reaching of maturity and to be limited only by mortality, a mode usually observed in brachiopods (WESTERMANN, 1964). The last septa are rarely approximated and the aperture is almost never preserved probably due to lack of shell thickening which

usually occurs on adult apertures (HÖLDER, 1952; OECHSLE, 1958, p. 70). Furthermore, the majority of specimens from Bradford Abbas do not show any significant change in whorl section, coiling or ornamentation of the body chamber (if known to be preserved) even if of large diameter. Consequently, it is difficult or often impossible to distinguish juveniles from small fully grown specimens from the plates — even from inner whorls. Almost certainly an exception is the "group of dwarfs", the "*subdecorata* group", of which "*S. subdecorata*" and "*S. decora*" are very probably fully grown.

Since the parameters whorl section (H/W) and relative umbilical width (U/D) do not change significantly during intermediate and only exceptionally during latest growth, covariation studies can be based on the whole sample between about 60 and 150 mm diameter or on all phragmocones larger than 60 mm.

Sonninia **BAYLE 1878**

S. (Euhoploceras) BUCKMAN 1913

[syn.: *Sherbornites*, (?) *Stiphromorphites* BUCK., 1923]

Type-species by original designation is *S. acanthodes* BUCKMAN (1889, mature stage first figured in 1892, pl. 58), a subjective synonym of *Am. adicrus* WAAGEN (1876). It remains doubtful if this subgenus is clearly distinguished from *Sonninia* s. s.; the type-species of the latter, *Am. propinquans* BAYLE, resembles *S. adicra* in many respects and appears to be morphologically connected by several intermediate species. Thus "*S. spinifera*" BUCKMAN (here No. 17) from the *L. discites* Subzone of Bradford Abbas and from Germany was a "garbage pile" for forms intermediate between the close *S. propinquans* relative *S. sowerbyi* and *S. adicra* (HILTERMANN, 1939, OECHSLE, 1958) but is here shown to be another morphotype of *S. adicra*, and *S. sowerbyi adicroides* HILTERMANN appears to intergrade with *S. adicra* according to OECHSLE (1958) and to represent another morphotype of *S. adicra*. The German authors who have studied sonninias extensively (DORN, 1935; HILTERMANN, 1939, and OECHSLE, 1958) have therefore all regarded BUCKMAN's genus *Euhoploceras* as synonymous with *Sonninia* (s. s.). Nevertheless, the characters for which it was retained as a subgenus in the Treatise (ARKELL, 1957) remain as "tendencies", i.e. evolute rounded whorls with rursiradiate strong costae which are retained beyond the spinous stage onto the body chamber. There is always a thin and rather low hollow-floored keel.

Sonninia s. s. has usually more and stronger secondaries while *S. (Papilliceras)* is more compressed and somewhat weaker costate (see below) with longer retained or "revived" spinous stage.

The subgenus is known almost throughout central and western Europe and from the west coast of North America. Of about 80 described "species" only a very few are here recognized. All flourish in the lower *S. sowerbyi*

Sonninia (Euhoploceras) adicra (WAAGEN 1876)

Table of measurements

a) The Bradford Abbas "sample", BUCKMAN's *Sonninia (Euhoploceras)* "species" from the *L. discites* Subzone of Bradford Abbas, DORSET (pl. 48—77, 1892; pl. 78—87, 1893; pl. 87, pars., 103, 1894).

Name	pl.	Nr.	abundance	Db	(b/ph)	Dph	H	W	H/W	U	Dsp	P
crassispinata	48	1	r	—		115	37	32(.28)	1.2	48(.42)	115	10—13
,,	57	1	r	170			54	—	—	73	170	12
						110	36	37(.34)	.95	43(.39)		9—10
acanthodes	58	2	m	242			80	—	—	99	110+	16
					180		60	50(.28)	1.2	78(.43)		~14
,,	59	2	m	—		94	30	31(.33)	.97	43(.46)	85	10
,,	60	2	m	220			62 ~	63	~1.0	104	110	18
					174		56	48(.275)	1.15	79(.45)		18
irregularis	61	3	m	265			81	65	1.25	121(.41)	170	~21
						175	60	—	—	69(.40)		13
marginata	62	4	m?	225			66	54	1.2	105	60	18
						168	55	43(.255)	1.3	72(.43)		19
,,	64	4	m	312			98	68	1.45	133(.425)	<60	18
						170	58	—	—	65(.37)		17
,,	65	4	m	—		108	38	33(.305)	1.15	42(.39)	35	14
dominans	66	5	cc	302			100	78	1.3	120	30	19
						210	80	~58(.275)	1.4	175(.36)	30	~19
,,	94	5	cc	—		164	64	45(.275)	1.45	49(.30)	38	16—18
"intermed."	67	—	sg	—		102	41	31(.30)	1.32	37(.36)	50	18
modesta	68	6	c	~185/170			64	46	1.4	56	~18	(14 obsol.)
						120	50	31(.26)	1.6	33(.27)		(14 obsol.)
,,	95	6	c	166			66	43	1.55	56	(<20)	0
						120	50	~33	~1.5	35(.29)		~20 (obsol.)
,,	96	6	c	—		56	22.5	18	1.25	18(.32)	25	~24

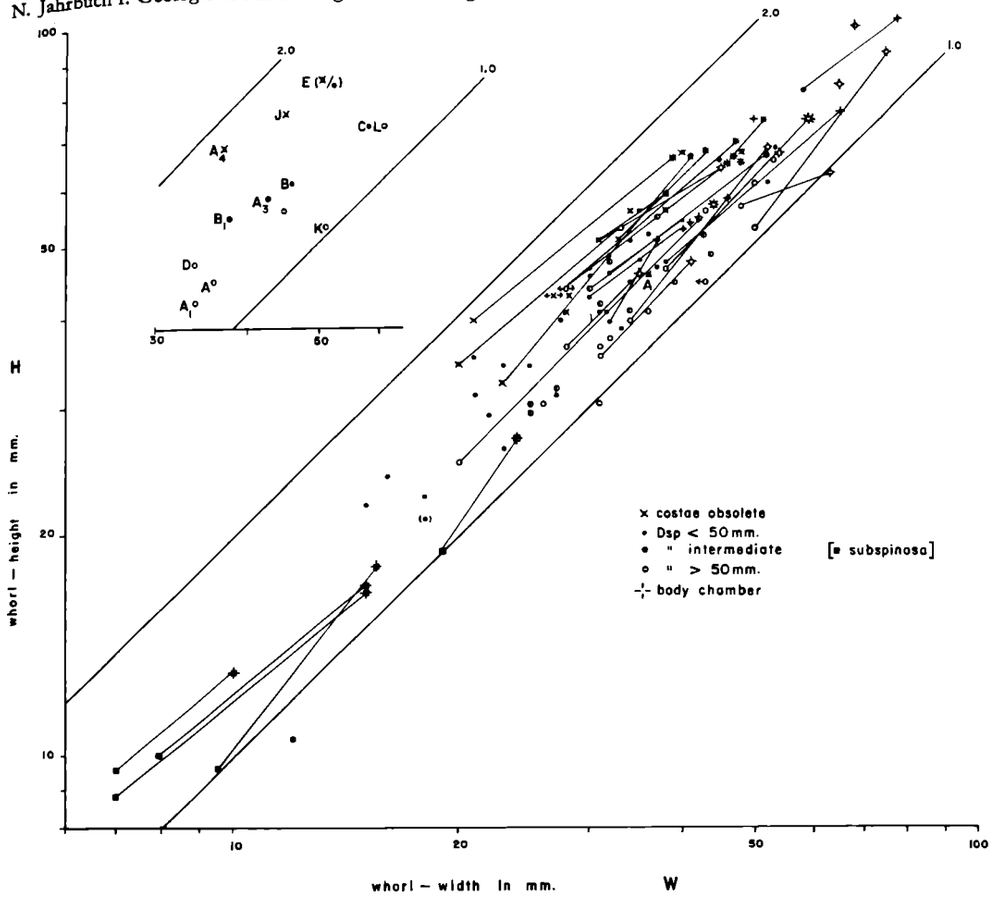
Name	pl.	Nr.	abundance	Db	(b/ph)	Dph	H	W	H/W	U	Dsp	P
revirescens	70	7	rr		110		40	—	—	45(.41)	~25	11 (obsol.)
simplex	70	8	r	~165			68	47	1.45	63	0	0
						~95	42	~27	~1.55	24(~.25)		0
substriata	71	9	r	~150			58	38	1.53	52	0	0
						~75	34	~20	~1.7	23		19
subcostata	71	10	r	—		124	46	30(.24)	1.55	44(.36)	15	~23
submarginata	71	11	r		~125		47	35	1.35	~56(~.44)	~45	~22
"intermed."	72	—	sg		82		35	21	1.65	25(.305)	0	19
obtusiformis	72	12	sg	~200			60	52	1.15	~90(~.45)	(30—40)	~14
ptycta	73	13	r	225			65	—	—	130(.50)	75	17
cymatera	73	14	r	—		99	34	25(.25)	1.35	40(.40)	28	16
spinicostata	73	15	sg	222			67	52	1.3	105	(~120)	17
						128	39	~34	~1.15	54(.42)		17
costata	74	16	c	220			67	53	1.25	101	(0?)	13
						107	45	30(.28)	1.5	46(.43)		13
spinifera	74	17	m?		90		31	27	1.15	38(.42)	35	18 (obsol.)
,,	100	17	m?		196		53	41(.21)	1.3	78(.40)	~40	15
parvicostata	75	18	m	~200			65	39	1.65	72	0	0
						105	39	21	1.85	35(.33)		(~18 obsol.)
brevispinata	75	19	m		66		24	16	1.5	23(.35)	25	17
magnispinata	76	20	r		82		30	26(.32)	1.15	32(.39)	60+	12
,,	76	20	r	132			45	35	1.3	56	70	17
						70	25	~20	~1.25	30(.43)		7
,,	98	20	r		128		44	44(.34)	1.0	57(.45)	55+	15
alternata	98	21	r	—		58	22	15	1.45	20(.34)	15+	17—20
,,	77	21	r		115		43	30(.26)	1.45	40(.35)	45	14—18
semispinata	77	22	r	—		129	47	32(.25)	1.47	49(.38)	30+	18
"sp. indet."	77	(=?63)	sg		75		26	23	1.15	28(.375)	45+	13
biplicata	78	23	r	—		150	51	42.5(.285)	1.2	59(.39)	40+	12—15

