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Palaeontology and biostratigraphy of the Middle–Upper Coniacian and Santonian inoceramids of the US Western Interior

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ABSTRACT:

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The taxonomy of the Middle-Late Coniacian and Santonian inoceramids of the US Western Interior, including some specimens from the Canadian Western Interior, is revised, based mainly on the extensive collections of the US Geological Survey. The classic Meek and Hayden material is discussed. Forty-four species are described of which 5 are new: *Inoceramus americanus*, *Inoceramus sokolovi*, *Inoceramus robertsoni*, *Inoceramus glacierensis*, and *Sphenoceramus gilli*. The Middle Coniacian to Santonian inoceramids of the Western Interior represent a uniform Euramerican fauna. This allows the application of a uniform biostratigraphical zonation throughout the whole biogeographical region. Starting in the Late Coniacian, inoceramid faunas are characterised by relatively strong north–south biogeographic differentiation.

The inoceramid zonation applied is discussed, diagnosed, and compared to previously used schemes, and to the ammonite zonation commonly used in the US Western Interior.

Key words: Coniacian, Santonian, US Western Interior, Inoceramids, Taxonomy, Biostratigraphy.

INTRODUCTION

This paper deals with the Middle-Upper Coniacian and Santonian inoceramids of the US Western Interior, and it is the fourth part of our survey of the Upper Cretaceous inoceramids of the region. As in preceding parts, those devoted to the inoceramids of the Upper Turonian/Lower Coniacian (WALASZCZYK & COBBAN 1999, 2000), Upper Cenomanian–lower Middle Turonian (WALASZCZYK & COBBAN in KENNEDY & *al*. 2000), and Campanian–Lower Maastrichtian (WALASZCZYK & *al*. 2001), the aim of this paper is to provide palaeontological descriptions of the inoceramids in question, based on the extensive collections of the Geological Survey in Denver, also including the old 19th century collections, and to present their biostratigraphic potential.

The Middle Coniacian through Santonian time of the Western Interior, and actually of the whole Euramerican biogeographic region, represents one of the most interesting intervals in the Late Cretaceous inoceramid history. It was the time of their highest taxonomic and morphological diversity and also the time of a clear Boreal–Tethyan geographical pattern, with parallel occurrence of widely distributed, cosmopolitan species. However, as discussed herein, a large number of inoceramid taxa are still very poorly known, with some, even very distinctive morphotypes, known from single specimens. Consequently, in spite of the rich representation of Inoceramidae in the Middle Coniacian through Santonian of the region, the biozonation applied is rather crude, and inevitably much below its expected stratigraphical potential.

GEOLOGICAL SETTING

The Middle-Upper Coniacian and Santonian deposits of the US Western Interior were formed in a broad elongated seaway, extending from the Gulf of Mexico in the south to the Arctic Ocean in the north (Text-fig. 1). It was a seaway filling a foreland basin, formed east of the active Sevier Orogenic belt, due to subduction along the western margin of the North American plate (GILL & COBBAN 1973, KAUFMANN 1977a, 1984; DYMAN & *al*. 1994a, b; ROBINSON ROBERTS & KIRSCHBAUM 1995). Although tectonic activity highly influenced the observed geometry and facies pattern of the Upper Cretaceous succession of the basin, the succession simultaneously records large scale cyclicity, at least in part globally recognisable, representing eustatically induced transgressive-regressive cycles (KAUFFMAN 1977a). The Coniacian–Santonian succession represents part of the seventh Niobrara cyclothem (KAUFFMAN 1977a, 1984), characterised by several smaller trangressive peaks separated by regressive pulses.

Measured sections

A large part of the material studied is not precisely located in the succession but comes from

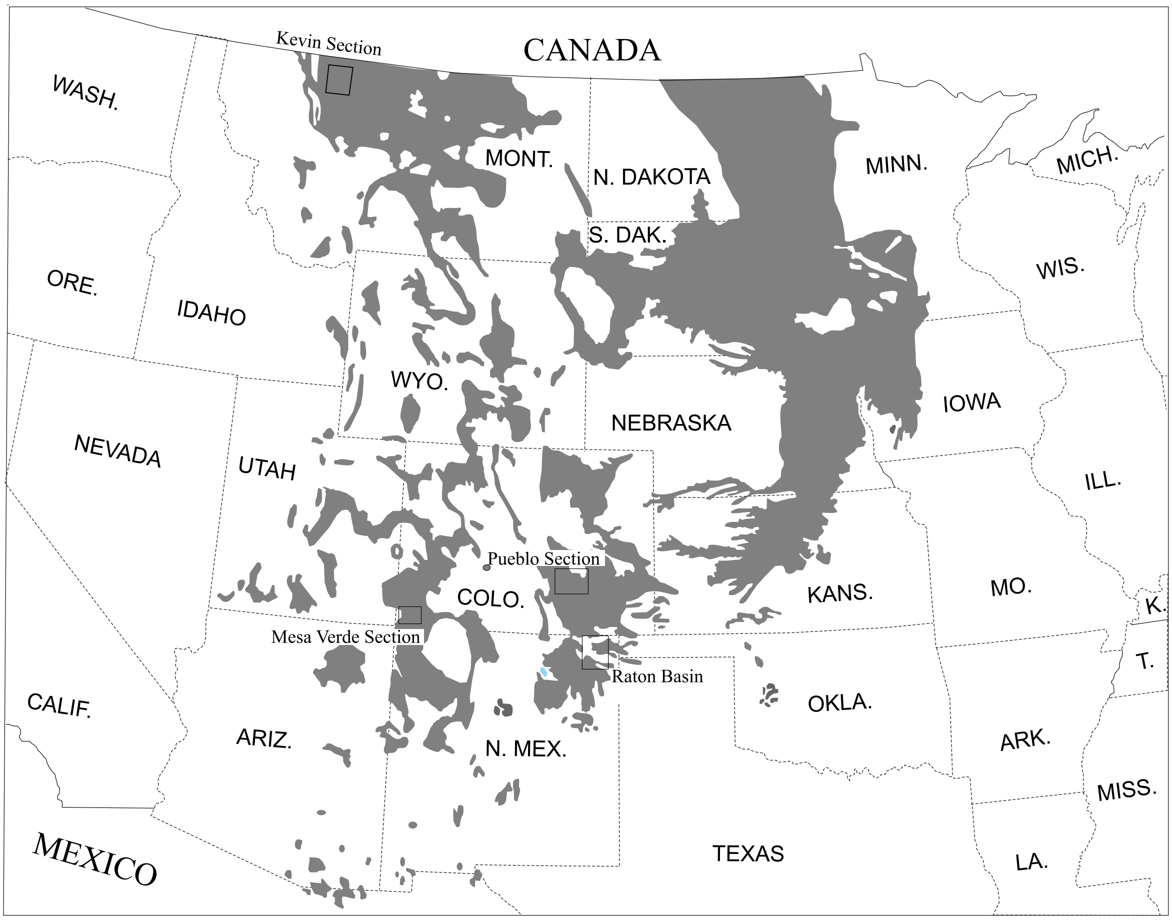

Fig. 1. Upper Cretaceous deposits of the US Western Interior with the location of the main study areas

localities with limited stratigraphical extent and with good ammonite dating. Of primary importance are four expanded successions, which provided precisely localised inoceramid material, spanning the whole Middle Coniacian through Santonian. The best documented is the Pueblo section, in SE Colorado. This succession was described in detail and documented palaeontologically by SCOTT & COBBAN (1964), and the inoceramid material presented herein is almost entirely from that work. Additionally of importance is the material from the Raton Basin section, NE New Mexico, described and illustrated by SCOTT & *al*. (1986). Also discussed below is the Mesa Verde section, SW Colorado, documented recently by LECKIE & *al*. (1997), but not studied by us. However, the precision of field documentation and the illustration of the rich inoceramid material allows this section to be included in the compilation of the general inoceramid record for the US Western Interior and the proposed biostratigraphic zonation based on that

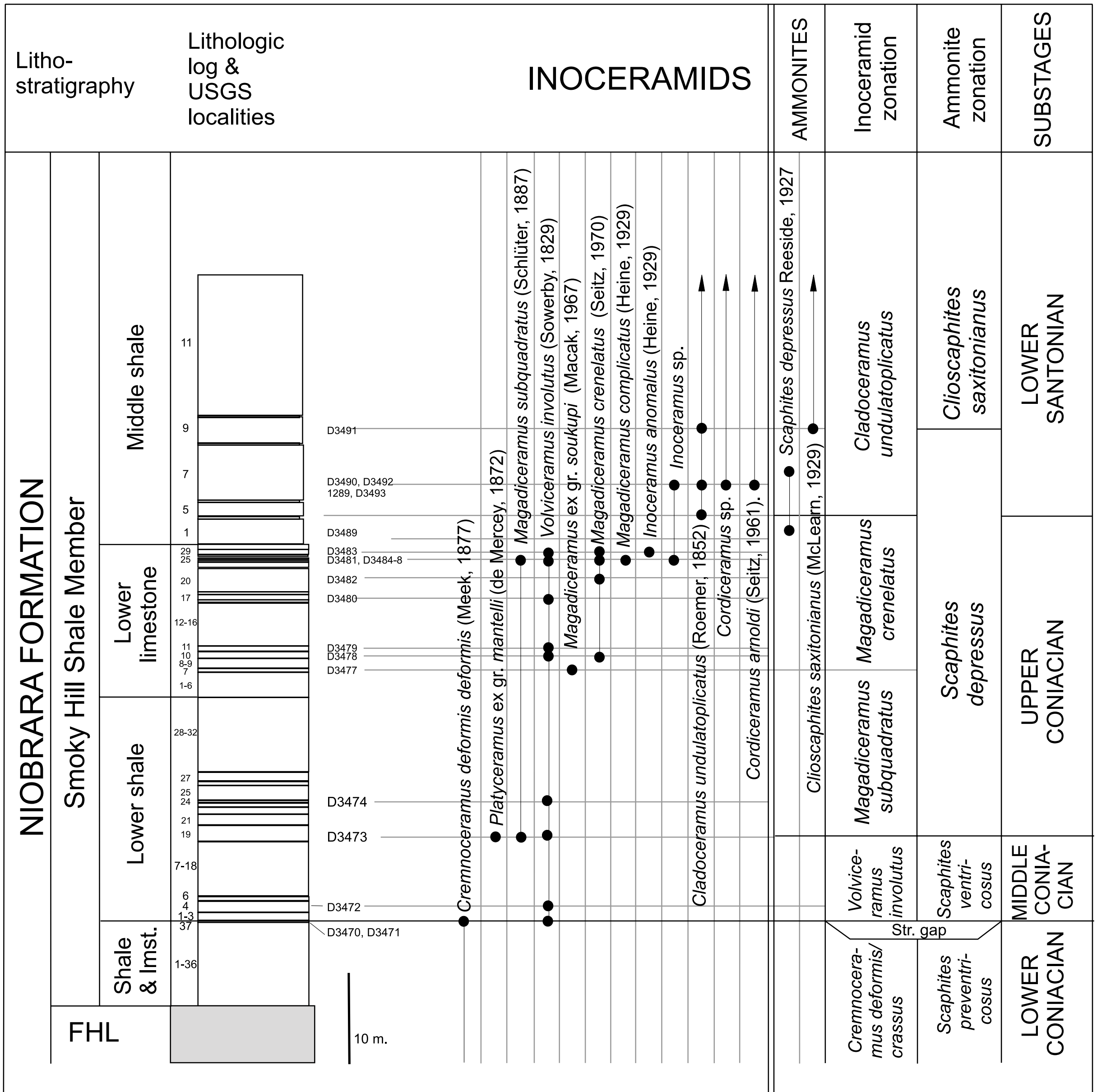

Fig. 2A. Lithological log, stratigraphical ranges of inoceramids and ammonites, and the ammonite and inoceramid zonations in the Middle Coniacian through Santonian of the Pueblo section [compiled after SCOTT & COBBAN 1964]

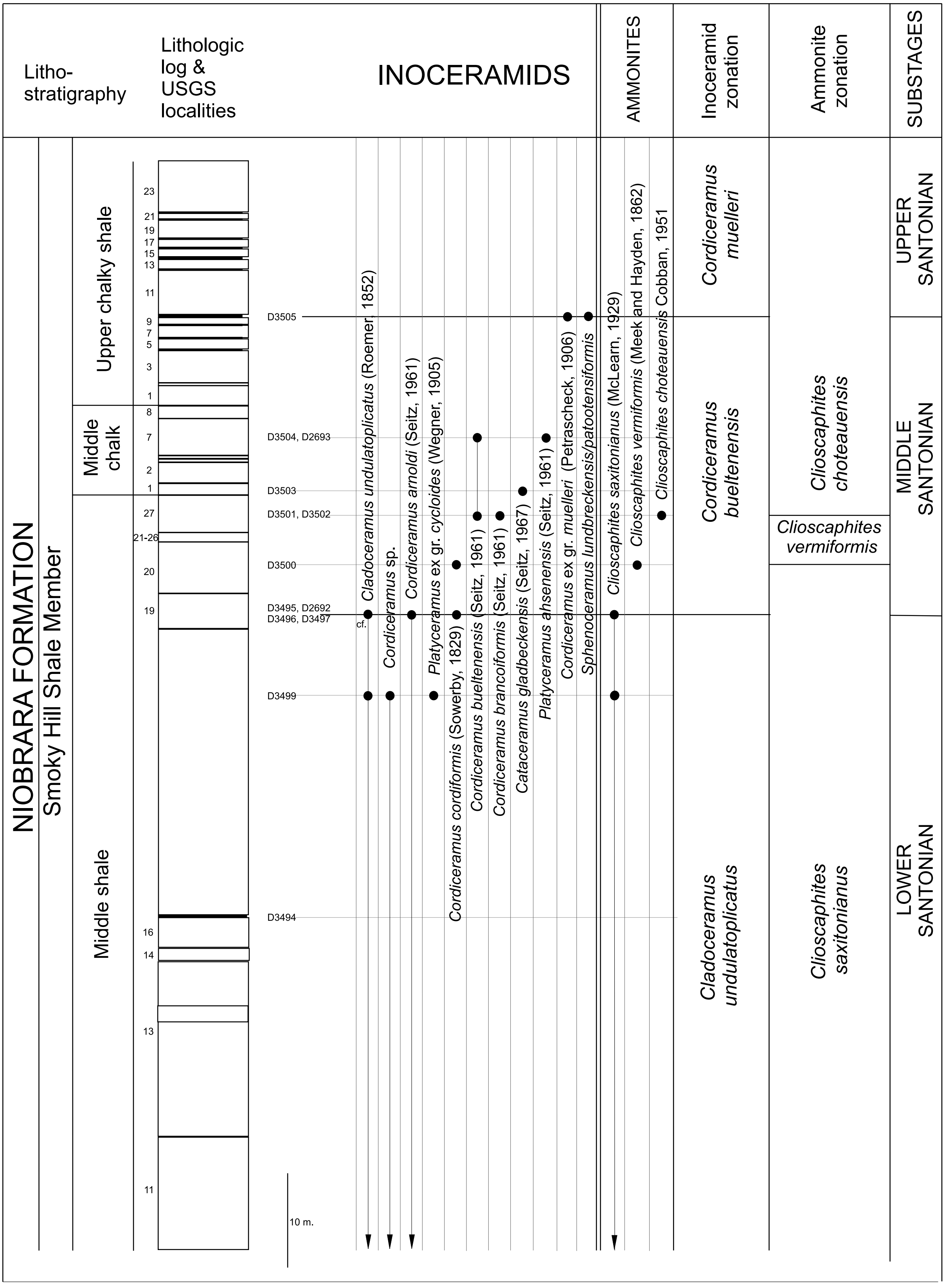

Fig. 2B. Lithological log, stratigraphical ranges of inoceramids and ammonites, and the ammonite and inoceramid zonations in the Middle Coniacian through Santonian of the Pueblo section [compiled after SCOTT & COBBAN 1964] group. Also of importance is the Kevin section, north-central Montana, of which the succession and ammonite stratigraphy was presented recently by COBBAN & *al*. (2005; see also COBBAN & *al*. 1976).

Pueblo section

The succession, described in detail by SCOTT & COBBAN (1964), is exposed in the Lake Pueblo State Park, west of the town of Pueblo, Colorado (see also KAUFFMAN & PRATT, 1985). The Middle Coniacian through Santonian succession is represented by the Smoky Hill Shale Member of the Niobrara Formation, and ranges from the base of the lower shale unit up to the upper chalky shale (see Text-fig. 2 and SCOTT & COBBAN 1964). The part of the succession yielding inoceramids studied herein is about 180 m thick, with almost half of it represented by the middle shale unit. Inoceramids are best represented in the lower limestone unit, in the upper part of the middle shale, and within the middle chalk units.

Springer section

The Springer section is located within the Raton Basin, in the north-eastern part of New Mexico. As in the case of the Pueblo section, the Middle Coniacian through Santonian succession of the Springer section is represented by the Smoky Hill Shale Member of the Niobrara Formation (Text-fig. 3). The succession was described in detail by SCOTT & *al*. (1986). The base of the Middle Coniacian lies in the lower part of the lower shale unit, a little higher than the last *Cremnoceramus*, which is still noted at the base of this unit. Like the Pueblo section, the Springer indicates a strongly reduced Middle Coniacian in the Raton Basin, most probably due to a gap spanning its lower part. Higher within the lower shale unit appears the first *Magadiceramus subquadratus* (SCHLÜTER), marking the base of the Upper Coniacian. The Coniacian/Santonian boundary, marked by the FO of *Cladoceramus undulatoplicatus* (ROEMER) is in the upper part of the sandy unit above. The first *Cordiceramus* ex gr. *muelleri* (PETRASCHECK), which is taken herein to mark the base of the Upper Santonian, appears in the lower part of the upper shale unit. At the same level is noted the first *Sphenoceramus lundbreckensis* (MCLEARN).

Mesa Verde section

The Mesa Verde section, in the SW corner of Colorado, was recently studied in detail by LECKIE & *al*. (1997). The Coniacian–Santonian succession is represented by the Smoky Hill and Cortez Members of the Mancos Shale. The Middle Coniacian, which begins at the base of the Smoky Hill Member, is represented by monotonous calcareous shales and foraminiferal marlstones. The boundary to the underlying Montezuma Valley Member is marked by a disconformity, associated with a stratigraphical gap, spanning the topmost Turonian through the Middle Coniacian. The Coniacian/Santonian boundary lies in the upper part of the Smoky Hill Member. The base of the Upper Santonian, marked by the first occurrence of *Cordiceramus* ex gr. *muelleri* and *Sphenoceramus lundbreckensis*, is just above the base of the overlying Cortez Member (see LECKIE & *al*. 1997, text-fig. 19).

Kevin section

The Middle Coniacian through Middle Santonian succession of the Kevin section is represented by the Kevin Member of the Marias River Shale. The succession and its ammonite and inoceramid content were recently described by COBBAN & *al*. (2005). The succession is well documented and dated by scaphitid ammonites. The inoceramids are less diverse than the assemblages farther south. The Middle Coniacian is reprented by *Volviceramus*, a genus which is also well represented in most of the Upper Coniacian. Not observed in the Kevin section, as well as in the other sections in Montana, is *Magadiceramus subquadratus*, a marker of the Upper Coniacian and of the base of the substage. Also missing from Montana is *Cladoceramus undulatoplicatus*, although this species was reported from the Wapiabi Formation of British Columbia, in Canada (STELCK 1962). The Santonian succession in Montana and farther north is dominated by a *Cordiceramus*–*Sphenoceramus* assemblage.

Locality details

Prefix D indicates Denver Mesozoic locality numbers; all other are Washington, D.C. Mesozoic

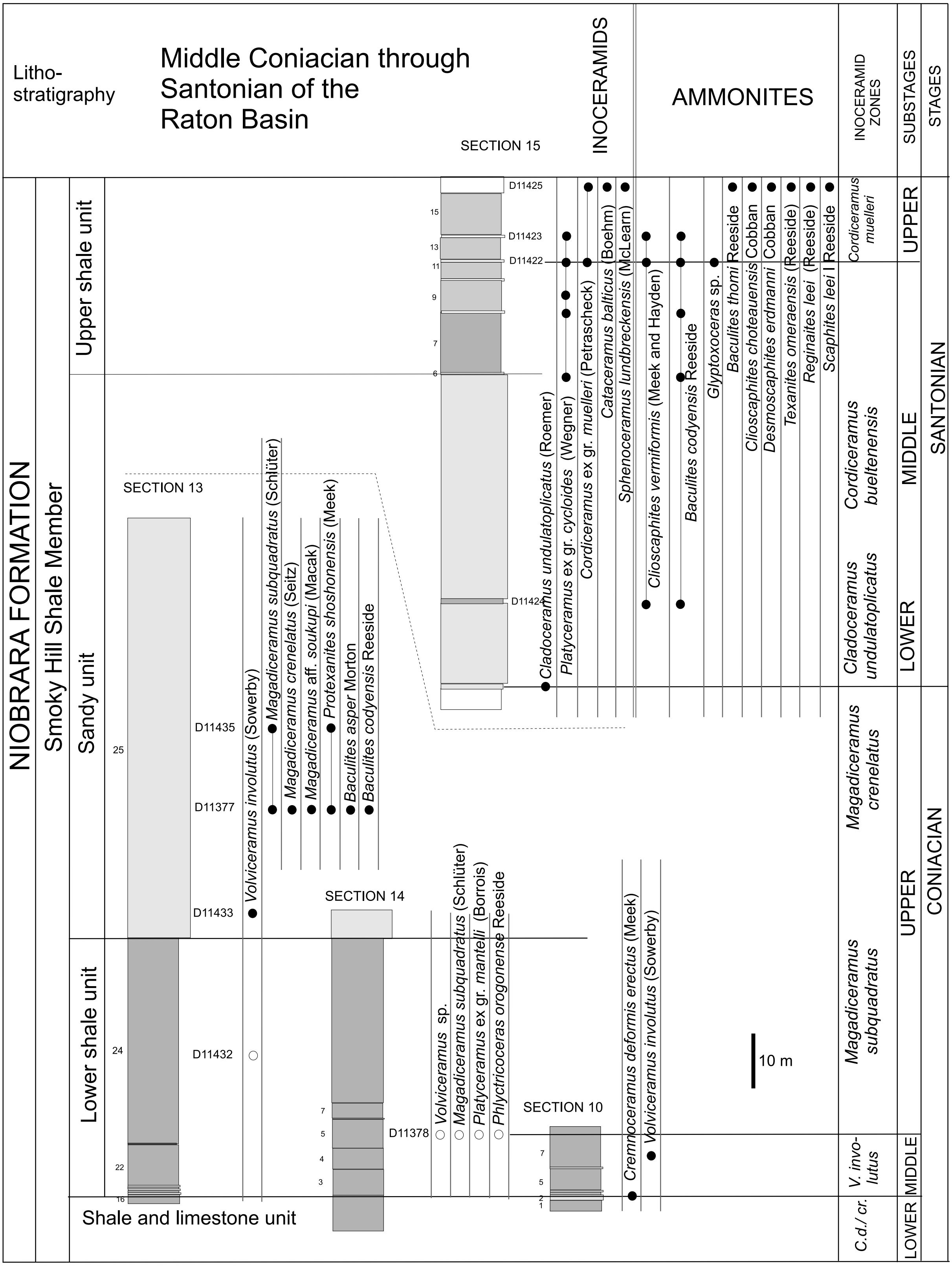

Fig. 3. Lithological log, stratigraphical ranges of inoceramids and ammonites, and the inoceramid zonation in the Middle Coniacian through Santonian of the Raton Basin [compiled after SCOTT & *al.* 1986]; *C.d / cr.* – *Cremnoceramus deformis / crassus* Zone

locality numbers. The data contain: number of locality, name of collector, year of collection, geographical location of the locality, and stratigraphic assignement. The number in parantheses, at the left, refers to numbers on the map in Text-fig. 4.

3079. C.A. FISHER, 1904. Shoshone River, at Cody, Park County, Wyoming. Cody Shale. Zone of *Scaphites depressus*.

(30) 3383. A.C. VEATCH, 1907. Centre of sec. 27, T. 22N., R. 116 W., Lincoln County, Wyoming.

(31) 5032. T.W. STANTON, 1907. Shoshone River at Cody, Wyoming. Cody Shale. Ammonite zone of *Scaphites depressus*.

(32) 6625. V.H. BARNETT, 1910. NW 1/4 sec. 10, T. 49 N., R. 67 W., Crook County, Wyoming. Fox Hills Sandstone.

(33) 7369. D.F. HEWETT, 1911. Cody, Wyoming. Cody Shale.

(12) 8048. T.W. STANTON, 1912. Sec. 29, T. 35 N., R. 4 W., Toole County, Montana. Near top of the Marias River Shale. Zone of *Desmoscaphites erdmanni*.

(13) 8605. E. STEBINGER, 1913. NW 1/4 sec. 24, T. 35 N., R. 4 W., Toole County, Montana. [Probably Telegraph Creek Formation, Zone of *Desmoscpahites bassleri*]

(14) 8968. E.R. LLOYD, W.T. THOM & W.B. WILSON, 1914. NW 1/4 sec. 24, T. 26 N., R. 11 E., Chouteau County, Montana. Marias River Shale. Zone of *Scaphites ventricosus*.

(34) 9625. C.J. HARES, 1916. Sec. 24, T. 58 N., R. 100 W., Park County, Wyoming. Telegraph Creek Formation. Zone of *Desmoscaphites bassleri*.

(47) 11951. E.M. SPIEKER & J.B. REESIDE, Jr., 1923. Price, Carbon County, Utah. Mancos Shale. Zone of *Scaphites depressus* or *C. saxitonianus*.

(1) 11621. F.P. LAINE, 1923. Sec 5, T. 25, R. 8, 5th meridian. Alberta, Canada. Zone of *Clioscaphites saxitonianus*.

(15) 11990. A.J. COLLIER, 1923. Sec. 9, T. 25 N., R. 9 E., Chouteau County, Montana. Marias River Shale. Zone of *Scaphites ventricosus*.

(35) 17942. W.G. PIERCE, 1938. SE 1/4 sec. 10, T. 57 N., R. 103 W., Park County, Wyoming, Cody Shale, 120 m above base. *Scaphites depressus* Zone.

(36) 17955. W.G. PIERCE & J.B. REESIDE, Jr., 1938. SW 1/4 sec. 26, T. 58 N., R. 103 W., Park County, Wyoming. Cody Shale, 192 m above base. Zone of *Scaphites depressus*.

(37) 17956. W.G. PIERCE & J.B. REESIDE, Jr., 1938. SW 1/4 sec. 26 T. 58 N., R. 103 W., Park County, Wyoming. Cody Shale, 180 m above base. Zone of *Scaphites depressus*.

(16) 20953. W.A. COBBAN, 1947. NE 1/4 sec. 25, T. 1 S., R. 34 E., Bighorn County, Montana. Cody Shale, 7-10 m below top of Niobrara Member.

(38) 21097. E.M. THOMPSON, 1948. Ray Lake in NE 1/4 sec. 25, T. 25., R. 1 W., Fremont County, Wyoming. Cody Shale, 244 m above base. Zone of *Scaphites depressus*.

(39) 21109. J.D. LOVE, 1947. NW 1/4 sec. 20, T. 42 N., R. 112 W., Teton County, Wyoming. Cody Shale, 152 m above base. Zone of *Scaphites ventricosus*.

(17) 21406. W.A. COBBAN, 1948. SE 1/4 sec. 5, T. 14 N., R. 31 E., Garfield County, Montana. Marias River Shale. 43-53 m above Niobrara Member.

(18) 21419. W.A. COBBAN, 1948. NE 1/4 sec. 31, T. 32 N., R. 3 W., Toole County, Montana. Marias River Shale, 3 m below top. Zone of *Desmoscaphites erdmanni*.

(19) 21425. W.A. COBBAN, 1949. SE 1/4 sec. 14, T. 31 N., R. 4 W., Toole County, Montana. Marias River Shale, 71-77 m below top. Zone of *Clioscaphites vermiformis*.

(20) 21483. W.A. COBBAN, C.T. MOORE & B.R. ALTO, 1949. NE 1/4 sec. 4, T. 35 N., R. 3 W., Toole County, Montana. Marias River Shale, 93-119 m

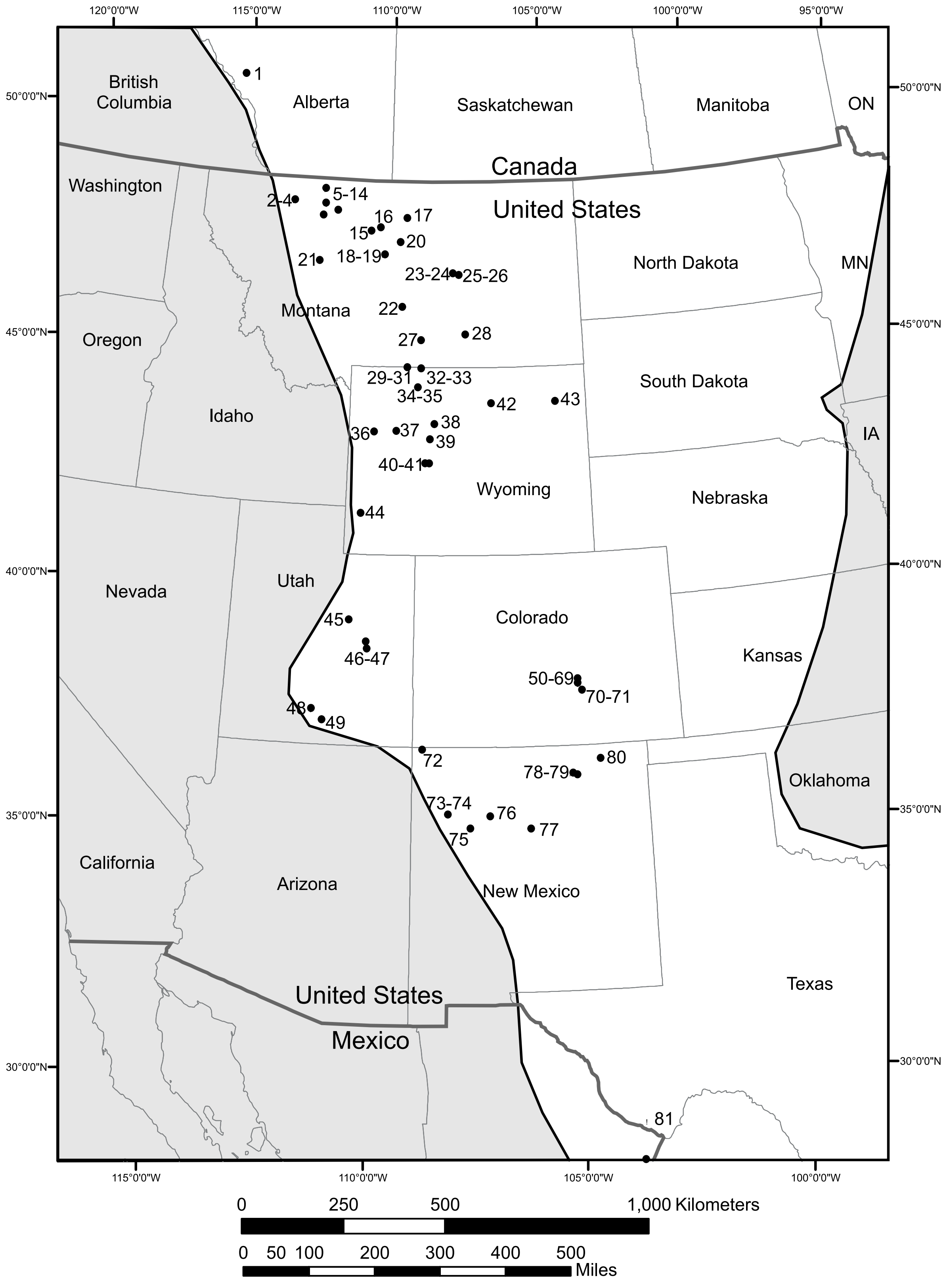

Fig. 4. Index map of the Western Interior of the United States and southernmost Canada showing USGS localities listed in the text. A single dot may indicate one or several nearby localities. Map illustrates probable extent of late Coniacian seway (*Scaphites depressus* Zone)

below top. Marias River Shale. Probably zone of *Scaphites ventricosus*.

(40) 21548. J.B. REESIDE, Jr., J.D. LOVE, E.M. THOMPSON & M.L. TROYER, 1949. NE 1/4 sec. 25, T. 1 S., R. 1 E., Fremont County, Wyoming. Cody Shale, 175-181 m above base. Zone of *Scaphites depressus*.

(21) 21568. W.A. COBBAN, J.B. REESIDE, Jr. & C.T. MOORE, 1949. NW 1/4 sec. 13, T. 22 N., R. 16 E., Fergus County, Montana. Lower part of Eagle Sandstone. Zone of *Scaphites hippocrepis* II.

(41) 23152. R.K. HOSE & W.J. MAPEL, 1950. Sisters Hill area in T. 49 N., R. 83 W., Johnson County, Wyoming. Cody Shale, Niobrara Member.

(42) 23113. J.B. REESIDE, Jr., & *al*., 1950. NW 1/4 sec. 24, T. 6 N., R. 2 E., Fremont County, Wyoming. Cody Shale, 20 m below top. *Scaphites hippocrepis* III Zone.

(43) 23425. W.A. COBBAN & *al*., 1951. W 1/2. 1, T. 42 N., R. 107 W., Fremont County, Wyoming. Lower part of Cody Shale. Probably *Clioscaphites saxitonianus* Zone.

(22) 23689. K.H. HOLMES, 1951. NE 1/4SE 1/4 sec. 8, T. 31 N., R. 4 W., Pondera County, Montana. Marias River Shale, 6 m below top of *Desmoscaphites ermanni* Zone.

(44) 24556. J.B. REESIDE, Jr., 1951. Sec. 35, T. 58 N., R. 103 W., Park County, Wyoming. Cody Shale. Zone of *Scaphites depressus*.

(25) 24596. W.J. PECORA & *al*., 1953. NW 1/4 sec. 4, T. 28 N., R. 18 E., Blaine County, Montana. Telegraph Creek Formation, *Desmoceras bassleri* Zone.

(23) 24649. W.A. Cobban, 1953. SE 1/4 sec. 13, T. 30 N., R. 1. W., Toole County , Montana. Marias River Shale, 20 m below bed F. Zone of *Scaphites ventricosus*.

(81) D100. W.S. ADKINS. Just north of Terlingua, Brewster County, Texas. Austin Chalk.

(24) D494. W.A. COBBAN, 1955. SE 1/4 sec. 5, T. 14 N., R. 31 E., Garfield County, Montana. Claggett Shale, 5 m above base.

(11) D666. B.R. ALTO, 1955. NE 1/4 sec. 28, T. 29 N., R. 4 W., Pondera County, Montana. Telegraph Creek Formation, 32 m above base. Zone of *Desmoscaphites bassleri*.

(10) D690. W.L. ROHRER, 1955. NE 1/4 sec. 31, T. 32 N., R. 3 W., Toole County, Montana. Marias River Shale, 25 m below top. Zone of *Desmoscaphites erdmanni*.

(9) D694. W.L. ROHRER, 1955. NW1/4 sec. 31, T. 32 N., R. 3 W., Toole County, Montana. Marias River Shale, 3 m below top. Zone of *Desmoscaphites erdmanni*.

(8) D940. B.R. ALTO, C.H. CLARK & W.A. COBBAN, 1958. SW 1/4 sec. 3, T. 31 N., R. 12 W., Glacier County, Montana. Marias River Shale. Zone of *Scaphites depressus*.

(7) D934. B.R. ALTO & C.H. CLARK, 1956. SE 1/4 sec. 34, T. 32 N., R. 12 W., Glacier County, Montana, Marias River Shale. Zone of *Scaphites depressus*.

(6) D937. B.R. ALTO, 1956. NE 1/4 sec. 25, T. 32 N., R. 12 W., Glacier County, Montana. Virgelle Sandstone. Zone of *Desmoscaphites bassleri*.

(29) D1655. G.R. SCOTT, 1958. NW 1/4 sec. 14, T. 44 N., R. 97 W., Hot Springs County, Wyoming. Cody Shale. Zone of *Scaphites depressus*.

