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Mid-Jurassic Ammonitina from the Central Ranges of Irian Jaya and the origin of stephanoceratids

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(with 2 figures and Plates 14–17)

Abstract

Selected specimens from the Seo and Suzuki ex-situ collections of mainly Bajocian Ammonitina from the Central Ranges of Irian Jaya are described and their phylogeny and/or paleobiogeography discussed. *Riccardiceras* gen. nov., type species *Coeloceras longalvum* VACEK from (late) Aalenian–Early Bajocian of the Alps, is named to distinguish serpenticone *"Docidoceras"* (lately placed in *Stephanoceras*) from the sub-spherocone *Docidoceras* s. str. *Riccardiceras* is the phylogenetic link between the *Erycites* gr. *gonionotus-Abbasitoides* [Erycitidae], and *Stephanoceras* s. l. [Stephanoceratidae], i.e. in parallel to the lineage *Erycites*(?) gr. *fallifax* – *Docidoceras* – *Emileia* etc. [Otoitidae]. Macroconch shape and sculpture of *Riccardiceras* resemble early *Stephanoceras*, but also intergrade with contemporary *Docidoceras*; septum/suture and the microconch morphology are close to *Docidoceras*. *Riccardiceras suzukinense* sp. nov. is most closely allied to *G. limatum* (POMPECKJ).

Key words: Ammonoidea, Irian Jaya, taxonomy, biostratigraphy, new species

Introduction

In the seventies, H. SUZUKI, then a student at Kyoto University (presently professor at Doshita University in Kyoto), and H. J. SEO, of Painai Lake Minerals Inc., made ex-situ collections of Middle and Upper Jurassic ammonoids in the Central Ranges of eastern (mainland) Irian Jaya. The ammonites from the Suzuki collection were kindly lent to me through the auspices of professor T. SATO of Tsukuba University, whereas the Seo collection was gifted to me by the exploration company in return for their study. Whereas the Mid-Bathonian to Early Callovian Macrocephalitinae and associated taxa from these collections have been described earlier (WESTERMANN & CALLOMON, 1988), the remaining Mid-Jurassic Ammonitina of exceptional preservation or unique occurrence are presented here.

The Jurassic litho- and biostratigraphy of eastern Indonesia, including Irian Jaya on the island of New Guinea, has recently been reviewed by SUKAMTO & WESTERMANN (1992). The only relatively recent taxonomic study of Middle Jurassic ammonites from Irian Jaya (WESTERMANN & GETTY, 1970) was based on an earlier ex-situ collection from the Central Ranges, i.e. the Le Roux collection stored in the Rijksmuseum van Geologie en Mineralogie in Leiden, The Netherlands. Extensive discussions of previous works on Middle Jurassic ammonoids on eastern Indonesia are found in that work.

The Mid-Bathonian to Early Callovian ammonite taxa of Eastern Indonesia and Papua New Guinea and their ages are now relatively well known, based on my recent field work (partly accompanied by T. SATO, S. SKWARKO and F. HASIBUAN), that resulted in the first significant in-situ collections. Several formal ammonite assemblage zones have been established for the Sula Islands, Irian Jaya and Papua New Guinea, based on relatively rich *Macrocephalites* associations with tulitids, cadomitines and oppeliids (WESTERMANN & CALLOMON, 1988; HILLEBRANDT et al., 1992), i.e. Macrocephalites bifurcatus Zone (Middle Bathonian), M. apertus Zone (Late Bathonian), and M. keeuwensis Zone (late Early Callovian). However, most of the Callovian remains poorly known.

The earlier Mid-Jurassic biostratigraphy, however, remains an enigma owing to poor outcrop conditions, inaccessibility, and very limited field work. In particular, the presence of marine Aalenian has so far not been established, nor indicated by the numerous large ex-situ collections which may contain abundant Early Bajocian ammonites.

1. The oldest Mid-Jurassic ammonite species so far identified, *Fontannesia kiliani* (KRUIZ.) and *"Docidoceras longalvum* cf. *limatum* (POMP.)" = *Riccardiceras suzukinense* n. sp. from the Central Ranges (WESTERMANN & GETTY, 1970), could be as old as latest Aalenian, but

more probably are of early to mid-Lower Bajocian age. *F. kiliani* probably indicates the Laeviuscula Zone according to its occurrence in Tibet (WESTERMANN & WANG, 1988), i.e. about the age of *Pseudotoites* cf. *robiginosus* (CRICK). *P. robiginosus* is rare in Irian Jaya, but occurs abundantly in the Laeviuscula Zone of Western Australia, together with *Fontannesia (Newmarracaroceras)* spp. After many years of hyphonated existence, the *"D." longalvum* group is here given the generic name *Riccardiceras*.

2. The next-younger, larger fauna is known mainly from the Vogelkop Peninsula and Geelvink Bay, consisting of diverse cosmopolitan species of the late-Early Bajocian Stephanoceratinae and a few Sphaeroceratinae (WESTERMANN, 1956 and review by WESTERMANN & GETTY, 1970). Among the endemic species are *Stephanoceras*(?) *etheridgei* (GERTH), *Teloceras*? *indicum* KRUIZINGA, and *Chondroceras boehmi* WEST. But most were based on single, poorly preserved specimens. The holotype of *T.*? *indicum* is almost complete, but with a strongly corroded outer whorl (refigured by WESTERMANN & GETTY, 1970, text-fig. 9). Whereas the inner whorls resemble extremely coarse-ribbed *Teloceras/conchsStemmatoceras*? gr. *subblagdeni* WEISERT, the body-chamber uncoils markedly and becomes much more rounded and, probably, much more smoother (unless this is entirely due to corrosion). This, together with its small size for a macroconch (D=115 mm), suggests that *T.*? *indicum* could be the only known western Pacific *Zemistephanus* (HALL & WESTERMANN, 1980). It is distinguished from *Irianites* WEST. & GETTY by the conical umbilicus of the inner whorls. The problematic ages of *Irianites*, *"Bullatimorphites" costidensus* WEST. & GETTY and similar, but lappeted microconchs are dicussed below.

3. Only very few Late Bajocian ammonites are known. Very rare Leptosphinctinae (previously misidentified as Kimmeridgian *Idoceras*) have been found. One specimen of the early–Late Bajocian genus *Caumontisphinctes* was collected in-situ on Sula (WESTERMANN & CALLOMON, 1988), and two came ex-situ from Irian Jaya (one illustrated by WESTERMANN & GETTY, 1970, pl. 51, figs 3a–b).

4. The endemic *Praetulites kruizingai* WEST., known from Irian Jaya and Sula (WESTERMANN, 1956; WESTERMANN & CALLOMON, 1988), is probably Late to latest Bajocian, possibly ranging into the earliest Bathonian.

5. *Satoceras* WEST. & CALLOMON also occurs mainly in eastern Indonesia, but is also known from Japan. *S. hataii* (TAKAHASHI) was first described as a Callovian perisphinctid from Honshu and is here illustrated from Irian Jaya. *Satoceras* has recently been found in-situ on Sula, where its age can be bracketed between latest Bajocian and early Middle Bathonian (WESTERMANN & CALLOMON, 1988).