Name	pl.	Nr.	abundance	Db	(b/ph)	Dph	H	W	H/W	U	Dsp	P
piplicata	78	23	r	—		95	47	32(.34)	1.45	36(.38)	45+	20
crassiformis	79	24	r	—		115	40	36(.31)	1.1	44(.38)	110	10
,,	79	24	r	290			90	75	1.2	124	125+	15.5
						160	~52	50	~1.05	60(.375)		13
crassibullata	80	25	r		190		65	53(.275)	1.23	71(.38)	70	11
crassicostata	80	26	r		130		40	31(.30)	1.3	35(.33)	30—45	10
crassinuda	81	27	m		~115		45	36	1.25	40(~.35)	50	0
diversa	81	28	r		100		40	28(.28)	1.45	35(.35)	25—30	20—25 (obsol.)
,,	83	28	r			87	31	25	1.25	32(.39)	~50	12—23
spinosa	83	29	r		148		54	37(.25)	1.45	57(.38)	45+	10—12
crassa	82	30	r	225			73	59	1.25	87	50—60	15
						~125	46	~38	~1.2	45(~.35)		15
nuda	82	31	r	~190			73	51	1.43	64	0	0
						~95	42	~28	~1.5	22		0
laevigata	82	32	r		~155		66	48	1.4	58(~.37)	~15+	0
omphalica	83	33	r		106		39	27.5(.26)	1.42	39(.37)	12	21
umbilicata	84	34	r		83		31	21	1.48	33(.40)	0	16
euromphalica	85	39	r		80		27	24	1.12	35(.44)	31	22
						60	19	19	1.0	24(.40)		22
abnormis	85	40	sg		82		29	22	1.3	33(.40)	30	16.5
multicostata	86	41	r?		135		50	34(.35)	1.47	48(.355)	15+	18.5
spinea	86	42	r?		135		42	34(.25)	1.25	59(.44)	55+	14—16
scalpta	87	43	sg		98		34	23(.24)	1.5	42(.43)	15+	22
gibbera	87	44	r?		133		44	39(.29)	1.12	58(.43)	50+	(irr.) 15—20
contusa	88	45	r?	200			64	47	1.35	78	(<25)	(12—14 ob.)
						144	55	38(.265)	1.45	52(.36)		(12—14 ob.)
densicostata	88	46	sg		178		55	~35	~1.55	82(.46)	(0)	19
nodata	89	47	r			120	40	31.5(.26)	1.27	48(.40)	30+	16

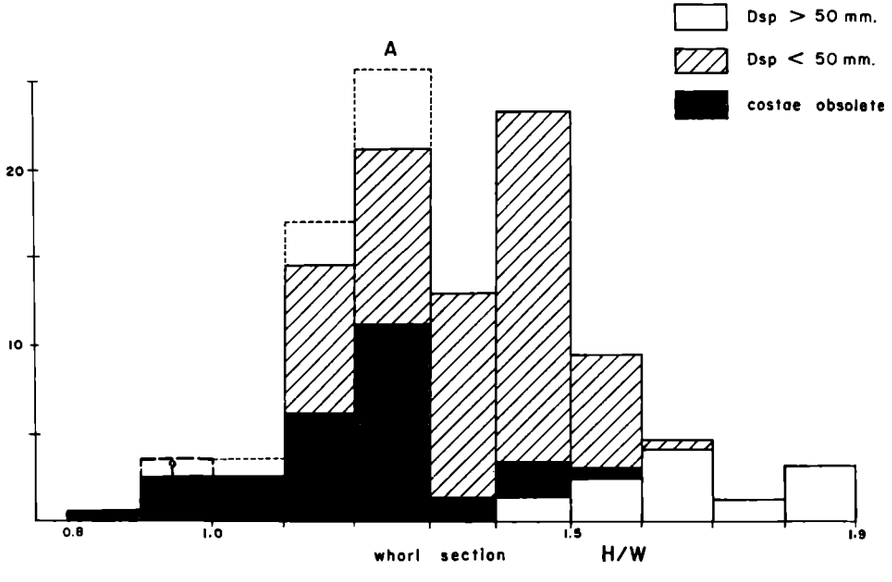
Name	pl.	Nr.	abundance	Db	(b/ph)	Dph	H	W	H/W	U	Dsp	P
reformata	89	48	r?			61	21	18	1.16	24(.39)	15—45	18—20
papilionacea	90	49	r	166			56	44	1.27	62	(≤20)	16.5
						90	36	~27	~1.35	30(.33)		~20 (obsol.)
attrita	90	50	r			166	66	40(.24)	1.65	48(.29)	(≤20)	15 (obsol.)
quadrifida	91	52	r	160			53	41	1.3	59	40	17
						120	45	32(.27)	1.4	41(.34)		23 (obsol.)
mutans	91	53	r?	140			47	41	1.15	56	75+	20
						107	35	~35	~1.0	42(.39)		~15
paucinodata	91	54	r	154			52	40	1.3	56	25—35	16
						114	42	30(.265)	1.4	38(.33)		16
locuples	92	55	r?		190		65	52(.275)	1.25	54(.28)	40—50	16
loculosa	92	56	r?	~155			65	41	1.6	46	0	0
						75	32	23	1.4	20(.27)	0	(~25 obsol.)
renovata	93	57	r		187		57	~46	~1.25	82(.44)	35+	14
,,	93	57	r		113		40	34(.30)	1.18	43(.38)	40+	16—18 (obsol.)
dominatrix	94	58	r—m		170		64	48(.28)	1.33	64(.38)	30	12
subsimplex	94	59	m	214/160			55	34(.21)	1.62	53(.32)	0	(17—18 obsol.)
regularis	94	60	r		140		48	43.5(.31)	1.1	59(.42)	45+	~18
dominata	97	61	r	192/145			49	—	(~1.25)	58(.40)	40	16—18
plicata	97	62	r		190/103		46	~37	~1.25	43(.42)	15+	~16
subirregularis	97	63	r	271/190			63	—	(~1.1—1.2)	81(.43)	50+	~17
duplicata	99	64	r	164			53	42	1.25	67	45+	14—16
						90	30	~25	~1.2	33(.37)		12—15
camura	99	65	r	228			73	50	1.45	—	20	18—20
						112	47	32(.285)	1.45	30(.27)		16—20
tridactylia	101	66	r		92		31	27(.295)	1.15	36(.40)	45—55	14.5
costigera	102	67	r		255 /	140	46	~38	~1.2	48(.34)	35—45	17.5

Name	pl.	Nr.	abundance	Db	(b/ph)	Dph	H	W	H/W	U	Dsp	P
multispinata	50	68	sg			40	12	15	0.8	18.7(.405)	40(+)	9
dominica	103+69	69	r?		190/115		43	~28	~1.5	41(.355)	60	26
b) The "dwarf *subdecorata*-group", associated with (a)												
subspinosa	84	35	r		50		18	15.5	1.16	20(.40)	20+	16—19
						27	9.5	9.5	1.0	8.5(.31)		10—12
subdecorata	84	36	m	48			17	15	1.13	18.5(.385)	23	~30
						24	8.5	7	1.2	9(.375)		6—7
decorata	84	37	m		50		17	15	1.13	18(.36)	25	~20
						28	10	~8	~1.25	10(.36)		~12
decora	84	38	sg	38			13	10	1.3	12.5(.33)	(<10)	~25
						24	9.5	7	1.35	8(.33)		~25
c) Broad Windsor, Dorset, *S. discites* Subzone (BUCKMAN, 1894)												
inaequa	101	70	r		135		51	36	1.42	46	<10	17
d) Top of *L. concava* Zone (F) and *S. trigonalis* Subzone of *S. sowerbyi* Zone, Dorset.												
palmata	90	F	sg	156			50	37	1.35	64	~35	13
BU. 1894						116	39	~32	~1.22	46(.40)		13—15
Sherbornites projectifer	T.A., pl. 411			263	/	149	55	44.5	1.23	44.5	150+	9
BU. 1923		G	r?									
Stiphromorphites nodatopinguis	T.A., pl. 398			115			40	37	1.15	42.5	(0?/80?)	obsol.
BU. 1923		H	sg?			65	26.5	26	1.0	20		9—10