(5) D2150. W.A. COBBAN, 1959. SW 1/4 sec. 15, T. 19 N., R. 12 E. Fergus County, Montana. Marias River Shale, just below MacGowan Concretion Bed. Zone of *Scaphites ventricosus*.

(69) D3473. G.R. SCOTT, 1961. NW 1/4 sec. 16, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Scaphites ventricosus*.

(70) D3481. G.R. SCOTT, 1961. NE sec. 16, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Scaphites depressus*.

(68) D3482. G.R. SCOTT, 1961. NW 1/4 sec. 16, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Scaphites depressus*.

(67) D3483. G.R. SCOTT, 1961. NE 1/4 sec. 16, T. 20 N., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Scaphites depressus*.

(66) D3485. G.R. SCOTT, 1961. SE 1/4 sec. 9, T. 20 S., 65 W., Pueblo County, Colorado. Niobrara Formation, Smoly Hill Member. Zone of *Scaphites depressus*.

(65) D3487. G.R. SCOTT, 1961. NW 1/4 sec. 21, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Scaphites depressus*.

(64) D3488. G.R. SCOTT, 1961. NE 1/4 sec. 8, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Fomration, Smoky Hill Member. Zone of *Scaphites depressus*.

(62) D3490. G.R. SCOTT, 1961. SE 1/4 sec. 9, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphits saxitonianus*.

(63) D3491. G.R. SCOTT, 1961. NW 1/4 sec. 21, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites saxitonianus*.

(61) D3492. G.R. SCOTT, 1961. SW 1/4 sec. 21, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites saxitonianus*.

(60) D3493. G.R. SCOTT & W.A. COBBAN, 1961. NW 1/4 sec. 16, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites saxitonianus*.

(59) D3495. G.R. SCOTT, 1961. NE 1/4 sec. 34, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites saxitonianus*.

(57) D3499. G.R. SCOTT, 1961. NW 1/4 sec. 10, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites saxitonianus*.

(58) D3501. G.R. SCOTT & W.A. COBBAN, 1961. SW 1/4 sec. 10, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites choteauensis*.

(54) D3503. G.R. SCOTT, 1961. NW 1/4 sec. 15, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites choteauensis*.

(55) D3505. G.R. SCOTT, 1961. SE 1/4 sec. 10, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Desmoscaphites erdmanni*.

(56) D3504. G.R. SCOTT, 1961. NW 1/4 sec. 15, T. 20 S., W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites choteauensis*.

(52) D3506. G.R. SCOTT, 1961. NE 1/4 sec. 22, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member.

(51) D3508. G.R. SCOTT, 1961. SW 1/4 sec. 34, T. 19 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member.

(53) D3509. G.R. SCOTT, 1961. NW 1/4 sec. 15, T. 20 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member.

(4) D3629. J.R. GILL, 1961. SW 1/4 sec. 14, T. 17 N., R. 5 W., Lewis and Clark County, Montana. Top of Virgelle Sandstone. Zone of *Desmoscaphites bassleri*.

(73) D3645. S.D. THEODOSIS, 1957. SE 1/4 sec. 18, T. 25 N., R. 20 E., Colfax County, New Mexico. Niobrara Formation, Smoky Hill Member. Zone of *Clioscaphites vermiformis*.

(72) D3648. G.R. SCOTT, 1962. Sec. 6, T. 12 N., R. 9 E., Santa Fe County, New Mexico. Mancos Shale, upper part. Zone of *Clioscaphites vermiformis*.

(50) D4307. G.R. SCOTT, 1963. NW 1/4 sec. 10, T. 21 S., R. 65 W., Pueblo County, Colorado. Niobrara Formation, Smoky Hill Member. Zone of *Scaphites depressus*.

(2) D4371. K. YENNE & E.D. PATTERSON, 1962. W 1/4 sec. 5, T. 3 S., R. 23 E., Carbon County, Montana. Cody Shale, 88 m below top. *Clioscaphites saxitonianus* Zone.

(45) D5308. F. PATERSON & B. LAW, 1966. NE 1/4 sec. 18, T. 38 S., R. 5 E., Kane County, Utah. Straight Cliffs Formation, 12 m below top.

(46) D5186. H.D. ZELLER, 1965. SW 1/4 sec. 3, T. 36 S., R. 2 W., Garfield County, Utah. Straight Cliffs Formation, about 150 m above base.

D5427. H.D. ZELLER, G.H. HORN & W.C. BOWERS, 1966. SW 1/4 sec. 12, T. 36 S., R. 1. E., Garfield County, Utah. Straight Cliffs Fo-r mation.

(26) D5634. J.R. GILL & *al*., 1966. SW 1/4 sec. 26, T. 15 N., R. 29 E., Petroleum County, Montana. Telegraph Creek Formation, zone of *Scaphites hippocrepis* I.

(27) D5636. J.R. GILL & *al*., 1966. SW 1/4 sec. 26, T. 15 N., R. 29 E., Petroleum County, Montana. Telegraph Creek Formation, zone of *Scaphites hippocrepis*.

(71) D6075. G.R. SCOTT, 1967. SE 1/4 sec. 6, T. 22 S., R 64 W., Pueblo County, Colorado. Smoky Hill Shale Member of Niobrara Formation, Zone of *Scaphites depressus*.

(76) D8282. C.M. MOLENAAR, 1971. SE 1/4 sec. 30, T. 13 N., R. 6 E., Sandoval County, New Mexico. Mancos Shale, zone of *Scaphites depressus*.

(77) D9781. W.A. COBBAN, 1976. SW 1/4 sec. 33, T. 29 N., R. 26 E., Colfax County, New Mexico. Niobrara Formation. Zone of *Scaphites depressus*.

(78) D10851. G.R. & J. SCOTT, 1977. SW 1/4 sec. 36, T. 32 N., R. 19 W., San Juan County, New Mexico. Mancos Shale, 2.4 m above the Stray sandstone bed, zone of *Scaphites ventricosus*.

(79) D11425. G.R. SCOTT, 1980. SW 1/4 sec. 7, T. 25 N., R. 19 E., Colfax County, New Mexico. Niobrara Formation, zone of *Clioscaphites vermiformis*.

(74) D12810. J.F. ROBERTSON, 1987. SW 1/4 sec. 10, T. 16 N., R. 12 W. McKinnley County, New Mexico. Basal part of Dalton Sandstone.

(80) D12888. J.F. ROBERTSON & W.A. COBBAN, 1991. SE 1/4 sec. 10 T. 16 N., R. 12 W., McKinley County, New Mexico. Lower part of Dalton Sandstone, upper part of zone of *Scaphites depressus*.

(48) D12987. T.D. FOUCH & *al*., 1988. NW 1/4 sec. 27, T. 19 S., R. 14 E., Emery County, Utah. Mancos Shale, from sandy unit, zone of *Scaphites depressus*.

(28) D13127. W.A. COBBAN, 1990. SW 1/4 sec. 15, T. 19 N., R. 12 E., Judith Basin County, Montana. Marias River Shale, zone of *Scaphites ventricosus*.

(49) D13269. C.M. MOLENAAR & W.A. COBBAN, 1992. NW 1/4 sec. 5, T. 21 S., R. 15 E., Emery County, Utah. Mancos Shale, top of ridge-forming sandy unit, zone of *Scaphites depressus*.

(75) D13972. W.A. COBBAN, 1999. NW 1/4 sec. 35, T. 16 N., R. 2 W., Sandoval County, New Mexico. Mancos Shale, basal part of El Vado Member. *Scaphites depressus* Zone.

(3) D14098. T.S. DYMAN, K. TAKAHASHI & W.A. COBBAN, 2001. NE 1/4 sec. 11, T. 6 N., R. 17 E., Wheatland County, Montana. Marias River Shale, a little below MacGowan Concretion Bed. Zone of *Scaphites ventricosus*.

STAGE AND SUBSTAGE DEFINITIONS

Lower/Middle Coniacian

At the Brussels Symposium the Coniacian Working Group recommended the FAD of the inoceramid species *Volviceramus koeneni* (G.

MÜLLER, 1888) as a marker of the base of the Middle Coniacian (KAUFFMAN & *al*. 1996). The first appearance of this species is a well recognisable event throughout the whole Euramerican biogeographical region (e.g. HEINZ 1926, 1928a; SEITZ 1952, 1956, 1959; TRÖGER 1969a, 1974, 1989; KAUFFMAN & *al*. 1994, 1996). In contrast to previous opinions, the first *Volviceramus* do not directly follow the Early Coniacian cremnoceramids. Both faunas are separated by a distinct fauna of a sulcate *lamarcki*-like forms, referred provisionally in Europe to *Inoceramus gibbosus* SCHLÜTER, 1877 (see WALASZCZYK & WOOD 1999 in NIEBUHR & *al*. 1999) and, consequently, representing the youngest Early Coniacian inoceramid assemblage so far recognised.

Middle/Upper Coniacian

The base of the Upper Coniacian, in agreement with the recommendation of the Brussels Symposium, is placed at the FO of the inoceramid species *Magadiceramus subquadratus* (SCHLÜTER, 1877) (see KAUFFMAN & *al*. 1996). This species is widely known in the Euramerican biogeographic region. So far, however, no report of this species is known from outside the region. The Japanese specimens of NAGAO & MATSUMOTO (1939, pl. 30, figs 4-7) compared to *Magadiceramus subquadratus subquadratus* and *M. austinensis* by KAUFFMAN (1977c, p. 185) are very unconvincing. *Inoceramus* (*Magadiceramus*) sp. nov. described by MATSUMOTO & YOSHIMATSU (1982) differ in outline and in ornament type from representatives of the genus. It is similarly the case with the New Zealand specimens referred to ?*Magadiceramus* by CRAMPTON (1996); heterochronous homeomorphy, so common among inoceramids, may well be the explanation here (see discussion in CRAMPTON 1996).

Coniacian/Santonian boundary

The lowest occurrence of *Cladoceramus undulatoplicatus* (ROEMER, 1847) was almost unanimously accepted as a basal boundary marker for the base of the Santonian during the Brussels Symposium (LAMOLDA & HANCOCK 1996). It is an easily identifiable inoceramid species and, moreover, it is characterised by a wide geographic occurrence, although it is not cosmopolitan in distribution as sometimes stated. It occurs regularly in the Euramerican biogeographic region. The species was also reported from the African–Madagascan Province (although referred to as *Cladoceramus* aff. *undulatoplicatus* v. *michaeli* – see SORNAY 1964) and from the Far Eastern Russian Province (PERGAMENT 1974); its presence in the latter area was not confirmed. In the African–Madagascan Province cladoceramids seem to appear first at or very close to the base of the Santonian.

The *Sphenoceramus pachti* (ARKHANGELSKY)–*Sphenoceramus cardissoides* (GOLDFUSS) group occurs regularly only in the northern part of the North European province and does not represent a good boundary marker. As will be shown later herein, sphenoceramid vertical distribution may be markedly diachronous outside the area of their regular occurrence.

Lower/Middle Santonian

No formal proposal was made concerning this boundary during the Brussels Symposium, although the LO of *Cladoceramus undulatoplicatus* (ROEMER) was suggested and provisionally accepted by members of the Santonian Working Group. Thus defined, it corresponds more or less to the concept of SEITZ (1961), who placed this boundary at the top of the *undulatoplicatus* Faunenzone (=the zone of radially ribbed inoceramids), which is marked by the disappearance of the radially-ribbed inoceramids. The main disadvantage of such a definition is the problem with a precise recognition of the LO of *C. undulatoplicatus* (as is the case with the LO of any species). Sporadic occurrences of a *Cladoceramus* were reported by SEITZ (1965) from a level within the Upper Santonian. These occurrences, markedly above the main range of *C. undulatoplicatus* are, however, difficult to interpret. Another possibility is to define the base of the Middle Santonian by the FO of *Cordiceramus cordiformis* (SOWERBY), as recently used e.g. by KENNEDY (1995) and also KAPLAN & KENNEDY (2000), KENNEDY & KAPLAN (2000), which would correspond to the concept of G. ERNST (ERNST & SCHULZ 1974, ERNST & *al*. 1979, SCHULZ & *al*. 1984), and to the base of TRÖGER's (1989) Zone 27. The problem is a poor recognition of the phylogenetic history of *C. cordiformis*. Moreover, there are more and more data suggesting that the first *C. cordiformis* may have appeared very close to, or event at the base of the Santonian, as defined by the FO of *C. undulatoplicatus* (Texas, Gulf Coast, own observations; England, C.J. WOOD, personal communication).

Middle/Upper Santonian

During the Brussels Symposium, the base of the Upper Santonian was proposed to be marked by the FO of the crinoid *Uintacrinus socialis* (LAMOLDA & HANCOCK 1996). This level approximates to the first occurrence of the inoceramid species *Cordiceramus muelleri* (PETRASCHECK), the taxon often used to mark this boundary (e.g. NIEBUHR & *al*. 1999). It seems that the FO of this inoceramid species may also be used as the Middle/Upper Santonian boundary proxy in the US Western Interior, where it is well represented at least in the southern and central part of the region (SCOTT & *al*. 1986, LECKIE & *al*. 1997, WALASZCZYK & COBBAN 2006 in press). In ammonite terms, its first occurrence is high within the *Clioscaphites choteauensis* Zone or even within the *Desmoscaphites erdmanni* Zone. Of interest is the co-appeareance of *C. muelleri* with members of the *Sphenoceramus lundbreckensis/cancellatus* group (Text-fig. 2; see also LECKIE & *al*. 1997, WALASZCZYK & COBBAN 2006, in press). In Europe, representatives of the latter species appear distinctly later than the first *C. muelleri*, at about the level of the FO of the crinoid *Marsupites testudinarius* (see e.g. SEITZ 1965, text-fig. 7; TRÖGER 1989, text-fig. 4). We regard the co-appearance of these inoceramid taxa in the Western Interior as attributable to the earlier appearance of sphenoceramids in that area.

Santonian/Campanian boundary

The biostratigraphical marker of this boundary proposed during the Brussels Symposim is the last occurrence (LO) of the crinoid *Marsupites testudinarius*. The inoceramid record is rather imprecisely known around the boundary level, although recent study of this fauna in the Wahaxachie section, Texas, a proposed Campanian basal boundary stratotype (see HANCOCK & GALE 1996), suggests a distinct turnover in platyceramids just below the boundary. A similar pattern was later confirmed at the Santonian/Campanian boundary succession in Madagascar. WALASZCZYK (1992), based on data from central Poland suggested, that there is a change in the ornament pattern in sphenoceramids of the *patootensis/angustus* group (=*cancellatus/lundbreckensis* in this paper) close to the base of the Campanian. This, however, requires further study.

INOCERAMID SUCCESSION, EVOLUTION AND ZONATION

Inoceramid succession and evolution

As demonstrated by the Pueblo section, the *Cremnoceramus* fauna, well represented in this section and elsewhere (WALASZCZYK & COBBAN 2000), is followed directly by the *Volviceramus* – *Platyceramus* assemblage, which is taken in the Euramerican biogeographical region to mark the base of the Middle Coniacian. In Pueblo the Lower/Middle Coniacian boundary succession looks continuous but, to judge from the record in Europe (WALASZCZYK & WOOD 1999, MORTIMORE & *al*. 2001), such an apparently complete succession may contain a discontinuity and a gap, spanning at least the topmost part of the Lower Coniacian and the basal part of the Middle Coniacian (Text-fig. 2; see also Text-figs 5-6). The missing Lower Coniacian interval is what is referred to in Europe as the *Inoceramus gibbosus* Zone (WALASZCZYK & WOOD 1999). Evolutionarily advanced volviceramids, occurring right at the base of the Middle Coniacian, additionally confirm the gap at the Lower/Middle Coniacian boundary, suggesting the absence of the lowermost Middle Coniacian. Disconformity at this level is nothing exceptional, and the gap was widely documented in the central and south-western part of the US Western Interior (e.g. LECKIE & *al*. 1997). The Pueblo and Raton sections were often reported as examples of continuous (in this interval) sections farther to the east, but this is apparently not the case, albeit the extent of the gap clearly decreases eastward.

The Middle Coniacian is characterised by a uniform Euramerican fauna, represented by volviceramids (*V. koeneni* and *V. involutus*) and platyceramids (*P. mantelli* group). In North America these taxa were most commonly referred to *Volviceramus umbonatus* and *Platyceramus platinus* respectively. Actually, the list of names offered by North American authors for *V. involutus* was quite long (see the synonymy list for *V. involutus*), with most of the taxa based on variable RVs of this species. At the same time, LOGAN's name *P. platinus* was applied to a series of various platyceramids, and even some large-sized and flat cordiceramids, spanning the Middle Coniacian through the Early Campanian. The genus *Inoceramus* is characteristic of the Middle Coniacian and lower Upper Coniacian in the study area. Many of these North American *Inoceramus* species seem to be descendants of the well known European species *Inoceramus kleini* G. MÜLLER, which appeared in the mid-Early Coniacian (see ČECH & ŠVABENICKÁ 1992; WALASZCZYK & WOOD 1999), and ranged apparently higher into the Middle Coniacian (e.g. ASSMUS 1963, TRÖGER 1989). The most confusing North American Coniacian *Inoceramus* species appears to be *I. undabundus* MEEK & HAYDEN. This species most probably first appeared at the beginning of the Middle Coniacian and continued to the early Late Coniacian, where it was often referred to *Inoceramus stantoni*, another name with no stable concept. The very poor representation of *V. koeneni* in North America most proba-

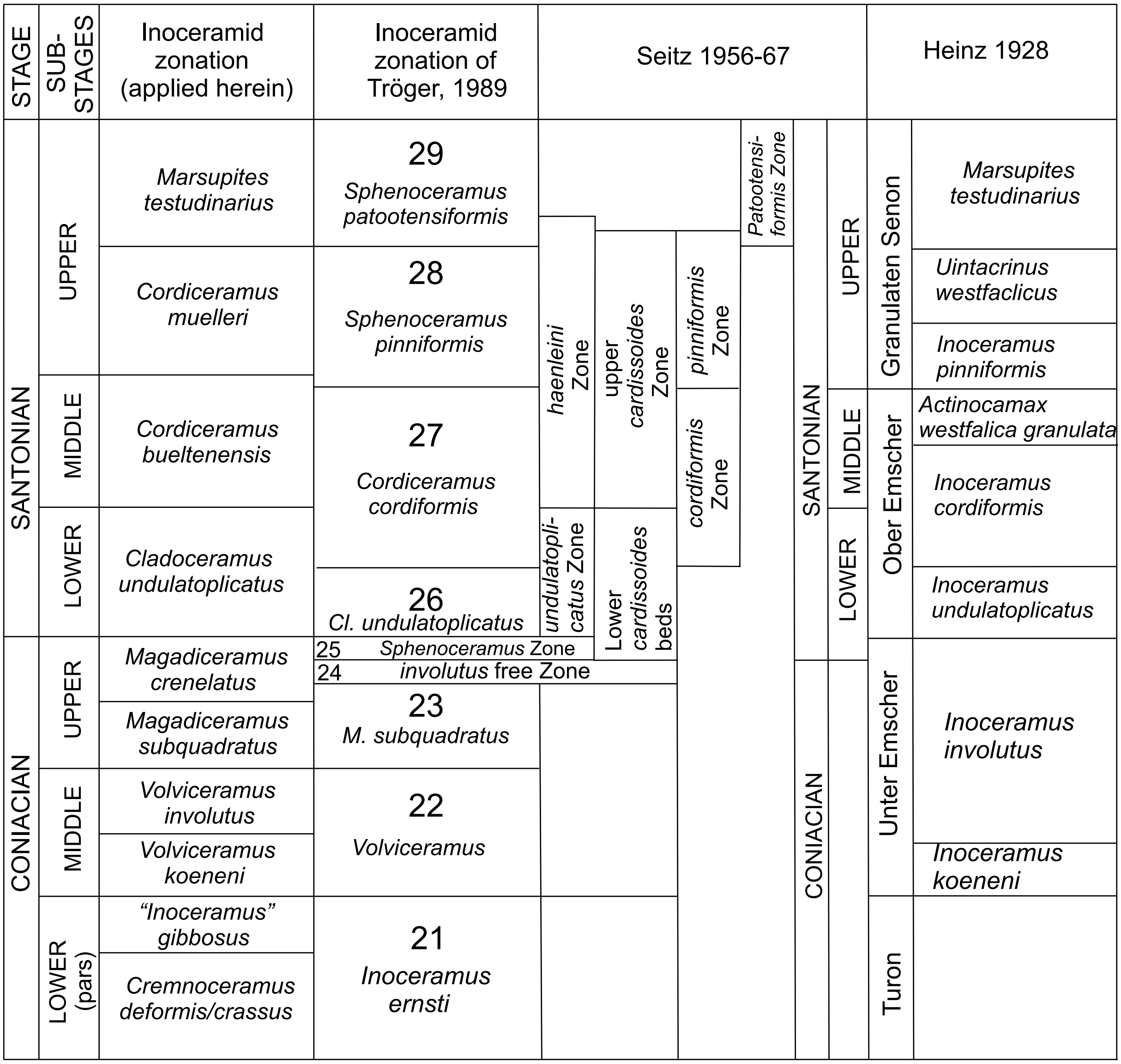

Fig. 5. Inoceramid zonation applied to the Middle Coniacian through Santonian of the US Western Interior and its comparison with the European zonations of HEINZ (1928a), SEITZ (1956 through 1967) and TRÖGER (1981b, 1989)

bly results from the poor record of the lowermost Middle Coniacian in the area, an interval characterised mostly by that taxon.

Almost all of the Middle Coniacian taxa continue into the Late Coniacian, although they do not form the most characteristic assemblage of the highest Coniacian substage. This substage, the lower boundary of which is marked by the first occurrence of *Magadiceramus*, provides the most taxonomically diversified inoceramid fauna, with 5 genera and 19 well defined species. Besides the characteristic magadiceramids, and the volviceramids and platyceramids ranging up from below, it is a time with a rich representation of *Inoceramus* (*I. gibbosus* SCHLÜTER, *I. frechi* FLEGEL, *I. americanus* sp. nov.) and the first *Sphenoceramus*, represented already by several species (*S. canaliculatus* HEINE, *S. latisulcatus* HEINE, *S.* sp. A, and *S. subcardissoides* SCHLÜTER).

In the Late Coniacian a very clear biogeographical differentiation of inoceramids begins, which is well visible even within the range of the North American Western Interior. Magadiceramids and platyceramids characterise mostly the southern parts of the region (*Magadiceramus subquadratus* is unknown north of Montana – see COBBAN & *al*. 2005), whereas in the north the inoceramids are represented by the *Inoceramus* – *Sphenoceramus* assemblage. In Europe volviceramids seem to disappear towards the south (e.g. LOPEZ 1992c, LOPEZ & *al*. 1992). This pattern is not observed within the Western Interior, and even south of this region, in the Gulf coast area, the genus is well represented.

The base of the Santonian is marked by the appearance of *Cladoceramus undulatoplicatus,* associated with *Platyceramus* of the *cycloides* group. *Cordiceramus cordiformis* also appears close to this level. Such an assemblage is known, however, only from the southern part of the area. To the north platyceramids and *Cladoceramus* disappear. Inoceramids are represented there by cordiceramids and, dominating in the north, *Sphenoceramus*. This *Cordiceramus*–*Sphenoceramus* assemblage dominates the northern parts of the Euramerican region throughout the Santonian, ranging even into the basal Campanian. In the southern part of the US Western Interior Basin sphenoceramids are virtually absent in the Lower and Middle Santonian and it is only in the lower Upper Santonian that representatives of the *Sphenoceramus cancellatus* (= *patootensiformis*) – *S. lingua* group appear. The apparent heterochrony of the first occurrences of this group within the Euramerican region is noteworthy: in Europe, the group first appears with the first *Marsupites* (middle Late Santonian) whereas in the US Western Interior it first appears with the first representatives of the *Cordiceramus muelleri* group, a level placed around the Middle / Late Santonian boundary. It means that zonal boundaries based on sphenoceramids, at least in areas outside their regular occurrence, may clearly be heterochronous. The sphenoceramids range far into southern Utah and New Mexico but they are unknown from Texas. In Europe, the southern limit of *Sphenoceramus* approximately corresponds to the northern edge of the Alpine area; the genus is noted only sporadically from Tethyan sections (e.g. in Austria – TRÖGER & SUMMESBERGER 1994). *Sphenoceramus* is limited to the northern hemisphere; both reports from South Africa – *Inoceramus patootensis* by HEINZ (1929) and *Sphenoceramus pachti* by KAUFFMAN (in KENNEDY & *al*. 1973) – are based on misidentifications (see discussion in KENNEDY & *al*. submitted).

Middle Coniacian – Santonian inoceramid zonation in Europe

The inoceramid zonation of the interval studied herein, i.e. of the Middle – Upper Coniacian and Santonian, was worked out in northern Germany (Text-fig. 5). HEINZ (1928a; but earlier also G. MÜLLER 1900) recognised the succession, which is generally valid today, and his scheme has been only slightly refined subsequently. HEINZ (1928a) reported the *Inoceramus koeneni* and *I. involutus* zones in the Middle–Upper Coniacian (his lower Emscherian), the *I. undulatoplicatus* and *I. cordiformis* zones in the Lower – Middle Santonian (his upper Emcherian), and in the Upper Santonian (his Granulaten-Senon) the belemnite *Actinocamax westfalicus-granulatus* Zone, the *Inoceramus pinniformis* Zone, the crinoid *Uintacrinus westfalicus* Zone and, at the top, the interval with *Inoceramus lingua* and *I. patootensis* (the latter interval he referred to the *Marsupites testudinarius* Zone) (Text-fig. 5).

Subsequently O. SEITZ intensively studied the inoceramids of that interval and found a number

Fig. 6. Inoceramid and amonite zonations applied to the Middle Coniacian through Santonian of the US Western Interior and its comparison with the inoceramid zonation proposed by KAUFFMAN & *al.* (1994)

of forms unknown to HEINZ. He recognised (SEITZ 1956) an *involutus*-free interval in the topmost part of HEINZ' *involutus* Zone, which he referred to as a separate zone. Moreover, he defined the base of the Santonian at the FO of the *Sphenoceramus cardissoides/pachti* group rather than that of *Cl. undulatoplicatus*. However, his main interest was the Santonian (SEITZ 1961, 1965, 1967). On the basis of rich material from numerous mineshaft sections in the Münsterland Basin (northern Germany), SEITZ recognised a number of species, which could potentially be used for stratigraphical purposes, and proposed, based on these species, a series of taxon range zones. The zones he proposed (excluding the *Sphenoceramus* Teilzone, which is below the *undulatoplicatus* Zone and should now be ascribed to the topmost Coniacian) are (the generic names are given according to the systematics applied herein): *Sphenoceramus cardissoides*, *Cladoceramus undulatoplicatus*, *Cordiceramus cordiformis*, *Cordiceramus cordiinitialis riedeli* and *spickernageli*, *Cordiceramus haenleini*, *Cordiceramus brancoiformis*, *Cordiceramus muelleri*, *Sphenoceramus pinniformis* and *Sphenoceramus patootensiformis* (Text-fig. 5; see e.g. SEITZ 1965, text-fig. 7). Some of the indexes proposed by SEITZ (1961, 1965) are, however, quite poorly defined (as e.g. *C. brancoiformis* or *C. cordiinitialis*) and their stratigraphical ranges are only roughly known. This led to a number of variable definitions of proposed zones [compare e.g. the *Cordiceramus brancoiformis* Zone in SEITZ 1961 and LOPEZ 1992c (and repeated in MARTINEZ &

al. 1996)].

A subsequent scheme, based on taxon first occurrence interval zones, was proposed by TRÖGER (1989). The interval discussed herein is contained within his zones 22 through 29 (see Text-fig. 5). Although TRÖGER (1989) introduced a numerical system, instead of index taxa, the ranges of taxa shown in his table plus short discussion gives a clear idea of his scheme. In the Upper Coniacian he distinguished the zone of *M. subquadratus* + *Volviceramus* (his zone 23), and the *Volviceramus*-free Zone, as introduced originally by SEITZ (his zone 24). Following SEITZ he defined the basal Santonian with the *Sphenoceramus* Teilzone (zone 25 of TRÖGER), and the successive early Santonian *Cl. undulatoplicatus* Zone (his zone 26) he defined as the interval zone from the FO of the index taxon to the FO of *C. cordiformis*. No zonal boundary is coeval in his scheme with the Lower/Middle Santonian boundary. The base of the Upper Santonian he put at the FO of *Sphenoceramus pinniformis*. The FO of *S. patootensiformis*, marking the base of the eponymous zone, was coeval with the base of the *Marsupites* Zone, in the middle part of the Upper Santonian.

Middle Coniacian through Santonian inoceramid zonation in the US Western Interior

The inoceramid zonation applied to the Middle Coniacian – Santonian sucession of the US Western Interior is presented in Text-figs 5- 7 and see also Text-figs 2-3). To a large extent it is the same standard zonation used in the North European Province (as recently compiled by ERNST & *al*. 1983 and TRÖGER 1989). The main difference is the exclusion of sphenoceramids, the major stratigraphical group among inoceramids in northern Europe, particularly in the Santonian (see e.g. WALASZCZYK 1992). In the US Western Interior the distribution of the group is still poorly known, but it seems to have a rather irregular occurrence.

To judge from the taxonomic diversity of the inoceramids in the interval studied, the stratigraphical potential of the group is expected to be much higher than currently recognised. The main problem, however, seems to be a rather rough knowledge of the stratigraphical distribution of several species, which is particularly the case in the Upper Coniacian (see Text-fig. 7).

The chronostratigraphical succession of inoceramid zones and their correlation with the ammonite zonation is presented in Text-figs 6-7 (see also Text-figs 2-3). Short definitions of particular zones/subzones are given below.

Volviceramus koeneni interval Zone: Its lower boundary is defined by the FO of the index taxon and its upper boundary by the FO of *V. involutus* (J. de C. SOWERBY). In the US Western Interior the zone is poorly documented.

Volviceramus involutus interval Zone: The interval from the FO of the index taxon to the first occurrence of *Magadiceramus subquadratus* (SCHLÜTER). Thus defined, the zone is recognisable only in the southern and central part of the US Western Interior; mainly south of Wyoming (COBBAN & *al*. 2005).

Magadiceramus subquadratus interval Zone: The interval from the FO of the index taxon to the FO of *Magadiceramus crenelatus* (SEITZ).

Magadiceramus crenelatus interval Zone: The interval from the FO of the index taxon to the FO of *Cladoceramus undulatoplicatus* (ROEMER).

Cladoceramus undulatoplicatus range Zone: The interval defined by the range of the index taxon.

Cordiceramus bueltenensis interval Zone: The base of the zone is defined by the LO of *Cladoceramus undulatoplicatus* and its top by the FO of *Cordiceramus* ex gr. *muelleri* (PETRASCHECK).

Cordiceramus muelleri interval Zone: The base of the zone is defined by the FO of any of the representatives of the *Cordiceramus muelleri* group, and its top by the FO of *Marsupites testudinarius*. The interval spanning the upper boundary of the zone was not observed in any of the sections studied.

Comparison of the proposed zonation with the Kauffman & al's (1994) scheme

In their comprehensive molluscan biostratigraphical scheme for the Western Interior Basin KAUFFMAN & *al*. (1994) proposed a number of taxon range and interval zones for the studied interval (Text-fig. 6). Some of these zones are easily correlated with the zones proposed herein but some of the others are based on taxa in open nomenclature, and/or taxa differently understood from their concept applied herein, and are difficult to follow (Text-fig. 6).

The correlation presented in Text-fig. 6 is based on selected zonal indexes and the rest of the KAUFFMAN & *al*. (1994) zones are presented according to their correlation.

The main problem is in the Middle Coniacian. Additionally, the interval of the *Volviceramus koeneni* Zone, KAUFFMAN & *al.* (1994) subdivided into a series of cremnoceramid-based zones. From bottom upwards these are the zones of *Cremnoceramus schloenbachi schloenbachi*, *C. schloenbachi woodsi* and *Cremnoceramus wandereri* + *C. inconstans* ssp. (late form). The latter zone, as may be inferred from their stratigraphical ranges, would actually be time equivalent of the range of *Volviceramus involutus* (SOWERBY). In Europe, cremnoceramids have never been observed to co-occur with *Volviceramus involutus*, and even the probable early volviceramids are reported from an interval stratigraphically well above the LO of *Cremnoceramus* (see WALASZCZYK & WOOD 1999). A possible explanation is a difference in the concept of early '*Inoceramus*' *undabundus* MEEK & HAYDEN, the not very well preserved material of which may easily be taken for the late cremnoceramids of the *schloenbachi* (=*crassus*) group (see also remarks in the taxonomic part). We cannot comment on the zones based on forms compared to '*Inoceramus*' *stantoni*, as even the interpretation of a typical *I. stantoni* presents a problem.

Although the general zonal succession in the Santonian may be followed (the correlation is quite certain), some of the zones (or rather zonal indexes) cannot. The base of our zone of *Cordiceramus muelleri* should correspond to the base of KAUFFMAN & *al.*'s (1994) zone of *Endocostea simpsoni* + *E. baltica* + *Sphenoceramus* cf. *patootensis*. The absence of *Cordiceramus muelleri* from the list of index taxa for this zone probably results from differing taxonomic concepts of the inoceramids from that interval. The *Sphenoceramus pachti pachti* Zone must be proposed for the northernmost part of the Western Interior, as representatives of the *S. cardissoides* – *S. pachti* group are sporadically noted in the US part of the Western Interior Basin.

RESPOSITORIES

USNM – United States National Museum of Natural History, Washington, DC
MGU – Museum of the Moscow State University
NMC – National Museum of Canada

PALAEONTOLOGICAL DESCRIPTION

Terminology and measurements of the external morphologic features of inoceramid shell is shown in Text-fig. 8.

Bivalvia LINNÉ, 1758
Pteriomorpha BUERLEN, 1944
Pterioida NEWELL, 1965
Pterioidea GRAY, 1847
Inoceramidae ZITTEL, 1881 (ICZN 473)

Genus *Inoceramus* SOWERBY, J. 1814

TYPE SPECIES: *Inoceramus cuvieri* SOWERBY, J. 1814, by subsequent designation of COX, 1969, p. 315.

The group of *Inoceramus kleini* – *Inoceramus undabundus* (*Inoceramus stantoni*) – *Inoceramus americanus* sp. nov.

The group represents an evolutionary lineage, beginning with *Inoceramus kleini*, which first gives rise to *I. undabundus* and then to *I. americanus* sp. nov. The lineage spans the latest Early Coniacian through to the Late Coniacian. The North American record reveals well only the later part of its history.

In the US Western Interior the group is well represented by *Inoceramus undabundus* MEEK & HAYDEN, 1862. This species is moderately to strongly inequivalve. The less inflated specimens of the species (e.g. USNM 519847 – Text-fig. 10) show the outline and the type of ornament characteristic of evolutionarily advanced *Inoceramus kleini* MÜLLER, 1888: sharp-edged and asymmetric concentric rugae, with a more or less well developed radial sulcus (on the posterior part of the disc), moderate obliquity and a short anterior margin. *I. kleini* is apparently equivalve.