Taxonomic descriptions

Family Sphaeroceratidae BUCKMAN, 1920
Genus *Satoceras* WESTERMANN & CALLOMON, 1988

Type-species (orig. des.): *Satoceras satoi* WESTERMANN & CALLOMON, 1988, from Early Bathonian of Irian Jaya and Sula.

Satoceras satoi WESTERMANN & CALLOMON
Plate 16, figs 3a, b

1988 *Satoceras satoi*, WESTERMANN & CALLOMON, p. 40, text-figs 10a–b, plate 16, figs 1–3 [and earlier synonymy therein].

Comments

The Suzuki ex-situ collection from Homejo, Kemabo River, which has furnished the holotype, also includes the topotype illustrated here. Its nucleus closely resembles the impression associated in the same concretion with *Irianites* (Pl. 16, figs 1a–b), which would suggest a mainly Early Bathonian age for *Irianites* (interpretation 2, above). This specimen also displays the sharp primaries ending in small lateral bullae, characteristic for the mature body-chamber. The inner whorls, however, are also closely similar to those of *"Bullatimorphites? (Treptoceras?)* n. sp. A ♂" of WESTERMANN and GETTY (1970), illustrated on plate 14, figures 2a, b and discussed below.

Satoceras hataii (TAKAHASHI)
Plate 14, figs 4 a, b

1969 *Obtusicostites hataii* TAKAHASHI, p. 71, pl. 7, fig. 9 and pl. 9, fig. 6.
1988 *Satoceras hataii* (TAKAHASHI), WESTERMANN & CALLOMON, p. 40.

Description

The phragmocone is subspherical with involute, depressed-oval whorls, similar but more inflated than in *S. satoi*; but the primary and secondary costae are much coarser and much less curved, almost rectiradiate. The body-chamber, 3/4 whorls long, uncoils and rounds gradually, and bears similarly coarse and almost rectiradiate costae as the phragmocone, with exceptionally coarse secondaries. Faint mid-lateral bullae are present at the end of the phragmocone and at the beginning of the bosy-chamber. Compared to *S. satoi* and *S.*? *subkamptum* (SPATH), the ribs are straighter and the secondaries much coarser. The (incomplete) aperture at c. 105 mm diameter is typically constricted and slightly oblique. The septal suture is as in *S. satoi* (WESTERMANN & CALLOMON, 1988, Text-fig. 10a–b), i.e. highly complicated, with radial saddle envelope, deep and narrow L, a U_2 of about half as large as L, and a rather well developed umbilical saddle.

Comments

Only the holotype from the Arato Formation of northwest Honshu, Japan, has been known. Its age is bracketed by the subjacent, early–Late Bajocian Leptosphinctes Zone (SATO & WESTERMANN, 1991) and the Mid– to Late Bathonian *Kepplerites*–(?)*Cadomites* assemblage (= ? Pseudoneuqueniceras yokojamai Zone of SATO & WESTERMANN, 1991) much higher in the sequence. A mainly Early Bathonian age is therefore indicated for the Honshu occurrence, similar as for *S. satoi* on Sula.

The single, large, but somewhat damaged specimen with aperture from the Suzuki collection from Homejo, which was recorded and reclassified by WESTERMANN & CALLOMON (1988), is a significant find and illustrated here. It closely resembles the holotype from Japan, which is a somewhat distorted specimen preserved with one side only and without venter. Poor preservation probably was the reason for its original misplacement in the superfamily Perisphinctaceae. The New Guinea specimen is thus the best preserved known specimen of *S. hataii* and an exceptional biogeographic link.

Tab. 1. Measurements (mm) of MM 19815

	Diameter	Whorl-width	Height	Ww/H	Umbil.	Prim.	& sec.
						1/2 whorl	
Aperture	105	c. 61 (.58)	49	1.25	31.4 (.30)	12	c. 35
end phr.	70	–	31	–	13.0 (.19)	13	36
	64	45 (.70)	28	1.6	12.2 (.)	13	–

Satoceras boehmi (WESTERMANN & GETTY)
Plate 14, figs 5a–c

1913 *Macrocephalites keeuwensis β-γ* BOEHM, p. 16, text-fig. 9, pl. 5, fig. 2 (holotype).
1970 *Subkossmatia obscura* SPATH *boehmi* WESTERMANN & GETTY, p.266, pl. 56, figs 3a–b, 4a–b only.
?1988 (?)*Satoceras boehmi*, WESTERMANN & CALLOMON, p.43, text-fig. 10c, pl. 17, figs 1a–b.

The specimens of the Suzuki collection from an unknown locality of Irian Jaya, here ilustrated, closely resembles the (lost?) holotype from Mamapiri, Irian Jaya. It is also a good match to the large fragment from Assemblage 1a of the Sula islands, described by WESTERMANN & CALLOMON (1988). The Sula assemblage includes *Cadomites* cf. *daubenyi* (GEMM.) and underlies the Mid-Bathonian Bifurcatus Zone, indicating a Late Bajocian–Early Bathonian age.

This species was originally classified (as subspecies) in the Callovian genus *Subkossmatia* of the Subfamily Eucycloceratinae (then a family), which is now known to have been restricted to the Indo-East African Bioprovince. The fragments of "?*Eucycloceras*", also Eucycloceratidae, illustrated on the same plate by WESTERMANN & GETTY (1970, pl. 56, figs 1–2) are probably incomplete microconchs of *Macrocephalites bifurcatus* (BOEHM) (cf. WESTERMANN & CALLOMON, 1988, pl. 9, figs 1–2, 4).

The complete size of the Suzuki specimen from Irian Jaya was c. 95 mm. The exposed ultimate whorl, including the 1/2 whorl body-chamber, is moderately involute with rounded-trapezoidal section, about as high as wide. The converging flanks are separated from the vertical umbilical wall by a rounded margin; the venter is gently rounded. The inner whorls are probably ovate with rounded umbilical slope, and also about as high as wide. The sculpture of the phragmocone (internal mould) consists of blunt, very dense and strongly forward-curved primaries and secondaries, which pass convexly over the venter. On the body-chamber, primaries and secondaries become coarser, but remain blunt on the internal mould and adorally inclined. Remnants of the shell show, however, that the last primaries were sharp and narrow, with maximum elevation (?bullae) at mid-flank. The aperture is obliquely constricted.

Tab. 2. Measurements (mm) of MM 19816

	Diameter	Whorl-width	Height	wW/h	Umbilicus	Prim.	Sec.
						1/2 whorl	
body-ch	89	37 (.42)	35.5	1.04	21.5	13	45
end phr.	64	35 (.48)	30	1.0	11.2	15.5	50

Superfamily Stephanocerataceae NEUMAYR 1875
Family Stephanoceratidae NEUMAYR 1875
Genus *Irianites* WESTERMANN & GETTY 1970

Type-species (orig. design.): *"Coeloceras" moermanni* KRUIZINGA, 1926; a microconch from Sula Islands

Irianites moermanni (KRUIZINGA) ♀/M & ♂/m
Text-figs 1–2 ; Plates 15–16

♂ 1926 *Coeloceras moermanni* KRUIZINGA, p. 44 with text-fig., pl. 13, fig. 2. [refigured in WESTERMANN & GETTY, 1970, text-fig. 14]
♂ 1970 *Irianites moermanni* (KRUIZINGA, 1926) ♂, WESTERMANN & GETTY, p. 274, text-figs 13–16, 20–24, pls. 57–58. [With additional synonymy]
♂ 1970 *Irianites* cf. *I. moermanni* (KRUIZINGA) ♀, WESTERMANN & GETTY, p. 281, text-figs 19–24, pls. 59–62.