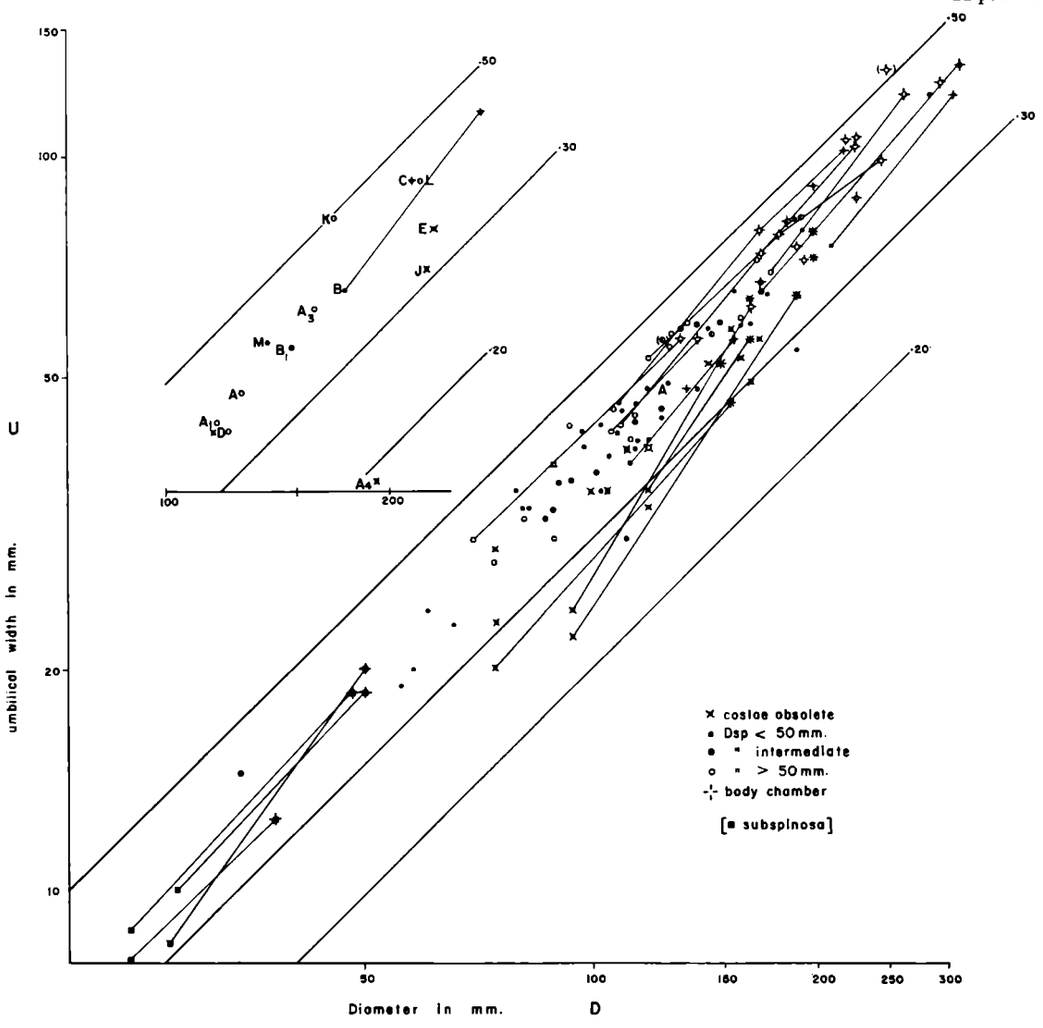
		Db	(b/ph)	DpH	H	W	H/W	U	D3p	P
c) (lower) *S. sowerbyi* Zone of central Europe										
Am. adicrus WAAGEN 1867, pl. 25	A	—		125	44	36	1.2	48(.385)	75	9
Am. polycanthus WAAGEN 1867, pl. 29	B	260			77	~57	~1.35	117		
				170	60	~46	~1.3	66	<35+	~14
"*S. costosa* QUEN." in Dorn 1935, pl. 4	C		205		72	58	1.25	93	~25+	9
S. berckhemeri DORN 1935, pl. 21	D			120	47	34	1.4	42(.31)	60+	10—11
S. sowerbyi adicroides HILTERMANN 1939, pl. 9	A_1		115		41	34	1.2	43	115	7—8
S. adicra externa OECHSLE 1958, p. 87 (nom. nud.)										
S. adicra interna OECHSLE 1958, pl. 18	A_3			157	57	43	1.32	62	~45+	8
S. modesta nenningensis OECHSLE 1958, pl. 19	A_4		190		67	37.5	1.78	36	0	0
S. grandiplex OECHSLE 1958, pl. 20	E			229	83	51	1.65	80	(<40)	0 (obsol.)
S. polyacantha intermedia OECHSLE 1958, pl. 18	B_1			148	54	38	1.43	55	40+	9
S. mussonensis MAUBEUGE 1951, pl. 2	J		220		75	45	1.65	70	0	(~16) obsol.
S. pseudogibbera MAUBEUGE 1951, pl. 16	K		168		52	51	1.05	82	90	12
[*S. pseudoirregularis* MAUBEUGE 1951, pl. 9	L		217		72	61	1.18	92	70+	~16]
[*S. pseudocostata* MAUBEUGE 1951, pl. 9	M		135		46	—	—	56	(<25)	12]



Text-fig. 1. Scatter of Whorl-Height against Whorl-Width (HXW), i. e. Whorl Section, for the Bradford Abbas „sample", in symbols for type of ornament and with some „true" growth lines connecting phragmocone end with end of preserved body chamber. The holotype of *S. adicra* is plotted on the same coordinates (A), while the synonyms from central Europe are plotted on a different abscissa for clarity. There is no significant change in growth rate but an obvious weakening of ornamentation with increasing compression of the whorls. The same association is evident for the European synonyms.



Text-fig. 2. Estimated frequency distribution of the Whorl Section (H/W) for mature phragmocones of the Bradford Abbas „sample", based on BUCKMAN's statements of abundance for 64 „species". Strength of ornament is evidently correlated with whorl section. *S. subdecorata* (fine dashes) and the holotype of *S. adicra* (A) are also plotted.



Text-fig. 3. Scatter of Umbilical Width against Diameter (UXD) for the Bradford Abbas „sample" with some „true" growth lines and symbols as in Text-fig. 1. The growth rate does not change significantly except for a few involute variants and probably some very large (old) specimens. Ornament strengthens with increasing relative umbilical width, in the Bradford Abbas „sample" as well as in the central European *S. adicra* with synonyms (in capital letters on inset at upper left, plotted on different abscissa).

Zone with a range from the *L. concava* Zone (very rare and local) to the middle *S. sowerbyi* Zone.

It appears that the species *S. adicra* correctly includes at least 64 or 65 if not all of the 69 Bradford Abbas "species", 3 more English "species" from other localities and/or the *S. trigonalis* Subzone, 4 "species" from northeastern France, and 4 "species" and 5 "subspecies" from the lower part of the *S. sowerbyi* Zone of northern and especially southern Germany. Up to date, neither geographical nor chronological subspecies can positively be distinguished.

The very probably microconchiate "*subdecorata* group" (including 4 "species") is here tentatively retained as *S. subdecorata*.

Variation and covariation of the Bradford Abbas "sample"

Besides reporting the extraordinary great variation of the Bradford Abbas sonninias, S. S. Buckman (1892, p. 313) clearly observed for the first time to the author's knowledge, a particular type of covariation [intercorrelation] between the ornament on the one hand and the whorl section and coiling on the other: "Roughly speaking, inclusion of the whorls correlate with the amount of ornament — the most ornate species being the most evolute, and having almost circular whorls". The same covariation was observed by him in *Amaltheus* which he believed to be the ancestor of *Sonninia*.

Buckman (loc. cit.) also stated that in *Sonninia* the complexity of the septal suture varies with the ornament and that he observed the same in *Amaltheus*: "In general the complexity of the suture-line increases in proportion to the decrease of ornament, a feature similar to what may be noted in the case of *Amaltheus*". — Without the original material, this alleged covariation, although of high interest with respect to the possible function of the septum, can here be neither supported nor disproved. However this relationship is in agreement with Oechsle's (1958, p. 86, 111) statements that the septal suture is only moderately incised in "*S. adicra*" and intensively incised in "*S. modesta*".

1) Variation

a) Diameter (D). — Because of poor knowledge of the original "sample" (which was studied in the Geological Survey Museum, London, only superficially by the author in 1962 and 1964), the presumed "unlimited" growth in *Sonninia*, and the almost always incomplete preservation, no size-frequency curve is plotted. As evident from the "growth curves" (Text-figs. 1 and 3) specimens with partially preserved body chambers are mostly from 150 to 300 mm in diameter and a maximum of 320 mm was certainly reached. However, Buckman also figured a number of supposed probable juvenile specimens which he was often unable to distinguish from septate

inner whorls. The representation of the sample is fair above 50 mm and good above 80 mm diameter.

The only small specimens (40—50 mm) which are almost certainly fully grown belong to the "group of dwarfs" or "*subdecorata*-stock/group", comprising the two "common species" *S. subdecorata* and *S. decorata* and presumably also the "rare species" *S. subspinosa* and the "single specimen" of *S. decora* (all BUCKMAN, 1893). Another microconch may be the "rare species" *S. euromphalica* BU. (1893) with 80 mm diameter. As always, no aperture is preserved.

b) Whorl section (H/W). — The plot of whorl-height against whorl-width (Text-fig. 1) includes a number of "true" growth lines made on the preserved body chamber. It is evident from these as well as from allomorphosis that the whorl section does not change significantly or becomes only slightly more rounded during growth (satisfactory sample beyond 30 mm H and 20 mm W, > 80 mm D), i.e. the H/W growth rate is approximately constant or slightly negative. The whorl section varies from slightly depressed subcircular (H/W 0.85) to strongly compressed oval — subrectangular (H/W 1.85). The distribution does not show any apparent clustering. The "dwarf" (microconchiate) "*subdecorata*-group" is well within this range down to a diameter of 24 mm.