In Europe, *I. kleini* appeared in the late Early Coniacian (see WALASZCZYK & WOOD 1999, see

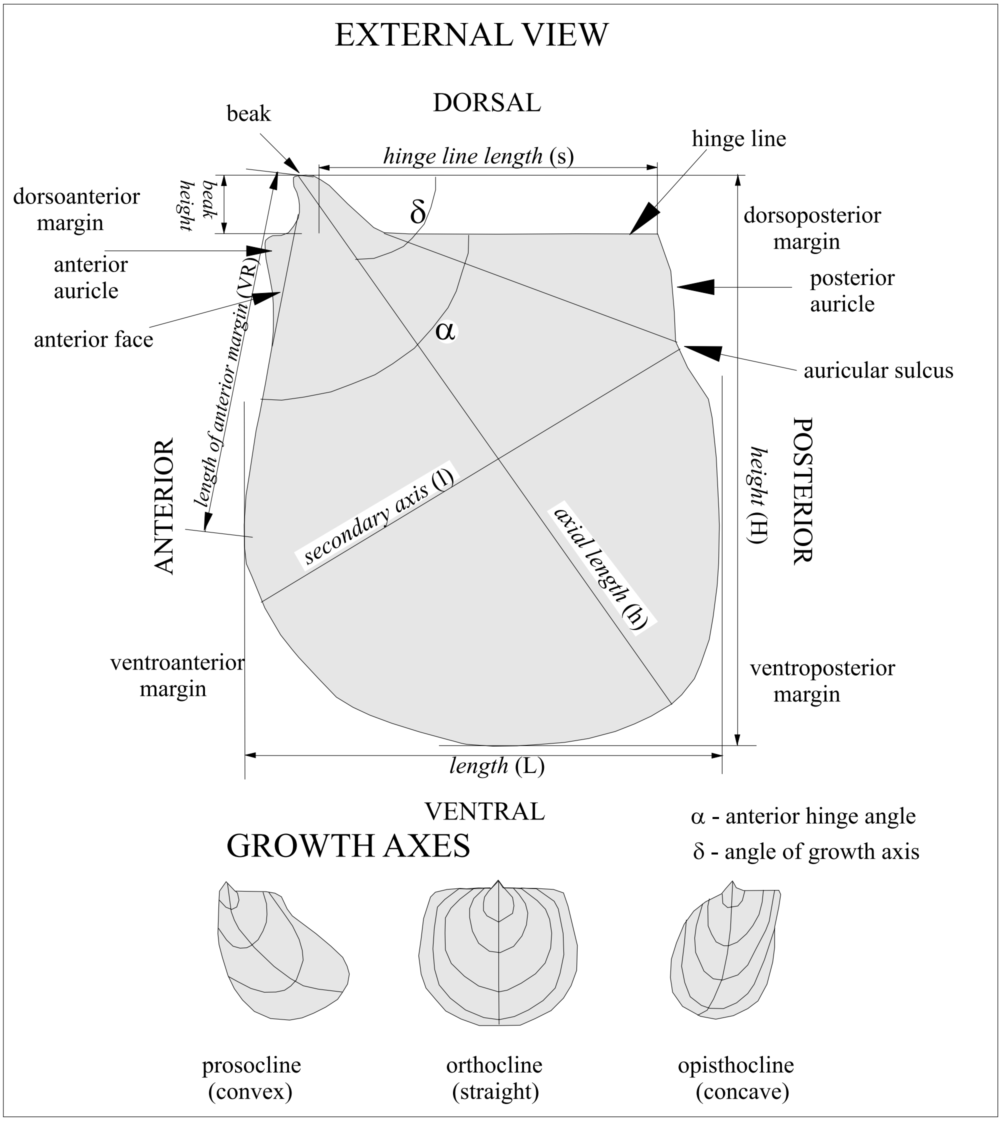

Fig. 8. Terminology and measurements of the external morphologic features of inoceramid shell [after HARRIES & *al*. 1996, modified]; RV – right valve; LV – left valve

also ČECH & ŠVABENICKÁ 1992) and continued into the Middle Coniacian (ASSMUS 1963, TRÖGER 1974, 1989; the type material actually comes from the lower Middle Coniacian). Although forms closely resembling the *kleini* morphotype appear still higher, ranging up to the lower Upper Coniacian (e.g. STANTON's 1899, pl. 75, figs 9-10, small specimens of his *Inoceramus acuteplicatus* (=*stantoni*) or USNM 519888 – Text-fig. 12.8 illustrated herein), these are interpreted as small-sized (juvenile) *Inoceramus undabundus*.

To the group of *Inoceramus kleini* – *Inoceramus undabundus* – *Inoceramus americanus* sp. nov. also belongs *Inoceramus stantoni* SOKOLOV, 1914, based on Upper Coniacian material from northern Wyoming (see discussion in SCOTT & COBBAN 1964), and interpreted herein as a synonym of *Inoceramus undabundus*. STANTON (1899, pl. 75, figs 9-10 and pl. 76, fig. 1) illustrated three specimens; the two smaller represent the *I. kleini* morphotype; the third one – the holotype – is a large right valve, which displays all of the features of the RV of *I. undabundus* (see discussion below).

Summing up, both species *I. kleini* and *I. undabundus* (with *I. stantoni* being a junior synonym of the latter) form a single clade. The evolutionary interpretation of this clade remains, however, unclear; it either constitutes a simple phyletic lineage or a phylogenetic one, with *I. undabundus* being an evolutionary successor which appeared by a cladogenetic event early in the Middle Coniacian. The direct reading of the character of this clade from the palaeontological record is difficult. Although specimens representing the *kleini* morphotype are still present in the Upper Coniacian their interpretation is not straightforward; as noted above under the description of *I. kleini*, they are interpreted as juveniles of *I. undabundus*. At about the Middle/Late Coniacian, *I. kleini* gave rise to another characteristic member of this clade, namely *Inoceramus americanus* sp. nov., a typical form of the Upper Coniacian of the Western Interior.

To the same clade also belong *Inoceramus incurvatissimus* (TRÖGER 1969b, and also 1974) and *Inoceramus balli* NEWTON 1909 (see also SEIBERTZ 1996); neither species was recognised in the material studied.

Inoceramus undabundus MEEK & HAYDEN, 1862
(Text-figs 9.2, 9.4, 10, 11.4-?5, 12.8, ?13.2, 22.?4, 5-6, 27.2, 28.2, 38.6)

1862. *Inoceramus undabundus* MEEK & HAYDEN, p. 26.
1876. *Inoceramus undabundus* MEEK & HAYDEN; MEEK, p. 60, pl. 3, fig. 2.
1894. *Inoceramus undabundus* MEEK & HAYDEN; STANTON, p. 84, pl. 16, figs 1-2 [the illustration and description after MEEK, 1876].
1898. *Inoceramus undabundus* MEEK & HAYDEN; LOGAN, p. 455, pl. 105, figs 1-2. [the illustration and description after MEEK, 1876]
1899. *Inoceramus acuteplicatus* n.sp., STANTON, p. 634, pl. 76, fig. 1 [non pl. 75, figs 9-10 = *Inoceramus kleini*]
? 1901. *Inoceramus undabundus* MEEK & HAYDEN; STURM, p. 92, pl. 10, fig. 4.
pars 1914. *Inoceramus stantoni* SOKOLOV, p. 52, pl. 5, figs 7-8.
1929. *Inoceramus undabundus* MEEK & HAYDEN; HEINE, p. 100, pl. 11, figs 50-51; pl. 12, fig. 55; pl. 13, fig. 57; pl. 19, figs 70-71.
non 1964. *Inoceramus stantoni* SOKOLOV; SCOTT & COBBAN, pl. 4, figs 1-3.
non 1971. *Inoceramus stantoni* SOKOLOV emend; PERGAMENT, p. 145, pl. 51, figs 2-5; pl. 52, figs 2-3; pl. 53, figs 2-5; pl. 54, fig. 2; pl. 55, fig. 2; pl. 56, figs 3-6; pl. 58, figs 2-3; pl. 60, figs 2-3; pl. 62, figs 1-2; pl. 64, fig. 2; pl. 65, fig. 2; pl. 66, figs 1-2; pl. 67, figs 1-3; pl. 68, figs 1-3.
non 1979. *Mytiloides*? aff. *M.? stantoni* (Sokolov); HERM *& al*., p. 71, pl. 11C.

TYPE: The lectotype, here designated, is USNM 1909, the original of MEEK (1876, pl. 3, fig. 2) (illustrated herein in Text-fig. 9.2) from the Colorado Shale (now Marias River Shale) of Chippewa Point near Fort Benton, Choutea County, Montana.

MATERIAL: USNM 519838 from USGS locality 21109, USNM 519844 from USGS locality D10851, USNM 519933 from locality D13127, USNM 519841 from USGS locality 21109, USNM 519847 from USGS locality 5032, USNM 519861 from USGS locality D8282; USNM 519865, USNM 519866, USNM 519867, USNM 519871, USNM 519872; USNM 519888 from USGS locality D13269; and also USNM 519896 from USGS locality D940; and a number of specimens in the collection at the Denver Federal Center, Denver, Colorado.

DESCRIPTION: The species is of moderate size, inequilateral, according to MEEK (1876, p. 60) decidedly inequivalve, with the LV markedly more inflated. The LV is moderately to strongly inflated, elongated postero-ventrally, with anteriorly curved growth axis. The anterior margin is short, almost straight, passing into the very long, broadly convex antero-ventral margin, and thence into the rounded postero-ventral one. The hinge line is short and straight. The anterior face and the posterior slope of the disc toward the posterior auricle are steep. The ventral margin is flattened. The disc is massive. The posterior auricle is small, indistinct. In some specimens, including the lectotype, the valve in the anterior and antero-ventral parts is clearly geniculated.

Very characteristic is the surface ornament of the species, composed of strong, sharp-edged rugae, with interspaces increasing in width regularly in the juvenile and early adult stages, and then subregularly. No other ornament element is seen on the internal moulds examined by us.

REMARKS: According to MEEK's (1876) description the species is inequivalve; the LV is more inflated with a more strongly incurved beak; both valves are similarly ornamented, with regular, strong, subangular rugae, with wide rounded interspaces.

In Europe the species was first cited by SCHLÜTER (1877) but without illustration. It was subsequently reported from the Middle Coniacian

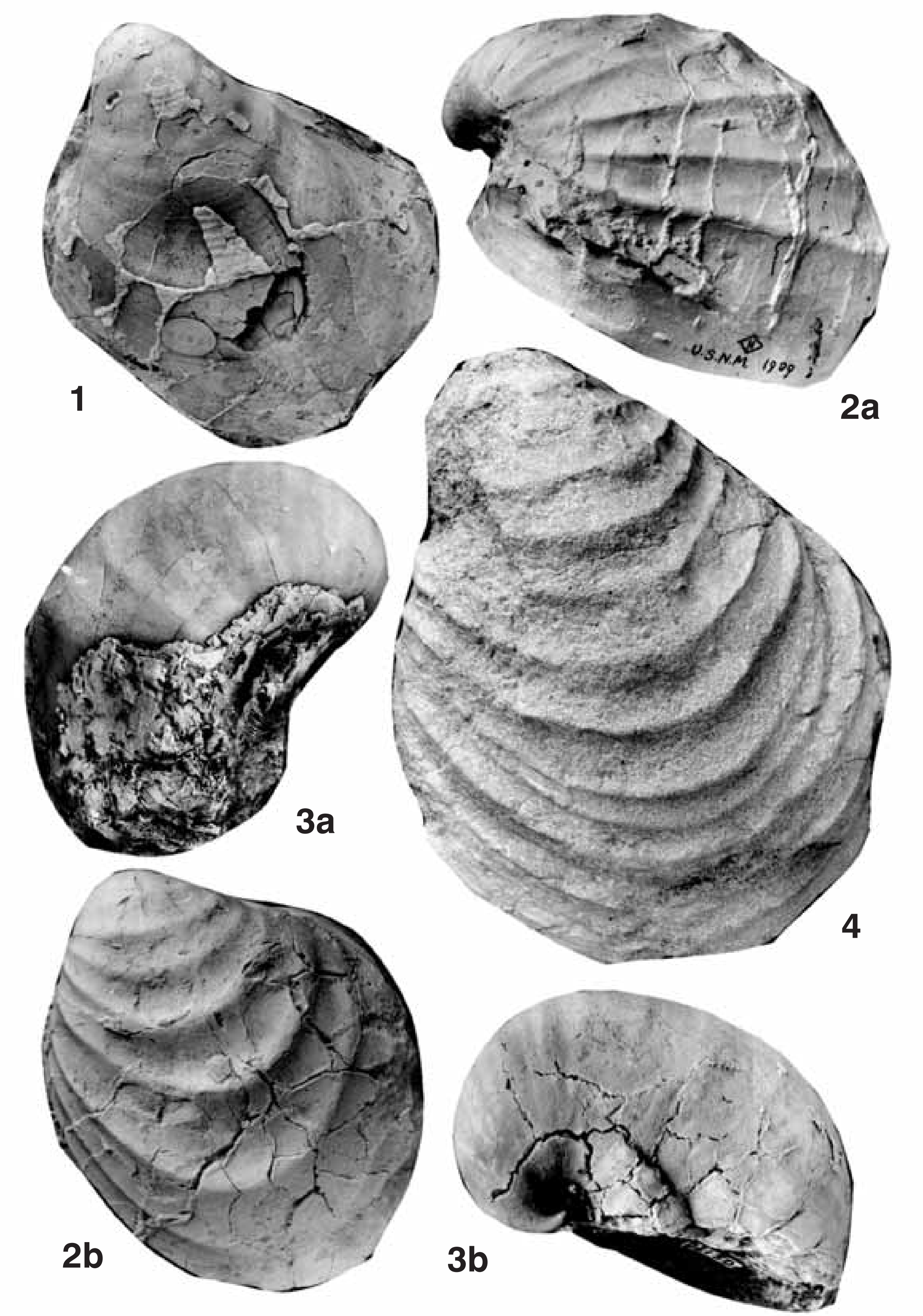

Fig. 9. **1** – *Inoceramus tenuirostratus* Meek & Hayden, 1862; USNM 519997, from USGS locality 17956; × 0.8. **2, 4**. – *Inoceramus undabundus* Meek & Hayden, 1862; 2 – photograph after the plaster cast, lectotype [figured by Meek 1876, pl. 3, fig. 2]; × 0.85; 4 – USNM 519844 from USGS locality D10851. **3**. – *Volviceramus involutus* (J. de C. Sowerby, 1829); USNM 519843 from USGS locality D2150; × 0.95.

Fig. 10. *Inoceramus undabundus* MEEK & HAYDEN, 1862; USNM 519847 from USGS locality 5032; × 0.7

of the Idzików sandstone (German *Sandstein von Kieslingswalde*) by STURM (1901, pl. 10, fig. 4). STURM's illustrated specimen looks like a RV, with a long, slightly concave anterior margin that is completely atypical of *I. undabundus*. However, the specimen is strongly deformed, and its ornament is undoubtedly of the *undabundus* type. A series of specimens showing well the features of *I. undabundus* was described by HEINE (1929, p. 100, pl. 11, figs 50-51; pl. 12, fig. 55; pl. 13, fig. 57, and pl. 19, figs 70-71) from Westphalia, northern Germany. Of particular interest are the double-valved specimens, displaying well the inequivalve character of the species and the range of this feature. Another very interesting specimen is a large RV (HEINE 1929, pl. 19, fig. 70) that resembles STANTON's type (STANTON 1899, pl. 76, fig. 1) of *Inoceramus stantoni* SOKOLOV, which we synonymised herein with *I. undabundus*. HEINE (1929, p. 95) referred this species to *Volviceramus* (his group of involutid inoceramids). However, based on the phylogeny of this species showing it clearly to be an evolutionary successor of *I. kleini*, *I. undabundus* should rather be retained in the genus *Inoceramus*.

Into the synonymy of *Inoceramus undabundus*, we put *Inoceramus stantoni* SOKOLOV, 1914. This name is a replacement name for *I. acuteplicatus* of STANTON, 1899, due to its homonymy with *I. acuteplicatus* SCHAFHÄUTL, 1863. In its original description STANTON (1899) illustrated three specimens, of which the large one, from his pl. 76, fig. 1, was designated by him the holotype. The two smaller specimens, his pl. 75, figs 9-10, differ from the holotype and represent a morphotype very close to *I. kleini*, to which they were subsequently commonly referred (see discussion in SCOTT & COBBAN 1964, and SEITZ 1965, p. 131). However, because distinguishing between isolated specimens of *I. kleini* and the juveniles of *I. stantoni* is practically impossible, we interprete all three STANTON's specimens as conspecific.

SOKOLOV (1914, p. 52) apparently applied *I. stantoni* to a common Early – ?Middle Coniacian North Pacific form, referred later by YEHARA (1924; and emended further by NAGAO & MATSUMOTO 1940) to *Inoceramus uwajimensis*. This concept was subsequently followed by PERGAMENT (1971, p. 145), who synonymised *I. uwajimensis* and

I. stantoni (=*I. acuteplicatus* Stanton), as well as *I. uwajimensis* var. *yeharai*. More recently a partial synonymy was suggested by KAUFFMAN (1977c, p. 183) who referred to *I. stantoni* those forms of *I. uwajimensis* which are 'more inclined, have more asymmetrical growth line-rugae, more evenly distributed rugae and have a twisted, strongly prosogyrous beak-umbo below which the anterior margin is projecting and rounded'. The synonymy of *Inoceramus uwajimensis* and *I. stantoni* was also regarded as highly probable by NODA & MATSUMOTO (1998, p. 449). The North American type of *I. stantoni* is a RV, characterised by a broadly convex anterior margin, a long and straight hinge line, and a weak and shallow radial sulcus; it is quite different from forms referable to *Inoceramus uwajimensis*.

OCCURRENCE: The species is known from the Western Interior and Gulf Coast of North America and from Europe. It appeared first in the early Middle Coniacian and ranged most probably to the early Late Coniacian.

Inoceramus americanus sp. nov.
(Text-figs 11.1, 12.7, ?12.9, 12.13, 12.14, 12.15, 23.2)

pars 1970. *Inoceramus* (*Magadiceramus*?) cf. *soukupi* MACÁK; SEITZ, p. 45, 49, pl. 8, fig. 6; pl. 12, fig. 2.

1986. *Inoceramus* (*Magadiceramus*) aff. *soukupi* MACÁK; SCOTT & *al.*, fig. 9j.

pars 2001. *Magadiceramus subquadratus complicatus* (HEINE); COLLOM, p. 486, pl. 13, figs 1-3 [non pl. 39, fig. 6]

TYPE: The holotype is USNM 519887 (Text-fig. 12.7) from the Upper Coniacian of USGS locality 21097 (Cody Shale, Fremont County, Wyoming).

DERIVATION OF NAME: From the name of the continent.

MATERIAL: USNM 519868 from USGS locality 17955, USNM 519887, USNM 519894 and USNM 519893 from USGS locality 21097, USNM 519889 from USGS locality D1655, USNM 519892 from USGS locality 17956; USNM 519918 from USGS locality 24556.

DIAGNOSIS: Moderate sized and moderately inflated, axially elongated species. Valves moderately oblique, with narrow, subtriangular posterior auricle. Valve disc with more or less developed posterior radial sulcus. Valves covered with regularly spaced rugae and radial ornament, well developed in the axial part of disc.

DESCRIPTION: The species is of small to moderate size, inequilateral, subequivalve. The valves are moderately inflated and strongly axially elongated, with the growth lines anteriorly convex and markedly oblique. The beak is small, pointed antero-dorsally, projecting slightly above the hinge line. The posterior auricle is small, subtriangular in outline, well developed and clearly separated from the disc. The disc is elongate ovate. Posterior to the growth axis there is a weakly to moderately developed radial sulcus. Sometimes the juvenile part of the valves is geniculated. The anterior margin is short to moderately long; it passes into the broadly rounded antero-ventral margin and then into the ventral margin, which is rounded besides the axis of the posterior radial sulcus. The posterior margin is almost straight.

The valves are ornamented with closely and regularly spaced rugae; sharp edged, asymmetrical, with their leading edges distinctly steeper. The rugae pass through the radial sulcus, and then curve sharply at the posterior margin of the disc, and run parallel to the growth axis on the posterior auricle. The valves bear usually more or less clearly developed radial ornament, which is developed mostly in the axial and anterior part of valves. The radial elements are usually rather weak, never dominating the concentric rugae. Sometimes the radial ornament is expressed mostly by crenellation of the edges of the concentric rugae.

REMARKS: The species closely resembles small-sized *I. kleini* with fine radial streaming. It shows a relatively narrow range of morphological variability, mostly the valve outline which ranges from subquadrate-rounded to more subquadrate, and the extent of the radial ornament.

Inoceramus americanus sp. nov. resembles ?*Magadiceramus soukupi*. The latter species differs in the smaller h/l rato, and consequently in a more subquadrate outline than *I. americanus*. Both species are definitely closely related although the nature of the relationship is not clear. Possibly they

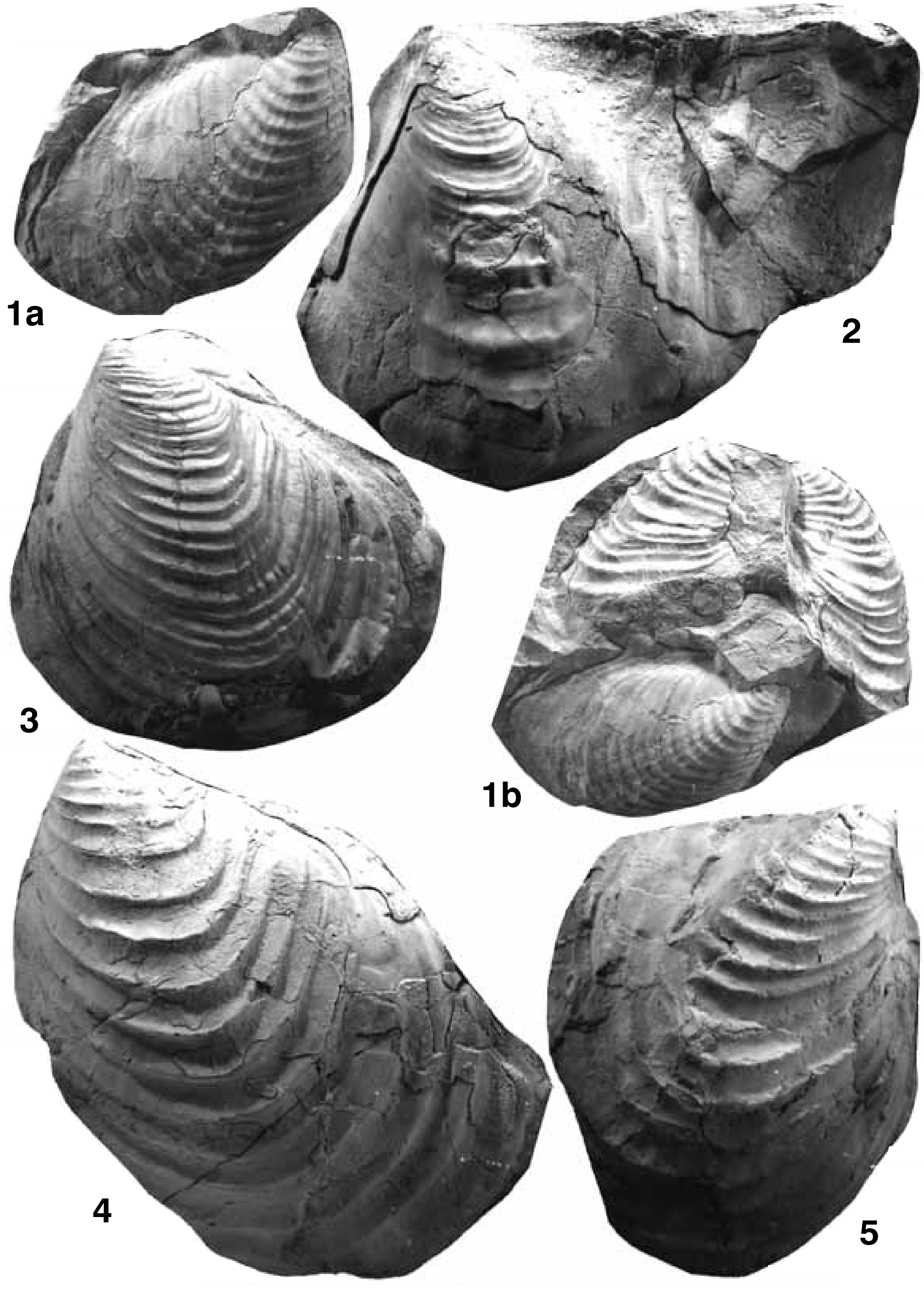

Fig. 11. **1** – *Inoceramus americanus* sp. nov., USNM 519868 from USGS locality 17955; × 0.8. **2** – *Sphenoceramus* sp. A., USNM 519869 from USGS locality D934; × 0.8. **3** – *Magadiceramus soukupi* (MACÁK, 1967), USNM 519870, locality unknown; × 0.8. **4, ?5** – *Inoceramus undabundus* MEEK & HAYDEN, 1862; 4 – USNM 519871 from USGS locality D940; × 0.9; 5 – USNM 519872 from USGS locality 17955; × 0.8

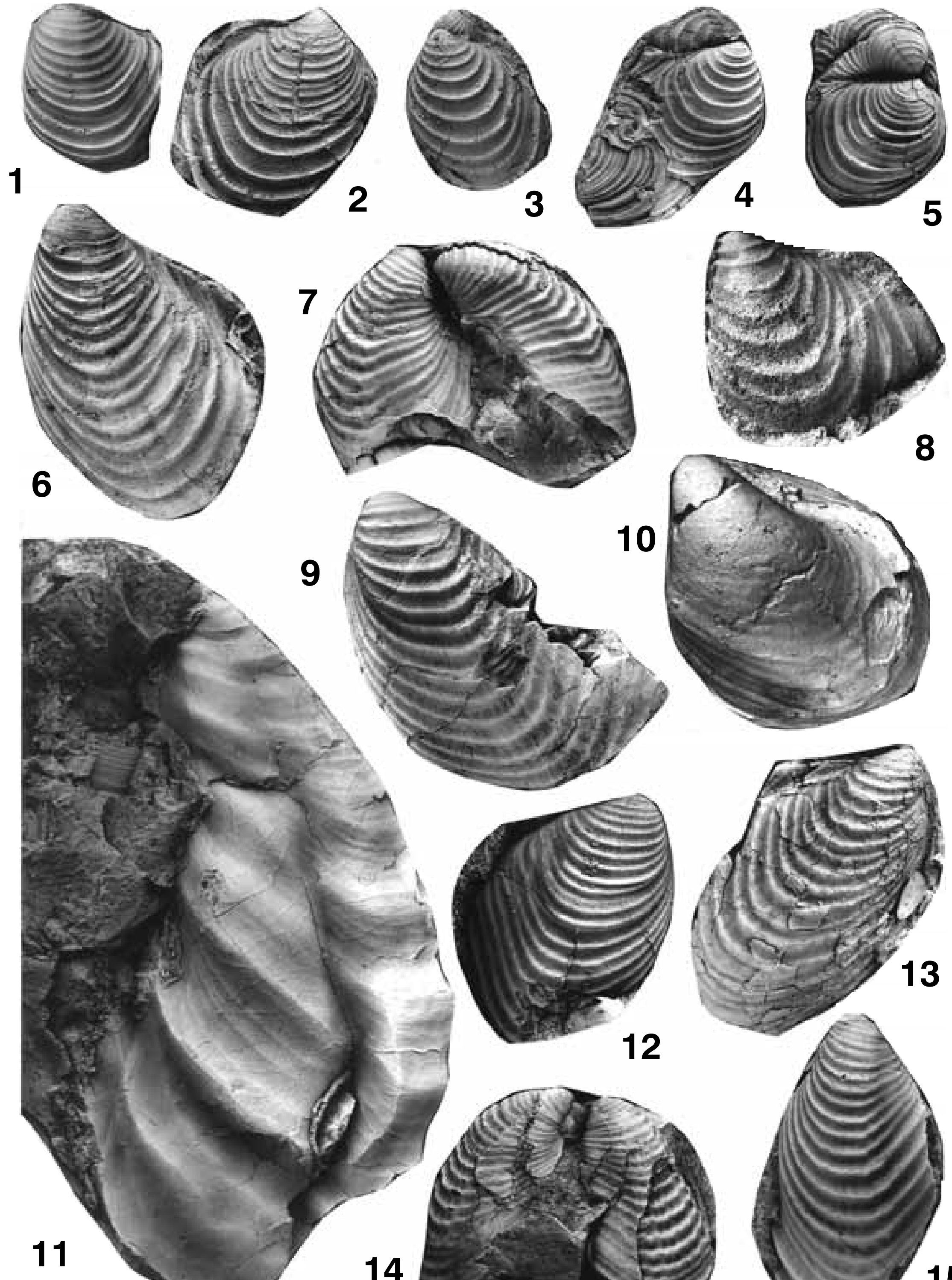

Fig. 12. **1, 6, 12** – *Magadiceramus soukupi* (Macák, 1967); 1 – USNM 519881 from USGS locality 21097; × 0.9; 6 – USNM 519886 from USGS locality D934; × 0.8; 12 – USNM 519891 from USGS locality 21097; × 0.8. **2-5** – *Magadiceramus subquadratus* (Schlüter, 1877) juveniles; 2 – USNM 519882 from USGS locality D1655; × 0.8; 3 – USNM 519883 from USGS locality 23426; × 0.85; 4 – USNM 519884 from USGS locality 17942; × 0.9; 5 – USNM 519885 from USGS locality 17942; × 0.8. **7, 9, 13-15** – *Inoceramus americanus* sp. nov., 7 – USNM 519887 from USGS locality 21097; × 0.85; 9 – USNM 519889 from USGS locality D1655; × 0.75; 13 – USNM 519892 from USGS locality 17956; × 0.8; 14 – USNM 519893 from USGS locality 21097; × 0.85; 15 – USNM 519894 from USGS locality 21097; × 0.8. **8** – *Inoceramus undabundus* Meek & Hayden 1862; USNM 519888 from USGS locality D13269; × 0.8. **10** – *Inoceramus tenuirostratus* Meek & Hayden, 1862; holotype; × 0.8. **11** – *Inoceramus gibbosus* Schlüter, 1877; USNM 519890 from USGS locality 21097; × 0.8

form a lineage leading from *Inoceramus* to *Magadiceramus*.

To *I americanus* belongs one of SEITZ' specimens of *Inoceramus* (*Ma*.?) cf. *soukupi* MACÁK (see SEITZ 1970, pl. 12, fig. 2). It is the specimen referred by SEITZ to his group 3 of *I*. cf. *soukupi*. Other specimens of the group are markedly distinct; the auriculate specimen Ko350 (SEITZ 1970, pl. 12, fig. 1), with straight and long anterior margin, is referred herein to *Inoceramus? sokolovi* sp. nov., whereas the third

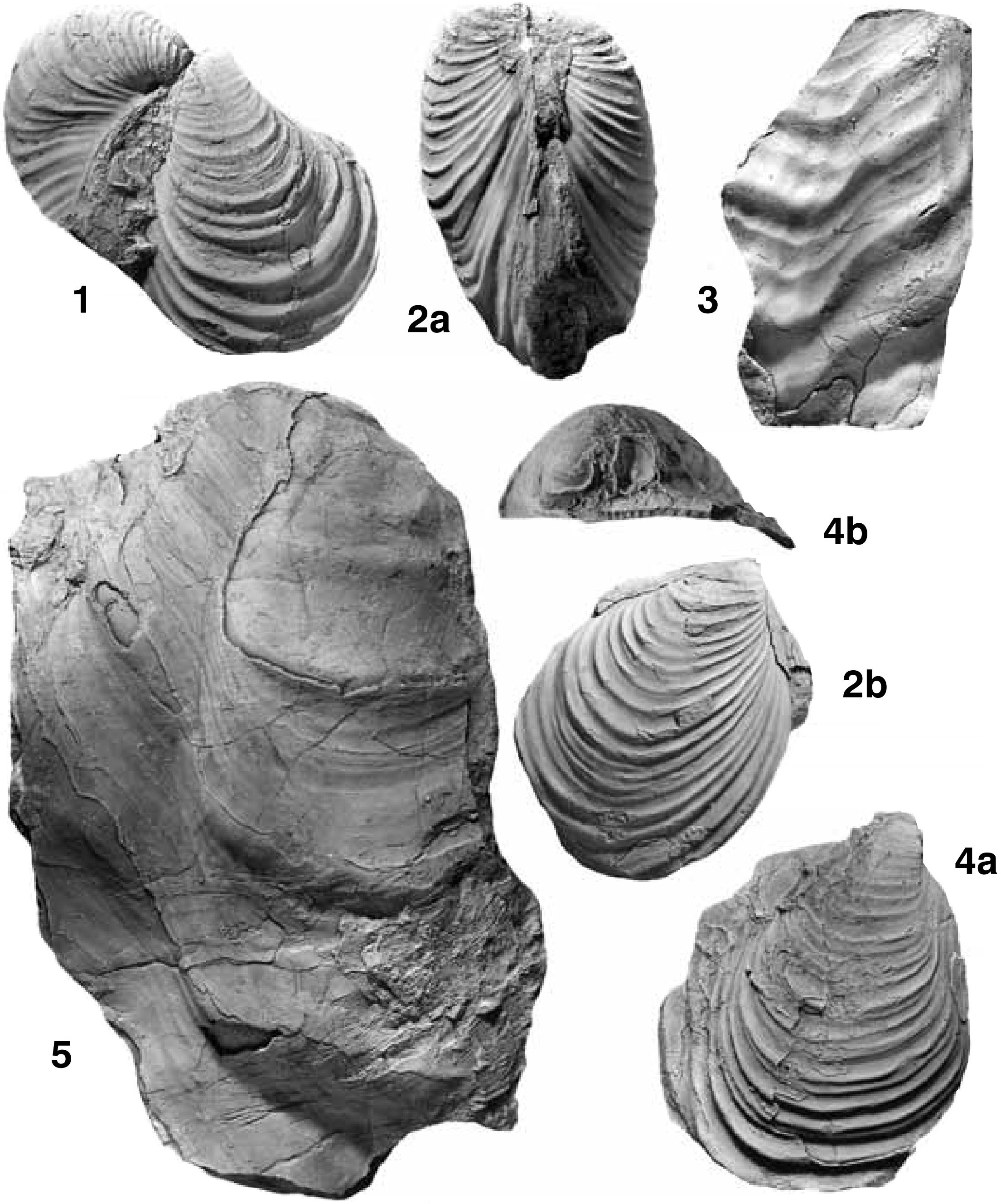

Fig. 13. **1, 4** – *Inoceramus sokolovi* sp. nov.; 1 – USNM 519895, 4 – USNM 519898; all from USGS locality D940. **2** – ?*Inoceramus undabundus* MEEK & HAYDEN, 1862; USNM 519896 from USGS locality D940. **3** – *Sphenoceramus* cf. *latisulcatus* (HEINE, 1929); USNM 519897, from USGS locality D940. **5** – *Inoceramus gibbosus* SCHLÜTER (1877), USNM 519899 from USGS locality D940. All specimens × 0.85

specimen, ZH1980 (SEITZ 1970, pl. 13, fig. 5) is a deformed *Magadiceramus* ex gr. *subquadratus*.

I. americanus is referred herein to the genus *Inoceramus*, although it resembles representatives of the genus *Magadiceramus*, particularly some of the specimens referred to *Magadiceramus complicatus* (but not the type) that possess sharp and relatively closely spaced rugae. The best examples are the specimens of SOUKUP (1956, pl. 1, figs 1-2) referred originally to *I.* ex gr. *subcardissoides* and then reassigned to *M. complicatus* (HEINE) by SEITZ (1970, p. 33); and those of COLLOM (2001), referred to *M. complicatus*. Such specimens differ markedly from HEINE's type, which is subquadrate, with typical *M. subquadratus* concentric ornament, and radial ornament limited to the adult part. Forms like those of SOUKUP present a considerable problem at the moment. The inadequate knowledge of these forms does not allow us to judge whether they represent extreme variants of *M. complicatus* or belong to *I. americanus*.

OCCURRENCE: The species is a common member of the Upper Coniacian inoceramid assemblages in the US Western Interior (and most probably also in Europe, although in the latter area the fauna from that interval is still rather poorly known).

Inoceramus sokolovi sp. nov.
(Text-fig. 13.1, 13.4)

pars 1970. *Inoceramus* (*Magadiceramus?*) cf. *soukupi* MACÁK; SEITZ, p. 45, 48; pl. 12, fig. 1 [only]

TYPE: Specimen Ko350, the original of SEITZ (1970, pl. 12, fig. 1), is here designated the holotype.

MATERIAL: 2 North American specimens: USNM 519895 and USNM 519898 fromUSGS locality D940, and the German specimen, the original of SEITZ (1970, pl. 12, fig. 1), from the Upper Coniacian of the Königsmühle mine shaft near Dortmund, Westphalia.