Morphology

Irianites is known only in the single, dimorphic type species, *I. moermanni*, from several islands of the Moluccas and from Irian Jaya (see WESTERMANN & GETTY, 1970). In addition to the approximately 75 microconchs and 25 macroconchs of *Irianites* known previously, the 18 microconchs and 4 macroconchs from the new collections also belong to the same morphs, with closely matching inner whorls. We therefore conclude, even in the absence of stratigraphic data, that only one biospecies is present.

The sculpture of the microconchs, collected by H.J. SEO at S. Bija in the S. Badai River bed, is particularly well preserved in the septate whorls illustrated on Plate 16, figs 1a–b.

A macroconch from the same SEO collection (Pl. 15, figs a–d) is the largest and most complete specimen known, yet it misses the aperture. There is almost perfect resemblance to the complete body-chamber whorl illustrated earlier from the Sula Islands (WESTERMANN & GETTY, 1970, text-figs 18a–b). The immature growth stages are as described previously: the platyconic juvenile stage, with lateral nodes and irregular umbilical bullae, is followed by depressed elliptical whorls (Pl. 16, figs 2 a–b). The body-chamber is *Teloceras*/*Stemmatoceras*-like. The ontogeny of shape and sculpture in the new, large specimens is as described previously and follows the developmental trend (Figs 1–2). The width/height ratio of the whorls develops from c. 1.2 in the juvenile (2–5 cm diameter), via c. 1.5 of the penultimate whorl, to c. 2.0 of the body-chamber. The same collections also contains an isolated, large apertural fragment (Pl. 16, figs 3a–b), which may belong to the same morph. It is broadly depressed and with prominent lateral bullae and dense, convex ventral lirae.

Affinity

In the original description WESTERMANN & GETTY (1970) were swayed mainly by the serpenticonic and compressed whorls of the microconch to place *Irianites* tentatively in the Perisphinctaceae, rather than the Stephanoceratacae. However, the characteristic umbilical bullae on evolute-compressed whorls are now known to be present in several stephanoceratid genera. The oldest-known taxon is *Gerzenites* WEST., the microconch to *Kumatostephanus* BUCK. from the Sauzei Zone of western Europe (WESTERMANN, 1964; SANDOVAL, 1983; FERNANDEZ LOPEZ, 1985). Umbilical bullae are developed especially in *K. (G.) aequicostatus* WESTERMANN (1954, fig. 99 and pl. 21, figs 4, 7), which resembles the *Irianites moermanni* microconch also in the evolute, platyconic whorls, and even in the simple septal suture with reduced U_2. Other stephanoceratids with umbilical bullae are the recently described genus *Duashnoceras* SANDOVAL & WEST. from the Lower/Upper Bajocian boundary of Mexico, e.g. *D. undulatum* (BURCK.), *D. paucicostatum* (FELIX), and *D. floresi* (BURCK.), as well as some specimens of *Phaulostephanus* (SANDOVAL & WESTERMANN, 1986, figs 18, 26). On the other hand, blade-like primaries with sharp drop from a high elevation at the umbilical shoulder, and a reduced U_2 lobe, are also developed in the serpenticonic *Parabigotites crassicostatus* IMLAY and its microconch *"Normannites" kialagvikensis* IMLAY, from the Crassicostatus Zone (Sauzei Chron) of North America (IMLAY, 1964, pl. 13, figs 1–8, 10, 11; pl. 29, figs 1–15). But this endemic form could be an early perisphinctid (e.g. TAYLOR, 1988).

The adult *Irianites* macroconch (♀), however, is a close homeomorph to *Teloceras* and *Stemmatoceras* with its trapezoidal, highly sculptured outer whorls (Pl. 15). In fact, without exposure of the flat umbilicus of the inner whorls (i.e. the platyconic inner whorls that can be seen in sagittal section), most mature *Irianites* macroconchs cannot be clearly distinguished from typical late-Early Bajocian stephanoceratids, with the exception of the incipient ventral depression if clearly developed.

Perhaps, *Irianites* can find its place in the Garantianinae [Stephanoceratidae], rather than in the Stephanoceratinae, or it may even be distinct enough for subfamily-status. Again, stratigraphically controlled collections with datable associated fauna are needed to solve this problem.

Age according to one associated spherocone

The only hint at the age of *Irianites* comes from an ex-situ concretion which contained the impressions of a *Sulaites* sp. indet. together with that of a small spherocone, which cannot be identified precisely (Pl. 14, figs 1a–b) (WESTERMANN & GETTY, 1970, pl. 55, figs 4a–b). This important important incomplete specimen is a phragmocone with body-chamber fragment that belonged to a small, relatively evolute spherocone with rounded whorls and very dense, projected costae. There appear to be two plausible alternatives for the affinity and age of this spherocone.

Interpretation 1: Sauzei Chron. The spherocone is a small, fully grown, densely isocostate and lappeted microconch *"Bullatimorphites? (Treptoceras?)*, n. sp. A ♂" of WESTERMANN & GETTY (1970 , pl. 55, figs 1–3) of which the best specimen is shown on Plate 14, figs 2a–b. According to this interpretation, this morph corresponds to the macroconch *"B.? (T.?)" costidensus* WEST. & GETTY (1970, pl. 54, figs 1–4), which is also isocostate, but with "simple" aperture. The septal suture with tri- or multifid lobes and retraction at the umbilicus indicates that this is not a tulitid. If this is indeed a dimorphic pair – which can only be surmised in the absence of stratigraphy – then the dense, isocostate ribbing with long primaries and the moderately involute, gradually uncoiling whorls of the macroconch and microconch suggest that this "species" belongs to *Labyrinthoceras* BUCKMAN of the Early Bajocian family Otoitidae. *Labyrinthoceras* is known from Europe and North America where it is restricted to the Sauzei Chron. Our supposed macroconch is relatively small and not very inflated, resembling the West European *L. intricatum* (BUCKMAN); the rare microconchs with lappets have been illustrated from Spain (SANDOVAL, 1983, pl. 3, fig. 4), Portugal (FERNANDEZ LOPEZ et al., 1994), and the United States, i.e. *"Otoites?" delicatus* IMLAY (1964).

The originally supposed microconch of *Labyrinthoceras* (WESTERMANN, 1964), i.e. the small *Frogdenites* BUCKMAN with lappets, has later been disposed on stratigraphic and morphological grounds (PARSONS, 1974; GALÁCZ, 1980). In contrast to the lappeted microconchs suggested for *Labyrinthoceras* by SANDOVAL and FERNANDEZ LOPEZ (see above), GALÁCZ (1990) has recently described *L. manselli* BUCK., with "simple" aperture, as the corresponding microconch. (He consequently transferred *Labyrinthoceras* from the Otoitidae to the Sphaeroceratidae). This interpretation and GALÁCZ'S suggestion that SANDOVAL'S lappeted [*Labyrinthoceras*] microconch could be a *Kumatostephanus*, i.e. *Gerzenites* [Stephanoceratinae], are not accepted here.