The estimated frequency histogram (Text.-fig. 2) is based on the whole sample and shows a roughly unimodal, normal distribution. The mode approximates and is probably slightly above 1.3. The variation coefficient can be roughly estimated as 12—15 % assuming that the weighting of frequency of occurrence is approximately correct. This value is unusually high for infraspecific variation which usually approximates 10 %.

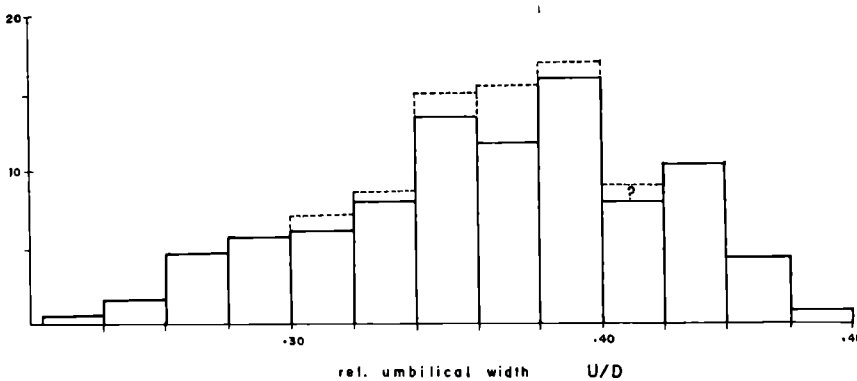
The distribution of the "*subdecorata*-group" agrees with the large sample.

c) Umbilical width (U). — The plot of umbilical width against diameter (Text.-fig. 3) shows random distribution of measurements, nearly constant "growth ratio" within the well represented sample, ranging from about 80 mm to 150—200 mm diameter, except for a very few variants with extremely narrow umbilicate (U < .30) intermediate growth stages, and finally minor and possibly insignificant increase in relative umbilical width for the larger body chambers (150—200 mm D) for average forms (U < .30) and a strong increase for the few involute "variants" (U < .30), which have average body chamber coiling.

The higher positive allometry of body chambers of narrowly umbilicate forms as compared with widely umbilicate forms is commonly observed within infra- and interspecific variation (WESTERMANN, 1954). Large body chambers over 210 mm D have .40 to almost .50 umbilical width, still within the range for middle and large sized phragmocones. Similarly, the few measurements below 80 mm D, including the "*subdecorata*-group" do not differ significantly in umbilical width from intermediate- and large-sized specimens.

The estimated frequency histogram (Text.-fig. 4) excludes whorls over 150 mm D. Again the distribution is similar to normal, but may be platykurtic (low-peaked). The range is from 0.235 to 0.465, the mean approximates a value of .38 and the variation coefficient is again 13—15 %.

Again, the "*subdecorata*-group" is randomly distributed about the mean.



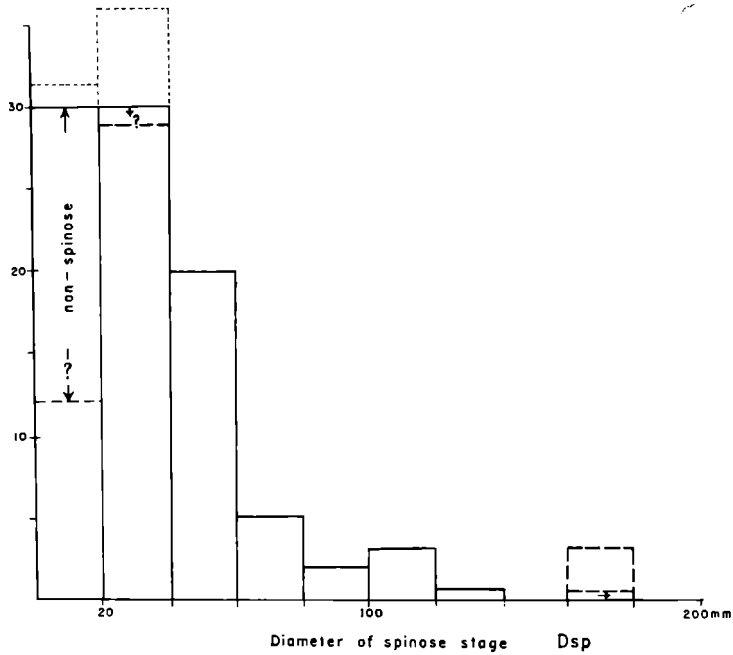
Text-fig. 4. Estimated frequency distribution of the Relative Umbilical Width (U/D) of average size phragmocones (> 150 mm D) for the Bradford Abbas "sample", based on BUCKMANN's statements of abundance for 64 "species". Fine dashes for *S. subdecorata*.

d) Ornament: Diameter of the spinose stage (Dsp). — The estimated frequency distribution (Text-fig. 5) is extremely strong positively skewed and probably leptokurtic. Measurements for small and intermediate-sized specimens are only plotted if D > Dsp. The distribution is discontinuous because the spinose stage is probably absent in 15—20 % of the population. However, incomplete knowledge of the nuclei often does not allow one to differentiate between very small (Dsp < 10—15 mm) and absent spinose stage and both are therefore included in the first interval, 0—20 mm Dsp. This first interval is about as frequent as the second (20—40 mm) but approximately reduced to one half if probably non-spinose forms are excluded. The mean is close to 40 mm. Beyond the 40—60 mm interval the frequency drops sharply and only "single" and "rare species" occur at Dsp > 120 mm. However, the specimen with 170 mm Dsp is spinose up to the end of the preserved shell. The measurement for the "moderately common species" tentatively plotted at 170 mm is based on a single specimen irregularly spinose throughout.

The "*subspinosa*-group" plots around the mode. In all "dwarfs" the spinose stage ceases before the end of the preserved shell.

2) Covariation (association/inter-correlation)

a) Inter-dimensional. — The plot of whorl section against relative umbilical width (H/W X U/D; Text-fig. 6) for measurements close to the end of the phragmocone demonstrates weak but apparently significant negative



Text-fig. 5. Estimated frequency distribution of the Diameter of the Spinose Stage (Dsp) for the Bradford Abbas "sample", based on Buckman's statements of abundance of 64 "species". The first interval includes very approximately 50 per cent non-spinose specimens. Fine dashes for *S. subdecorata*.

correlation; however, both characters are at least partially logically correlated (SOKAL & SNEATH, 1963, p. 67), since whorl-height is part of the diameter. Thus the fact that evolute whorls are much more rounded than involute whorls is at least in large part due to a single varying "dorso-ventral" growth vector, although the estimated regression (based on the empirical growth rate of 1.9 for diameter increase per whorl) may be slightly less steep that exhibited by the scatter. Relative whorl-width and relative umbilical width (W/D X U/D Text-fig. 7) are not clearly inter-correlated except for positive shift of maximum values; it can only be stated that evolute whorls are usually as wide ("thick") as involute ones, but are often somewhat "thicker" rather than "thinner". — All measurements are intercostal, but appearance of "thickness" is increased by strong lateral ornament.

b) Dimensions-ornament. —
"Buckman's Law of Covariation"

The scatter of the whorl-section (near end of phragmocone) against the diameter of the spinose stage (H/W X Dsp) (Text-fig. 8) establishes the moderately strong but apparently highly significant negative correlation;

the plots for BUCKMAN's "species" are more or less evenly distributed over most of the range without any obvious clusters, thinning down towards the ends. All non-spinose or very weakly (< 20 mm Dsp) spinose specimens are moderately to strongly compressed (H/W ⩾ 1.4), and only this interval includes specimens with obsolete or absent costation of the last whorls. Moderately spinose forms (Dsp 20—60 mm) range from almost sub-circular to moderately compressed (H/W 1.1—1.5) and are costate throughout, while all strongly spinose specimens (> Dsp 60 mm) are more or less subcircular (H/W .95—1.2).

Probably significant is the marginal and possibly clustered distribution of the "*subdecorata*-group", which appears to be comparatively too rounded in whorl-section and/or too weakly spinose (Text-fig. 9).