DERIVATION OF NAME: After D.V. SOKOLOV, Russian palaeontologist.

DIAGNOSIS: Small to moderately sized species, weakly oblique, subrectangular in outline, with subtriangular disc and well separated, triangular posterior auricle. Beak projecting above hinge line, Valve ornamented with closely, subregularly spaced commarginal rugae.

DESCRIPTION: The species is of small to moderate size for the genus, inequilateral, ?equivalve. The valve is composed of a subtriangular disc and a well separated posterior auricle. The posterior auricle is triangular and elongated. The valve is moderately inflated, with maximum inflation in the dorso-central part. The umbo is well developed, with the beak projecting above the hinge line. The hinge line is straight and moderately long. The anterior margin is relatively long, being more than three-quarters of the axial length, and is straight to concave. It passes into the broadly rounded ventral margin. The outline of the adult posterior margin is not observed, but judging by the earlier stages, it is concave, with a distinct auricular sulcus.

The valves are ornamented with commarginal, closely spaced, irregular rugae, well developed only on the disc. The posterior auricle is smooth or bears only growth lines. Although in general the interspaces are wider in the ventral margin, a clear, ventralward trend of increasing interspaces is not observed. Radial ornament is not observed.

REMARKS: *Inoceramus sokolovi* corresponds to a concept of group 3 of *Inoceramus* (*Ma*.?) *soukupi* of SEITZ (1970) as represented by his specimen Ko350; the two other specimens referred by Seitz to this group are quite different and obviously represent different taxa. His specimen Lü 201 (SEITZ 1970, pl. 12, fig. 2) belongs to *Inoceramus americanus* sp. nov., whereas ZH 1980 (SEITZ 1970, pl. 13, fig. 5) is a markedly deformed *Magadiceramus* ex gr. *subquadratus*.

OCCURRENCE: Upper Coniacian of the US Western Interior and of northern Germany.

Inoceramus cf. *albertensis* MCLEARN, 1926
(Text-fig. 14)

Compare:
1926. *Inoceramus albertensis* MCLEARN, p. 123, pl. 20, figs 3-4.

TYPE: By original designation the holotype is 6107, the original of MCLEARN (1926, pl. 20, figs 3-4).

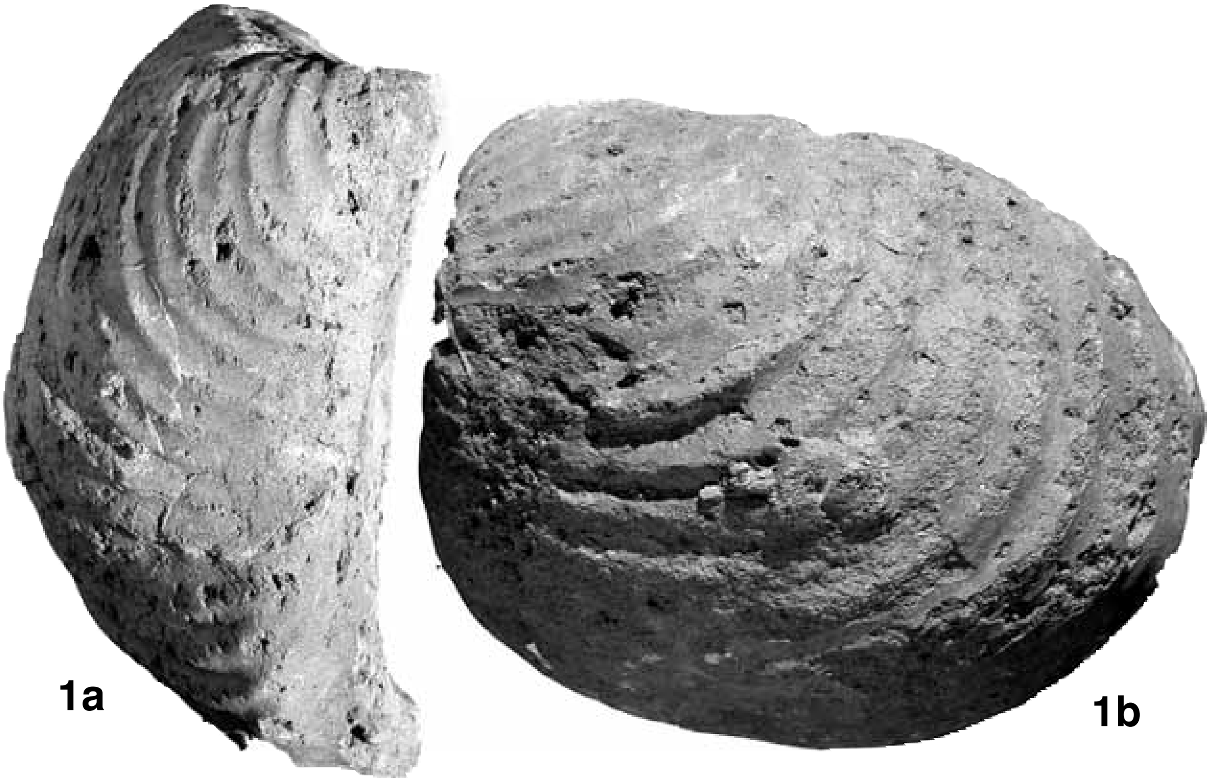

Fig. 14. *Inoceramus* cf. *albertensis* McLearn, 1926; USNM 519848 from the basal part of the Dalton Sandstone; USGS locality D5427

MATERIAL: A single specimen, USNM 519848, from USGS D5427.

DESCRIPTION AND REMARKS: The only specimen in the material studied is an internal mould of a single LV. The specimen is moderately large, moderately inflated, longer than high. The umbo is small, located anteriorly. The anterior margin is moderately long, almost straight, and passes into the very long, broadly convex ventral margin. The hinge line is long and straight. In the juvenile stage the valve grows obliquely, after which the obliquity decreases gradually. No clear geniculation is visible. The valve is ornamented with quite regular rugae, with the interspaces increasing in width slowly ventralward.

The specimen resembles the type of *I. albertensis*. The species, however, can hardly be regarded as very characteristic.

OCCURRENCE: Known from North American Western Interior; ?Middle Coniacian.

Inoceramus robertsoni sp. nov.
(Text-figs 15-20, 23.3)

HOLOTYPE: USNM 519850

MATERIAL: 6 specimens; USNM 519849 through USNM 519854.

DERIVATION OF NAME: After Jacques F. Robertson, US Geological Survery, who discovered and collected most of the specimens.

DESCRIPTION: It is a medium to large-sized *Inoceramus* species, prosocline, inequilateral, strongly inflated. Only left valves are represented in the material studied. All the valves are distinctly geniculated, the geniculation being associated with a change in ornament. The juvenile stage is subquadrate in outline, moderately inflated, the inflation is stronger in the adult part. The umbo is relatively small, with the beak not projecting, or projecting only slightly above the hinge line. The anterior margin is straight and long, with a steep and high anterior face. The posterior margin is flattened. The posterior auricle is generally small; it becomes larger at the adult stage. Posterior to the growth axis in the posterior part of the disc there is a quite well developed radial sulcus. The sulcus is best developed in the juvenile part and weakens gradually ventralward.

The juvenile stage is covered with subregularly spaced concentric rugae, sharp edged, with the interspaces increasing gradually ventralward. The adult stage is ornamented with irregular, very widely spaced, low rugae, or the valve becomes smooth.

REMARKS: Unfortunately, the species is represented in the material studied exclusively by LVs.

Fig. 15. **1, 2** – *Inoceramus robertsoni* sp. nov.; 1 – USNM 519849 (see Text-fig. 16.1 for the dorsal and anterior views), USGS locality D12888; 2 – USNM 519850 (see Text-fig. 16.2 for the dorsal and anterior views), USGS locality D12810

The high, flat anterior wall suggests, however, that it was equi- or at most weakly inequivalve and lying on the anterior side when adult.

Despite the considerable inflation, the species is clearly a representative of the genus *Inoceramus*, with the inflation due partly to geniculation.

I. robertsoni resembles *Inoceramus incurvatis-*

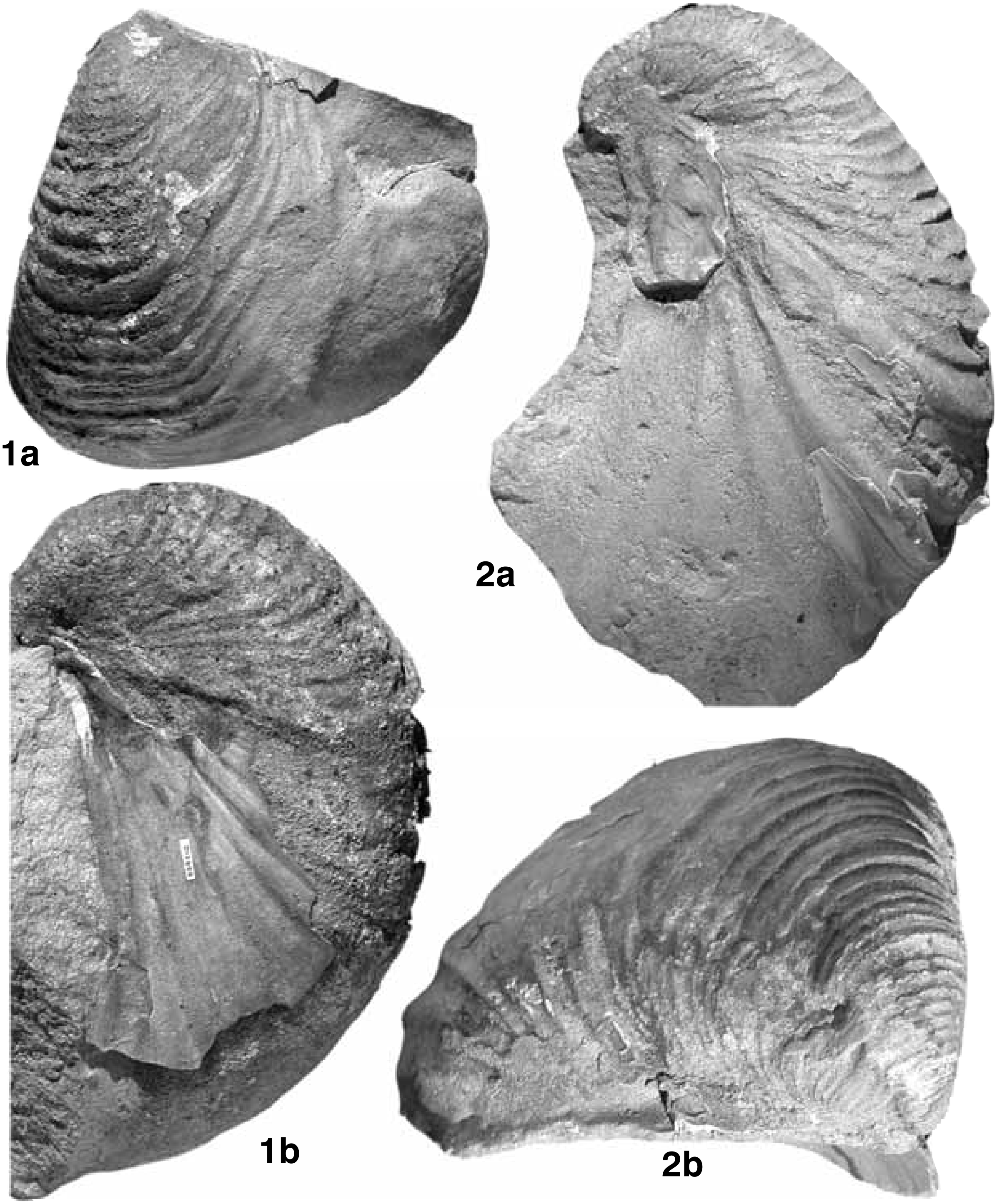

Fig. 16. **1, 2** – *Inoceramus robertsoni* sp. nov.; 1 – USNM 519849 (see Text-fig. 15.1 for lateral view), USGS locality D12888; 2 – USNM 519850 (see Text-fig. 15.2 for lateral view), USGS locality D12810

Fig. 17. **1, 2** – *Inoceramus robertsoni* sp. nov.; 1 – USNM 519851 (see Text-fig. 18.1 for the dorsal and anterior views), USGS locality D12888; 2 – USNM 519852 (see Text-fig. 18.2 for the dorsal and posterior views), USGS locality D12810

simus TRÖGER, 1974, described from the Middle Coniacian of the Subhercynian Cretaceous, Germany (TRÖGER 1969b and 1974). The latter possesses much more regular ornament and does not show the presence of the posterior radial sulcus that is so characteristic of the American species.

OCCURRENCE: US Western Interior; most probably Middle Coniacian.

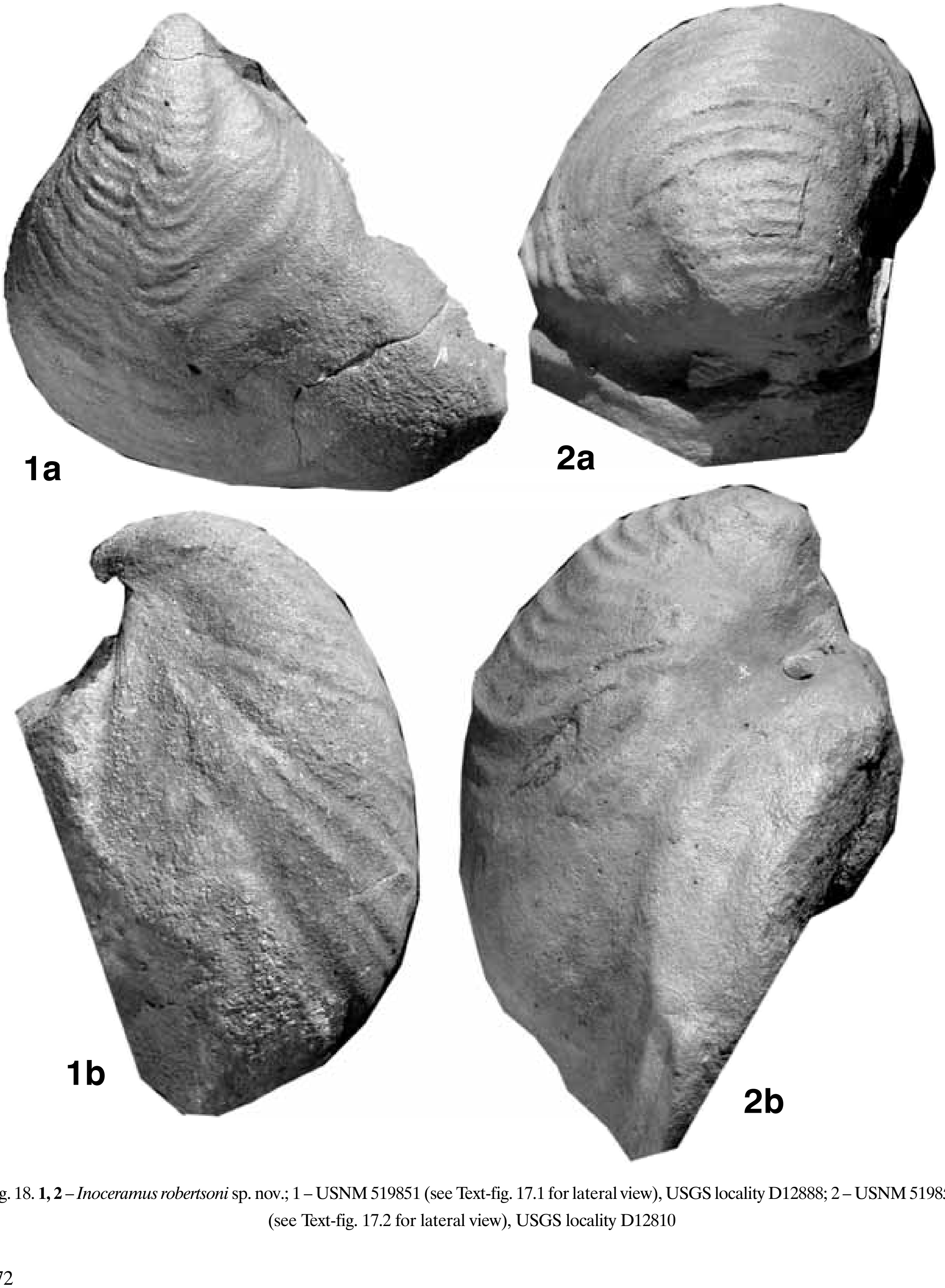

Fig. 18. **1, 2** – *Inoceramus robertsoni* sp. nov.; 1 – USNM 519851 (see Text-fig. 17.1 for lateral view), USGS locality D12888; 2 – USNM 519852 (see Text-fig. 17.2 for lateral view), USGS locality D12810

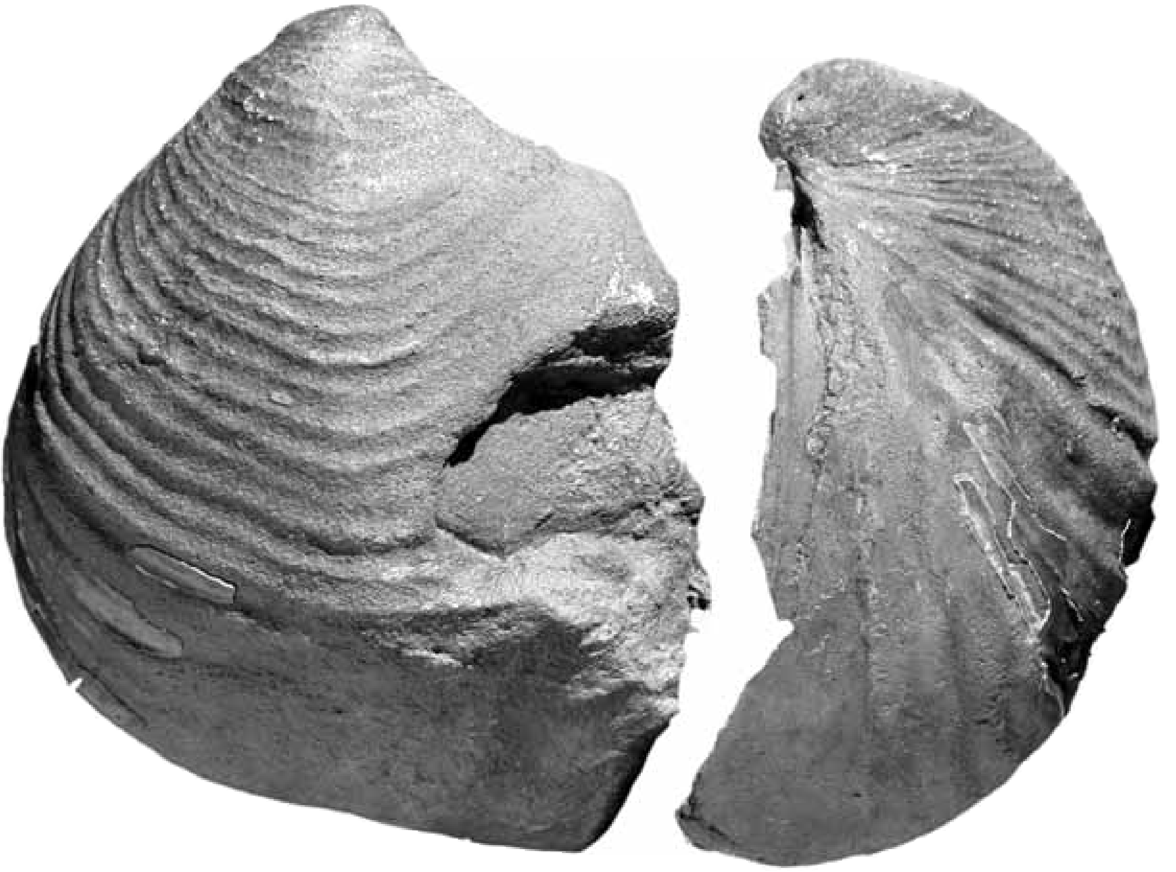

Fig. 19. *Inoceramus robertsoni* sp. nov.; USNM 519853; USGS locality D12888

Inoceramus gibbosus SCHLÜTER, 1877
(Text-figs 12.11, 13.5, 21)

1877. *Inoceramus gibbosus* SCHLÜTER, p. 271.
1888. *Inoceramus percostatus* MÜLLER, p. 413, pl. 17, fig. 3.
non 1904. *Inoceramus percostatus* MÜLLER, FLEGEL, p. 24 [=*Inoceramus lusatiae* ANDERT; see JERZYKIEWICZ, 1969, p. 175.
?non 1911. *Inoceramus percostatus* MÜLLER; ANDERT, p. 56, pl. 5, fig. 4.
1928a. *Inoceramus dankeri* HEINZ, p. 75.
1929. *Inoceramus dankeri* HEINZ var. *anderti* HEINZ; HEINZ, p. 686, figs 4-5.
1929. *Inoceramus gibbosus* SCHLÜTER; HEINE, p. 50, pl. 4, figs 20-22.
1929. *Inoceramus percostatus* MÜLLER; HEINE, p. 46, pl. 3, figs 14-17.
1929. *Inoceramus bilobatus* MÜLLER; HEINE, p. 49,pl. 4, figs 18-19.
1932. *Aulacoceramus dankeri* HEINZ; HEINZ, p. 8.
?non 1934. *Inoceramus percostatus* MÜLLER; ANDERT, p. 119, pl. 5, fig. 4.
1958. *Inoceramus russiensis* NIKITIN; BODYLEVSKI, p. 78, pl. 29, fig. 1; pl. 31, fig. 1.
1959. *Inoceramus percostatus* MÜLLER; DOBROV & PAVLOVA, p. 145, pl. 12, fig. 3.
non 1963. *Inoceramus percostatus* MÜLLER; ASSMUS, p. 45, pl. 9, fig. 1.
?non 1969. *Inoceramus percostatus* MÜLLER; KHALAFOVA, p. 177, pl. 13, fig. 4; pl. 14, fig. 1 [pl. 13, fig. 4 =*deformis* group; pl. 14, fig. 1 = ?*Tethyoceramus* sp.]
1972. *Inoceramus percostatus* MÜLLER; GLASUNOVA, p. 59, pl. 2, figs 1-2; pl. 3, fig. 2; pl. 9, fig. 1, pl. 13, fig. 6.
1972. *Inoceramus percostatus* MÜLLER subsp. *gorenkaensis* subsp. nov., GLASUNOVA, p. 60, pl. 4, figs 1-2; pl. 6, figs 1-2; pl. 7, fig. 1; pl. 9, fig. 2.

TYPE: The holotype, by monotypy, is the original of SCHLÜTER (1877, p. 271) first illustrated by

HEINE (1929, pl. 4, figs 20-22) from the Upper Coniacian of Westpahlia (Osterfeld Mine near Oberhausen), Germany.

MATERIAL: Two specimens: USNM 519855 and USNM 519890 from USGS locality 21097; and USNM 519899 from USGS locality D 940.

Fig. 20. *Inoceramus robertsoni* sp. nov.; USNM 519854; USGS locality D12810

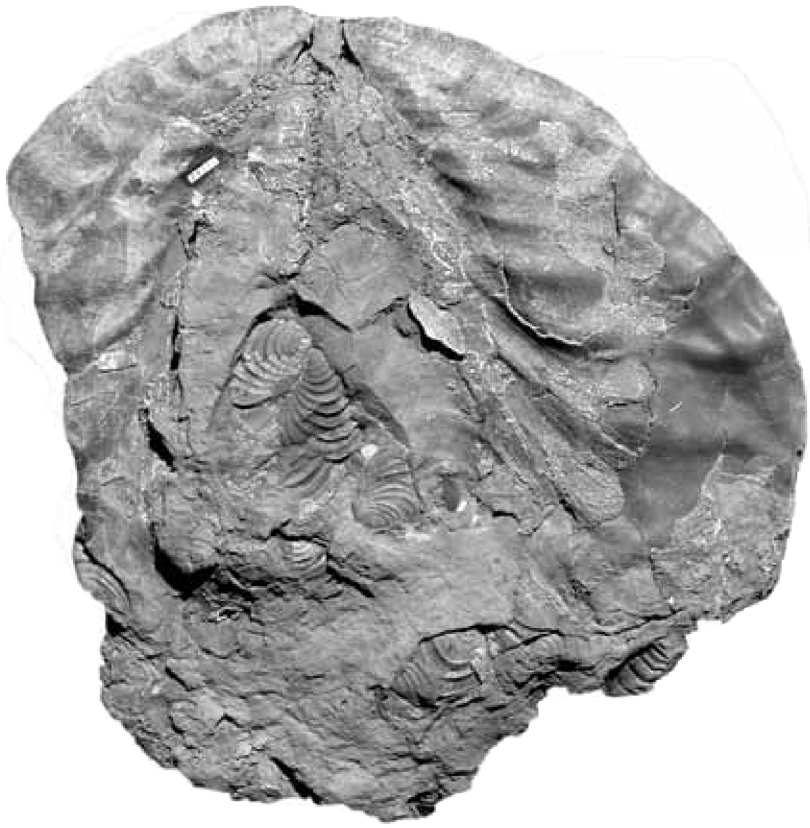

Fig. 21. *Inoceramus gibbosus* SCHLÜTER, 1877; USNM 519855 from USGS locality 21097; × 0.4

DESCRIPTION: USNM 519855 (Text-fig. 21) is a large, double-valved internal mould with fragments of shell preserved in the posterior part of the RV. The RV is more complete. Both valves are bent along the axis and moderately compressed. It is equivalve and inequilateral; the valves are triangular in outline, prosocline, axially strongly elongated with a long anterior margin, and a moderately high anterior face. The triangular posterior ear is well separated from the disc, with a distinct step along the posterior margin of the disc. The disc possesses a well developed radial sulcus, located posterior to the growth axis. The umbo is narrow, pointed, curved antero-dorsally. The hinge line is straight and moderately long.

The valves are ornamented with regularly spaced rugae, with interspaces increasing distinctly ventralward. In the juvenile stage, sharp-edged, slightly lamellate growth lines are superimposed on the rugae; these become less distinct in the middle and adult parts. The rugae weaken slightly when entering the posterior sulcus, and are again stronger on the posterior margin of the disc. They disappear on the posterior auricle. In the axial part of the disc the concentric undulations are crossed by discontinuous, slightly irregular radial ribs that are well developed in parts close to concentric rugae, particularly in the adult stage.

USNM 519890 (Text-fig. 12.11) is a large (h max = 133 mm), deformed and incompletely preserved single RV. The specimen lacks the anterior face and is incomplete toward the venter. Its extended posterior auricle is deformed. The specimen is similar to USNM 519855 (Text-fig. 21).

This specimen shows well the typical ornament of the species, composed of distinct concentric rugae, with interspaces increasing relatively quickly ventralward; it also possesses a well developed radial sulcus, posterior to the growth axis.

The third specimen, USNM 519899 (Text-fig. 13.5), only questionably referred to this species, is an incomplete RV of the adult stage, with the umbonal, anterior and auricular parts missing. It has very widely spaced concentric rugae, which are relatively sharp-edged, with flat-floored interspaces, and with superimposed growth lines. The rugae weaken on the posterior part of the disc, posterior to the radial sulcus. The radial sulcus is relatively shallow and wide.

REMARKS: The name *Inoceramus gibbosus* is applied herein in accordance with the concept presented by WALASZCZYK & WOOD (1999, pp. 189-190), i.e. this name is used provisionally for radially sulcate late Early – Late Coniacian *Inoceramus,* which are referred currently to at least four distinct species. These are: *Inoceramus gibbosus* SCHLÜTER, 1877, *Inoceramus lezennensis* (DECOCQ, 1874), *Inoceramus russiensis* NIKITIN 1888, and *Inoceramus percostatus* MÜLLER, 1888. The apparent differences between the types of these species are mainly the result of ontogenetic variability (*I. percostatus* is a juvenile stage, whereas *I. gibbosus* and *I. lezennensis* are adult individuals; the type of *I. russiensis* is an adult fragment) and additionally may result from evolutionary changes within the lineage (the type of *I. percostatus* is from the lower Middle Coniacian; the stratigraphical position of the types of *I. gibbosus* and of *I. russiensis* is unknown, and any location within the interval spanning the Middle – Upper Coniacian is possible). The range of morphological evolution of the lineage is inadequately known. Based on the record from Schacht Stafhorst (Westphalia, Germany) it seems that the lineage displays at least an up-section increase with following decrease in the sulcation (WALASZCZYK & WOOD 1999). Proper recognition of the pattern of the evolution of the *I. gibbosus* lineage may prove useful in its subdivision into chronosubspecies and is currently under study by one of us (I.W.) together with Christopher J.WOOD, Mineahead.

The two American specimens from locality 21097 (Text-figs 12.11, 21) are close to the *percostatus* morphotype. They do not have the strong sulcation characteristic of the types of *I. gibbosus* or *I. russiensis*. The third specimen (Text-fig. 13.5), referred provisionally to SCHLÜTER's species, has relatively subdued morphology, such as is observed only rarely in the *gibbosus* lineage (e.g. *Inoceramus percostatus* from the Saratov area in GLASUNOVA, 1972, pl. 9, fig. 1).

It is very probable that *Inoceramus dankeri* HEINZ, at least its variety *anderti* HEINZ [although according to HEINZ (1929) this variety differs from the type only in being a little bit smaller and less inflated] is a synonym of *Inoceramus percostatus*. The two specimens of *I. dankeri* var *anderti* from Lüneburg illustrated by HEINZ (1929, figs 4-5) appear to be juvenile fragments of *I. gibbosus*.

HEINZ (1928a, plate 3) regarded *Inoceramus gibbosus* and *I. percostatus* as varieties of the North Americam species *Inoceramus flaccidus* WHITE, 1876. However, WHITE's species came from the Middle Turonian and there is no proof of evolutionary continuity between this species and the group of *I. gibbosus* appearing in the latest Early Coniacian.

As is demonstrated by the originals of *Inoceramus percostatus* of MÜLLER (1888, pl. 17, figs 3a-c) the species varies considerably in its l/h ratio. Whether there are two distinct morphotypes – a slender and a wide one – or a continuous variation in this respect, requires further study. The presence of two morphotypes was suggested by GLASUNOVA (1972), who, based on the material from the Saratov Region on the Volga River, referred a slender morphotype to a separate subspecies *gorenkaensis*.

To *Inoceramus gibbosus* belongs the specimen illustrated and referred to *I. bilobatus* by HEINE (1929, pl. 4, figs 18-19). HEINE's specimen is compressed antero-posteriorly and this probably resulted in its bi-sulcate appearance. Apart from this, it possesses the typical *I. gibbosus* ornament, as well as a steep and long anterior face which differs from the short and low anterior face in the type of *I. bilobatus*.

OCCURRENCE: The species is known from the mid-Upper Coniacian of the Preussen mine shaft, Westphalia, northern Germany (see SCHLÜTER 1877, HEINE 1929, SEITZ 1962, p. 370), from the lower Middle Coniacian (*V. koeneni* Zone) of the Subhercynian Cretaceous (MÜLLER 1888, ASSMUS 1963), from apparently Middle Coniacian around Moscow, Russia (NIKITIN 1888), Caucasus (DOBROV & PAVLOVA 1959), from Lezenne, north-eastern France (BARROIS 1878, 1879); in the US Western Interior the species is known from the the Upper Coniacian *Scaphites depressus* ammonite Zone of Wyoming and Montana. Outside the Euramerican biogeographical region the species is known from the Taymyr Peninsula of northern Siberia, Russia (BODYLEVSKI, 1958).

Inoceramus cf. *frechi* FLEGEL, 1904
(Text-fig. 22.2, 34.7)

Compare:

1912-13. *Inoceramus Frechi* FLEGEL; SCUPIN, p. 208, pl. 11, fig. 10.

1996. *Inoceramus frechi* FLEGEL; WALASZCZYK & TRÖGER, fig. 3.

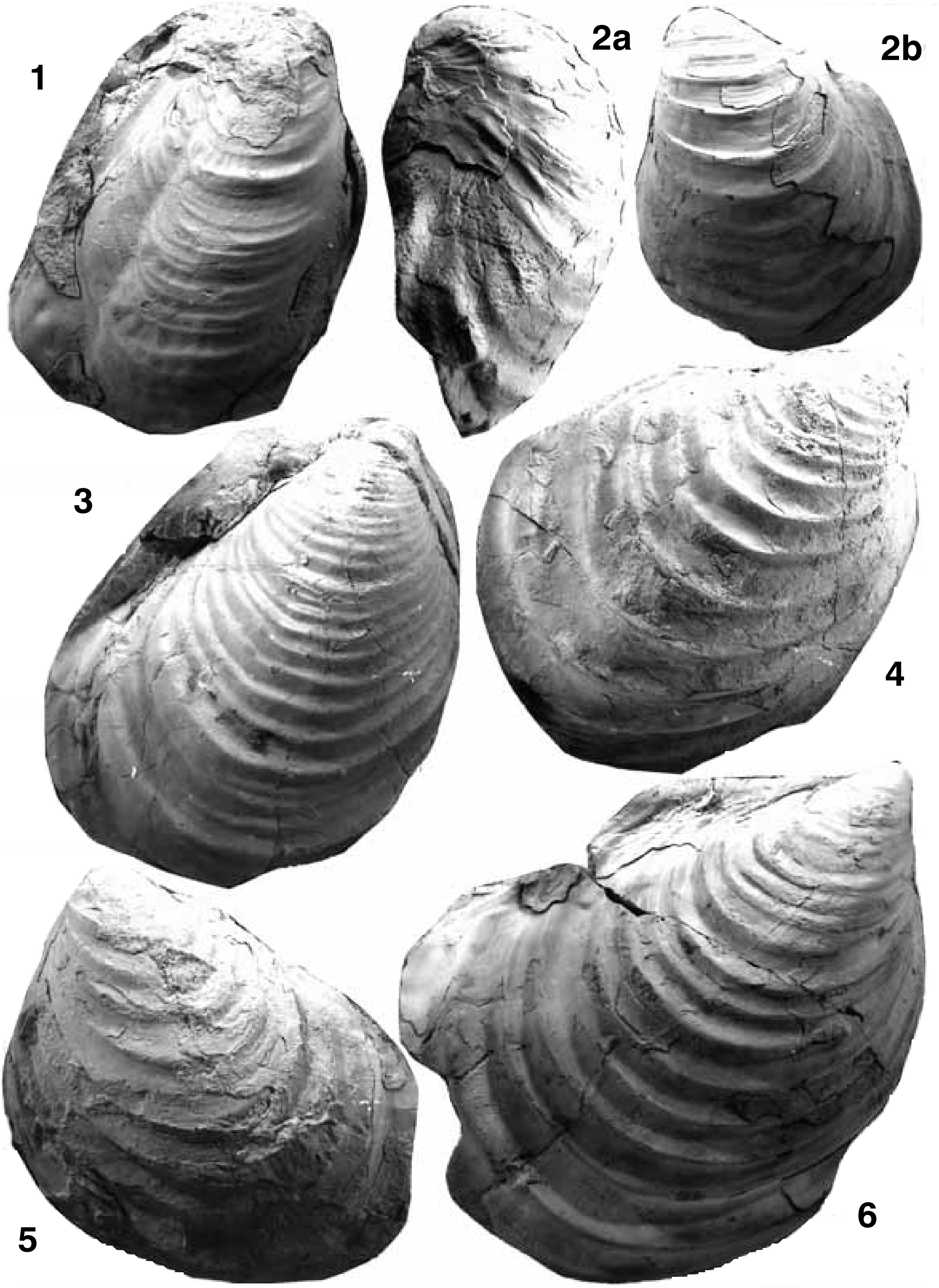

Fig. 22. **1** – *Sphenoceramus canaliculatus* (HEINE 1929); USNM 519862 from USGS locality D940; × 0.8. **2** – *Inoceramus* cf. *frechi* FLEGEL, 1904; USNM 519863 from USGS locality D 940; × 0.7. **3** – *Magadiceramus* cf. *soukupi* (MACÁK, 1967); USNM 519864 from USGS locality D940; × 1. ?**4, 5-6** – *Inoceramus undabundus* MEEK & HAYDEN, 1862; 4 – USNM 519865 from USGS locality D940; × 1; 5 – USNM 519866 from USGS locality D934, × 0.9; 6 – USNM 519867 from USGS locality D940; × 0.7

TYPE: The neotype, designated by WALASZCZYK & TRÖGER (1996) is the original of SCUPIN (1912-13, pl. 11, fig. 10) from the topmost Lower or, more probably, lower Middle Coniacian of Hockenau, Löwenberger Kreide, Outer Sudetic Trough, Poland.