Interpretation 2:. (Late Bajocian–) Early Bathonian. The impression attached to *Irianites* is of the inner whorls of *Satoceras*, so far known only as a macroconch (WESTERMANN & CALLOMON, 1988, pl. 16, fig. 2). According to CALLOMON (in WESTERMANN & CALLOMON, 1988, p. 40), however, *"Bullatimorphites ?" costidensus* WEST. & GETTY could be a *Satoceras* microconch (not a *Labyrinthoceras* macroconch as in 1). The juvenile whorls of *Satoceras satoi* WEST. & CALL., ♀, closely resembling the mentioned impression, are again illustrated on Pl. 14, fig. 3a.

Tab. 3. Measurements (mm) of *Irianites moermanni* ♀ (ROM ....)

Diameter		Whorl-width	height	Umbilicus	Prim.	Second.
					1/2 whorl	
body-ch	132	69.5	37	68 (57)	21.5	c. 28
	87	47	28	39 (45)	26	–

Genus *Riccardiceras* gen. nov.

Type-species: *Coeloceras longalvum* VACEK 1886 (holotype refigured by WESTERMANN, 1964, pl. 6, fig. 1) from the (upper) Aalenian – basal Bajocian of the Southern Alps.

Diagnosis: Resembling early *Stephanoceras* in the platyconic to serpenticonic, rounded whorls with complete, plicate costae; but with biaxial (bullate) septum, suture with two internal saddles and large, subvertical "2nd lateral lobe" U_2.

Origin of name:

yHonouring my long-standing friend and collaborator, Professor Alberto C. RICCARDI, eminent Argentine paleontologist and geologist.

Comments

The new generic name formally separates the serpenticonic species group of *"Docidoceras" longalvum* from the subcadiconic group of *D. cylindroides* BUCKMAN, type species. Intermediate morphospecies, however, existed between these extreme morphologies around the Aalenian-/Bajocian stage boundary (WESTERMANN, 1964, fig. 14 right). This broad species "complex", however, included two major, largely co-existent, cosmopolitan clades, both derived from the mid-Aalenian Erycitidae: (1) the Otoitidae, an offshoot from the *Erycites fallifax – Abbasites* group and with typical *Docidoceras* as oldest-known member, and (2) the Stephanoceratidae, going back to the *"Erycites" gonionotus – Abbasitoides* group and first represented by *Riccardiceras*. Significantly, the septal surfaces and sutures are astonishingly constant across this broad range of coiling (WESTERMANN, 1956a), with the *Riccardiceras* structures clearly distinct from that of typical early *Stephanoceras* with similar coiling and sculpture, or even forms with more depressed whorls, e.g. the *Skirroceras* microconch *Epalxites anceps* (QU.) (Pl. 17, 2c vs. fig. 5).

There remains, however, some confusion about the species-level classification and age of the type-species, *R. longalvum*. The serpenticonic, densely costate lectotype (designated as "holotype") and one or two syntypes (WESTERMANN, 1964, pl. 6, figs 1–2) came from a thin, lenticular grainstone bed on top of the Oolite di San Vigilio at Cap St. Vigilio in the Italian Alps. This level is