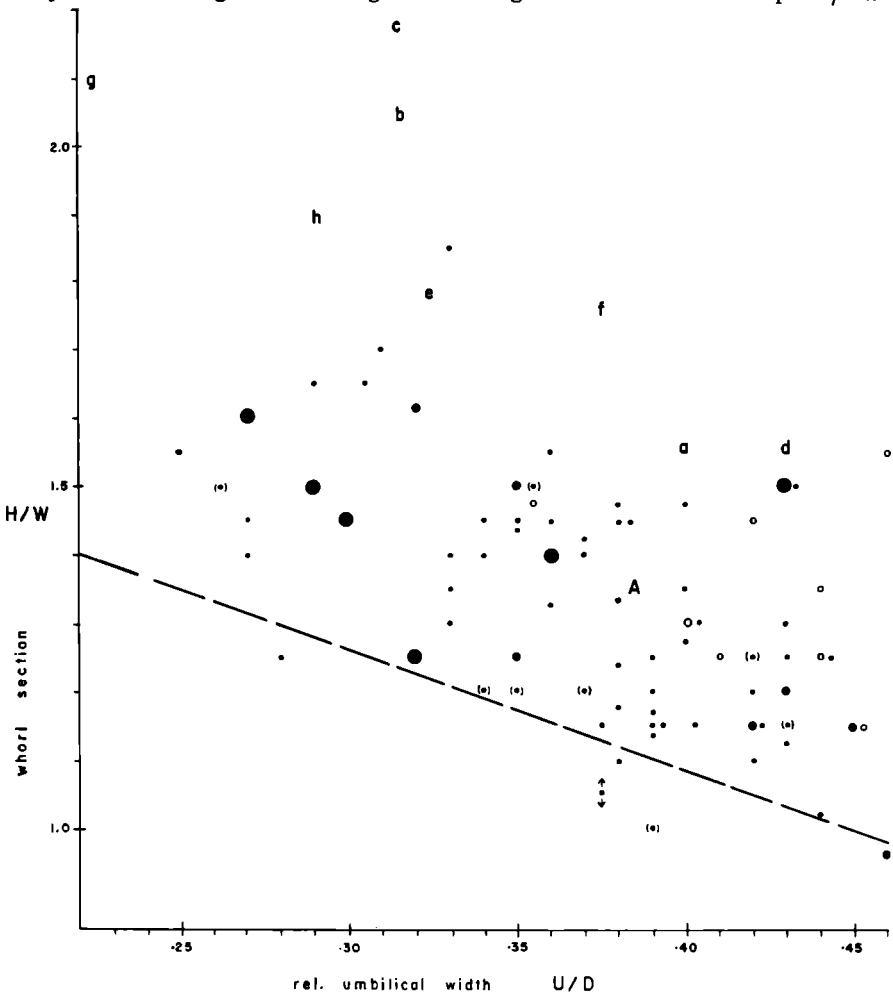
The same inter-correlation is also evident from the HXW scatter, discussed above, where four different symbols were employed for 4 ornament types. As expected, this covariation is also present between relative umbilical width and ornament, as evident from the UXD scatter (Text-fig. 3), because of the correlation of umbilical width with whorl-section. In the frequency histogram for whorl-section the three major ornament types are distinguished and show the broadly overlapping distribution of this association. If whorl-width would be measured on instead of between costae and spines, the resulting correlation would be stronger, but be partly derived from logical correlation.

The scatter of whorl section against number of primaries (H/W X P), (Text-fig. 10) suggests very weak positive correlation. This is expected since weaker ornament is usually denser. The distribution of the major ornament types shows that a prolonged spinose stage is usually associated with more distant and therefore usually stronger primaries of the last whorl(s).

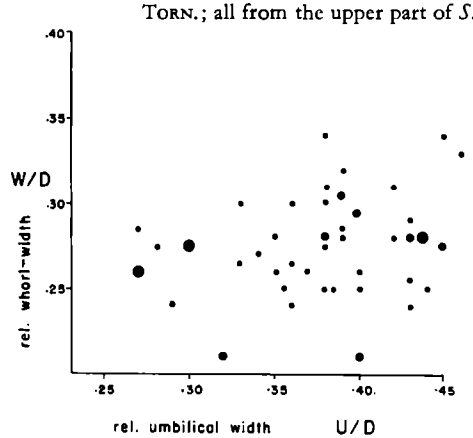
Interpretation of Variation and Covariation

The Bradford Abbas "sample" of middle to large sized specimens does not display any appreciable clustering in the measured characters, and appears to form a continuous morphological series also with respect to all other observable features. BUCKMAN's subdivision of this morphological continuum into 65 "species", additional infraspecific categories and, significantly, intermediate forms, is equivalent to naming each square of a matrix, based on arbitrary intervals, or of a multiple Mendelien cross. The conclusion is therefore that this "sample" is representative of only a single paleo-(chrono-)species and, very probably, a single chronodeme.

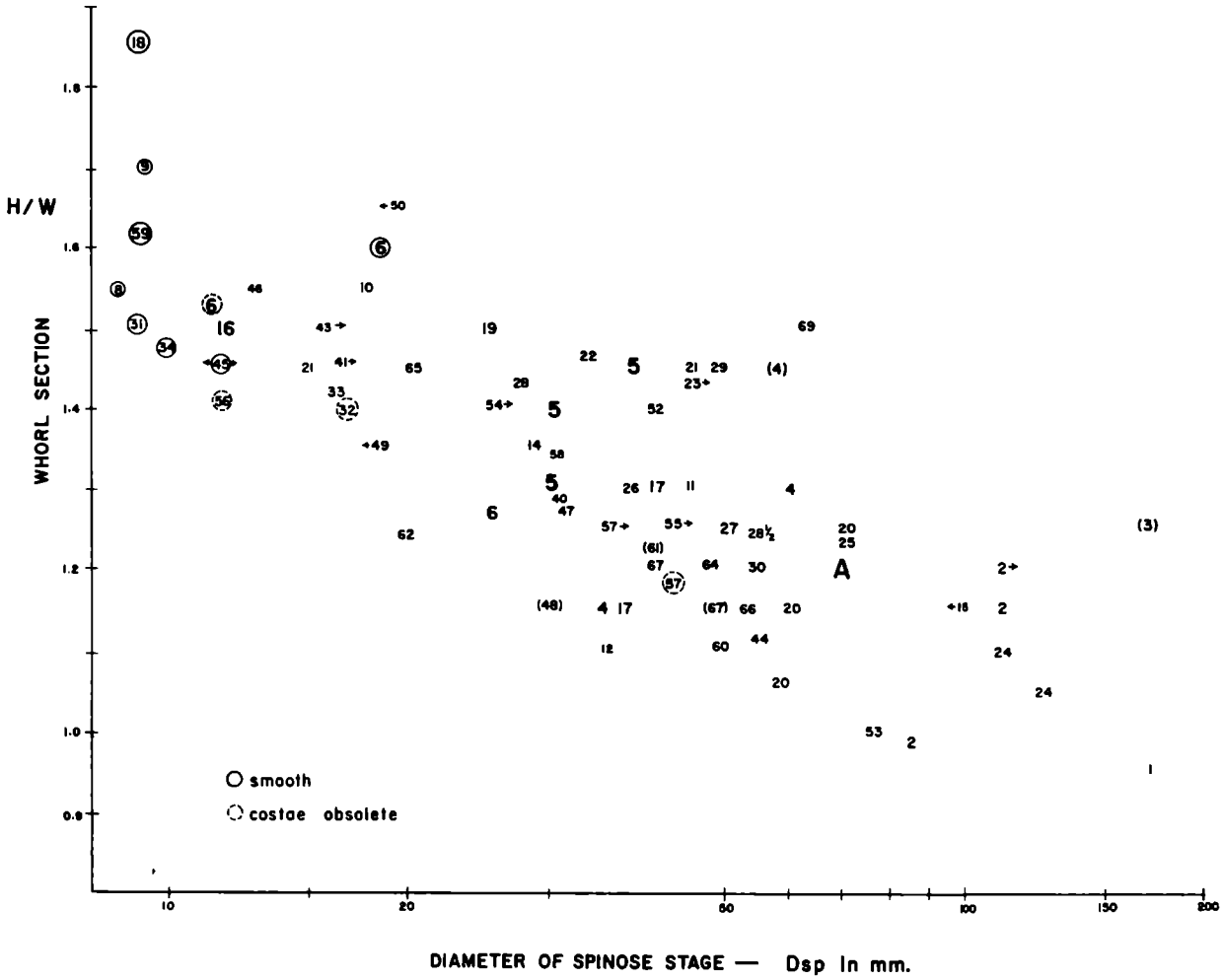
Since the strong variability of all measured characters within this supposed single chronodeme cannot be attributed to a steep ecocline, the adaptive significance of, or alternatively, the selection "pressure" on, all these characters appears to have been extremely low. Also, the variability appears to be similar in other occurrences of the species, such as in southern