MATERIAL: USNM 519863 and USNM 519877, from USGS locality D940; *Scaphites depressus* ammonite Zone.

DESCRIPTION AND REMARKS: Of the three specimens referred herein to *I*. cf. *frechi*, two are single LVs and one is a double-valved specimen with its RV only partially preserved. The specimens studied are of medium size and are strongly inflated; in USNM 519887 the strong inflation seems to be due to geniculation. The beak is pointed antero-dorsally and projects above the hinge line. The anterior margin is straight and long, with a high and steep anterior face. The disc is subtriangular in outline, with a regularly rounded ventral margin and a distinct posterior margin. The posterior auricle is well separated from the disc, along a well developed step. The hinge line is moderately long and straight. The ornament is composed of sharp-edged rugae, which are spaced regularly in the middle part of the disc; in the juvenile and in the gerontic stages the rugae become much less regular. The interspaces are relatively wide, flat-floored, with well developed growth lines.

The American specimens closely resemble the European neotype from the ?Middle Coniacian of Hockenau, Outer Sudetic Trough, from which they differ in a less well developed posterior auricle. However, as has been demonstrated in numerous cases, the size of the posterior auricle of an inoceramid often varies to a considerable extent (see e.g. NODA 1975). We therefore refer the specimens studied to *I. frechi* using open nomenclature.

OCCURRENCE: The North American specimens are from the Upper Coniacian; the European type comes from the ?Middle Coniacian of the Outer Sudetic Trough, SW Poland.

Inoceramus glacierensis sp. nov.
(Text-fig. 34.1, 34.3, 34.6)

?1929. *Inoceramus* cf. *glatziae* FLEGEL; HEINE, p. 60; pl. 6, fig. 31 [in the plate caption mistakenly called *Inoceramus* cf. *frechi*].

TYPES: The holotype is USNM 519873 (Text-fig. 34.1) from USGS locality D 934 (*Scaphites depressus* Zone of the Upper Coniacian); a small double-valved specimen. USNM 519874, USNM 519878 are paratypes.

DERIVATION OF NAME: After Glacier County, Montana, where the holotype and a paratype were collected.

TYPE LOCALITY: USGS locality D934, *Scaphites depressus* ammonite Zone, Marias River Shale, in SE 1/4 sec. 34, T. 32 N., R. 12 W., Glacier County, Montana.

MATERIAL: 3 specimens from USGS locality 21548 and 2 specimens from USGS locality D934; both localities from the *Scaphites depressus* ammonite Zone.

DIAGNOSIS: Small-sized, equivalve, inequilateral species with highly inflated juvenile and steep, almost straight anterior face. Ornament composed of fine concentric rugae. Disc with shallow radial posterior sulcus.

DESCRIPTION: The species is small-sized, equivalve and inequilateral. The valve is subtriangular in outline, higher than long. The beak is small, pointed antero-dorsally, projecting only slightly above the hinge line. The anterior margin is straight and long, passing into the narrowly rounded ventral margin, which runs obliquly toward the posterior margin. The hinge line is straight and moderately long. The anterior face is steep and high. The valve is strongly inflated; the juvenile part is small and contacts the adult stage at almost a right angle. The posterior auricle is very small, but well separated from the disc. In the posterior part of the disc is a shallow, radial sulcus, visible only in the adult stage.

The ornament is uniform, composed of fine, closely spaced, sharp-edged rugae. The rugae pass onto the posterior auricle.

REMARKS: Fine, closely, evenly to subevenly spaced rugae and the distinct geniculation of the adult stage against the small juvenile stage, characterise the species. *Inoceramus* cf. *glatziae* FLEGEL of HEINE (1929, pl. 3, fig. 31) is very similar to our species; these are axially elongated, small-sized forms, with fine, closely-spaced rugae. Markedly different, however, are ANDERT's (1911, pl. 1, figs 3-4) originals of *I. glatziae*, with which HEINE compared his specimens. ANDERT's specimens are subquadrate in outline, instead of axially elongated; moreover, the juveniles of his specimens are much higher than the adult, which is the exact opposite of HEINE's specimens. Both of ANDERT's specimens represent *Cremnoceramus waltersdorfensis* (ANDERT) (see WALASZCZYK 1992, 1996).

OCCURRENCE: The species is known from the *Scaphites depressus* ammonite Zone of the Upper Coniacian of the US Western Interior, and probably from the Middle Coniacian of Westphalia, Germany.

Inoceramus tenuirostratus MEEK & HAYDEN, 1862 (Text-figs 9.1 and 12.10)

1862. *Inoceramus tenuirostratus* MEEK & HAYDEN, p. 27.
1876. *Inoceramus tenuirostris* MEEK & HAYDEN; MEEK, p. 59, text-fig. 5.
1894. *Inoceramus tenuirostratus* MEEK & HAYDEN; STANTON, p. 83, pl. 16, figs 3-4.
1898. *Inoceramus tenuirostratus* MEEK & HAYDEN; LOGAN, p. 455, pl. 95, figs 3-4.
1911. *Inoceramus tenuirostris* MEEK & HAYDEN; BÖHM, p. 405.
1911. *Inoceramus tenuirostratus* MEEK & HAYDEN; BÖHM, p. 405.
1972. *Inoceramus obliquus* GLASUNOVA, p. 63, pl. 8, figs 2-3.

TYPE: The holotype, by monotypy, is USNM 1906, the original of MEEK (1876, text-fig. 5) from the Fort Benton Group (now Marias River Shale) of the Chippewa Point, Montana. MEEK & HAYDEN (1862) originally called this species *Inoceramus tenuirostratus*; the name was changed later (MEEK 1876), probably by mistake, into *Inoceramus tenuirostris*, which consequently becomes a junior synonym of the original name.

MATERIAL: Single specimen USNM 519997 from USGS 17956, and plaster cast of the type.

DESCRIPTION: The holotype is a single LV, medium-sized (h max = 61 mm), highly inflated, strongly oblique, with obliquity inceasing with age (with δ decreasing from 75° at h = 15 mm to 45° at h max). The umbo is narrow and pointed anterodorsally. It projects markedly above the hinge line. The disc is narrow (l/h ratio ranging between 0.66 and 0.73), axially elongated, with the growth axis anteriorly convex. The posterior auricle is very small, subtriangular, indistinctly separated from the disc. The anterior margin is almost straight, weakly concave in the dorsalmost part, and short (slightly below 50 % of the respective axial length). It passes abruptly into the long, broadly convex antero-ventral margin and thence into the narrowly rounded ventral margin. The posterior margin is rounded and short. The hinge line is long and straight. The anterior face is steep and high, the other sides are flattened.

The shell is almost smooth or, mostly in the adult part, covered with superimposed irregular, low rugae. On the posterior auricle the ornament elements are curved toward the beak.

The other specimen USNM 519997 (Text-fig. 9.1) is also a LV, but larger, with h max = 87 mm. It is slightly less slender than the holotype (with l/h ratio between 0.70 and 0.75), and slightly less inflated (to some extent this could have resulted from secondary lateral compression). The small fragments of the prismatic shell preserved show the growth lines to be distinctly raised, regular, symmetrical in cross section. Similarly as in the holotype, the rugae are mostly limited to the adult part, where they are irregularly spaced, low, with wide interspaces.

REMARKS: Both the holotype and USNM 519997, the second specimen available, are single LVs. The strong ligament, with concave ligamental plate, as observed in USNM 519997, and general shape of the LV suggests, however, that the species was inequivalve (as suggested also by MEEK 1876), with the RV slighly smaller and less convex.

Apparently identical to MEEK & HAYDEN's species is *Inoceramus obliquus*, described by GLASUNOVA (1972, p. 63, pl. 8, figs 2-3) from the 'upper' Coniacian of the village of Belovode in the Ulianovsk region upon Volga river (SE of the European part of Russia). It is characterised by a long and straight hinge line, high obliquity and strong inflation, particularly in the juvenile part, and a smooth or almost smooth shell surface. Its ligament is characterised by a distinctly concave ligamental surface. Although no double-valved specimen was found, the inequivalveness is suggested by the shape of the ligament, and the small RV interpreted as belonging to this species (GLASUNOVA 1972, pl. 8, fig. 3).

STANTON (1894) suggested that *I. tenuirostratus* may represent only an immature *Volviceramus umbonatus* (MEEK & HAYDEN), assuming that some of the differences could have resulted from secondary distortion. However, the other specimen studied herein suggests that the secondary distortion of the holotype is really slight and that all the features observed are primary. In contrast to *V. umbonatus* (and other volviceramids) the LV of *I. tenuirostratus* is not coiled and possesses only a strongly curved dorsally umbonal part. Moreover, it has a very short anterior margin and strong obliquity, which are not observed in *V. umbonatus*.

OCCURRENCE: The type came from the "Fort Benton Group of Chippewa Point, Montana" [now Marias River Shale near Fort Benton, Montana], where it occurs together with *V. umbonatus*, *I. undabundus* and *V. involutus*, which indicate its Middle Coniacian age. The other specimen studied herein comes from the Upper Coniacian, as did the specimens of this species referred to *I. obliquus* from the Volga area (eastern European part of Russia).

Inoceramus anomalus HEINE, 1929
(Text-fig. 23.1, 23.6)

1929. *Inoceramus anomalus* sp.n., HEINE, p. 86, pl. 14, figs 61-62.
2006. *Inoceramus anomalus* HEINE; WALASZCZYK & COBBAN, figure 3A.

TYPE: The lectotype, here designated, is the original of HEINE (1929, pl. 14, fig. 62) from the Preussen 2 mine; Westphalia, northern Germany; Upper Coniacian.

MATERIAL: Two specimens, USNM 519917 and USNM 519922, both from the USGS locality D3483.

DESCRIPTION AND REMARKS: Both specimens in our material are internal moulds of single LVs. The valves are robust although the specimens are secondarily laterally compressed. The valves are massive, moderately oblique. The posterior auricle is relatively small and well separated from the disc. The beak is small, located anteriorly. The hinge line is straight and of moderate length. The surface ornament is composed of strong, irregular rugae, with the interspaces in the adult stage up to 25 mm; the interspaces are flat-floored, the rugae edges are sharp. Raised growth lines superimpose the rugae.

All specimens of the species, both those described herein as well as the German originals of HEINE (1929), are all LVs, thus the actual character (equi- or inequivalve) is unknown. Although the strongly inflated LV may indicate the inequivalve nature of the species, the delicate ligament suggests its equivalve character. The strong rugae, with raised growth lines, are among the most charactersitic features of the species. The radial elements, visible in HEINE's species, we regard as deformations.

OCCURRENCE: According to SEITZ (1962, p. 370), HEINE's (1929) specimens are from the very high Upper Coniacian. The American specimens studied herein came from approximately the same level.

Genus *Volviceramus* STOLICZKA, 1871

TYPE SPECIES: *Inoceramus involutus* J. de C. SOWERBY, 1828. *Cymatoceramus* HEINZ, 1932, with its type species *Inoceramus koeneni* G. MÜLLER, 1888, is a synonym. The genus *Tactoceramus*, proposed by HEINZ (1932, p. 21) for volviceramids with regularly spaced rugae in the juveniles of the LV is a *nomen nudum*. HEINZ (op. cit.) based his concept of this genus on his new species *Volviceramus epigonus*, which is a *nomen nudum*.

DESCRIPTION: Strongly inequivalve, inequilateral, of moderate to large size. The LV is markedly more inflated than the RV or distinctly coiled, distinctly coiled for up to one and a half whorls. Its surface is often ornamented in the juvenile stage and later smooth, or it is smooth throughout. The RV is almost flat or weakly to moderately inflated, but always distinctly less inflated than the LV. It is usually regularly ornamented.

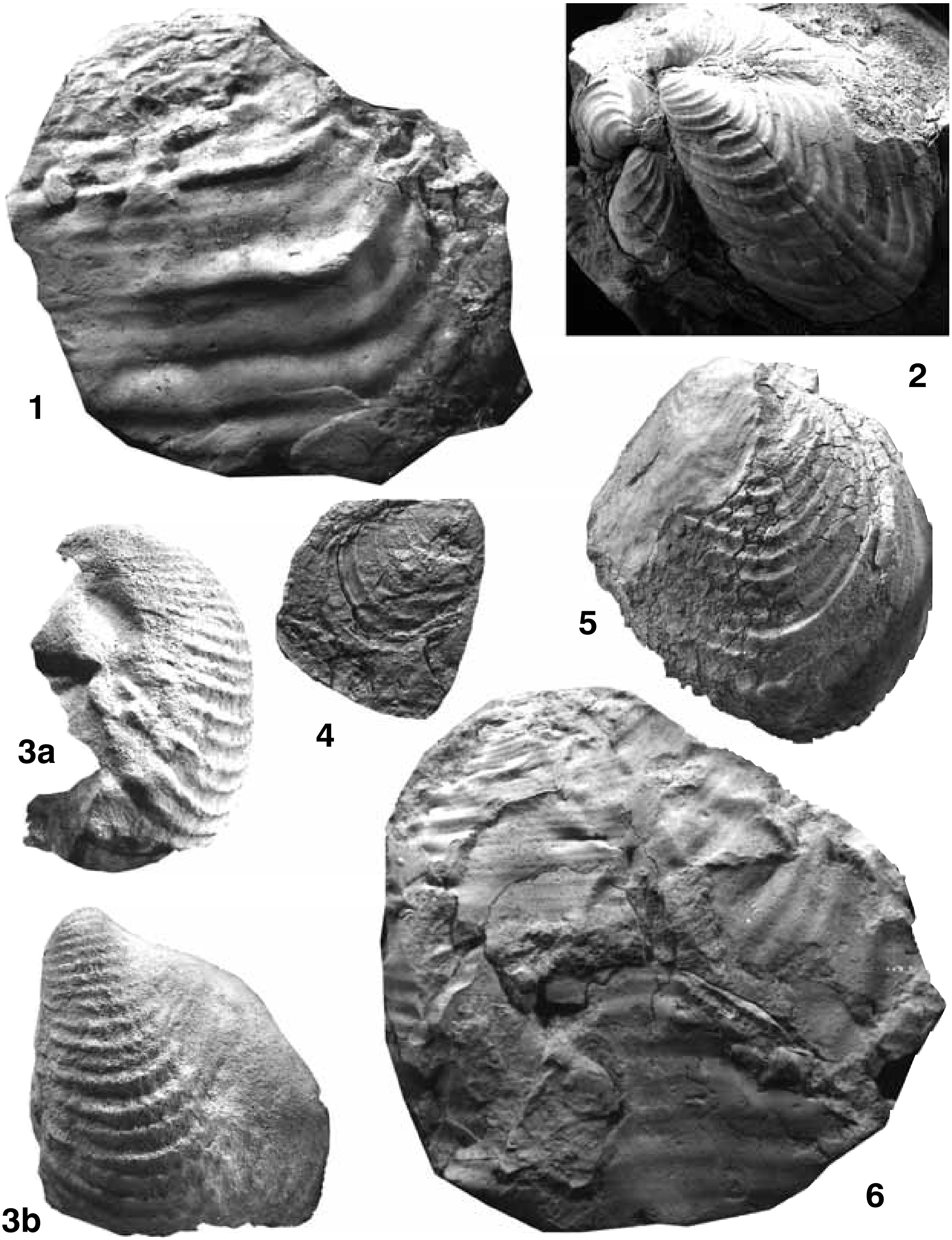

Fig. 23. **1, 6** – *Inoceramus anomalus* Heine, 1929; 1 – USNM 519917 from USGS locality D3483; 6 – USNM 519922 from USGS locality D3483; both × 0.6. **2** – *Inoceramus americanus* sp. nov.; USNM 519918 from USGS locality 24556; × 1.1. **3 –** *Inoceramus robertsoni* sp.nov., USNM 519919 from USGS locality D12910; × 0.55. **4** – *Magadiceramus subquadratus* (Schlüter, 1877), USNM 519920 from USGS locality D3473; × 1. **5**. *Magadiceramus* sp.; USNM 519921 from USGS locality D12910

REMARKS: Only a few species of the genus *Volviceramus* are recognised so far. Besides the type species, these are: *Volviceramus exogyroides* (MEEK & HAYDEN) and *V. koeneni* (MÜLLER). The generic affiliation of *V. anomalus* (HEINE, 1929) is unclear and the species is referred herein to *Inoceramus*. *Inoceramus allievimusiensis* IVANNIKOV, referred by TRÖGER (in TRÖGER & CHRISTENSEN 1991) to *Volviceramus* should be referred to *Cremnoceramus*. *Inoceramus incurvatissimus* TRÖGER, 1974 (=*Inoceramus incurvatus* TRÖGER, 1969b), *Inoceramus balli* NEWTON, and *Inoceramus selwyni* MCLEARN, 1926, all referred to *Volviceramus* by SEIBERTZ (1996), are moderately inflated, more or less equivalve species, not showing any signs of coiling, and belong to the genus *Inoceramus sensu stricto*.

HEINZ (1932) considered that there was a remarkable taxonomic diversity within forms regarded herein as belonging to the genus *Volviceramus* STOLICZKA, referring them to three monogeneric subfamilies: Cymatoceraminae, Tactoceraminae, and Volviceraminae, albeit suggesting that the last two were synonyms. The genus *Cymatoceramus*, the only genus within the subfamily Cymatoceraminae (however with 4 subgenera) was based on the concept of *Inoceramus koeneni* and is regarded herein as a younger synonym of *Volviceramus*. *Tactoceramus* is based on HEINZ' *Volviceramus epigonus*, which is a *nomen nudum*.

The phylogeny of the genus *Volviceramus* is problematic. According to WOODS (1912a, b) and TRÖGER (1969a), it stems from the *Inoceramus lamarcki* group but this phylogeny has never been convincingly documented.

OCCURRENCE: The genus is known from the Middle and Upper Coniacian of Europe, western Asia (Central Asia), and North America. Reports from Madagascar (HEINZ 1933) and from Far Eastern Asia (PERGAMENT 1971) are based on misidentifications. Similarly, the North African species *Inoceramus balli* Newton, referred to *Volviceramus* by SEIBERTZ (1996) belongs to the genus *Inoceramus*.

Volviceramus koeneni (MÜLLER, 1888)
(Text-fig. 24, 25.2-25.4, 29.2)

1888. *Inoceramus* (*Volviceramus*) *koeneni* MÜLLER, p. 412, pl. 17, fig. 1.
1891. *Inoceramus paradoxus* v. HAENLEIN; LANGENHAN & GRUNDEY, p. 12, pl. 5, figs 3-4.
1891. *Inoceramus varius* v. HAENLEIN; LANGENHAN & GRUNDEY, p. 12, pl. 5, figs 1; ?pl. 5, fig. 2.
1912a. A variety connecting *Inoceramus lamarcki* with *I. involutus*; WOODS, p. 332, text-figures 86-87.
1912b. *Inoceramus* connecting *I. lamarcki* with *I. involutus*; WOODS, pp. 7, 9, text-figs 42-43.
1913. *Inoceramus* (*Volviceramus*)(aff.?) *involutus* SOWERBY; SCUPIN, p. 213, pl. 12, fig. 3.
1928b. *Inoceramus koeneni* MÜLLER; HEINZ, p. 37, pl. 3, fig. 2. [*Rhadinoceramus regalis* HEINZ, 1932, p. 21]
1929. *Inoceramus koeneni* MÜLLER; HEINE, p. 98, pl. 15, fig. 63; pl. 17, fig. 66; pl. 18, fig. 67.
1932. *Rhadinoceramus regalis* HEINZ, p. 21. [=*Inoceramus koeneni* MÜLLER; HEINZ, 1928, pl. 3, fig. 2]
1934. *Inoceramus koeneni* MÜLLER; ANDERT, p. 132, text-figs 16a-c; pl. 8, figs 2-3.
1969a. *Inoceramus koeneni* MÜLLER; TRÖGER, p. 69, pl. 1, figs 1-6; pl. 2, figs 1-5.
1991. *Inoceramus* (*Volviceramus*) *koeneni* MÜLLER; TRÖGER & CHRISTENSEN, p. 31, pl. 3, fig. 7; ?pl. 2, figs 2-3.
non 1994. *Inoceramus* (*Volviceramus*) cf. *koeneni* MÜLLER; MALCHUS & *al*., p. 116, text-fig. 4a, pl. 1, fig. 7 [=*Cordiceramus cordiformis*]

TYPE: The lectotype, designated by TRÖGER (1969a, p. 70), is the original of MÜLLER (1888, pl. 17, fig. 1), from the Middle Coniacian of Lehofsberg near Quedlinburg, Subhercynian Cretaceous, Germany.

MATERIAL: 5 specimens; two double-valved specimens: USNM 519845 from USGS locality D5427 and USNM 519836 from USGS locality 24649; and three single RVs: USNM 519830, USNM 519831, from USGS locality 21483, and USNM 519832 from USGS locality D2150.

DESCRIPTION: The species is strongly inequivalve, inequilateral, of moderate to large size for the genus. The LV is more inflated and the juvenile stage is usually smooth. The smaller RV is regularly to subregularly rugate. The RV has a distinct disc, a well separated posterior auricle, and a dorsalward curved umbo. The valve is weakly to moderately inflated.

USNM 519830 (Text-fig. 29.2) is a double-valved internal mould, with small parts of the shell pre-

Fig. 24. *Volviceramus koeneni* (MÜLLER, 1888); USNM 519845 from USGS locality D5427; × 0.45

served on the RV. The RV is well ornamented with regularly and moderately closely-spaced rugae. The disc is slender and moderately inflated. The umbo projects markedly above the hinge line. The posterior auricle is well separated from the disc. In the adult stage, the valve bears a shallow radial sulcus posterior to the growth line. The LV is more inflated, with poorly visible, irregular ornament.

USNM 519845 (Text-fig. 24) is a huge double-valved internal mould, with a large, well inflated LV and a distinctly smaller and less inflated RV. The juvenile stage of the LV is ornamented with regular concentric asymmetrical rugae, with steeper leading edges. The posterior auricle is small, subtriangular, elongated parallel to the hinge line. The RV shows a less massive umbo, projecting well beyond the the hinge line. The valve is ornamented with fine rugae. No shell fragments are preserved.

USNM 519830, USNM 519831 and USNM 519832 are internal moulds of single RVs. All three valves are relatively small-sized and moderately well preserved.

REMARKS: The two double-valved specimens (USNM 519845 and USNM 519830) display well the characteristics of *V. koeneni*, i.e. the distinct inequivalveness, albeit without the coiling typical of *Volviceramus involutus*, and the regularly ornamented juvenile and early adult stages of the LV. From *Volviceramus involutus*, which is very close morphologically, *V. koeneni* differs in the lack of coiling of the LV, the much smaller difference in inflation between the LV and RV, and the rugation of the juvenile and early adult stages of the LV, which is almost smooth in *V. involutus*.

OCCURRENCE: All specimens studied herein are from the Middle Coniacian of the Marias River Shale, Montana, *Scaphites ventricosus* ammonite Zone; the species is known from the Middle Coniacian of Europe and western Asia.

Volviceramus involutus (J. de C.SOWERBY, 1829)
(Text-figs 9.3, 25.1, 26.1-26.3, 27.3-27.4, 28.3, 30.2)

1829. *Inoceramus involutus* J. de C SOWERBY, p. 160, pl. 583, fig. 1.
1843. *Inoceramus involutus* SOWERBY; D'ORBIGNY, p. 520, pl. 413, figs 1-3.
pars 1843. *Inoceramus Lamarcki* BRONGNIART; D'ORBIGNY, p. 518, pl. 412, figs 1-2 [non fig. 3]
1850. *Inoceramus involutus* SOWERBY; DIXON, p. 355, pl. 28, fig. 32. [=*Volviceramus anglo-germanicus* HEINZ, 1932, p. 22]
1858. *Inoceramus umbonatus* MEEK & HAYDEN, p. 50.

1876. *Inoceramus umbonatus* MEEK & HAYDEN; MEEK, p. 44, pl. 3, fig. 1; pl. 4, fig. 1-2.
1898. Inoceramus umbonatus MEEK & HAYDEN; LOGAN, p. 454, pl. 89 [re-illustration of MEEK' (1876) pl. 4, fig. 2]
1898. Inoceramus concentricus LOGAN, p. 490, pl. 116, fig. 1 [the photograph is in mirror view; see pl. 10, fig. 3 of the present paper]
1898. *Inoceramus truncatus* LOGAN, p. 492, pl. 114. [see pl. 7, fig. 2 of the present paper]
1898. *Haploscapha grandis* CONRAD; LOGAN, p. 492, pl. 94, figs 1-4.
1898. *Haploscapha niobrarensis* n.sp., LOGAN, p. 493, pl. 116, fig. 2.
1898. *Haploscapha eccentrica* CONRAD; LOGAN, p. 494, pl. 93.
? 1901. *Inoceramus involutus* SOWERBY; STURM, p. 91, pl. 9, fig. 4. [?= *Volviceramus koeneni* (MÜELLER)]
1912a. *Inoceramus involutus* SOWERBY; WOODS, p. 327, text-figs 88-94.
1912b. *Inoceramus involutus* SOWERBY; WOODS, pp. 9-10, text-figs 44-47.
1929. *Inoceramus involutus* SOWERBY; HEINE, p. 95.
non 1930. *Inoceramus* (*Volviceramus*) aff. *involutus* SOWERBY; BESAIRIE, p. 94. [="*Inoceramus*" *modestoides* SORNAY]
1932. *Volviceramus anglo-germanicus* Heinz, p. 22. [=*Inoceramus involutus* Sowerby; DIXON, 1850, pl. 28, fig. 32]
non 1933. *Volviceramus* cf. *involutus* SOWERBY; HEINZ, p. 254, pl. 20, fig. 1 [="*Inoceramus*" *modestoides* SORNAY]
1955. *Inoceramus involutus* SOWERBY; PAVLOVA, p. 203, pl. 10.
pars 1955. *Inoceramus involutus* SOWERBY; COBBAN, p. 204, pl. 2, figs 6-9 [6-7 = ?*Volviceramus koeneni* (MÜLLER, 1888)].
1958. *Inoceramus involutus* SOWERBY; KOTSUBINSKY, p. 15, pl. 6, figs 25-26.
? 1959. *Inoceramus involutus* SOWERBY; DOBROV & PAVLOVA, p. 153, pl. 10, fig. 1.
1963. *Inoceramus* (*Volviceramus*) *involutus* SOWERBY; DVOŘÁK, pl. 8.
1963. *Inoceramus involutus* SOWERBY; TSAGARELLI, p. 94, pl. 3, fig. 1.
1964. *Inoceramus involutus* SOWERBY; SCOTT & COBBAN, pl. 3, fig. 4.
?non 1971. *Inoceramus involutus* SOWERBY; PERGAMENT, p. 130, pl. 41, fig. 2.
? 1972. *Inoceramus involutus* SOWERBY; GLASUNOVA, p. 61, pl. 10, figs 1-2; pl. 11, figs 1-6.
1974. *Inoceramus involutus* SOWERBY; KOTSUBINSKY, p. 81, pl. 18, fig. 1.
1977b. *Volviceramus grandis* (CONRAD)(?=*V. involutus* (SOWERY)); KAUFFMAN, pl. 11, fig. 2; pl. 13, fig. 3.
1979. *Inoceramus involutus* SOWERBY; IVANNIKOV, p. 59, pl. 13, fig. 1.
1982. *Inoceramus* (*Volviceramus*) *grandis* (CONRAD); HATTIN, pl. 2, figs 1-4; pl. 3, fig. 1; pl. 4, fig. 6.
1986. *Inoceramus* (*Volviceramus*) *grandis* (CONRAD); SCOTT & *al*., fig. 9i.
1992. Volviceramus involutus (SOWERBY); WALASZCZYK, p. 57, pl. 37, fig. 5.

TYPE: The lectotype, by subsequent designation of WOODS (1912, p. 334) is BM 43268, the original of J. DE C SOWERBY (1929, pl. 583, fig. 1; refigured in WOODS 1912a, text-fig. 88) from the Upper Chalk, England; the locality unknown.

MATERIAL: USNM 519829 and USNM 519843 from USGS locality D2150, USNM 519834 from USGS locality D940, USNM 519835 from USGS locality 8968, USNM 519839 from USGS locality 11990, USNM 519842 from the USGS locality D9781, and numerous specimens in the collections of the Geological Survey in Denver.

DESCRIPTION: This is a strongly inequivalve, inequilateral species, of moderate to large size for the genus. The left valve is strongly coiled, gastropod-like, low trochospiral, with the anterior side planar or almost planar, and the posterior margin curved distinctly posteriorly. The coiling, at least within the first whorl, is gradual, with h/l and l/B ratios, measured at h = 100 mm reaching between 0.35-0.45 and 0.30-0.40. This causes the shape of the aperture (and of the right valve), to be distinctly longer than high. The shell is almost smooth, with irregular, indistinct rugae usually visible in the juvenile and early adult parts.

The right valve is much smaller and much less inflated. The valve outline is subrounded, usually higher than long, but the valve shows relatively high variability in this respect. This valve usually possesses an inflated umbo, well separated from the rest of the valve, and a subtriangular posterior auricle, with a long and straight hinge. The disc is ornamented with more or less distinct, regularly-spaced concentric rugae, which weaken markedly or completely disappear when passing onto the posterior

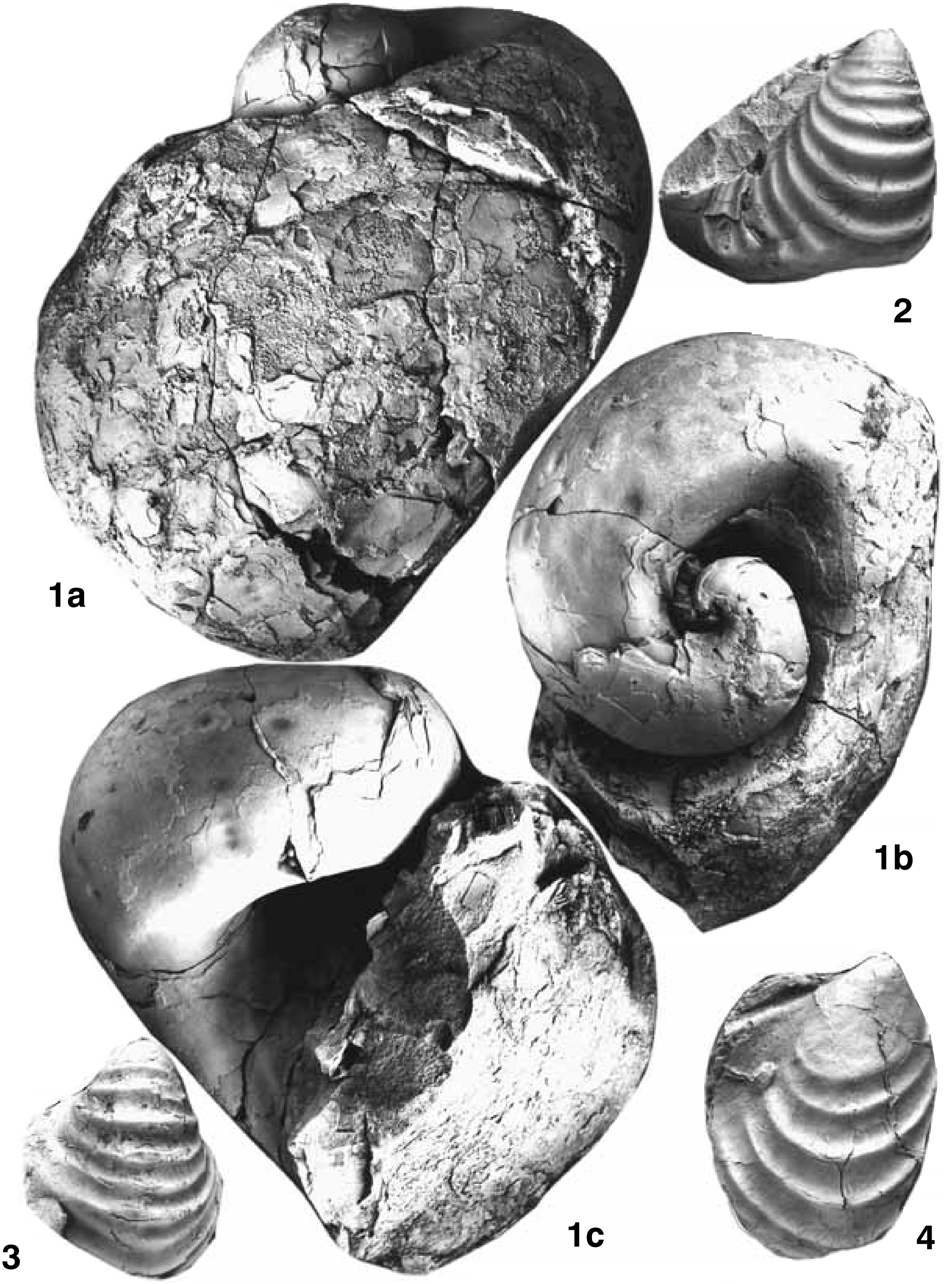

Fig. 25. **1** – *Volviceramus involutus* (J. DE C. SOWERBY, 1829); USNM 519829 from USGS locality D2150; × 0.7; **2-4** – *Volviceramus koeneni* (MÜLLER, 1888); 2 – USNM 519830 from USGS locality 21483; × 0.9; 3 – USNM 519831 from USGS locality USGS 21483; × 0.8; 4 – USNM 519832 from USGS locality 21483; × 0.85

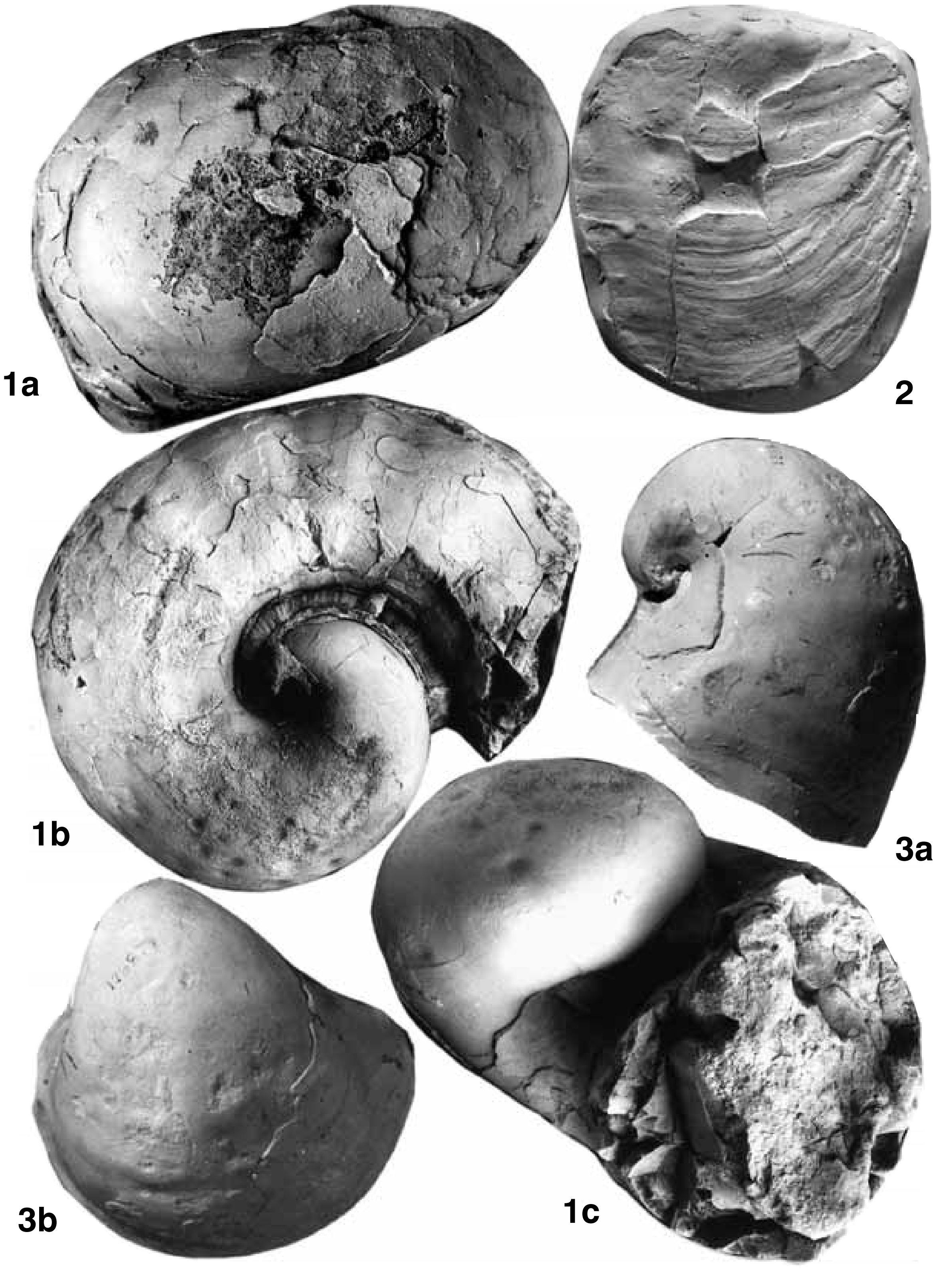

Fig. 26. **1-3** – *Volviceramus involutus* (J. DE C. SOWERBY, 1829); 1 – USNM 519835 from USGS locality 8968; × 0.8; 2 – fragment of the LV [= type of *Inoceramus truncatus* LOGAN, 1898, pl. 114; × 0.55; 3 – USNM 128874 from the Marias River Shale, northwestern Montana [original of COBBAN 1955, pl. 2, figs 8-9]; × 0.8