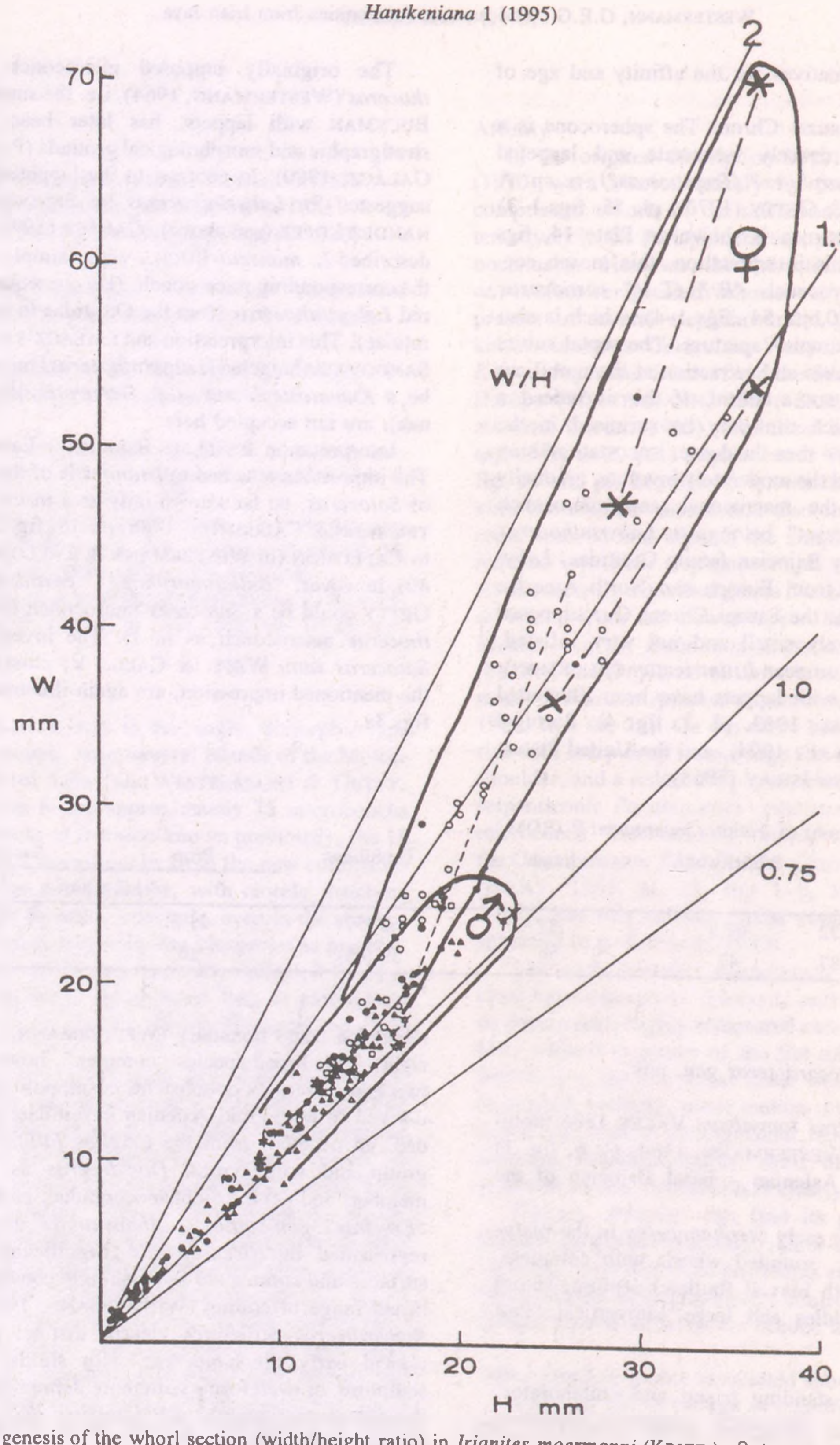
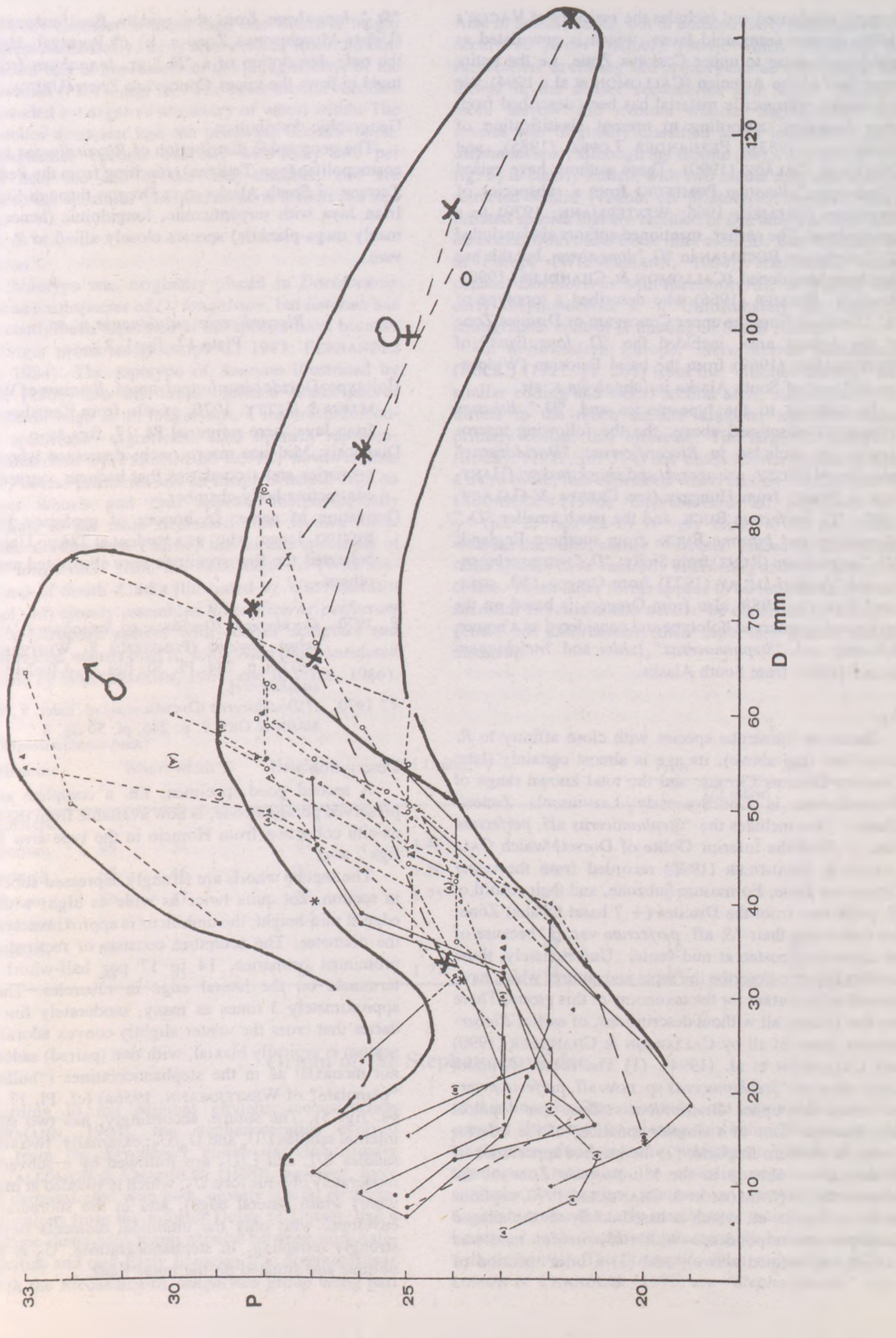


Fig. 1. Morphogenesis of the whorl section (width/height ratio) in *Irianites moermanni* (KRUIZ.), ♀ (macroconch) & ♂ (microconch); heavy crosses mark the new specimens, a large circle the Sula specimen; note the strongly positive allometry for whorl width in the macroconch

Fig. 2. Morphogenesis of sculpture in *Irianites moermanni* (KRUIZ.) ♀ & ♂; number of primary (P) and secondary (S) costae per half-whorl; note the adult modification mainly in the secondaries.


D mm
10
20
30
40
50
60
70
80
100
120
P
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30
33

strongly condensed and includes the majority of VACEK's (1886) diverse ammonoid fauna, which is now dated as mid-Murchisonae to upper Concava Zone, i.e the entire upper half of the Aalenian (CALLOMON et al., 1994). No indubitably conspecific material has been described from other localities, according to present classification of SANDOVAL (1983), FERNANDEZ LOPEZ (1985), and CRESTA & GALÁCZ (1990). These authors have raised *"Coeloceras" limatum* POMPECKJ from a subspecies of *longalvum* (BREMER, 1966; WESTERMANN, 1970) to a species level. The earlier, mentioned authors also included *"D." perfectum* BUCKMAN in *"D." longalvum*, but this has also been abandoned (CALLOMON & CHANDLER, 1990). However, BREMER (1966) who described a topotype of *"C." limatum* from the upper Concavum or Discites Zone of the Ankara area, included the *"D. longalvum"* of WESTERMANN (1969) from the basal Bajocian (Widebayense Zone) of South Alaska in *longalvum* s. str.

In addition to the type-species and *"D." limatum* (POMPECKJ) discussed above, the the following macroconchs are included in *Riccardiceras*: *"Docidoceras" telegdirothi* GÉCZY, *wysogorski* and *chocksinskeyi* (HANTKEN in PRINZ) from Hungary (see CRESTA & GALÁCZ, 1990); *"D. perfectum* BUCK. and the much smaller *"D." planulatum* and *biforme* BUCK. from southern England; *"D." trapanicum* (RENZ) from Sicily; *"D." warmspringensis* and *?lupheri* IMLAY (1973) from Oregon (*"D. striatum"* TAYLOR, 1988, also from Oregon, is based on the very poorly preserved holotype and considered as a nomen dubium); and *"Stephanoceras" juhlei* and *?nelchianum* IMLAY (1964) from South Alaska.