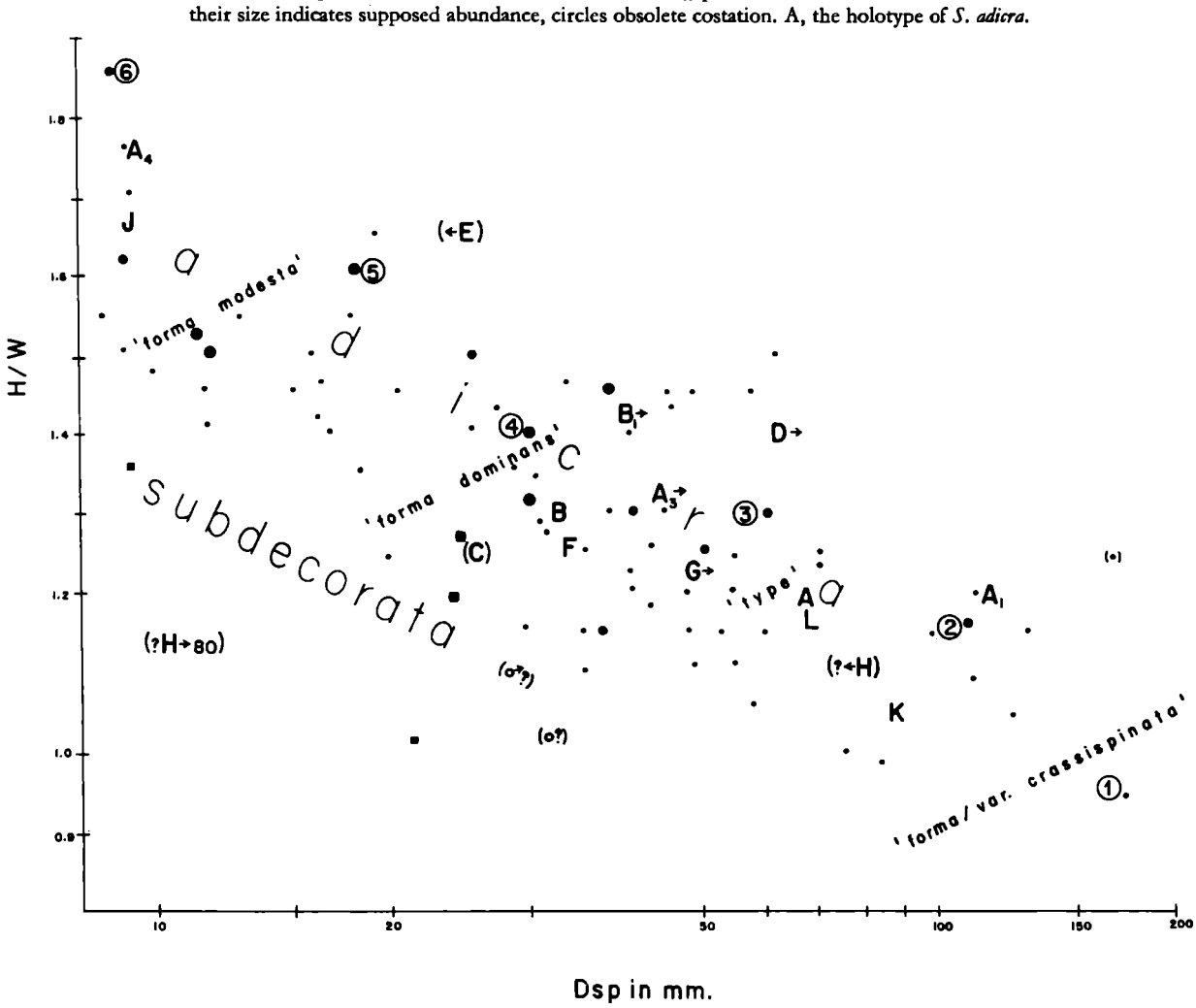
Text-fig. 6. Scatter of Whorl Section against Relative Umbilical Width (H/W X U/D), individual allomorphosis of mature phragmocones in the Bradford Abbas „sample". Size of dots according to supposed abundance. The dashed line represents the approximate slope of the expected logical correlation between the parameters, since H is contained in D. — Lower case letters mark the position of species of *Sonninia (Papilliceras)*: a, *S. papillata* (Bu.), b, *S. mesacantha* (Waag.), c, *S. arenata* („Dorn", non Qu.), d, *S. acanthera* (Bu.), e, *S. micracantha* (Bu.), f, *S. pseudoarenata* Maub., g, *S. gracilis* Torn., h, *S. espinazitensis* Torn.; all from the upper part of *S. sowerbyi* or the *O. sauzei*-Zone.



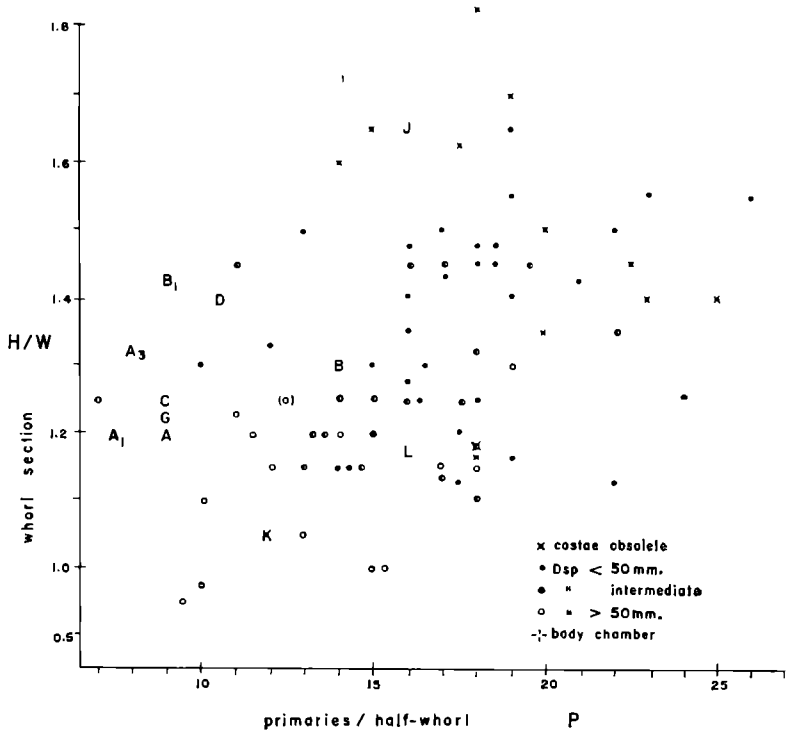
Text-fig. 7. Scatter of Relative Whorl-Width against Relative Umbilical Width (W/D X U/D), individual allomorphosis of the Bradford Abbas „sample" as in Text-fig. 6.



Text-fig. 8. Scatter of the Whorl Section against the Diameter of the Spinose Stage (H/W X Dsp) of the mature phragmocone for the Bradford Abbas „sample"; the numbers stand for BUCKMAN's „species" as listed in the table of measurements and their size indicates supposed abundance, circles obsolete costation. A, the holotype of *S. adicra*.



Text-fig. 9. Scatter as in Text-fig. 8, the dots representing the Bradford Abbas „sample"; the numbered dots indicate specimens figured in Text-fig. 11. The holotype and central European synonyms of *S. adicra* are plotted i capital letters and are listed in the table of measurements. For descriptive purposes, the „forma modesta", „forma dominans", „type", and „forma/var. crassispinata" may be distinguished. The squares represent the plots for *S. subdecorata*.



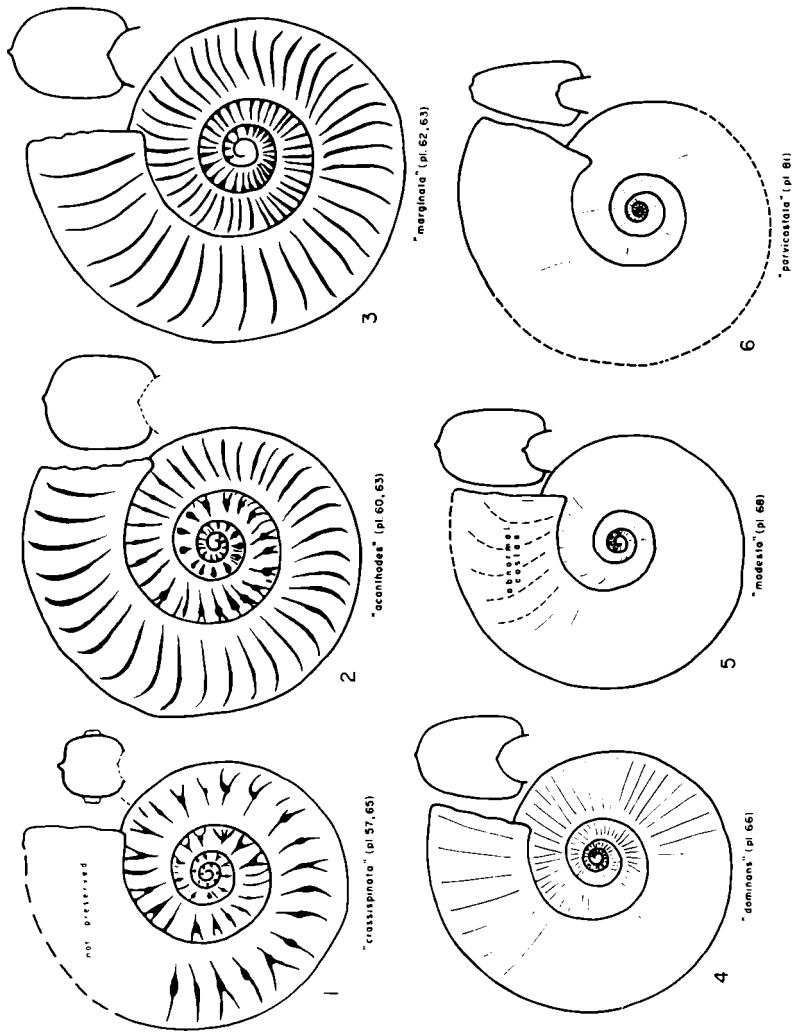
Text-fig. 10. Scatter of Number of Primaries per Halfwhorl against Whorl Section (P × H/W), individual allomorphosis of mature phragmocones of the Bradford Abbas "sample" in symbols for types of ornament. The capital letters indicate the plots of the holotype (A) and central European synonyms of *S. adicra*. Very weak positive correlation and weakening ornament with increasing H/W (compression of whorls section) and P are evident.

Germany, where it is sufficiently well known (see below). Thus it appears, in the case of this species, fallacious to attribute to strong costation the function of stiffening (corrugation of the shell, WESTERMANN, 1964a), protection or mimicry; similarly the much better "streamlining" of the smooth and involute over the evolute and highly ornate conchs (KUMMEL & LLOYD, 1955) was apparently non-functional in this species.