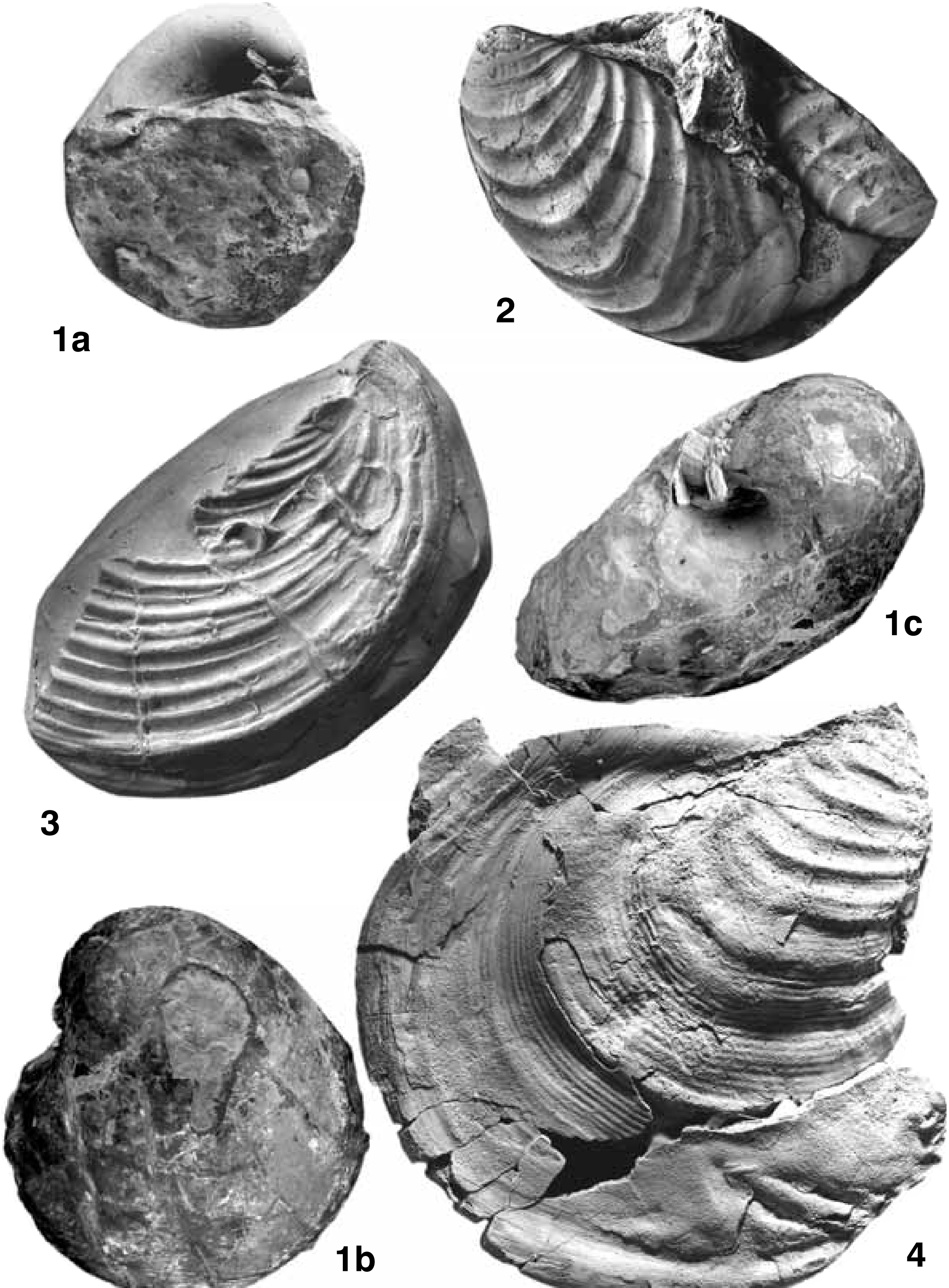

Fig. 27. **1** – *Volviceramus exogyroides* (MEEK & HAYDEN, 1862); USNM 519840 from USGS locality D2150; × 0.85. **2** – *Inoceramus undabundus* MEEK & HAYDEN, 1862; USNM 519841 from USGS locality 21109; × 0.85. **3** – *Volviceramus involutus* (J. DE C. SOWERBY 1829) [original of *Inoceramus concentricus* LOGAN, 1898, pl. 116, fig. 1; the photograph in LOGAN's plate is mirror-reversed]; × 0.55. **4** – *Volviceramus involutus* (J DE SOWERBY, 1829); USNM 519842 from USGS locality D9781; × 0.85

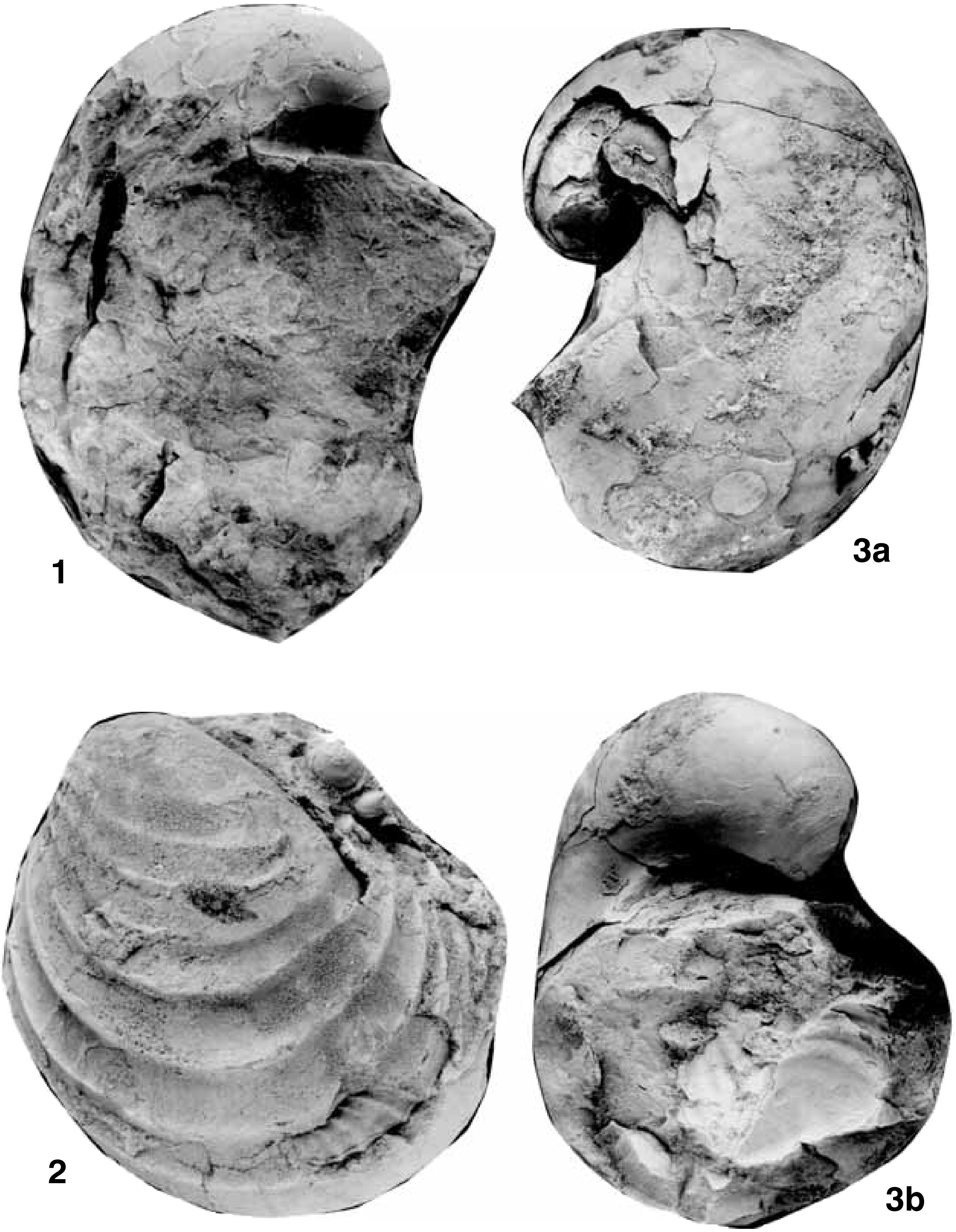

Fig. 28. **1** – *Volviceramus exogyroides* (Meek & Hayden, 1862); USNM 519837 from USGS locality 8968. **2** – *Inoceramus undabundus* Meek & Hayden, 1862; USNM 519838 from USGS locality 21109. **3** – *Volviceramus involutus* (J. de C. Sowerby, 1829); USNM 519839 from USGS locality 11990. All are × 0.9

auricle. In some specimens radial ribbing appears in the early adult part of the disc (see Text-fig. 30.2).

REMARKS: The highly involute and almost smooth left valve with the distinctly smaller and much less inflated right valve, similar to an operculum, makes *V. involutus* one of the most distinctive inoceramid species.

The observed morphological variation of the species is caused mainly by the differences in the ontogenetic change of h to l ratio in the LV. Specimens growing faster along the growth axis become slender, with the aperture higher than wide, whereas slow-growing specimens become massive in appearance and their aperture becomes wider than high. The latter morphotype is well represented by the type of *Inoceramus umbonatus* MEEK & HAYDEN (MEEK 1876, pl. 3, fig. 1a, b) [the other specimens illustrated by MEEK (1876, pl. 3, fig. 1c and pl. 4, fig. 2) are already 'typical' *V. involutus*]. The slender morphotype is well represented by DIXON's specimen (DIXON 1850, pl. 28, fig. 32; reillustrated by WOODS, 1912a, text-fig. 89), which was referred subsequently by HEINZ (1932) to a new species *Volviceramus anglo-germanicus*. The variation dicussed above is regarded herein as of infraspecific character, and consequently *I. umbonatus* and *V. anglogermanicus* are put into the synonymy of *V. involutus*.

The close similarity of *Volviceramus umbonatus* (MEEK & HAYDEN, 1858) and of *V. involutus* was mentioned already by MEEK (1876) (see also COBBAN 1955, SCOTT & COBBAN 1964, WALASZCZYK 1992). Besides the differences mentioned above, i.e. the higher h/l ratio of the LV, resulting from a faster ontogenetic length increase, and consequently the shape of the aperture being higher than wide in the English species, MEEK's main argument to keep these two species separate was their different stratigraphical position, in which point, as we know now, he was wrong.

Similar to *V. involutus* is *Volviceramus exogyroides* (MEEK & HAYDEN, 1862). However, it differs from *V. involutus* in its strongly anteriorly curved umbo and much faster relative length increase.

Also similar to *V. involutus* is *Volviceramus koeneni* (MÜLLER, 1888). In contrast to *V. involutus*, typical representatives of this species have the juvenile part of the LV distinctly rugate and the RV is markedly more inflated. Both species seems to represent a single lineage (see TRÖGER 1969a, text-fig. 8) and thus transitional morphotypes occur.

Although *V. involutus* may be generally very easily identified, its RV caused numerous misidentifications. D'ORBIGNY (1843, pl. 412) illustrated a form which he referred to *Inoceramus lamarcki*, which evidently represents a RV of *V. involutus*. Similarly, the type of *Inoceramus concentricus* of LOGAN (1898, pl. 116, fig. 1) is a single RV of *V. involutus*. This specimen was illustrated originally in a false, mirror image, that suggested it is a LV, but it is actually a fragmentarily preserved RV (see Text-fig. 27.3 of the present paper). LOGAN (1898) also described another new species based on a fragmentarily preserved shell of a *Volviceramus* which, judging from the size and outline, most probably belongs to *V. involutus*; this is his *Inoceramus truncatus* (see Text-fig. 26.2 of the present paper), based on a fragment of a large adult LV. Right valves of *Volviceramus* represent at least some of the species referred by CONRAD (1875, 1876) and subsequently LOGAN (1898) to the genus *Haploscapha* CONRAD. These are CONRAD's *Haploscapha grandis*, *Haploscapha eccentrica*, and LOGAN's (1898) *Haploscapha niobrarensis*. Judging from the morphology of these *Haploscapha* species, they all belong to *Volviceramus involutus*.

Volviceramus cf. *involutus* described by HEINZ (1933, pl. 20, fig. 1) from Manasoa, Madagascar, also represents a different species. Although it is markedly inflated and its beak is curved dorsally, the illustrated specimen is not coiled, and resembles the left valve of *Inoceramus inaequivalvis*. The recent study of inoceramids from Manasoa (SORNAY 1980, WALASZCZYK 1997, WALASZCZYK & *al*. 2004) shows it to be a LV of *Inoceramus modestoides* SORNAY, 1980.

The interpretation of PERGAMENT's (1971, pl. 41, fig. 2) *Inoceramus involutus* from the Coniacian of Kamtchatka is not quite clear. Although the umbonal part of the illustrated specimen is well curved inward, the position of the ligament is not seen in the illustration [and the original specimen is most probably lost]. The specimen resembles the fast growing morphotypes (such as *Volviceramus umbonatus*), but it is also possible that it is some strongly inflated *Inoceramus* species. The proper interpretation of the PERGAMENT specimen is very important for the palaeobiogeographical interpretation of middle Coniacian inoceramids.

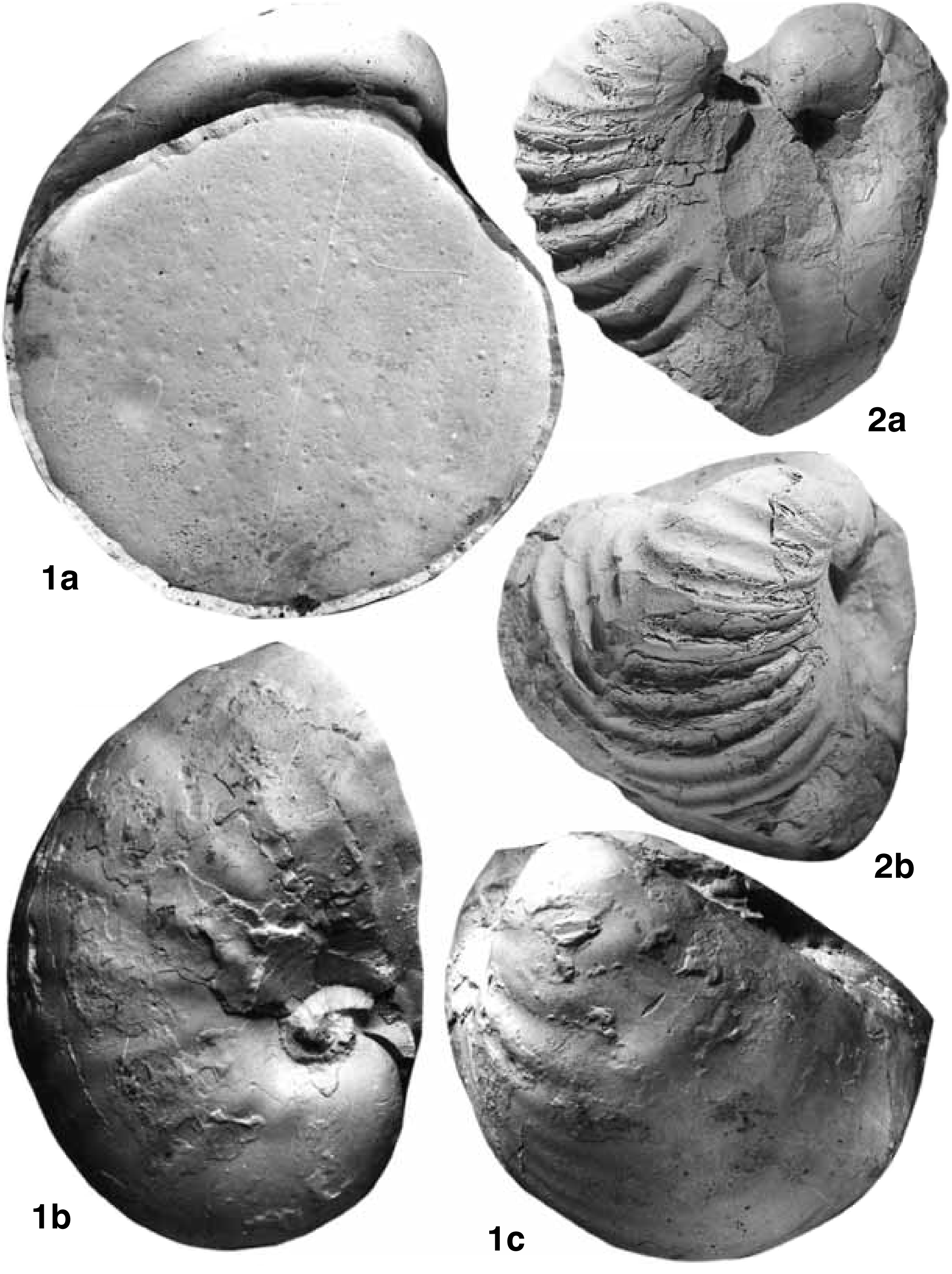

Fig. 29. **1** – *Volviceramus exogyroides* (MEEK & HAYDEN, 1862), photograph based on plaster cast; lectotype [figured in MEEK 1876, pl. 5, fig. 3]. **2** – *Volviceramus koeneni* (MÜLLER, 1888); USNM 519836 from USGS locality 24649. All are × 0.9

OCCURRENCE: *Volviceramus involutus* is known so far exclusively from Europe and from North America, excluding the Pacific Coast of this continent. According to its sparse precise datings (e.g. TRÖGER 1974, WALASZCZYK & WOOD 1999) it appears some way above the lower boundary of the Middle Coniacian and ranges high into the Upper Coniacian, not reaching the Coniacian/Santonian boundary. Its occurrence in the Far Eastern Russia (as suggested by PERGAMENT's 1971 report) requires further study.

Volviceramus exogyroides (MEEK & HAYDEN 1862)
(Text-figs 27.1, 28.1, 29.1, 30.1)

1862. Inoceramus exogyroides MEEK & HAYDEN, p. 26.
1876. *Inoceramus exogyroides* MEEK & HAYDEN; MEEK, p. 46, pl. 5, fig. 3.
1894. *Inoceramus exogyroides* MEEK & HAYDEN; STANTON, p. 83, pl. 17, figs 1-2 [reillustration of MEEK's 1876, pl. 5, fig. 3, specimen]
1898. *Inoceramus exogyroides* MEEK & HAYDEN; LOGAN, p. 454, pl. 88, figs 1-2 [reillustration of MEEK's 1876, pl. 5, fig. 3, specimen]

TYPE: The holotype, by monotypy, is the original of MEEK (1876, pl. 5, fig. 3; reillustrated herein in Text-fig. 29.1) from the "Fort Benton Group [Marias River Shale], twenty miles below Fort

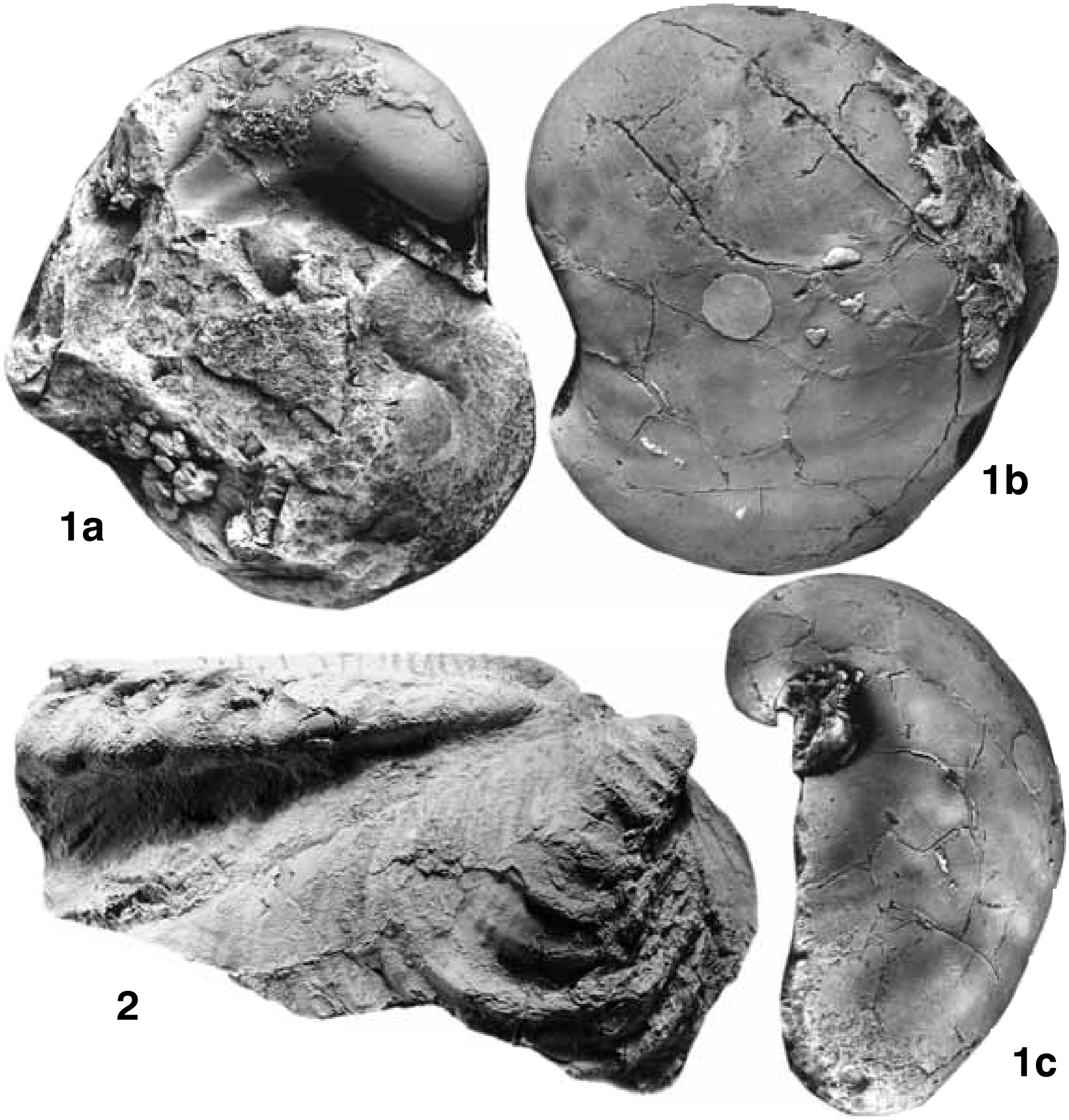

Fig. 30. **1** – *Volviceramus exogyroides* (MEEK & HAYDEN 1862); USNM 519833 from USGS locality 11990. **2** – *Volviceramus involutus* (J. DE C. SOWERBY, 1829); USNM 519834 from USGS locality D940. All are × 0.8

Benton", on the upper Missouri River, in north-central Montana.

MATERIAL: Thres internal moulds of single LVs; USNM 519833 from USGS locality 11990, USNM 519837 from USGS locality 8968, and USNM 519840 from USGS locality D2150.

DESCRIPTION: The species is known only from its LV; the RV was also missing in the original material of MEEK & HAYDEN (see MEEK 1876, p. 46). The LV is small to medium sized for the genus, inequilateral; to judge from the preserved ligamentarium in the umbonal parts of some of the specimens. There is, however, little doubt that the species is inequivalved, with the RV much smaller than the LV. The rest of the description refers only to the LV.

The valve shows two growth stages: the juvenile, markedly oblique, narrow, strongly inflated, with incoiled umbo; and the adult stage, weakly oblique, subquadrate in outline and with moderate inflation. As observed on the internal mould, which is partly covered with the inner, nacreous layer, the valve is ornamented with low, indistinct concentric rugae, or is almost smooth.

REMARKS: In contrast to *V. involutus*, the LV of *V. exogyroides* does not grow with approximately the same obliquity throughout ontogeny. After very oblique growth in the juvenile stage, the growth axis turns to the anterior and the valve starts to grow almost perpendicularly to the hinge [its general architecture is thus similar to e.g. strongly geniculate cremnoceramids or cataceramids]. As a result, the adult valve, just after the change in the growth direction, becomes very long, subquadrate in outline, and weakly or only moderately inflated; never coiled as in *V. involutus*.

When compared to the type, the specimens described herein are either completely smooth or the rugae are very poorly developed. To some extent this may result from the poorer state of preservation of the material studied, and to some extent it may be because of infraspecific variation.

OCCURRENCE: All specimens come from the lower Middle Coniacian of the Marias River Shale, Montana. Not reported from outside this area.

Genus *Platyceramus* HEINZ, 1932

TYPE SPECIES: *Inoceramus mantelli* (DE MERCEY) BARROIS, 1879.

REMARKS: Although HEINZ (1932) proposed the name *Platyceramus* without diagnosis and illustration, he indicated its type species (*Platyceramus mantelli*) and consequently his concept is clear enough to regard him as the author of the genus. COX's (1969) proposal to synonymise *Platyceramus* with *Inoceramus* is not accepted. The genus *Cladoceramus*, synonymised with *Platyceramus* by some authors (MATSUMOTO & *al*. 1982, NODA 1983, LOPEZ 1992b), is regarded a separate genus (see discussion by the description of the former genus).

Platyceramus is one of the most difficult taxa to understand and to work with. The material available for study is usually incomplete and, because of the morphological features defining the genus, the recognition of particular species is often difficult. The known record of *Platyceramus* from the US Western Interior is still very patchy and does not give a chance to follow a continuous evolutionary history of the group in that area. However, all of the morphotypes recognised here are the same as known from Europe.

In the North American Western Interior the representatives of the genus were commonly referred to *Inoceramus platinus* LOGAN 1898. Unfortunately, although LOGAN gave brief characteristics of his species, the taxon was never illustrated; the illustration (LOGAN 1898, pl. 116, fig. 2, lower left specimen) referred to – apparently by mistake – being of another LOGAN new species, *Inoceramus subconvexus* (see also COBBAN's comments in SEITZ 1965, p. 132). Because LOGAN's description is not sufficient to diagnose his species and his original specimen can no longer be found (see COBBAN's comment in SEITZ 1965, p. 132), *Inoceramus platinus* is a *nomen nudum*.

NODA & MATSUMOTO (1998) interpreted *Platyceramus* as an evolutionary successor of the genus *Inoceramus*, with the earliest representative, *Platyceramus tappuensis* (NODA & MATSUMOTO 1998), supposedly descending from *Inoceramus teshioensis* close to the Turonian/Coniacian boundary. The phylogeny of *Platyceramus* clearly requires further study, but we would like to draw attention to *Cremnoceramus waltersdorfensis han-*

novrensis (HEINZ), from the middle Early Coniacian, as a form morphologically very close to *Pl. tappuensis* (= *Platyceramus troegeri* of NODA 1992), and consequently suggest the possible descent of *Platyceramus* from Early Coniacian *Cremnoceramus*.

OCCURRENCE: The oldest representatives of the genus are known from the mid-Lower Coniacian and it ranges probably to the mid-Maastrichtian; it is apparently cosmopolitan.

Platyceramus ex gr. *mantelli* (DE MERCEY) BARROIS, 1879 (Text-figs 31, 35.3, 36.2-3)

1962. *Inoceramus* (*Platyceramus*) *mantelli* MERCEY (BARROIS); SEITZ, pp. 355-369; pls 10-13.
1985. *Inocerams mantelli mantelli* MERCEY, 1872; SZASZ, p. 171, pl. 33, figs 1-2; pl. 34, fig. 1.
1985. *Inoceramus mantelli beyenburgi* SEITZ; SZASZ, p. 171, pl. 33, fig. 3; pl. 34, fig. 2; pl. 40, fig. 1.
1990. *Inoceramus* (*Platyceramus*) *mantelli* DE MERCEY, 1877; NODA & TOSHIMITSU, pp. 487-505; figs 2-8.

Fig. 31. *Platyceramus* ex gr. *mantelli* (DE MERCEY) BARROIS, 1879; USNM 519846 from USGS locality D10851; × 0.8

TYPE: The lectotype, by subsequent designation of SEITZ (1962, p. 356) is the original of BARROIS (1979, pl. 4, fig. 1; photographically illustrated by SEITZ, 1962, pl. 10, fig. 1a) from the Coniacian of Lezennes near Lille, France.

DIAGNOSIS: Large, flat, equivalve; anterior margin low, concave, with anterior ear. Beak pointed, curved anteriorly. Growth axis anteriorly convex. Ornament composed of growth lines and irregular, low rugae.

DESCRIPTION AND REMARKS: The name *Inoceramus mantelli* was introduced by DE MERCEY in 1872, without description. Subsequently, a short description of the species, again without illustration, was given by DÉCOCQ (1874), based on the material from Lezennes near Lille. The first illustration was given by BARROIS (1879, pl. 4, figs 1-2).

SEITZ (1962) distinguished 5 subspecies within *Pl. mantelli*; these are: *mantelli*, *undatus*, *rhenanus*, *subrhenanus* and *angustus*. The last, because of homonymy, he renamed subsequently (SEITZ 1965) *Platyceramus mantelli beyenburgi*. *Platyceramus mantelli mantelli* embraces forms of *Pl. mantelli* with relatively more or less subquadrate outline; *Platyceramus mantelli undatus* represents a subspecies with relatively regular, widely spaced, ventrally curved rugae; *Pl. rhenanus* may or may not belong to *Pl. mantelli*; *Pl. subrhenanus* possesses a pointed and raised beak, and then circular outline of rugae. *Pl. beyenburgi* (=*angustus* SEITZ 1962) possesses oval rugae, elongated parallel to valve height, and a pointed beak, which does not project above the hinge line.

SEITZ' (1962) splitting approach was criticised by NODA & TOSHIMITSU (1990), who pointed out as biologically unnatural the co-occurrence of a number of subspecies of a single species and regarded *Platyceramus mantelli* as a single, albeit morphologically variable species.

A number of new subspecies and some new *Platyceramus* species closely allied to *Platyceramus mantelli* were described by LOPEZ (1992b). Besides forms described by SEITZ (1962), he described: *Platyceramus mantelli lamoldai*, a subspecies very close to *Pl. mantelli beyenburgi*; *Platyceramus mantelli turzoensis*, very close to *Pl. mantelli mantelli*; *Platyceramus mantelli herasensis*; *Platyceramus barronensis*, a form very close to *Platyceramus mantelli subrhenanus*; *Platyceramus roberti*. *Pl. lamoldai* is certainly a younger synonym of *Platyceramus beyenburgi*. Unfortunately, in the case of all the other new taxa only single specimens were available.

The material studied herein is mostly poorly preserved, either fragmentary or deformed, and consequently, the specimens are simply referred to a group of *Pl. mantelli*, understood to comprise all Middle and Late Coniacian platyceramids.

OCCURRENCE: *Platyceramus mantelli* appears at the base of the Middle Coniacian and ranges high within the Upper Coniacian. Known from the Euramerican biogeographical region and reported from the North Pacific Province.

Platyceramus cycloides (WEGNER, 1905)
(Text-figs 32.1, 44.1)

1905. *Inoceramus cycloides* nov. sp., WEGNER, p. 162, pl. 7, fig. 3 and Text-fig. 6.
1961. *Inoceramus* (*Platyceramus*) *cycloides cycloides* WEGNER; SEITZ, p. 58, pl. 1, figs 1, 6, 8 [and literature cited herein]
1982. *Inoceramus* (*Platyceramus*) *platinus* LOGAN; HATTIN, pl. 5, fig. 5.
?1986. *Inoceramus* (*Platyceramus*) *cycloides* WEGNER; SCOTT & *al*., fig. 13d.
1997. *Inoceramus* (*Platyceramus*) *cycloides* WEGNER; LECKIE & *al*., fig. 43B, E.
pars 1997. *Inoceramus* (*Platyceramus*) *platinus* LOGAN; LECKIE & *al*., fig. 40E [non fig. 41A, B = *Cordiceramus bueltenensis*].

TYPE: The lectotype, indicated by BÖHM (1915) and formally designated by SEITZ (1961, p. 55), is the original of WEGNER (1905p. 163, fig. 6 and pl. 7, fig. 3) from the Santonian of the Blumenthal mineshaft (Schacht V), Münster Basin, northern Germany.

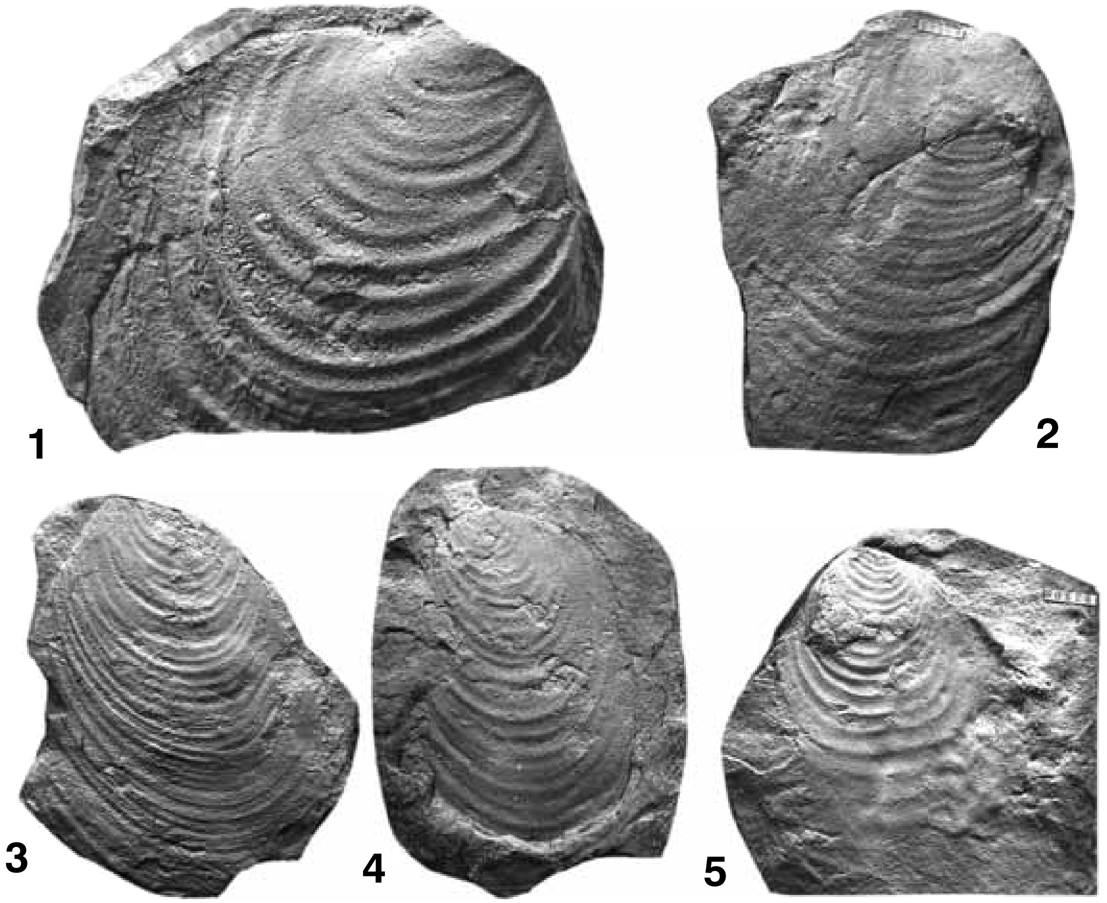

Fig. 32. **1** – *Platyceramus cycloides* (WEGNER, 1905), USNM 519967 from USGS locality D3509; × 1. **2-5** – *Platyceramus ahsenensis* (SEITZ, 1961), 2 – USNM 519968 from USGS locality D3508; × 0.6; 3 – USNM 519969 from USGS locality D3506; × 0.6; 4 – USNM 519970 from USGS locality D3509; × 0.7; 5 – USNM 519971 from USGS locality D3508; × 0.6

MATERIAL: USNM 519934 from USGS locality D3499 and USNM 519967 from USGS locality D3509.