Age

Based on numerous species with close affinity to *R. longalvum* (see above), its age is almost certainly (late) Concava–Discites Chrons, and the total known range of *Riccardiceras* is Concava–early Laeviuscula Zones/-Chrons. This includes the *"Stephanoceras* aff. *perfectum* var. γ" from the Inferior Oolite of Dorset, which CALLOMON & CHANDLER (1990) recorded from the upper Concavum Zone, Formosum Subzone, and their record of *G. perfectum* from the Discites (+ ? basal Ovalis) Zone; but it excludes their *"S.* aff. *perfectum* var. β" because of its alternating costae at mid-venter. Unfortunately, these authors failed to describe the septa and sutures which have proved so important for the taxonomy of this group. There are few claims, all without descriptions, of earlier *Riccardiceras*, most of all by CALLOMON & CHANDLER (1990) and CALLOMON et al. (1994). (1) The record (without illustration) of *"Stephanoceras* sp. nov. aff. *perfectum* var. α" from the upper Bradfordensis Zone (or topmost Murchisonae Zone of a simpler zonation) of the Inferior Oolite in southern England; (2) the implied appearance of *R. longalvum* already in the Murchisonae Zone of the Inferior Oolite (CALLOMON & CHANDLER, 1990, captions to Pl. 1, figs 2a–c), which is based solely on the alleged dimorphic correspondence with *Abbasitoides modestus* (which was refuted above); and (3) a brief mention of *"St." longalvum* from the middle Bradfordensis Zone (Upper Murchisonae Zone s. l.) of Portugal. However, the only description of a *"D."* gr. *longalvum* from Portugal is from the upper Concavum Zone (URETA, 1985).

Geographic distribution

The geographic distribution of *Riccardiceras* is quasi-cosmopolitan (pan-Tethyan), reaching from the Peninsular Terrane of South Alaska over Oregon through Europe to Irian Jaya with serpenticonic, longidomic (hence presumably mega-planktic) species closely allied to *R. longalvum*.

Riccardiceras suzukinense n. sp.

Plate 17, figs1–2

Holotype: *Docidoceras longalvum* cf. *limatum* of WESTERMANN & GETTY, 1970, ex-situ from Kemaboe River, Irian Jaya, here refigured Pl. 17, figs 1a–c.

Diagnosis: Mid-size macroconch; depressed whorls with primaries and secondaries that become coarser on the contracting body-chamber.

Derivation of name: In honour of professor Hiroyuki SUZUKI, Japan, who, as a student at Tokyo University, collected the fine specimen here illustrated and many others.

♀ 1970 *Docidoceras (Docidoceras) longalvum* (VACEK) cf. subsp. *limatum* (POMPECKJ) ♀, WESTERMANN & GETTY, p. 244, Pl. 50, figs 1a–d [holotype of *R. suzukinense*].

♀? 1970 (?)*Docidoceras (Docidoceras)* sp. indet. ♀, WESTERMANN & GETTY, p. 246, pl. 50 fig. 3.

Description

A second good specimen, i.e. a complete and well preserved phragmocone, is now available from the SUZUKI ex-situ collection from Homejo in the type area (Pl. 17, figs 2 a–c).

The septate whorls are strongly depressed-subelliptical in section, not quite twice as wide as high, with lateral edge at mid-height; the umbilicus is approximately 50% of the diameter. The sculpture consists of rectiradiate and prominent primaries, 14 to 17 per half-whorl, which terminate on the lateral edge in tubercles. There are approximately 3 times as many, moderately fine secondaries that cross the venter slightly convex adorally. The septum is typically biaxial, with two (paired) saddle axes, not monaxial as in the stephanoceratines ("bullate" vs. "planulate" of WESTERMANN, 1956a) (cf. Pl. 17, fig. 2c vs. fig. 5). The suture, accordingly, has two sub-equal internal saddles I/U_n and U_n/U_3; externally, two sub-equal saddles E/L and L/U_2 are followed by a subvertical or moderately oblique lobe U_2, which is situated at maximum whorl width (lateral edge); and in the subradial saddle envelope, with only the umbilical elements beyond U_2 strongly retracting. In stephanoceratines, U_2 is strongly oblique and situated on the inner flank.

The body-chamber is more than one whorl in length and degresses markedly, as is also evident from the umbilical seam that is impressed on the phragmocone of the new specimen (Pl. 17, fig. 2a). The cross-section becomes more rounded by negative allometry of whorl width. The lateral nodes disappear and the primaries become blunt. The secondaries become coarser, with only two per primary near the end of the body-chamber, and are retained to the aperture. The peristome is constricted and oblique.

Discussion

The holotype was originally placed in *Docidoceras limatum* as a subspecies of *D. longalvum*, but *limatum* has more recently been separated at the species-level because of its longer primaries (SANDOVAL, 1983; FERNANDEZ LOPEZ, 1984). The topotype of *limatum* illustrated by BREMER (1966) has the same flattened flanks and/or absent lateral edge as in *longalvum*, a feature here considered specifically significant. The Spanish representatives illustrated by FERNANDEZ LOPEZ, however, has relatively coarse primaries and an incipient lateral edge on the inner whorls and thus appears morphologically intermediate to the more depressed New Guinea form. Along the northeastern Pacific, the superb specimen of "*D.* aff. *longalvum*" from the basal Bajocian (Widebayense Zone) of South Alaska illustrated by WESTERMANN (1969, pl. 33) closely resembles *Riccardiceras perfectum* BUCK., a European species with coarser sculpture and more depressed whorls than *R. longalvum* (but considered conspecific by WESTERMANN, 1964, and BREMER, 1966).

Also in South Alaska, but in undated Early Bajocian beds, occurs *R. juhlei* (IMLAY, 1964), which resembles *R. suzukinense* in coiling and primary costae with nodes, but differs in the denser secondaries and larger, probably more narrow and evolute whorls. Significantly, this species was originally classified as an indubitable early *Stephanoceras*, although the septum (IMLAY, 1964, pl. 16, fig. 6) is clearly bullate with two saddle axes and weakly retracted suture (visible on plastotype). Several, more inflated species that are retained in *Docidoceras* were also described from these Cook Inlet sections. But, similarly as in Europe (WESTERMANN, 1964), transitional forms connect *Docidoceras* with *Riccardiceras*, as well as with early *Stephanoceras* s. l. Unfortunately the required stratigraphic control is missing in South Alaska.

In northwestern Europe, *Riccardiceras planulatum* (BUCK.) (1921, pl. 264) from the "discites hemera" has similar coiling and whorl section as *R. suzukinense*, but differs in the much smaller diameter and the denser primary costae, that bifurcate. The large *R. perfectum* (BUCK). (1922, pl. 314) has much shorter primaries and a more ovate, less depressed whorl section. CALLOMON & CHANDLER's (1990) "*Stephanoceras* aff. *perfectum* var. γ" (pl. 2, figs 2a–b) is very close to *R. perfectum*, whereas the other, earlier "variants" placed by them in the same species have ventrally alternating and/or interrupted costae. These latter forms appear to be intermediate to the ancestral Erycitidae and need to be classified as a distinct genus, but unfortunately their septa and sutures remain unknown.