Perhaps even more perplexing is the dimensions-ornament covariation which is here named BUCKMAN's Law of Covariation. The possibility of genetical correlation is probably to be excluded since the same association has been observed in a number of different, unrelated ammonoid stocks such as the Triassic ceratitine *Protrachyceras* (SILBERLING, 1956), the Aalenian hammatoceratid *Erycitoides* (WESTERMANN, 1964c, p. 374), and the Creatceous hoplitid ammonitine *Neogastroplites* (COBBAN & REESIDE, 1960). In *Neograstroplites*, 5 successive species were described each including the morphotypes "compressed costate", "stout nodose", and "subglobose

spinose" in different modifications. BUCKMAN's Law of Covariation can be observed in any large, intergrading ammonoid sample which includes ornate forms (Text-fig. 11).

Functional correlation between ornament and relative dimensions is unlikely for the reasons stated above for exceptionally high variability. The only causal relationship between whorl shape and ornament which the author is able to tentatively propose is that at least the amplitude of shell



Text-fig. 11. Selected morphotypes of the intergrading morphological series of *S. adicra* in the Bradford Abbas "sample"; numbers of BUCKMAN's "species" as in the "spinosity" x whorl section plot in Text-Fig. 9. All "species" approximately one quarter natural size.

plication and domal structure (nodes, spines) is a function of the growth rate for whorl-width and thus varies with whorl roundness. Spines are clearly associated with strong ornament in general and the diameter up to which spines are retained varies roughly with the strength of costation of the last whorls, i.e. with the diameter of the subsequent costate stages. This relationship also applies for at least most other, unrelated species, whenever costae and spines are both developed. Thus one could say that the mantle margin secreting the shell tended to more intense rythmic lateral contraction in relatively broad ("depressed") specimens than in relatively narrow ("compressed") specimens. But such a statement is almost nonsensical since we know so good as nothing about the anatomy of the animal.

If the supposed covariation between septal suture and shell plication can be shown to exist also in other, not closely related genera (it may then be called BUCKMAN's 2nd Law of Covariation), functional correlation has to be taken into account; i.e. the stiffening of the phragmocone, a strongly incised suture furnishing a better fixture of the septum against shear and a more even distribution of stresses from the septum onto the outer shell and vice versa. The inverse relationship between sutural complexity and costation (plication) intensity would then be a result of compensation in this mechanical function. Consequently, strong variability does not necessarily invalidate the assumption that costation serves a stiffening function. On the other hand, this type of covariation would support the theory of mechanical function of the fluted ammonite septum (WESTERMANN, 1956, 1958).

Taxonomy

Other synonyms of *Sonninia adicra*

England. — From the *L. discites* Subzone of Broad Windsor, near Bradford Abbas, Dorset, the holotype of *S. inaequa* BUCKMAN (1894, pl. 101) was figured. This "species" was also reported from Bradford Abbas (loc. cit.) and belongs to the morphotype "*S. modesta*" of *S. adicra*.

From the top of the *G. concavum* Zone of the Sandford Lane quarry, Dorset, comes *S. palmata* BUCKMAN (1894, pl. 90) which in all characters is close to the mode of the Bradford Abbas "sample" of *S. adicra*. In the *S. trigonalis* Subzone (middle *S. sowerbyi* Zone) of the same quarry originates *Sherbornites projectifer* BUCKMAN (1923, pl. 411) which certainly cannot be distinguished from BUCKMAN's (1926, pl. 669) own identification of a "*Sherbornites adicrus* WAAGEN" with which it was associated. *Sherbornites* is therefore a synonym of *S. (Euhoploceras)*. (However, "*Sherbornites undifer*" BUCKMAN, 1923 from the same subzone and quarry is probably a variety of the more involute *S. ovalis* (QUENSTEDT)).

Also from the *S. trigonalis* Subzone ("*mollis* hemera") of the near Clatcomb quarry, Dorset, comes *Stiphromorphites nodatopinguis* BUCKMAN (1923, pl. 398), type-species and only known specimen of the "genus". It has evo-

lute subcircular whorls but no typical spinose stage except for prominent and somewhat pointed bullae on the last phragmocone whorl (80 mm). If regarded as non-spinose, it falls well outside of the distribution of *S. adicra* (Text-fig. 9). If, however, this single specimen is regarded as a variant or pathological specimen of *S. adicra* with spines missing on the nucleus, the plot is perfectly in the Bradford Abbas "sample".

Central Europe. — The *L. discites* Subzone is present but the other subzones of the *S. sowerbyi* Zone are differently and often poorly developed rendering difficult correlation with the Dorset section.

From the northeastern Paris Basin, MAUBEUGE (1951) described four allegedly new species of *Sonninia*, of which *S. mussonensis* and *S. pseudogibbera* are certainly and *S. pseudoirregularis* and *S. pseudocostata* probably synonymous with *S. adicra*. Already OECHSLE (1958, p. 87) had placed the first name in synonymy with "*S. modesta*" and the others with "*S. polyacantha* BUCKMAN" which intergrades with *S. adicra*.

From northwestern Germany, HILTERMANN (1939) has reported and partly described typical *S. adicra* from the lower and middle parts of the *S. sowerbyi* Zone of the Weser Mountains; "*S. modesta*" was reported from the lower part of the zone. *S. sowerbyi adicroides* HILT. is certainly another *S. adicra*.

The species is again common in the Swabian Jura of Württemberg. Both WAAGEN's holotypes of *S. adicra* and *S. polyacantha* are from the Sowerbyi-Bank of Gingen, which has recently been reinvestigated by OECHSLE (1958). The famous, highly fossiliferous bed (also "Grundkonglomerat-Bank", Dogger/Mittlerer Jura Unter-γ) is usually developed as about 0.2 m impure often ironoolitic limestone with bored pebbles and concretions, and probably is a winnowed ("condensed") deposit representing the lower and middle *S. sowerbyi* Zone. Locally a sandy bed of similar thickness is superimposed. Both contain a rich fauna of *Sonninia sowerbyi* (MILL.), *S. trigonata* (QU.), *S. ovalis* (QU.), *S. fissilobata* (WAAG.), *S. jugifera* (WAAG.), *S. stephani* (BU.), *S. tessonia* (ORB.), *S. (Euhoploceras) adicra* (WAAG), *Ludwigia (Hyperlioceras) discites* (WAAG.), et al. This is overlain by about 15 m almost unfossiliferous "Mittel-γ" containing only rare *S. propinquans* (BAYLE) and *S. corrugata* (SOW.). They belong probably in the upper *S. sowerbyi* Zone, which is in turn overlain by the "Blaukalke" of the *O. sauzei* Zone.

OECHSLE (1958, p. 85, 89) admitted the morphological integration of *S. polyacantha* (WAAG.) with *S. adicra* (WAAG.) the latter of which has "page priority". *Am. Sowerbyi costosus* QUENSTEDT (1886), also from the Sowerbyi-Bank of Gingen, was placed in synonymy with *S. adicra* (loc. cit.). *S. berckhemeri* DORN (1935), from the same bed and locality, is another synonym, although it is a relatively compressed variety considering its strong ornamentation. Besides the "subspecies" *S. adicra externa* [nomen nudum], *S. adicra interna*, *S. modesta nenningensis* and *S. polyacantha intermedia*, OECHSLE (1958) also added *S. grandiplex* to the long list of synonyms. The latter

"species" is the exact counterpart to the "abnormal *S. modesta*" of BUCKMAN (1892, pl. 68), distinguished in the "revived" ornamentation on the large body chamber.

The probable microconch *S. subdecorata* BUCKMAN

BUCKMAN's (1893, pl. 84) "*subdecorata*-group/stock" from Bradford Abbas includes 4 allegedly "dwarfed" species, of which *S. subdecorata* and *S. decora* are almost certainly adult because of their modified body chambers. From the figures this is doubtful, however, of *S. subspinosa* and *S. decorata;* their apertures are unknown, and the phragmocones and body chambers if present are not clearly distinct from inner whorls of the associated large conchs. Again, spinose and non-spinose forms are represented. However, on the whorl-section x spinosity scatter (Text-fig. 9) for the Bradford Abbas "sample" the whole "group" plots at or slightly below the lower limit of distribution.

Without good first-hand knowledge of the type-specimens, the author does not feel justified in placing these "species" in synonymy with *S. adicra*, but prefers to consider them as a distinct single nomenclatorial species *S. subdecorata* which may be the males (microconchs) of *S. adicra* (see WESTERMANN, 1964a).

Other microconchs may be among the many small and alleged probable juveniles figured by BUCKMAN (1892–94) from Bradford Abbas, such as *S. euromphalica*. It is emphasized that it appears unlikely that this strong similarity exists between sympatric (bio-)species, and that further study may end the nomenclatorial distinction.

Taxonomic Conclusions

As argued elsewhere at some length (WESTERMANN, 1964 a, p. 41) the author attempts to adhere strictly to the "biospecies concept". At least 64—65 "species" from Bradford Abbas, 3—4 other "species" from elsewhere in Dorset, 2—4 "species" from France, and 4 "species" (and 5 "subspecies") from Germany, almost certainly belong to the single highly variable paleo-(chrono-)species *S. adicra*. In addition, the "dwarf *S. subdecorata*-group" probably contains the corresponding microconchs which because of lack of evidence, are still included in a different (nomenclatorial) species. Furthermore, since no significant morphological change can as yet be observed throughout the very restricted vertical range and the large geographical range (Dorset to, probably, Marocco), no subspecies can positively be distinguished.