DESCRIPTION: USNM 519934 is a single LV represented by an internal mould of the juvenile and early adult parts, slightly incomplete. The ornament is composed of very regular concentric rugae; rare growth lines are superimposed.

USNM 519967 is an internal mould of a single RV. It lacks the umbonal and antero-ventral parts. The juvenile part is ornamented with regularly and closely spaced concentric rugae, characteristic of the *Pl. cycloides* group; farther ventralward the interspaces increase stepwise and become typical of representatives of the *Pl. ezoensis* group.

REMARKS: *Pl. cycloides* was already reported from the US Western Interior (e.g. HATTIN 1982; SCOTT & *al.* 1986); however, numerous reports of WEGNER's taxon were referred in the American literature to *Inoceramus* (*Platyceramus*) *platinus* LOGAN (e.g. HATTIN, 1982, pl. 5, fig. 5; LECKIE & *al.*, 1997, fig. 40E). As LOGAN's species was never precisely diagnosed, it was often treated very broadly, comprising all Middle-Late Coniacian – Santonian platyceramids.

OCCURRENCE: The species appears very close to the base of the Santonian and ranges up to its top, and possibly higher. It is known from the Euramerican biogeographical region, South African – Madagasan and North Pacific Provinces.

Platyceramus ahsenensis (SEITZ, 1961)
(Text-figs 32.2-32.5)

pars 1964. *Inoceramus platinus* LOGAN; SCOTT & COBBAN, pl. 9 [non pl. 11, fig. 1 = *Platyceramus ezoensis* group]

1931. *Inoceramus cycloides* WEGN. var. *quadrata* n. var.; RIEDEL, p. 662, pl. 74, fig. 4.

1961. *Inoceramus* (*Platyceramus*) *cycloides ahsenensis* n. nom.; SEITZ, p. 63, pl. 1, figs 3, 7, 9-10.

MATERIAL: USNM 519968 and USNM 519971 from USGS locality D3508; USNM 519969 from USGS locality D3506; and USNM 519970 from USGS locality D3508.

DESCRIPTION AND REMARKS: All four specimens are internal moulds of single valves, with the juvenile and early adult parts preserved. All specimens show the subquadrate outline and closely spaced concentric rugae that are characteristic of the species; USNM 519970 resembles *Platyceramus rhomboides*.

OCCURRENCE: The species is characteristic of the Santonian and earliest Campanian of the Euramerican biogeographical region; it is also known from the Santonian and Early Campanian of the Madgascan – South African Province.

Platyceramus ex gr. *ezoensis* (YOKOYAMA, 1890)
(Text-fig. 47.1)

1964. *Inoceramus platinus* LOGAN; SCOTT & COBBAN, pl. 11, fig. 1.

?1982. *Inoceramus* (*Platyceramus*) *cycloides* WEGNER; HATTIN, pl. 6, fig. 12.

1986. *Inoceramus* (*Platyceramus*) sp.; SCOTT & *al.*, fig. 14h.

MATERIAL: USNM 519937 from the *Clioscaphites vermiformis* ammonite Zone of USGS locality D3648.

DESCRIPTION AND REMARKS: USNM 519937 studied herein, represented by a fragmentarily preserved internal mould of a single RV, is not a particularly typical representative of the group. However, it shows the widely spaced, rounded concentric rugae that are characteristic of these mostly late Santonian–earliest Campanian platyceramids. More typical are other specimens illustrated earlier by SCOTT & COBBAN (1964, pl. 11, fig, 1) and SCOTT & *al*. (1986, fig. 14h), from the Late Santonian of the Pueblo section and the Raton Basin respectively.

Several very similar species have so far been placed in the group. Besides the eponymous *Platyceramus ezoensis* (YOKOYAMA), these were: *Platyceramus vanuxemiformis* (NAGAO & MATSUMOTO, 1940), *Pl. chicoensis* (ANDERSON, 1958), *Pl. miyahisai* (NODA, 1983), *Pl. pacificus* (WOODS, 1917) and finally *Pl. colossus* (SORNAY, 1969). The stratigraphical position and evolutionary history of particular species remain, however, unclear. Of interest is the succession of Santonian platyceramids as observed in the Waxahachie section, Texas. Forms of the *ezoensis* group occur there in the very top of the Santonian (in the upper part of the *Marsupites testudinarius* Zone and range higher into the lowest Campanian), and clearly follow an older assemblage composed mostly of species of the *Platyceramus cycloides* group. Although very sparse, the Western Interior record seems to reveal the same (or at least a very similar) pattern.

OCCURRENCE: At least in the US Western Interior and in Texas, the group has its acme in the topmost Santonian and earliest Campanian; its range below and above this interval is uncertain. Representatives of the group are known from North America, Europe, Madagascar, and Pacific Asia.

?*Platyceramus heinei* (SEITZ, 1961)
(Text-fig. 47.4)

1929. *Inoceramus cycloides* WEGNER, var. *undulata*, n.v., HEINE, p. 43, pl. 2, fig. 9.
?pars 1961. *Inoceramus* (*Platyceramus*) *rhomboids heinei* n.sp. n.nom.; SEITZ, p. 87, pl. 3, fig. 1 [non fig. 8 which is most probably *Cl. undulatoplicatus*]; pl. 4, figs ?3, ?9.

TYPE: The holotype, by original designation, is the specimen illustrated by HEINE (1929, pl. 2, fig. 9) from the Ewald coal-mine, Schacht V, Westphalia, northern Germany, most probably from the Early Santonian *undulatoplicatus* Zone.

MATERIAL: Single specimen, USNM 519940 from USGS locality D3645, from the *Scaphites vermiformis* Zone; most probably Middle Santonian.

DESCRIPTION AND REMARKS: The specimen is represented by an internal mould of a single complete RV. Its ornament is composed of concentric rugae, with the outline characteristic of *Pl. rhomboides*, and of radial ribs that are well developed in the adult, posterior part of the valve. These radial elements are developed more as radial, widely spaced undulations, rather than regular ribs, as in *Cl. undulatoplicatus*.

The separation between radially ribbed platyceramids of the *rhomboides* group and *Cladoceramus undulatoplicatus* is not clear. Both forms are identical in respect of the concentric ornament, and they differ only in the development of the radial elements. Some of the forms illustrated and referred to *Pl. heinei* by SEITZ (1961, pl. 3, fig. 8; pl. 4, figs 3, 9) are very close to *Cl. undulatoplicatus* and may actually be easily referred to this species; although their radial ornament is not very strong, it possesses the pattern characteristic of *Cl. undulatoplicatus*. Our specimen possesses single, strong radial undulations in the posterior part of the valve, quite distinct from the typical cladoceramid ornament.

OCCURRENCE: The specimen studied comes from the Middle Santonian *Clioscaphites vermiformis* ammonite Zone of Colfax County, New Mexico; the German specimens of HEINE (1929) and of SEITZ (1961) are from the *undulatoplicatus* Zone of Westphalia.

Genus *Magadiceramus* HEINZ, 1932

TYPE SPECIES: *Inoceramus subquadratus* SCHLÜTER, 1887

REMARKS: The subquadrate shape, the presence of a usually flat and wide radial sulcus in the posterior part of the disc, and a characteristic ornament, composed of delicate, raised growth lines superimposed on widely-spaced, sharp-edged rugae, with radial ribs in some species, makes *Magadiceramus* a very distinctive morphotype, which is regarded here as of genus rank (see also WIEDMANN & KAUFFMAN 1978, WALASZCZYK 1992, CRAMPTON 1996). Some shell characters, such as the presence of several umbonal septa and an umbonal chamber within the right valve, and a lack of blade microstructure, were listed by CRAMPTON (1996) for *Magadiceramus? rangatira* from the Coniacian of New Zealand. However, the magadiceramid affinity of this species, based on the known palaeogeography of the genus, is rather doubtful. From the genus *Cremnoceramus*, with which it was synonymised by COX (1969), *Magadiceramus* differs in ornament (e.g. the radial elements were never noted in *Cremnoceramus*) and in the presence of the posterior radial sulcus.

For diagnosis and discussion on *Magadiceramus* see SEITZ (1970) and CRAMPTON (1996).

OCCURRENCE: Upper Coniacian of Euramerica. Outside this region, CRAMPTON (1996) suggested *Magadiceramus* affinity of the New Zealand species *Inoceramus rangatira*, and *Magadiceramus* sp. nov. allied to *Magadiceramus subquadratus* was reported from Japan by MATSUMOTO & YOSHIMATSU (1982). At least one of the Japanese specimens looks convincing, whereas the *Magadiceramus* affinity of the New Zealand species, as underlined by CRAMPTON himself, is far from being proved. Taking into account the age relationships (*I. rangatira* is Late Turonian), we regard its morphological resemblance to magadiceramids as homeomorphic.

Magadiceramus subquadratus (SCHLÜTER, 1887) group

Based on ornament and valve outline, a number of varieties and/or subspecies were distinguished within SCHLÜTER's species. HEINE (1929) distinguished 3 varieties; var. *curvata* and var. *arrondata*, based on the outline of the concentric ornament, and the variety *complicata*, based on the presence of distinct radial ornament in the adult stage. The first two varieties were put by SEITZ (1970) into synonymy of the nominative species, which is followed herein. The variety *complicatus* was ranked by SEITZ (1970) as a distinct subspecies of SCHLUTER's species.

The four subspecies of *Magadiceramus subquadratus* (SCHLÜTER) as distinguished by SEITZ (1970) are regarded here as valid and ranked as species level taxa: *M. subquadratus* (SCHLÜTER), *M. crenelatus* (SEITZ), *M. crenistriatus* (HEINZ), and *M. complicatus* (HEINE). At least three of them seem to represent stratigraphically successive taxa. The nature of this succession is unclear. KAUFFMAN (1991) and KAUFFMAN & *al.* (1994) regarded this as a result of phylogenetic appearance of particular species (with their co-occurrence in the topmost part of the Coniacian). It seems, however, probable that we have a phyletic lineage with a relatively wide range of variability. The resolution of this question will depend on a detailed study of rich material collected bed-by-bed

A lengthy discussion of the group was given by SEITZ (1970).

Magadiceramus subquadratus (SCHLÜTER, 1887)
(Text-figs 12.2-12.5, 23.4, 33.1, 33.4-33.5, 34.2, 35.4, 38.5)

1887. *Inoceramus subquadratus* SCHLÜTER, p. 43
1909. *Inoceramus subquadratus* SCHLÜTER; SCHRÖDER, p. 62, pl. 15; pl. 16, figs 2-3.
non 1911. *Inoceramus subquadratus* SCHLÜTER; ANDERT, p. 60, pl. 5, fig. 7 [=*Cremnoceramus deformis erectus*]
1928c. *Inoceramus subquadratus* var. *petraschecki* HEINZ; p. 125
1928. *Inoceramus subquadratus* SCHLÜTER; ADKINS, p. 95, pl. 34, fig. 6.
1929. *Inoceramus subquadratus* var. *curvata* HEINE, p. 36, pl. 1, figs 3-4.
1929. *Inoceramus subquadratus* var. *arrondata* HEINE, p. 37, pl. 1, figs 5-6.
non 1955. *Inoceramus subquadratus* SCHLÜTER; EGOYAN, pl. 4, fig. 7 [=*Cremnoceramus deformis erectus*]
pars 1963. *Inoceramus subquadratus* SCHLÜTER; MACÁK & MÜLLER, pl. 1, fig. 1; pl. 2, fig. 2 [non pl. 1, fig. 2 = *Magadiceramus crenelatus* (SEITZ)].
1963. *Inoceramus pachti* ARKHANGELSKY; MACÁK & MÜLLER, pl. 2, fig. 1.
1968. *Inoceramus subquadratus* SCHLÜTER; KOTSUBINSKY, p. 136, pl. 22, fig. 2.
pars 1968. *Inoceramus subquadratus* SCHLÜTER; KUZNETZOV, p. 204, pl. 8, fig. 1 [non pl. 8, fig. 5]
non 1969. *Inoceramus subquadratus* SCHLÜTER; KHALAFOVA, p. 195, pl. 19, fig. 4 [=*Cremnoceramus deformis erectus* or *C. waltersdorfensis waltersdorfensis*]
1970. *Inoceramus* (*Magadiceramus*) *subquadratus subquadratus* SCHLÜTER; SEITZ, p. 17, pl. 1, fig. 1; pl. 2, figs 1, 3; pl. 4, fig. 1; pl. 8, figs 2, 3, 7; pl. 9, fig. 2; pl. 10, figs 1, 4.
1970. *Inoceramus* (*Magadiceramus*) *subquadratus* cf. *subquadratus* SCHLÜTER; SEITZ, p. 26, pl. 2, fig. 4; pl. 3, fig. 1; pl. 9, fig. 1; pl. 10, fig. 2.
pars 1970. *Inoceramus* (*Magadiceramus*?) cf. *soukupi* MACÁK; SEITZ, p. 45, 48; pl. 13, fig. 2.
1970. *Inoceramus* (*Magadiceramus*) *subquadratus* n. subsp.; SEITZ, p. 29, pl. 1, fig. 2; pl. 8, fig. 5.
1974. *Inoceramus* (*Magadiceramus*) *subquadratus subquadratus* SCHLÜTER; TRÖGER, pl. 8, X4314, X4316.
? 1978. *Magadiceramus subquadratus* (SCHLÜTER); WIEDMANN & KAUFFMAN, pl. 2, fig. 16.
1986. *Inoceramus* (*Magadiceramus*) *subquadratus subquadratus* SCHLÜTER; SCOTT & *al*., fig. 9a-b.
pars 1992. *Magadiceramus subquadratus* (SCHLÜTER); WALASZCZYK, p. 57, pl. 37, figs 1-2 [only].
? 1992a. *Inoceramus* (*Magadiceramus*) *subquadratus subquadratus* SCHLÜTER; LOPEZ, p. 121, pl. 4, fig. 4.

?pars 1997. *Inoceramus* (*Magadiceramus*) *subquadratus subquadratus* SCHLÜTER; LECKIE & *al*., figures 39J, 40A. [?non figures 39H, I]

TYPE: The lectotype is GPI Bo Adkins 1, the original to ADKINS (1928, pl. 34, fig. 6; see also discussion in SEITZ 1970 and his pl. 1, fig. 1) from the Austin Formation of Texas, USA.

MATERIAL: 9 specimens; USNM 519860 from USGS locality 21097, USNM 519882 from USGS locality D1655, USNM 519883 from USGS locality 23425, USNM 519884, USNM 519904 and 519885 from USGS locality 17942, USNM 519900 from USGS locality D9781, USNM 519916 from USGS locality D3488.

DESCRIPTION: The studied specimens are small to medium-sized. The valve outline is subquadrate to subrounded. The anterior margin is long, broadly convex, passing into the variably shaped, usually broadly rounded, ventral margin. The postero-ven-

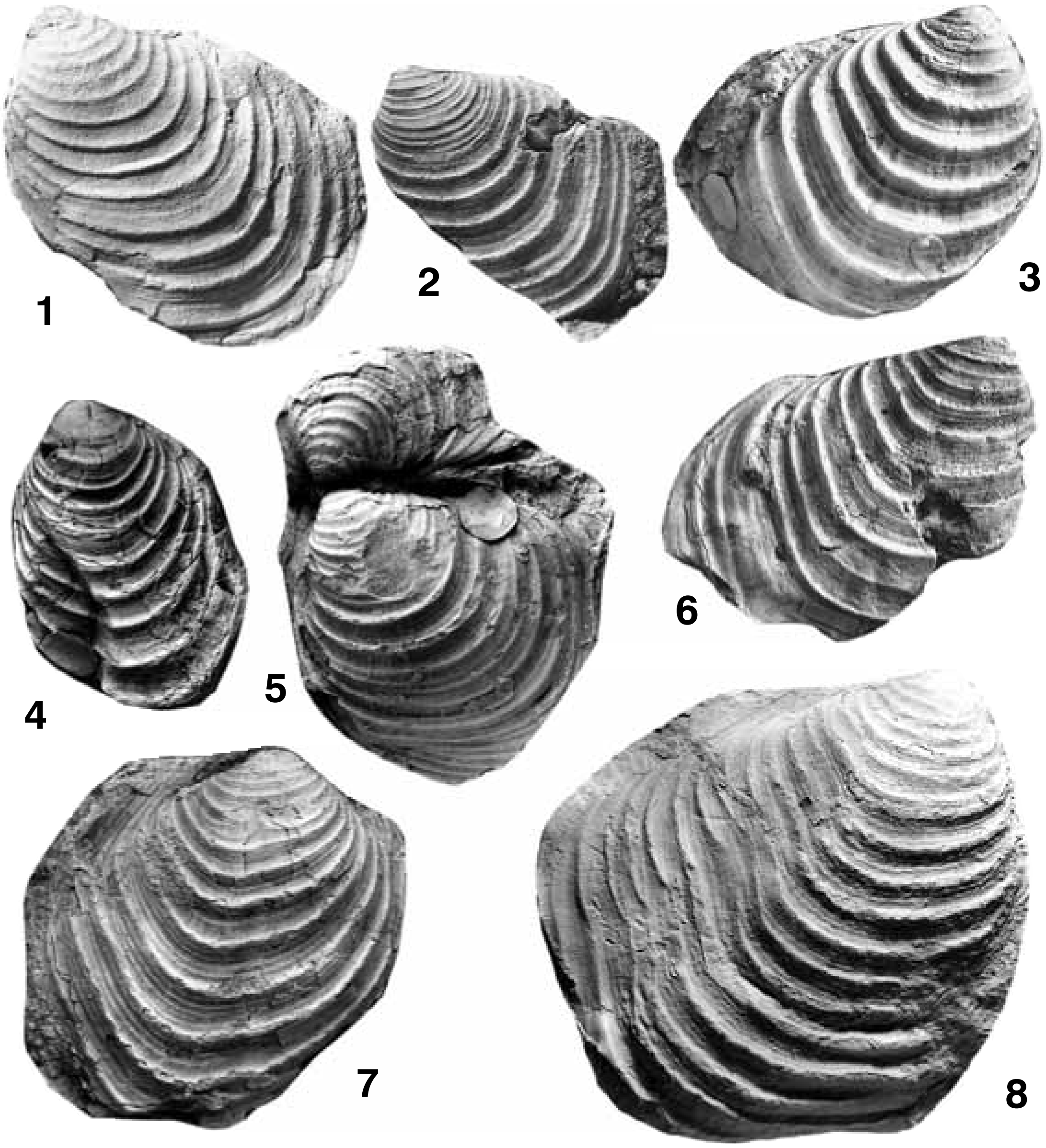

Fig. 33. **1, 4-5** – *Magadiceramus subquadratus* (SCHLÜTER, 1877); 1 – USNM 519900 from USGS locality D9781; 4 – USNM 519903 from USGS locality 7369; 5 – USNM 519904 from USGS locality 17942. **2, 6, 8** – *Magadiceramus crenelatus* (SEITZ, 1970); 2 – USNM 519901 from USGS locality D13269; 6 – USNM 519905 from USGS locality D13269; 8 – USNM 519907 from USGS locality D100. **3, 7** – *Magadiceramus crenistriatus* (HEINZ, 1928); 3 – USNM 519902 from USGS locality 7369; 7 – USNM 519906 from USGS locality D12987. All are × 0.8

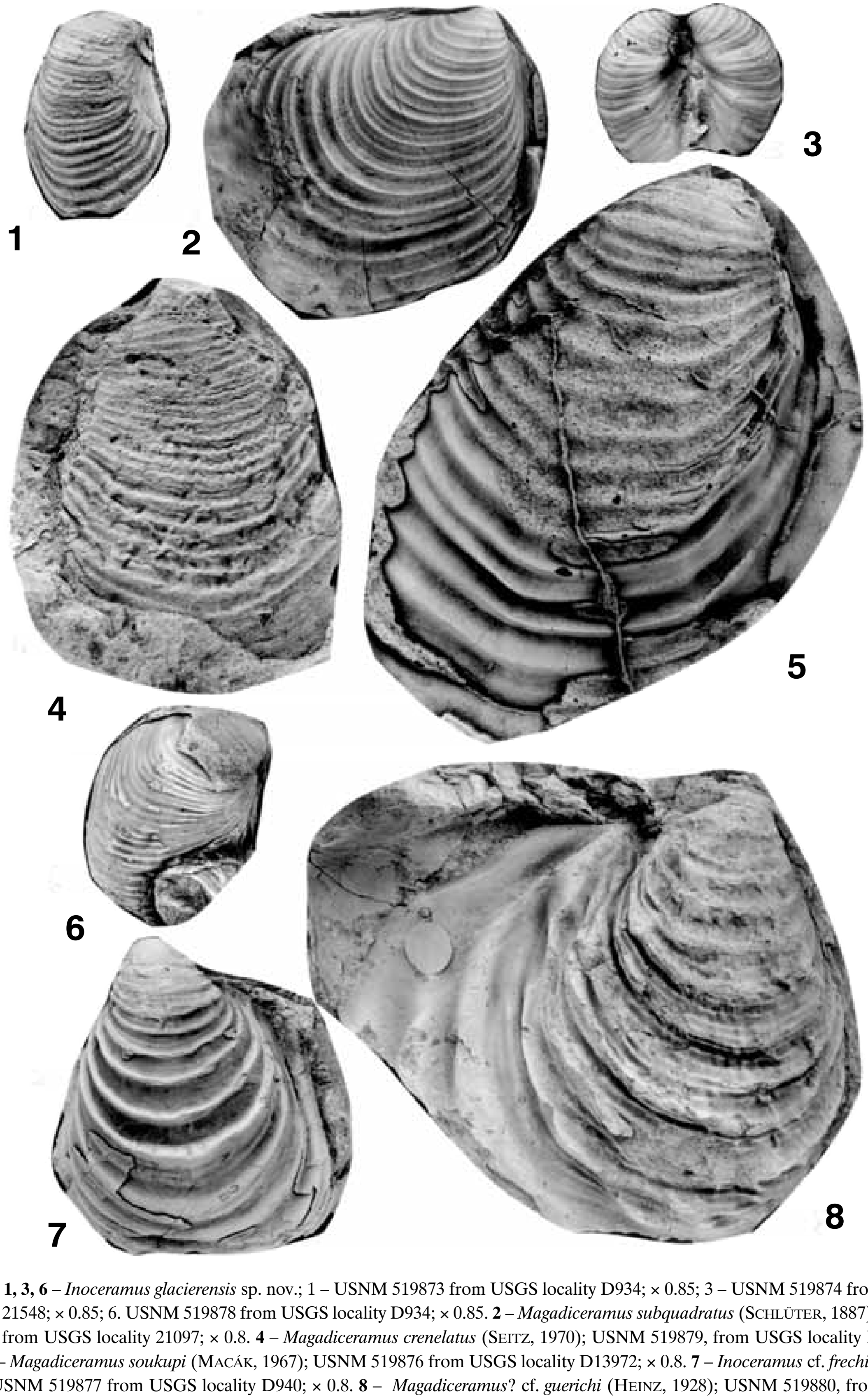

Fig. 34. **1, 3, 6** – *Inoceramus glacierensis* sp. nov.; 1 – USNM 519873 from USGS locality D934; × 0.85; 3 – USNM 519874 from USGS locality 21548; × 0.85; 6. USNM 519878 from USGS locality D934; × 0.85. **2** – *Magadiceramus subquadratus* (SCHLÜTER, 1887); USNM 519875 from USGS locality 21097; × 0.8. **4** – *Magadiceramus crenelatus* (SEITZ, 1970); USNM 519879, from USGS locality D4307; × 0.85. **5** – *Magadiceramus soukupi* (MACÁK, 1967); USNM 519876 from USGS locality D13972; × 0.8. **7** – *Inoceramus* cf. *frechi* FLEGEL, 1904; USNM 519877 from USGS locality D940; × 0.8. **8** – *Magadiceramus*? cf. *guerichi* (HEINZ, 1928); USNM 519880, from USGS locality 11956; × 0.85

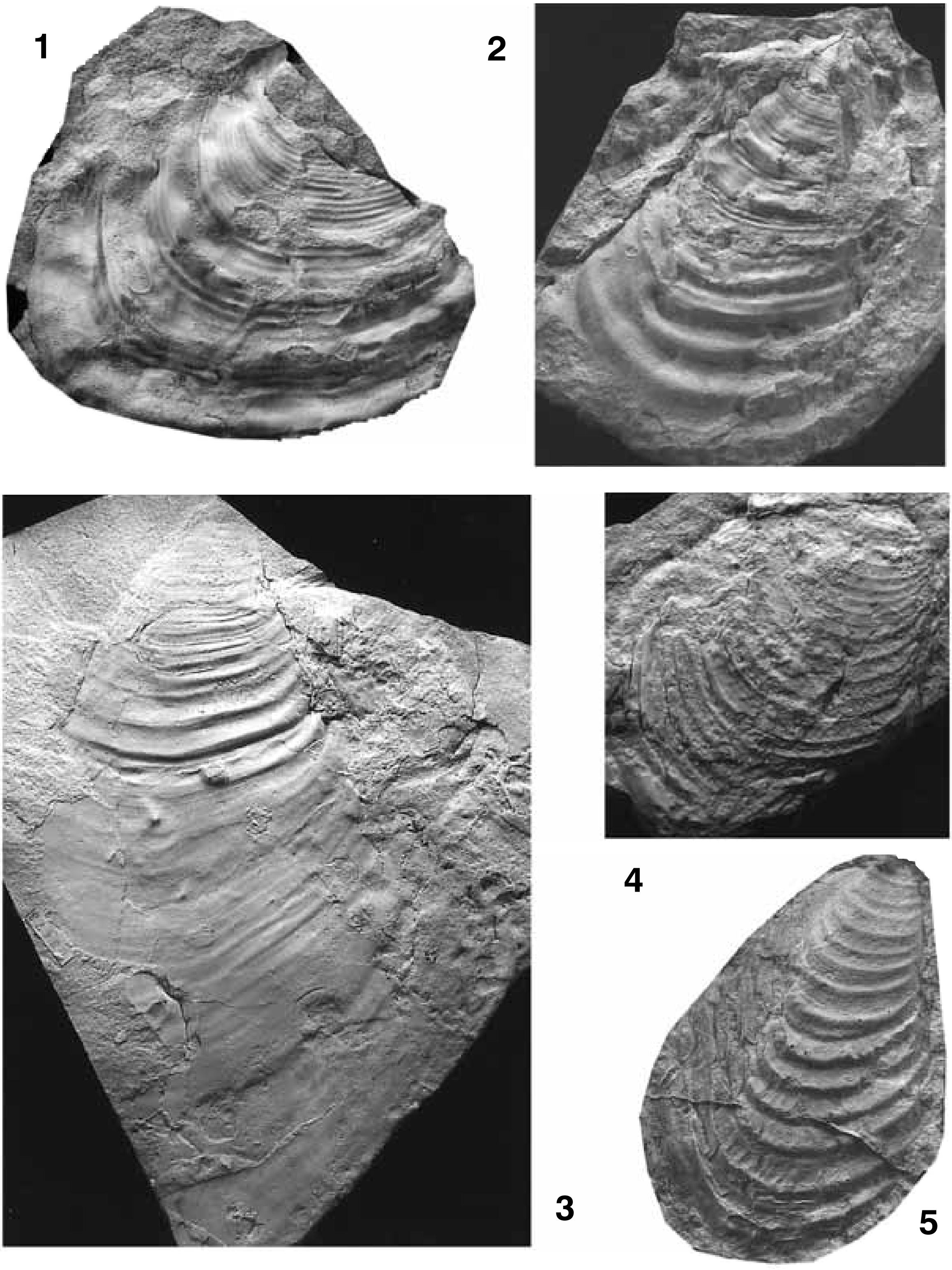

Fig. 35. **1-2** – *Inoceramus* cf. *bilobatus* MÜLLER, 1888; 1 – USNM 519913 from USGS locality D3490; × 0.85; 2 – USNM 519914 from USGS locality D3488; × 0.8. **3** – *Platyceramus* ex gr. *mantelli* (DE MERCEY) BARROIS, 1879; USNM 519915 from USGS locality D3473; × 0.8. **4** – *Magadiceramus subquadratus* (SCHLÜTER, 1877); USNM 519916 from USGS locality D3488; × 1.1. **5**. *Magadiceramus complicatus* (HEINE, 1929); USNM 131503 from USGS Mesozoic locality D3481 [original of SCOTT & COBBAN, 1964, pl. 4, fig. 2] ; × 0.75

tral margin, stretching approximately the width of the posterior sulcus on the disc, is straight and rather short. The posterior margin is straight, moderately long, approaching the hinge line at large angle, ranging between 130 and 160º. The hinge line is straight and rather short. The umbo is small with a rounded beak, projecting slightly above the hinge line. The disc is moderately inflated, subrounded to subrectangular in outline. Posterior to the growth axis lies the broad, shallow radial sulcus, which sometimes is very weakly developed, and marked only by a flattening of the posterior disc area. The posterior auricle, triangular in outline, is well separated from the disc by a distinct step.

The ornament is composed of regularly to subregularly spaced comarginal rugae, with superimposed, raised growth lines. The edges of the rugae are sharp and simple. Slight crenellation is observed in the most adult stage of some specimens.

REMARKS: The juveniles of *M. subquadratus* are very similar to juveniles of *Cremnoceramus deformis erectus* (MEEK), and representatives of the latter taxon were referred to the former species by some authors (see e.g. ANDERT, 1911, pl. 5, fig. 7; EGOYAN 1955, pl. 4, fig. 7; KHALAFOVA 1969, pl. 15, fig. 4). This apparently was a result of ANDERT's (1911) mis-identification (ANDERT 1911, pl. 5, fig. 7). Although juveniles of both species are similar, in *M. subquadratus* the posterior radial sulcus and characteristic sharp-edged rugae appear very quickly.

To *M. subquadratus* belongs *Inoceramus pachti* illustrated by MACÁK & MÜLLER (1963, pl. 2, fig. 1). Although their specimen is an axially elongated morphotype, possessing some resemblance to *Sphenoceramus pachti*, the type of ornament and the outline of the comarginal rugae are typical of *M. subquadratus*.

It is difficult to judge, based on illustration alone, whether WIEDMANN & KAUFFMAN's (1978, pl. 2, fig. 16) specimen really belongs to *M. subquadratus*. The same refers to the specimen illustrated by LOPEZ (1992a, pl. 4, fig. 4).

To *M. subquadratus* belongs one of SEITZ's specimens of *Inoceramus* (*Ma*?) *soukupi* MACÁK (SEITZ 1970, pl. 13, fig. 2). Although at first sight the specimen looks similar to other representatives of *M*. cf. *soukupi*, by closer examination and comparison, it appears to be a strongly deformed *M. subquadratus*.

OCCURRENCE: The species is known from most of Europe (and adjacent areas of Central Asia) and from North America; it ranges through the whole Upper Coniacian.

Magadiceramus crenelatus (SEITZ, 1970)
(Text-figs 33.2, 33.6, 33.8; 34.4, 36.1)

1929. *Inoceramus subquadratus* SCHLÜTER; HEINE, p. 34, pl. 1, figs 1-2.
pars 1963. *Inoceramus subquadratus* SCHLÜTER; MACÁK & MÜLLER, pl. 1, fig. 2 [non pl. 1, fig. 1 and pl. 2, fig. 2 = *Magadiceramus subquadratus* (SCHLÜTER)]
pars 1968. *Inoceramus subquadratus* SCHLÜTER; KUZNETZOV, p. 204, pl. 8, fig. 5 [non pl. 8, fig. 1]
non 1969. *Inoceramus subquadratus* SCHLÜTER; KHALAFOVA, p. 195, pl. 19, fig. 4 [=*Cremnoceramus deformis erectus*]
1970. *Inoceramus* (*Magadiceramus*) *subquadratus crenelatus* SEITZ, p. 31, pl. 2, fig. 2; pl. 3, figs 2-3; pl. 4, fig. 2.
1974. *Inoceramus* (*Magadiceramus*) *subquadratus crenelatus* SEITZ; TRÖGER, pl. 8, X4335, X4315, X4317, X4318.
1986. *Inoceramus* (*Magadiceramus*) *subquadratus crenelatus* SEITZ; SCOTT & *al*., fig. 9c-f.
pars 1992. *Magadiceramus subquadratus* (SCHLÜTER); WALASZCZYK, p. 57, pl. 38, fig. 1 [only].
1992a. *Inoceramus* (*Magadiceramus*) *subquadratus crenelatus* SEITZ; LOPEZ, p. 123, pl. 5, fig. 2.
pars 1997. *Inoceramus* (*Magadiceramus*) *subquadratus crenelatus* SEITZ; LECKIE & *al*., figure 40C [non figure 40B = *Magadiceramus complicatus* (HEINE)]

TYPE: The holotype, by original designation, is S 528 Wb, the original of SEITZ (1970, pl. 4, fig. 2) from the Upper Coniacian of mine section 5 of Minister Stein, in Westphalia, Germany.

MATERIAL: USNM 519879 from USGS locality D4307; USNM 519901 and USNM 519905 from USGS locality D13269; USNM 519907 from USGS locality D100; and USNM 519923 from USGS locality D3482.