Tab. 4. Measurements (mm)

	Diameter	Whorl-width %	Height %	W/H	Umbil. %	Prim.	Sec.
						1/2 whorl	
Holotype							
aperture	95	34	24	1.45	54	c. 22	45
body-ch.	65	46	31	1.50	50	19	55
phragm.	53	47	27	1.75	49	17	–
MM 19817							
phragm.	65	47	28	1.7	47	16	47
	40	51	28	1.77	48	14	–

Origin of the Stephanoceratidae

According to my original phyletic reconstruction (WESTERMANN, 1964), the stephanoceratids evolved directly from the *Erycites*(?) *gonionotus–Abbasitoides* group. CALLOMON & CHANDLER (1990), however, have recently demonstrated with new, closely spaced stratigraphic collections from the Inferior Oolite of Dorset, that a morphologic quasi-continuum existed between mid-Aalenian erycitids and mid-Early Bajocian true *Stephanoceras* s. l., with the *Riccardiceras longalvum* group being part of this lineage. They, however, not only applied extreme generic "lumping" by placing this entire lineage into the single genus *Stephanoceras* (unfortunately without investigating or recording the essential septal and sutural attributes), but also assumed a non-stephanoceratid dimorphism for the early members of their *Stephanoceras* lineage, i.e. the supposed microconchs bearing apertures without lappets. The dimorphic pairs suggested by CALLOMON & CHANDLER (1990) are "*Stephanoceras*" *[Ric-*

cardiceras] longalvum [M] – *Abbasitoides modestus* (VACEK) [m] (lectotypes designated and refigured by WESTERMANN, 1964, pl. 6, figs 1, 8); *"S."* aff. *perfectum* BUCK. [M] – *A.* aff. *modestus* [m]; and *"S." perfectum* [M] – *"S.?" planulatum* (BUCK.) [m]. I classify *"Docidoceras" planulatum* as a *Riccardiceras* macroconch, despite its small diameter (72 mm); the size ratio closely resembles that present in the Stephanoceratinae macroconchs, i.e. *Phaulostephanus* versus *Stephanoceras*, *Skirroceras*, *Teloceras*, etc. *A. modestus* contrasts with all known Stephanoceratidae microconchs in the "simple" aperture without lappets and, with micro- and macroconchs of that family, by the minute external lobe E that is characteristic of erycitids (Pl. 17, fig. 4). In my opinion, *Abbasitoides modestus* is almost certainly a small erycitid macroconch, to which the microconch has already been described from the same assemblage, i.e. the minute *A. pumilus* (VACEK) with(?) lappets. Furthermore, the lowest true Stephanoceratinae macroconchs recorded by CALLOMON & CHANDLER (1990) from the Inferior Oolite, i.e. *S. (Skirroceras) leptogyrale* (BUCK.) and *Mollistephanus* cf. *mollis* BUCK., came only from the upper Bradfordensis Zone (uppermost Laeviuscula Zone s. l.), immediately below the Sauzei Zone.

Microconchs

The minute, lappet-bearing microconchiate genus *Trilobiticeras* BUCK. was matched with *Docidoceras* s. l. (including *Riccardiceras*) long ago, because of resemblance of the immature whorls and similar vertical and lateral ranges, from Alaska to eastern Europe (WESTERMANN, 1964). Due to the high sex and size ratios in favour of the macroconchs (including collecting bias against small specimens), however, records of *Trilobiticeras* are very limited. For example, a single complete specimen was recovered from the Widebayense Zone of Wide Bay, South Alaska, in contrast to about one hundred complete macroconchs of *Docidoceras (Pseudocidoceras) widebayense* WEST. and *camachoi* WEST. (WESTERMANN, 1969). Most *Trilobiticeras* occurrences are recorded from the upper Concava–Discites Zones, including the respective type-species of macro- and microconchiate genera in the Inferior Oolite of England, which even CALLOMON & CHANDLER (1990) consider as a pair. But, in western Europe, *Trilobiticeras* ranges into the Laeviuscula Zone, above the range of *Docidoceras* (s. stricto). Here it is associated and has been paired with *Emileites* (GALÁCZ, 1972; SANDOVAL, 1983; FERNANDEZ LOPEZ, 1985; CALLOMON & CHANDLER, 1990), which CALLOMON & CHANDLER (1990) include in *Docidoceras* as a subgenus.

Together with *D. (Emileites)* in the Inferior Oolite occurs another poorly known genus affin to *Trilobiticeras*, i. e. *Frogdenites* BUCKMAN (1921, pl. 215). Originally considered as the microconch of *Labyrinthoceras* (WESTERMANN, 1964), *Frogdenites* was later separated on stratigraphic and morphologic grounds. The aperture is poorly known and *Frogdenites* may even include both dimorphs (PARSONS, 1974, 1977; GALÁCZ, 1982).

Hence, *Trilobiticeras* uniquely comprises the microconchs to several macroconchiate genera classified in the two families, Otoitidae and Stephanoceratidae. The generic name *Trilobiticeras* obviously needs to be retained for these microconchs, just as the Bathonian–Callovian microconchiate genus *Xenocephalites*, which corresponds to several macroconchiate genera of the Eurycephalitinae (RICCARDI & WESTERMANN, 1991).

The specific *Trilobiticeras* microconchs matching *Riccardiceras* are unknown and all are rare; it could be *T. punctum* (VACEK) (lectotype designated and refigured in WESTERMANN, 1964, pl. 6, figs 7a–b) which is kown from the Alps and England (GALÁCZ, 1972), whereas the *Docidoceras* microconchs probably include T. *trilobitoides* BUCK. *Abbasitoides*, on the other hand, has a much more restricted gepgraphic distribution than *Docidoceras* and *Riccardiceras*.

Early phylogeny and the classification of Stephanoceratinae

In my most recent discussion and classification (WESTERMANN, 1993) of the clade or clades leading from erycitids to *Stephanoceras* s. l., *Abbasitoides* is again placed in the Erycitidae (or Erycitinae of Hammatoceratidae), whereas the "group of *Stephanoceras? (Oecostephanus?) longalvum* (VACEK)" [here named *Riccardiceras*] is placed in the Stephanoceratidae (Stephanoceratinae or subfam. nov.?), tentatively as their first member. [*Oecostephanus* BUCK. was tentatively used as the best name available from a list of highly "split" late-Lower Bajocian "genera" named mostly by BUCKMAN for Inferior Oolite macroconchs [*Kallistephanus*, *Rhytostephanus*, *Skolekostephanus*, *Kreterostephanus*, *Freycinetia*, *Baylia*], which should be reduced to a couple of serpenticonic early subgenera of the genus *Stephanoceras*.]

The evolute to serpenticonic species of *Erycites* s. lato, i.e. the group of *E.*(?) *gonionotus* (BEN.) and *"E." modestus* (VACEK) (=*Abbasitoides* GÉCZY, 1966), have been considered ancestral to the stephanoceratids for a long time (e.g. WESTERMANN, 1964). *E.*(?) *gonionotus* differs from the much more inflated and involute *E. fallifax*, type-species, in a very similar way as does *Riccardiceras* from *Docidoceras*, i.e. serpenticonic coiling, and there also are intermediate forms. Hence, for reasons of conformity, these groups should perhaps be separated at generic or, at least, subgeneric level. (I will leave these to the specialists.) *Abbasitoides* is distinct by the broad ventral costae interruption and the small size (the lectotype of *A. modestus*, type-species, cf. Pl. 17, fig. 4, is here considered as a macroconch, as discussed above).