This type of "lumping" does not lead to the loss of taxonomical precision, as may be argued, because there simply is no "precision" in nature; i.e. this procedure does not minimize the stratigraphic or faunistic information available. If such information should come up in the future, chronological or geographic subspecies can be distinguished bearing the names of

former species. For purposes of reference to a certain morphotype within this variable species, particularly if no figure is to be given, the use of the infra-subspecific category is open for use (Internat. Code Zool. Nomenclature, 1961). Since the term "variety" does usually imply the exceptional (marginal position within the frequency distribution), the use of "forma" is preferable for the major morphotypes which include "common species" of BUCKMAN.

For reasons of common usage (as species in OECHSLE, 1958) the distinction of the following four "formae" is suggested (Text-fig. 9):

1) "forma modesta"; weakly ornate, compressed and rather involute.
2) "forma dominans"; fully costate but weakly spinose, somewhat evolute and moderately compressed forms (including *S. polyacantha*, a "variety" with revived spinose stage).
3) "type"; spinose forms with outer costate stage, slightly compressed and moderately evolute.
4) "forma/var. crassispinata"; throughout strongly spinose, whorls very evolute and subcircular (probably relatively rare).

Species "diagnosis" of *S. adicra*. — The attempt to define or diagnose a taxon with highly variable morphological characters is discouraging. Although this is quite common with higher categories, infrageneric taxa do normally possess common characters which enable one to "define" it. That the subgenus *Euhoploceras* can be circumscribed only on common trends as opposed to the "definition" given in the Treatise, has been shown above. Even on the specific level is there hardly a single "continuous character" which would not be found elsewhere among the large number of species within the suborder or superfamily. Subgenus and species can however be diagnosed on character associations, especially the dimensions — ornament covariation. The diagnostic description of *S. adicra* within the large genus *Sonninia* is now as follows:

A species of *Sonninia* varying from rather involute smooth forms with finely costose nucleus and compressed — oval or subrectangular whorl-section, over moderately evolute forms with slightly compressed-oval inner spinose and outer costate whorls, to very evolute forms with subcircular, heavy spineous whorls throughout. — Low, narrow, hollow-floored keel on flattened "ventre", spines placed irregularly mediolaterally, intermittant dense primaries and secondaries become obscure and finally obsolete with strengthening spines. Costation of outer whorls if present extremely heavy, distant and recti- to rursiradiate.

Occurrence and age: northwestern, central and southwestern Europe. *S. sowerbyi* Zone, *L. discites* Subzone; more rarely in *S. trigonalis* Subzone. [Very rare also in the *G. concavum* Zone of Dorset.]

Other species

From the Mormon formation of Shasta County, California, CRICKMAY (1933, pl. 28) has described "*Stiphromorphites schucherti*" based on a single

fragment of a probable *S. (Euhoploceras)*. The specimen came from a horizon below beds with *S. (Papilliceras)* s.p., *Normannites (Itinsaites)* and a sphaeroceratid and may therefore belong in the *S. sowerbyi* Zone, but accurate dating and comparison of this specimen is not possible. Yet undescribed *Sonninia (Euhoploceras)* also occur in the Weberg formation of the Colpits group in east-central Oregon (LUPHER, 1941), probably in the middle Fernie group near Banff, Alberta and in the basal Shelikov formation of Wide Bay, Alaska Peninsula. In Alaska and Oregon they occur together with certain evolute *Witchellia* aff. *W. sutneri* (BRANCO) and *Eudmetoceras (Euaptetoceras)* sp. and belong therefore in the *S. sowerbyi* Zone. Only the Wide Bay form is represented by a sufficiently large and well preserved sample (to be described separately by the author). It is distinguished almost solely in the stronger secondaries, especially near their distal termination, which do not fade in the presence of lateral-spines. Another, but very poorly known species is *S. playfordi* ARKELL from the Newmarracara Limestone of western Australia (ARKELL, 1954, pl. 27) which was figured only in the side view of a single fragment. It was also said to be distinguished from the English forms in the stronger secondaries. However, the material did not justify the naming of a new species and its character remains dubious. Compared with the Wide Bay species and the specimens from Alberta and Oregon, the primaries appear much denser on the last preserved whorl particularly in consideration of the spinose inner whorls. The Australian form is associated with *Pseudotoites*, as in Alaska. — The Alaskan species plots within the distributions of *S. adicra* in all measurements taken.

The distinction of *S. (Papilliceras)* is of biostratigraphical importance; while resembling *S. (Euhoploceras)* in geographical distribution it appears to clearly indicate the upper *S. sowerbyi* to *O. sauzei* Zone if properly delimited. However, the biostratigraphic use of *S. (Papilliceras)* has hitherto been dubious or misinterpreted because of taxonomical confusion due to the strong overlap present in "single characters" between the two subgenera which almost certainly represent an exceptionally complete ancestral-descendant lineage. This dilemma is solved if several characters are considered concurrently with respect to their covariation, such as whorl section and relative umbilical width (Text-fig. 6).

Thus *S. (Papilliceras) papillatum* (BU.), the type-species, very much resembles evolute *S. adicra*, i.e. the whorl section is as in "forma modesta" and the umbilical width as in *S. adicra* "type"; however, this association is at the very limit or just outside of the distribution for *S. adicra*. Even more subtle is the distinction of *S. (Papilliceras) acantherum* BU. (almost certainly assigned to this genus for biostratigraphic reasons) which besides a similar association of whorl section with umbilical width has also heavy spines; however, it falls well outside, i.e. above — too high "spinosity" or/and too compressed whorl-section — the range of the whorl-section x spinosity distribution for *S. adicra*.

References

Arkell, W. J., 1933: The Jurassic system in Great Britain: (Edinburgh and London) Oliver and Boyd, 806 p., 46 pl.

— 1957: Jurassic ammonoids, in Arkell, Kummel & Wright, Mesozoic Ammonoidea. — Treatise on Invertebrate Paleontology, part. L, Mollusca 4, Geol. Soc. Amer. and Univ. Kansas Press.

Buckman, S. S., 1887—1907: Monograph of the ammonites of the Inferior Ooolite Series. — Palaeontogr. Soc. (London), CCLXII + 456 p., 124 pl.

— 1889 (1889 a): The descent of *Sonninia* and *Hammatoceras*. — Quart. J. Geol. Soc. (London), **45** p. 651—663, pl. 22.

— 1893 (1893 a): The Bajocian of the Sherborne district. — Quart. J. Geol. Soc. (London), **49**, p. 479—522.

— 1909—1930: Type Ammonites. (London), **1—7**, text and 790 pl.

Dorn, P., 1935: Die Hammatoceraten, Sonninien, Ludwigien, Dorsetensien und Witchellien des süddeutschen, insbesondere fränkischen Doggers. — Paleaontographica, A, **82**, p. 1—124, pl. 1—29.

Hiltermann, H., 1939: Stratigraphie und Paläontologie der Sonninienschichten von Osnabrück und Bielefeld. — Palaeontographica, A, **90**, p. 109—209, pl. 9—13.

Hölder, H., 1952: Über Gehäusebau, insbesondere Hohlkiel jurassischer Ammoniten. — Palaeontographica, A, **102**, p. 18—48, pl. 3—7.

Kummel, B. & Lloyd, R. M., 1955: Experiments on relative streamlining of coiled cephalopod shells. — J. Paleont., **29**, p. 159.

Maubeuge, P. L., 1951: Les ammonites du Bajocien de la region frontière Franco-Belge. — Inst. Roy. Sci. Nat. Belgique, mem. (2) **42**, 104 p., 16 pl.

Oechsle, E., 1958: Stratigraphie und Ammonitenfauna der Sonninien-Schichten des Filsgebiets unter besonderer Berücksichtigung der Sowerbyi-Zone (Mittlerer Dogger, Württemberg). — Palaeontographica, A, **111**, p. 47—129, pl. 10—20.

Quenstedt, F. A., 1883—88: Die Ammoniten des Schwäbischen Jura. — (Stuttgart) 1140 p., 126 pl.

Reeside, J. B. & Cobban, W. A., 1960: Studies on the Mowry shale (Cretaceous) and contemporary formations in the United States and Canada. — U.S. Geol. Surv. Prof. Paper, **355**, 126 p., 58 pl.

Silberling, N. J., 1956: "Trachyceras" Zone in the Upper Triassic of the western United States. — J. Paleont., **30**, p. 1147—1153.

Sokal, R. R. & Sneath, P. H. A., 1963: Principles of Numerical Taxonomy. Freeman, 358 p.

Westermann, G. E. G., 1964 (1964 a): Possible mechanical function of shell plication in a Triassic brachiopod. — Canadian J. Earth Sci., **1**, p. 99—120.

— 1964 (1964 b): Sexual-Dimorphismus bei Ammonoideen und seine Bedeutung für die Taxionomie der Otoitidae (einschließlich Sphaeroceratinae: Ammonitina, M. Jura). — Palaeontographica, A, **124**, p. 33—73, pl. 6—9.

— 1964 (1964 c): The ammonite fauna of the Kialagvik formation at Wide Bay, Alaska Peninsula, Part I, Lower Bajocian (Aalenian). — Bull. Amer. Paleont., **47**, no. 216, p. 327—503.

Bei der Schriftleitung eingegangen am 16. Juni 1965.

Anschrift des Verfassers:

G. E. G. Westermann, Assoc. Prof. & Curator, Dept. Geology,
McMaster University, Hamilton, Ont., Canada.