By mid-Aalenian time, these forms tended to become *Stephanoceras*-like by closure of the ventral costae interruption and modification of the septum-suture complex. In the latest Aalenian and early Bajocian, typically serpenticonic *Riccardiceras* lived through much of the pan-Tethyan area, where they were planktic drifters in the upper water masses (WESTERMANN, in press). During the mid-Early Bajocian Laeviuscula Chron, *Riccardiceras* evolved into *Stephanoceras* s. l. (including *Skirroceras*, *Oecostephanus*, etc.) by the (gradual?) change of the monaxial ("planulate") into the biaxial ("bullate") septum. This is reflected in the suture by the reduction and increased obliquity of the "2nd lateral lobe" U_2 accompanied by strong retraction of the umbilical lobes, and, dorsally, by the similar reduction and increased obliquity of the "internal lateral lobe" U_1/U_n. The poorly known *Mollistephanus mollis* BUCKMAN (1922, pl. 344) from the Laeviuscula Zone of southern England appears to have been an important intermediate member of this lineage. According to the original illustrations, it has a subvertical U_2 (? and some poorly defined mid-ventral costae irregularity). Perhaps CALLOMON & CHANDLER's (1990) earlier "*Stephanoceras* cf. *perfectum* vars." with ventral costae alternation and/or interruption are best placed in *Mollistephanus*.

It is entirely possible that several parallel lineages existed, even in Europe, e.g. from strongly costate *Riccardiceras* to *Skirroceras*, which has a coarsely costate juvenile stage, and from finely costate *Riccardiceras* to the extremely serpenticonic *Stephanoceras (Oecostephanus)* gr. *baylei* (OPPEL), to *Stephanoceras* s. str.

Coeval clades

The radiation from late erycitids or the early otoitids and stephanoceratids included several other clades. Of particular interest is the basal Bajocian of Oregon. "*Docidoceras*" *amundsoni* TAYLOR (1988) closely resembles the rare, exceptionally evolute species placed in *Pseudotoites* from South Alaska, i.e. P. (?) *kialagvikensis* and *prestoni* WESTERMANN & RICCARDI (1989; respectively for *P.* cf. *argentinus* and *P.* cf. *transatlanticus* of WESTERMANN, 1969) from the very early Bajocian Widebayense Zone. They all have similar short, bullate primaries ending on the lateral edge that is situated well below mid-flank. In South Alaska, these forms are part of the much more abundant *Docidoceras (Pseudocidoceras)* fauna (WESTERMANN, 1969). "*Docidoceras*" *lupheri* IMLAY (1964) is more evolute and intermediate between *Riccardiceras* and "*D.*" *amundsoni* in sculpture and whorl section. The typical, more involute and inflated *Pseudotoites* occur in the Laeviuscula Chron (s. l.) of the Andes and Western Australia (WESTERMANN & RICCARDI, 1979). Significantly, what appears to be a broad-whorled, evolute *Pseudotoites* occurs also in the Aalenian/Bajocian boundary beds of Hungary, Spain and Morocco, i.e. "*Docidoceras*" *zemistephanoides* GÉCZY (1966; FERNANDEZ LOPEZ, 1985; BENSHILI, 1989). GÉCZY noticed that this species differed from *Docidoceras* in the bullate, short primaries, but compared it with the much younger Canadian genus *Zemistephanus*, a stephanoceratid of the Humphriesianum Chron (HALL & WESTERMANN, 1980); but not with *Pseudotoites*. These relationships are, of course, important biogeographically and phylogenetically. Curiously and again illuminating the close affinity between early otoitids and stephanoceratids, the Australian, New Guinean and ?Andean (typical) *Pseudotoites* appear to have originated from forms close to European species of intermediate *Docidoceras* and, especially, *D. (Emileites)*; the northeastern Pacific *Pseudotoites* from *Riccardiceras*. This would, of course, imply polyphyly and require taxonomic revision.

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Plate 14

All figures natural size

Figs 1a–b. Impression of *Irianites* sp. indet. attached to fragment of an evolute spherocone of doubtful affinity, as discussed in text, loose from Kemaboe River bed (reproduced from WESTERMANN & GETTY, 1970, Pl. 55, figs. 4a, b).

Figs 2a–b. Complete *"Bullatimorphites? (Treptoceras?)* n. sp. A ♂" of WESTERMANN & GETTY (1970, Pl. 55, figs. 1a, c reproduced), loose from Kemaboe River bed; this microconch of *?Labyrinthoceras* matches Fig. 1b (interpretation 1).

Figs 3a–b. Incomplete *Satoceras satoi* WEST. & CALL. ♀ (Tokyo Univ. Museum UMUT MM 19814); septate whorls with exposed nucleus (3a) and with (3b) body-chamber, ex-situ from Homejo; this nucleus also resembles Fig. 1b (interpretation 2).

Figs 4a–b. Damaged *Satoceras hataii* (TAKAHASHI) ♀ (Tokyo Univ. Museum UMUT MM 19815), ex-situ from Homejo; complete phragmocone and end of body-chamber (removed in 4b).

Figs 5a–c. Almost perfect specimen of *Satoceras boehmi* (WEST. & Getty) ♀ (Tokyo Univ. Museum UMUT MM 19816) with only the ventral part of aperture missing, from unknown locality of Irian Jaya; note septal suture with deep, trifid lobes characteristic of Sphaeroceratidae.

Plate 15

All figures natural size unless otherwise indicated

Figs a–d. Largest known *Irianites moermanni* (KRUIZ.) ♀ (Royal Ontario Museum 51413), with almost complete body-chamber, ex-situ from S. Badai River bed; a x 0.8.

Plate 16

All figures natural size unless otherwise indicated

Figs 1–2. *Irianites moermanni* (KRUIZ.) ♀ & ♂, ex-situ from S. Bidai River bed. 1 a–b, septate whorls of microconch (Royal Ontario Museum 51414), x 2; 2 a–b, damaged but almost complete macroconch (ROM 51415).

Figs 3a–b. End of large body-chamber of ?*Irianites* (ROM 51416), ex-situ from S. Bidai River bed.

Plate 17

All figures natural size

Figs 1–2. *Riccardiceras suzukinense* n. sp., ♀/M. 1a–c, Holotype, ex-situ from Kemaboe Valley (reproduced from WESTERMANN & GETTY, 1970, Pl. 50, figs. 1a–c); complete with damaged aperture. 2a, b. Probably complete phragmocone (UMUT MM 19817), ex-situ from Homejo; note biaxial ("bullate") septal surface, with two (paired) saddle axes (vs. Fig. 5).

Fig. 3. Topotype (?paralectotype) of *Riccardiceras longalvum* (VACEK) with septal suture inked in (reproduced from WESTERMANN, 1964, Pl. 6, fig. 8); note the large, slightly oblique U_2 situated on rounded lateral edge (max. whorl width), the retracted U_3, and that E is somewhat shorter than L.

Fig. 4. Oblique view of *Abbasitoides modestus* (VACEK), lectotype, with inked-in septal suture (reproduced from WESTERMANN, 1964, Pl. 6, fig. 8); note minute external lobe E and smooth ventral band.

Fig. 5. Septal surface of *Stephanoceras (Epalxites) anceps* (QU.) ♂ [microconch of *S. (Skirroceras)* gr. *macrum* (QU.) ♀], from Alfeld, Germany (reproduced from WESTERMANN, 1964, Pl. 6, fig. 3); note monaxial ("planulate") architecture, with only one (paired) saddle axis (vs. Fig. 2c).