DESCRIPTION AND REMARKS: The species possesses the same valve outline as *M. subquadratus* and differs from it only by the crenellation of the

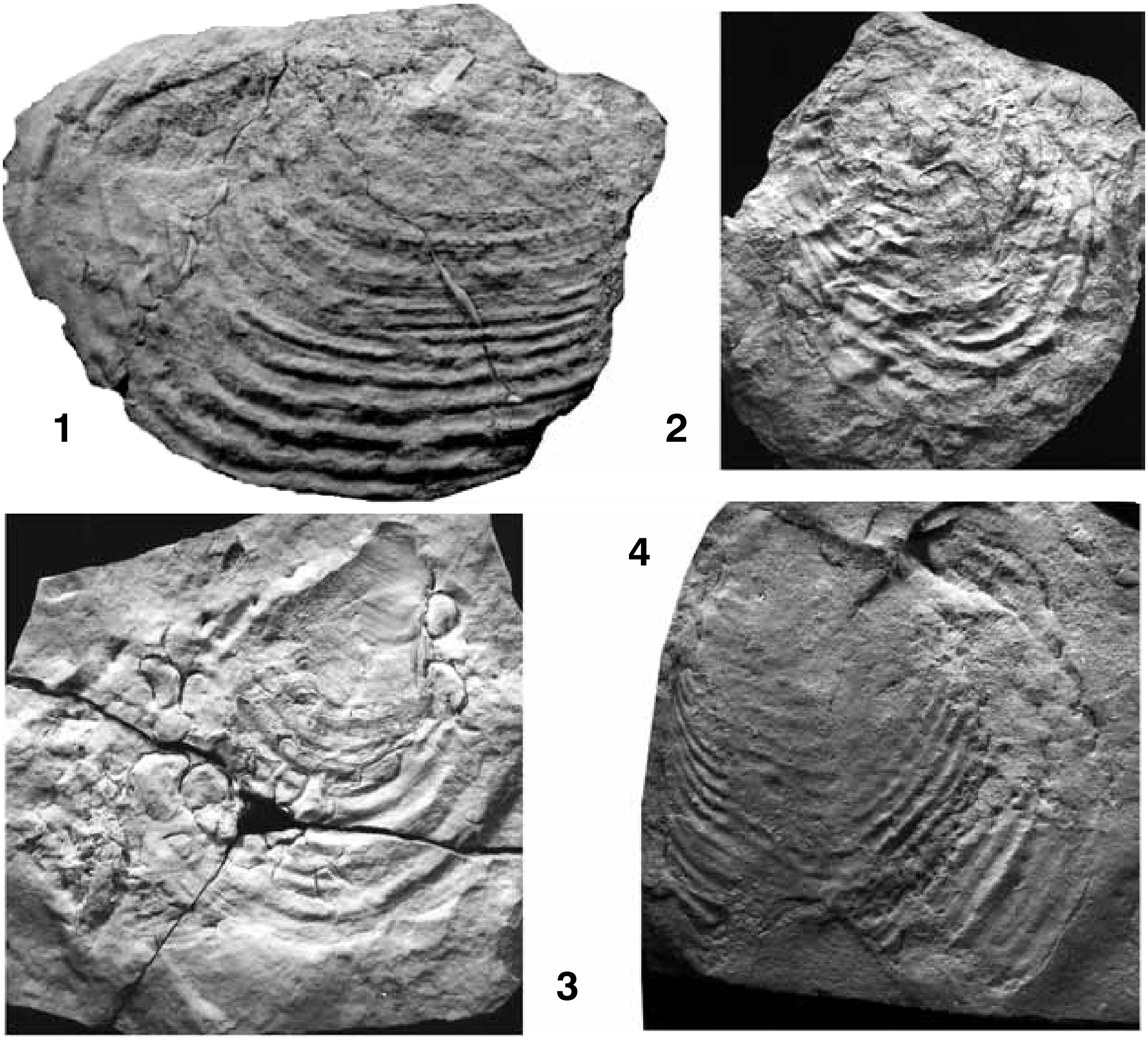

Fig. 36. **1** – *Magadiceramus crenelatus* (SEITZ, 1970); USNM 519923 from USGS locality D3482; × 0.7. **2-3** – *Platyceramus* ex gr. *mantelli* (DE MERCEY) BARROIS, 1879; 2 – USNM 519924 from USGS locality D3482; × 0.6; 3 – USNM 519925 from USGS locality D3487; × 0.6; **4**. – *Magadiceramus* sp.; USNM 519926 from USGS locality D3483; × 0.6

edges of rugae in the late juvenile and adult stages. The crenellation is best developed anterior to the posterior radial sulcus, and also disappears in the most anterior part. The characteristics of the concentric ornament, both rugae and growth lines, are the same as in *M. subquadratus*. Distinguishing the juveniles of these two species, as well as those of the third species, *M. complicatus*, may be impossible.

OCCURRENCE: The species appears stratigraphically higher than *M. subquadratus* and seems to continue almost to the top of the Coniacian. It is known throughout the Euramerican biogeographic region.

Magadiceramus crenistriatus (HEINZ, 1928c)
(Text-figs 33.3, 33.7)

non 1904. *Inoceramus crenistriatus* ROEMER; AIRAGHI, p. 197, pl. 4, fig. 16.
part 1909. *Inoceramus subquadratus* ROEMER; SCHROEDER, p. 63, pl. 16, fig. 1.
1928c. *Inoceramus subquadratus* var. *crenistriatus* F. ROEMER; HEINZ, p. 125.
?non 1970. *Inoceramus* (*Magadiceramus*) *subquadratus* cf. *crenistriatus* (Ferd ROEMER) HEINZ; SEITZ, p. 32, pl. 9, fig. 3.

MATERIAL: 2 specimens; USNM 519902 from

USGS locality 7369 and USNM 519906 from USGS locality D12987.

DESCRIPTION: Both specimens are well preserved single right valves of moderate size and inflation. The umbo is relatively small, projecting above the hinge line. The latter is rather short, straight. The anterior margin is short and straight and passes into the long, broadly convex antero-ventral margin, and then into the rounded or distinctly curved ventral margin. The valves bear a shallow, albeit distinct, posterior sulcus, starting early in ontogeny.

The ornament is composed of sharp-edged rugae, with interspaces increasing quite regularly ventralward, and with distinctly raised growth lines. The intersection of weak radials with the concentric elements produces a kind of regular reticulation.

REMARKS: The two specimens referred to *M. crenistriatus* (HEINZ, 1928) differ from the other species of the *Magadiceramus subquadratus* group in possessing strong, widely spaced rugae and raised, strong growth lines. The edges of the rugae are crenellated. The presence of delicate radials produces the reticulate appearance.

The species was established by F. ROEMER, based on material from Texas. ROEMER, however, never described his new species and the present concept of this species comes from HEINZ (1928c) who studied ROEMER's original material in Breslau (Polish Wrocław), and referred to this species one of the specimens from Timmenrode (Subhercynian Cretaceous Basin, Germany), illustrated by SCHRÖDER (1909). Both of the specimens referred to *M. crenistriatus* herein clearly differ from other members of the *M. subquadratus* group, and consequently the name *crenistriatus* is applied. However, study of more material may show that *M. crenistriatus* falls into the variability range of *M. crenelatus*, and should not be distinguished as a separate species.

OCCURRENCE: Known from Texas, US Western Interior and from Germany; Upper Coniacian.

Magadiceramus complicatus (HEINE, 1929)
(Text-figs ?35.5, 37.1-37.3, ?37.4, 37.5)

1929. *Inoceramus subquadratus* var. *complicata* HEINE, p. 38, pl. 2, fig. 7.

?pars1956. *Inoceramus* ex gr. *subcardissoides* SCHLÜTER; SOUKUP, p. 109, pl. 1, fig. 3 [?pl. 1, figs 1-2]

1964. *Inoceramus stantoni* SOKOLOV; SCOTT & COBBAN, pl. 4, figs 1-3

1974. *Inoceramus* (*Magadiceramus*) *subquadratus crenulatus* SEITZ; TRÖGER, pl. 8, X4315, X4319.

pars 1992. *Magadiceramus subquadratus* (SCHLÜTER); WALASZCZYK, p. 57, pl. 38, fig. 2 [only].

TYPE: The lectotype is B666, the original to HEINE (1929, pl. 2, fig. 7) from the Wetterschacht of the Grimberg Mine 3, depth 140 m; Upper Coniacian, Westphalia, Germany.

MATERIAL: USNM 519908 and USNM 131503 from USGS locality D3481; USNM 519909 from USGS locality D3483; USNM 519910 and USNM 519912 from USGS locality D3485; and most probably USNM 519911 from USGS locality D3481.

DESCRIPTION: All the specimens studied are from the Pueblo section, Colorado, from shaly facies, and consequently are more or less compressed. Additionally, they are incomplete or deformed. Besides USNM 131503 (Text-fig. 35.5), which we regard as deformed, all the other specimens (Text-fig. 37) preserve their subquadrate outline, the shallow radial sulcus in the posterior part of the disc, and the elongated triangular posterior auricle. The valves bear typical magadiceramid concentric ornament, composed of sharp-edged rugae with relatively wide and flat-floored interspaces. The juvenile stages are almost invariably covered with concentric rugae; the adults are additionally radially ornamented. The radial ornament varies from almost continuous radial ribs (like in USNM 519910 and USNM 519911 – Text-figs 37.3 and 37.4) to radial riblets, limited to particular interspaces (e.g. USNM 519912 and USNM 131503 – Text-figs 37.5 and 35.5). With the exception of USNM 519908 (Text-fig. 37.1), in which the radial riblets are relatively thick, the riblets cut through the concentric rugae. In most of the specimens the concentric rugae dominate and are not, or are only weakly disturbed by, the radial ornament.

REMARKS: *Magadiceramus complicatus*, as demonstrated by its type (HEINE 1929, pl. 2, fig. 7), possesses two variably ornamented growth stages: the juvenile stage with concentric, crenellated rugae, and the adult stage with radial riblets. In the type, the radial riblets are strong, cutting the concentric rugae. As demonstrated by the American material studied herein, the juvenile ornament may be of *M. subquadratus* or *M. crenelatus* type.

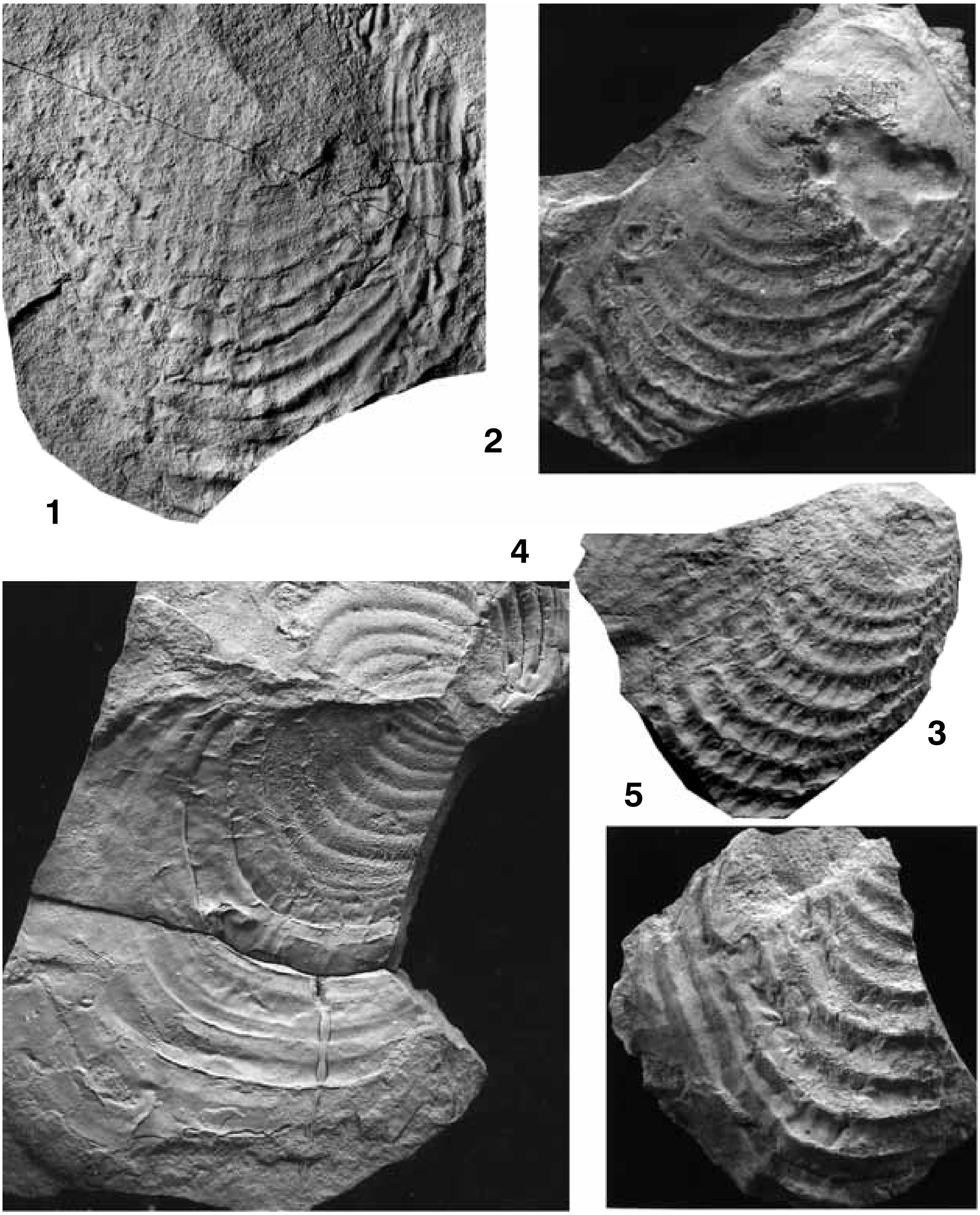

Fig. 37. *Magadiceramus complicatus* (HEINE, 1929); Pueblo; top of the lower limestone unit; topmost part of the Coniacian; 1 – USNM 519908 from USGS locality D3481; × 0.85; 2 – USNM 519909 from USGS locality D3483; × 0.9; 3 – USNM 519910 from USGS locality D3485; × 0.95; 4 – USNM 519911 from USGS locality D3481; × 0.9; 5 – USNM 519912 from USGS locality D3485; × 1.1

M. complicatus, particularly slightly deformed specimens, resembles *Inoceramus americanus* (Text-figs 12.7, 12.13, 12.14-12.15). The latter, however, is distinctly subtriangular in outline, possesses different concentric ornament composed of closely-spaced, narrow rugae, and its radial ornament begins well within the juvenile stage.

OCCURRENCE: The species occurs in the Upper Coniacian of the Euramerican biogeographical region; it seems to be characteristic of the higher parts of the substage. The species – similarly as other magadiceramids – seem to be limited to southern and central parts of the North American Western Interior; it is unknown north of Wyoming. The reports of the species from Canada (COLLOM 2001) represent *Inoceramus americanus* sp. nov.

Magadiceramus? cf. *guerichi* (HEINZ, 1928a)
(Text-fig. 34.8)

Compare:
1928a. *Inoceramus gürichi* n.sp., HEINZ, p. 75, pl. 2, fig. 1.

MATERIAL: Single specimen; USNM 519880 from USGS locality 11956; *Scaphites depressus* Zone.

DESCRIPTION: The species is represented in our material by the internal mould of a single, three-dimensionally preserved, RV. The valve is composed of a moderately inflated disc, giving a massive appearance, and of a relatively large posterior auricle, well separated from the disc. The umbonal part is neither well preserved nor exposed. Up to 35 mm axial length, the juvenile part of the disc is subquadrate in outline, with a well developed radial sulcus in its posterior part. Farther ventralward the disc becomes subrounded in outline. The anterior margin is long (being approximately 70 % of the corresponding axial length) and straight, with the anterior wall almost perpendicular to the sagittal plane. The ventral margin is rounded, as is the posterior margin. The hinge line is poorly preserved, but judging from the preserved part, it is straight and moderately long.

The disc is ornamented with strong concentric rugae, with superimposed raised growth lines, and with radial riblets. The latter form discontinuous lines of short ribs and never dominate the concentric elements. With the raised growth lines, they form a reticulate ornament in the axial part of the adult stage of the disc. The disc ornament does not pass on to the posterior auricle, which bears only irregular rugae, without growth lines.

REMARKS: The disc, elongated parallel to growth axis, with long and straight anterior margin, and the widely, posteriorly elongated posterior auricle makes this specimen close to the type of *I. guerichi*. It differs from HEINZ' type in a much less distinct posterior sulcus (but this may result from deformation to some extent) and in the ornament. The rugae in ?*M. guerichi* possess well developed '*Anwachsmarken*', the radial ribs are distinct and relatively strong, and the growth lines are fine, not raised like in the American specimen. The differences in the ornament may result partly from the fact that HEINZ' type is preserved as a shell rather than a mould. HEINZ (1928a) regarded his new species as a member of the *Sphenoceramus pachti* group. We agree with SEITZ (1970), who referred this species to *Magadiceramus*, albeit with a question mark.

OCCURRENCE: Neither the German type nor the American specimen have a precise section location. HEINZ (1928a) inferred that the type came from the Middle Coniacian (lower Involutus beds), based on the lithological characteristics of the specimen. The specimen studied came from the Upper Coniacian or lower Santonian.

Magadiceramus cf. *soukupi* (*sensu* SEITZ, 1970)

REMARKS: SEITZ (1970, p. 45) described a series of forms regarded by him as transitional between *Magadiceramus subquadratus* (SCHLÜTER) and *Magadiceramus? soukupi* (MACÁK) and referred to as *Magadiceramus* cf. *soukupi*. From *M. subquadratus* these forms differ in the umbonal part, with the beak projecting distinctly above the hinge line, which gives all these specimens an axially elongated outline. SEITZ (1970) had 8 specimens at his disposal, which he referred to three groups; the first group embraced forms with a geniculated juvenile stage; the second group is characterised by regular, widely-spaced rugae; and the third one is characterised by closely- and partly irregularly-spaced rugae.

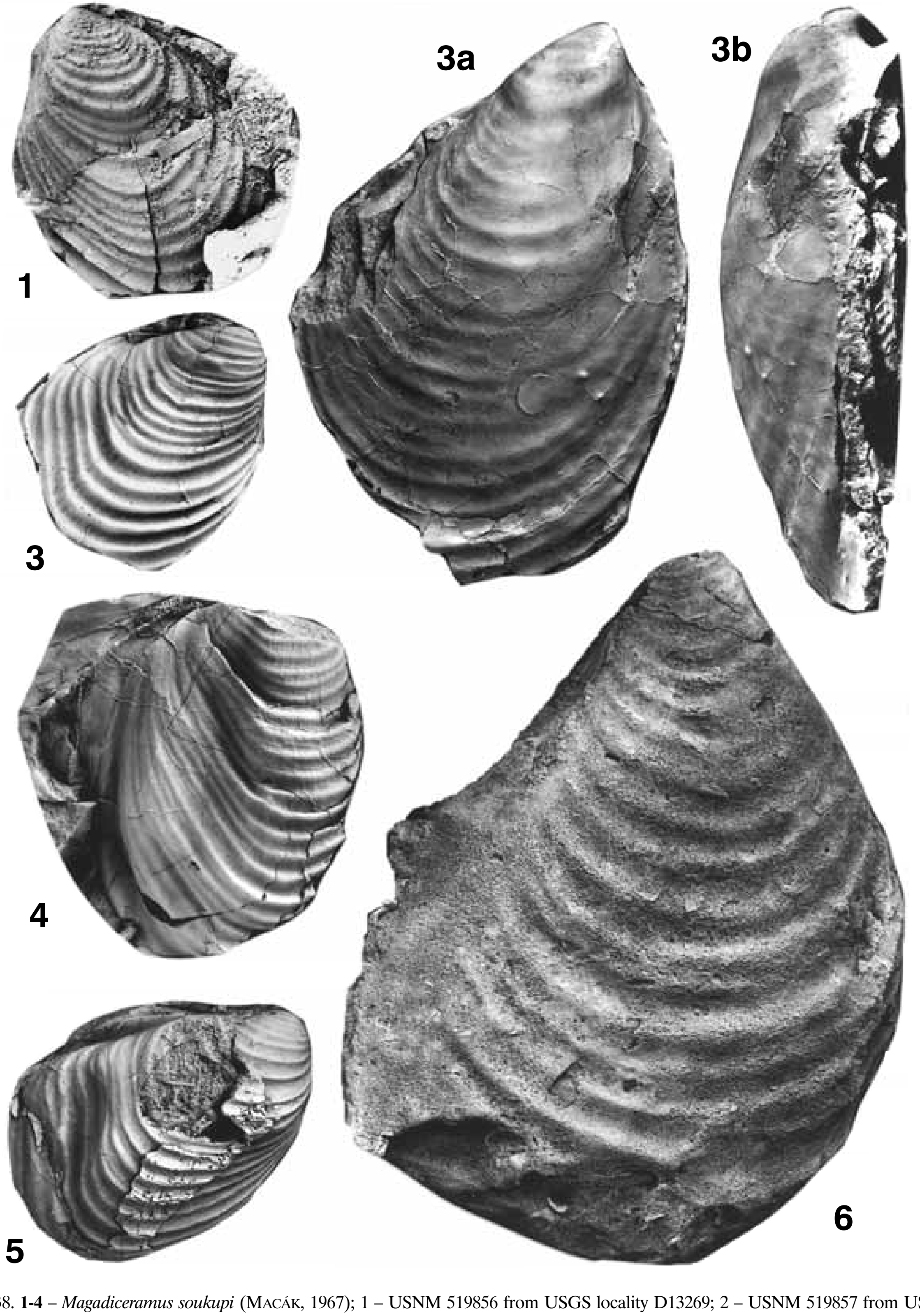

Fig. 38. **1-4** – *Magadiceramus soukupi* (MACÁK, 1967); 1 – USNM 519856 from USGS locality D13269; 2 – USNM 519857 from USGS locality 21097; 3 – USNM 519858 from USGS locality 3079; 4 – USNM 519859 from USGS locality 21097; all are × 0.85. **5** – *Magadiceramus subquadratus* (SCHLÜTER, 1877), USNM 519860 from USGS locality 21097; × 0.95. **6** – *Inoceramus undabundus* MEEK & HAYDEN, 1862; USNM 519861 from USGS locality D8282; × 0.8

Magadiceramus soukupi (MACÁK, 1967)
(Text-figs 11.3, 12.1, 12.6, 12.12, ?22.3, 34.5, 38.1, 38.2, 38.3, 38.4)

?pars 1970. *Inoceramus* (*Magadiceramus*?) cf. *soukupi* (group I); SEITZ, p. 46, pl. 6, fig. 1; ?pl. 13, fig. 1.

TYPE: The holotype, by original designation, is the original of MACÁK (1967, fig. 1), from the Upper Coniacian of borehole TH-10, in Předlice near Usti-upon-Elbe, northen Bohemia, Czech Republic.

MATERIAL: USNM 519856 from USGS locality D13269; USNM 519857, USNM 519859, USNM 519881 and USNM 519891 from USGS locality 21097; USNM 519864 from USGS locality D940; USNM 519870, locality unknown; USNM 519876 from USGS locality D13972.

DIAGNOSIS: Small to moderate size for genus, inequilateral, ?subequivalve. Valve moderately oblique, with usually more or less well marked geniculation; posterior auricle small, well separated from disc. Disc with radial sulcus posterior to growth line. Ornament of regular to subregular fine rugae, relatively closely spaced. Adult axial part usually with weakly developed radial ribs. Details of ligamentat and shell unknown.

DESCRIPTION: The species is small to medium sized, equivalve, inequilateral. The umbo is wide, not separated from the rest of the disc, with the beak not projecting above the hinge line. The anterior margin is short to moderately long, passing into the broadly rounded antero-ventral margin, and thence into the narrowly rounded ventral margin. The postero-ventral margin is short and straight, and passes into the weakly convex posterior margin. The hinge line is moderately long, straight. The valve is weakly inflated, markedly oblique, with the growth line straight. The posterior auricle is very small, well separated from the disc. In the posterior part of the disc runs a shallow radial sulcus, visible relatively early in ontogeny (Text-fig. 12.1). The juvenile and adult stages usually contact at variably developed geniculation; the ventral margin of the juvenile stage is usually well marked by the beginning of the radial sulcus.

The ornament is composed of regularly to subregularly spaced comarginal ribs, with narrow interspaces. In all specimens occur more or less well developed concentric rugae, which are low and roughly regular. Fine radial ribbing occurs rarely in the axial part of the adult stages (Text-figs 11.3, 38.2).

REMARKS: The axial valve elongation, the presence of a radial posterior sulcus, and relatively regular ornament, composed of closely-spaced rugae, makes our specimens very close to the type of the species. Although *Magadiceramus soukupi* was described based on a single specimen, with its anterior and dorsal parts not particularly well preserved, the main characteristics of the species are clear. To *M. soukupi* we refer also Ko 286, one of the specimens referred to *?M*. cf. *soukupi* by SEITZ (1970, pl. 6, fig. 1). As may be judged from the Western Interior material, the geniculation in the juvenile stage is variably developed, and seems not to be a permanent feature of the species.

OCCURRENCE: Upper Coniacian of the Western Interior and of Bohemia, Czech Republic.

Genus *Cladoceramus* SEITZ, 1961

TYPE SPECIES: *Inoceramus undulatoplicatus* var. *michaeli* HEINZ, 1928a (=*Inoceramus digitatus* SCHLÜTER 1877, non *Inoceramus digitatus* SOWERBY, 1829).

REMARKS: We follow SEITZ's (1961) concept of *Cladoceramus*, although similarly as DHONDT & DIENI (1990), we regard it a separate genus.

The genus is closely allied to *Platyceramus*, and is most obviously derived from it. The only difference between these two genera, as so far recognised, is a well-developed radial ribbing in *Cladoceramus*. Although this feature also characterises some of the *Platyceramus* species (see SEITZ 1961), it never dominates the concentric rugae. This distinction is not very strong and NODA's (1983, and also MATSUMOTO & *al*. 1982) view of *Cladoceramus* as a junior synonym of *Platyceramus* is very attractive. Neither of the two interpretations of *Cladoceramus* gained conclusive support subsequently. On the basis of a fauna from a single biogeographic area, Euramerican or North Pacfic, the resolution of this question on purely morphological considerations seems impossible, and accepting either of the two interpretations is a matter of taste. Palaeobiogeographical/evolutionary considerations of all the cladoceramids known so far may prove useful. Thus, when following DHONDT & DIENI's (1990) broad interpretation of *Cladoceramus undulatoplicatus* as a species comprising the Euramerican *undulatoplicatus* species group as well as the North Pacific "*I.*" *japonicus* group, it is easy to defend *Cladoceramus* as an independent (monospecific) genus, originating somewhere in the Euramerican biogeographic region and then moving throughout the Santonian to the east, into the Pacific area. If, however, an evolutionary independence of *I. japonicus* (as a Late Santonian evolutionary descendant of *Platyceramus ezoensis* as suggested by NODA 1983) and of *Cl. undulatoplicatus*, is accepted, NODA's interpretation of *Cladoceramus* would appear reasonable. Recent studies of the '*undulatoplicatus*' fauna from the Madagascan – South African Province (KENNEDY & *al.*. submitted; WALASZCZYK, in prep.), support the view of *Cladoceramus* as of independent genus.

OCCURRENCE: When the Japanese *japonicus* group is included, the genus ranges through the whole Santonian and ranges up into the Lower Campanian.

Cladoceramus undulatoplicatus (ROEMER, 1852)
(Text-figs 39.1-3, 40.4)

[1849. *Inoceramus undulato-plicatus* ROEMER, p. 402.
1852. *Inoceramus undulato-plicatus* ROEMER, p. 59, pl. 7, fig. 1.
1877. *Inoceramus digitatus* SOWERBY; SCHLÜTER, p. 267, pl. 36.
1877. *Inoceramus undulato-plicatus* ROEMER; SCHLÜTER, p. 270, pl. 38.
non 1879. *Inoceramus undulato-plicatus* ROEMER; WHITEAVES, p. 168, pl. 20, fig. 2.
1912a. *Inoceramus undulato-plicatus* ROEMER; WOODS, p. 304, text-figs 60-61.
1912a. *Inoceramus undulato-plicatus* var. *digitatus* SCHLÜTER, WOODS, p. 307, text-fig. 62.
1912b. *Inoceramus undulato-plicatus* ROEMER, WOODS, p. 18, text-fig. 94
?non 1958. *Inoceramus undulatoplicatus* ROEMER; ANDERSON, p. 102, pl. 22, fig. 4 [= *Sphenoceramus schmidti* (MICHAEL 1899)]; ?pl. 43, figs 3-5.
1959. *Inoceramus undulato-plicatus* ROEMER, DOBROV & PAVLOVA, p. 149, pl. 11, figs 3-4.
1961. *Inoceramus* (*Cladoceramus*) *undulatoplicatus undulatoplicatus* ROEMER; SEITZ, p. 98 text-figs 21-22; pl. 3, fig. 4, 9; pl. 4, fig. 6; pl. 5, figs 3, 6.
1961. *Inoceramus* (*Cladoceramus*) *undulatoplicatus michaeli* HEINZ, SEITZ, p. 102, text-figs 21-23, pl. 5, fig. 1-2, 4; pl. 6, fig. 2.
1961. *Inoceramus* (*Cladoceramus*) *undulatoplicatus* subsp. indet. SEITZ, p. 106, text-figs 22, 24-25, pl. 5, fig. 5; pl. 10, figs 1-2.
? 1961. *Inoceramus* (*Cladoceramus*) cf. *japonicus* NAGAO & MATSUMOTO; SEITZ, p. 109, pl. 7, fig. 3.
1963. *Inoceramus undulato-plicatus* ROEMER var. *digitatus* SCHLÜTER; GAMBASHIDZE, p. 83, pl. 8, fig. 2.
1963. *Inoceramus undulatoplicatus* ROMER, 1852; YOUNG, p. 128, pl. 81, figs 1-3; pl. 82, figs 1-4.
1964. *Inoceramus* (*Cladoceramus*) aff. *undulatoplicatus* var. *michaeli* HEINZ, SORNAY, p. 174, text-figs 6-7.
1964. *Inoceramus undulatoplicatus* RÖEMER; SCOTT & COBBAN, p. 15, pl. 5, figs 1, 5; pl. 6, figs 1, 4.
1969. *Sphenoceramus digitatus* (J. de C. SOWERBY); COX in MOORE, p. N320, fig. C48, 2b.
1974. *Inoceramus undulatoplicatus michaeli* HEINZ; PERGAMENT, p. 201, pl. 1, fig. 1.
1974. *Inoceramus undulatoplicatus michaeli* HEINZ; ATABEKIAN, p. 216, pl. 106, fig. 2; pl. 110, fig. 2.
1977b. *Inoceramus* (*Cladoceramus*) *undulatoplicatus* ROEMER; KAUFFMAN, p. 265, pl. 28, fig. 3.
1981. *Inoceramus* (*Inoceramus*) *undulatoplicatus undulatoplicatus* ROEMER; TZANKOV in TZNAKOV & *al*., p. 92, pl. 42, figs 3-4.
1981. *Inoceramus* (*Inoceramus*) *undulatoplicatus chumenensis* subsp. n., TZNAKOV in TZANKOV & *al*., p. 92, 212, pl. 43, figs 1-2.
1986. *Inoceramus* (*Platyceramus*) *undulatoplicatus michaeli* HEINZ; LOPEZ, p. 236, pl. 1, fig. 10.
1986. *Inoceramus* (*Platyceramus*) *undulatoplicatus undulatoplicatus* ROEMER; LOPEZ, p. 236.
1986. *Inoceramus* (*Platyceramus*) *undulatoplicatus* ROEMER; SCOTT & *al*., p. 16, text-fig. 9h.
1987. *Cladoceramus undulatoplicatus* (F. ROEMER); CLEEVELY & MORRIS, p. 107, pl. 21, fig. 7.
1988. *Inoceramus undulato-plicatus michaeli* HEINZ; ALIEV & KHARITONOV, p. 261, pl. 15, figs 1-2.
1994. *Cladoceramus undulatoplicatus* (ROEMER); subsp. indet.; TRÖGER & SUMMESBERGER, p. 174, pl. 3, fig. 2.

TYPE: The lectotype is the original of ROEMER (1852, pl. 7, fig. 1) from the *undulatoplicatus* Zone of the Austin Chalk, from a locality in 'Banks of the

Guadalupe River, below New Braunfels' in Texas, USA. ROEMER (1852) did not indicate the holotype, and it is clear from his text that he based the description on more than a single specimen. His single illustrated specimen, which was also the only quite complete specimen, is thus designated herein a lectotype.

MATERIAL: USNM 519927 from USGS locality D3493, USNM 519928 from USGS locality D3491, USNM 519929 from USGS locality D3490, and USNM 131504 from USGS locality D3490.

DESCRIPTION: The species is of medium to large size, weakly to moderately inequilateral, ?equivalve. Apart from the weakly inflated juvenile stage, the valves are flat. The posterior auricle is well separated only in the juvenile stage; later it is only weakly separated or not separated at all. The umbo is small, not projecting above the hinge line, which is short to moderately long and straight. The valve has an oval outline, much higher that wide, weakly oblique.

Very juvenile specimens are ornamented with concentric elements, which may consist exclusively of growth lines or also of superimposed rugae. Very quickly in ontogeny appear radial ribs which, where they are developed to the same extent as the concentric ornament, dominate the adult ornament. In some large specimens the next stage (?gerontic) is observed (see e.g. SCOTT & COBBAN 1964, pl. 5, fig. 5), where radial ornament becomes weaker or dis-

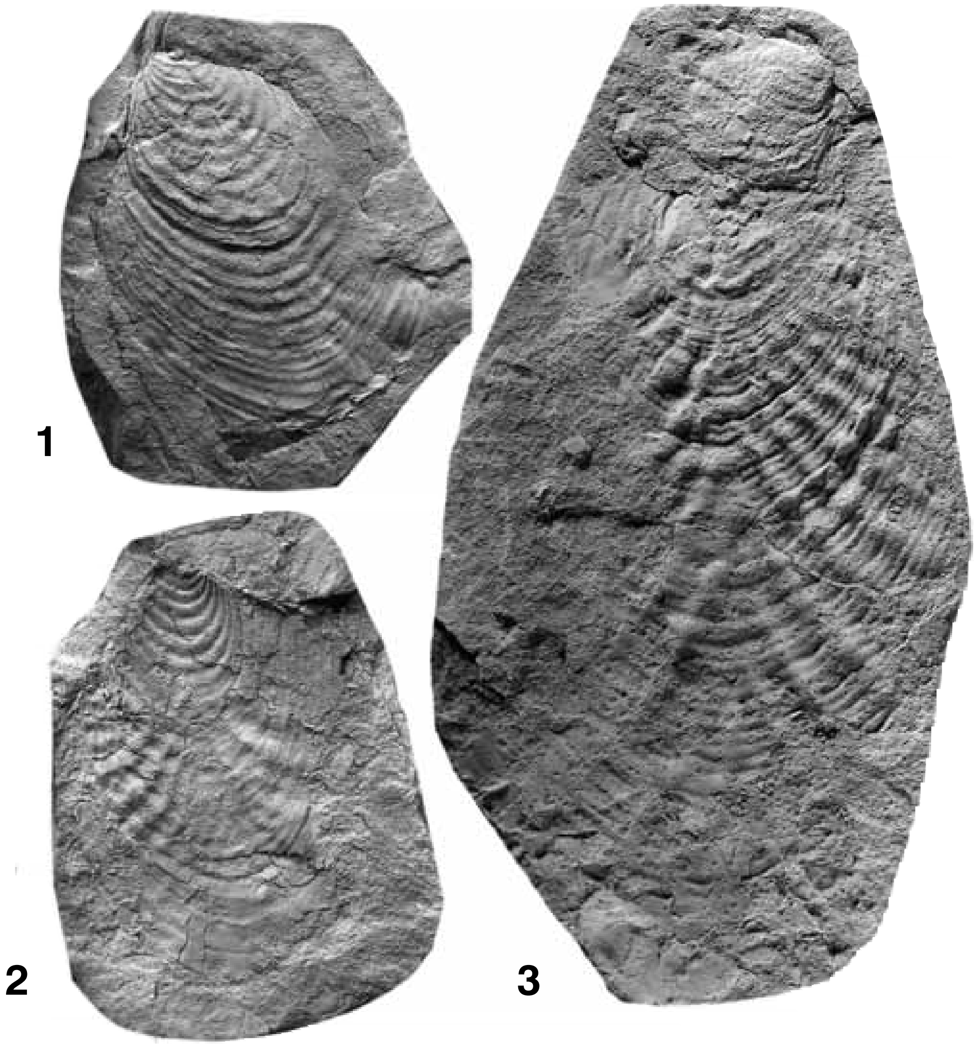

Fig. 39. **1-3** – *Cladoceramus undulatoplicatus* (ROEMER, 1852); 1 – USNM 519927 from USGS locality D3493; × 0.6; 2 – USNM 519928 from USGS locality D3491; × 0.6; 3 – USNM 519929 from USGS locality D3490; × 0.75

appears almost completely. In some specimens the radial ornament on the posterior part of the valve may be distinctly stronger than on the anterior side.

REMARKS: The species shows a wide range of morphological variability. Some of the parameters (such as valve inflation and to a large extent also valve outline) are difficult to assess because of the effects of preservation. The specimens studied are invariably from the Pueblo section, represented by shaly internal moulds, which are usually strongly compressed. The material clearly shows the variability in the size of the juvenile, concentrically ornamented stage, as well as the strength and pattern of the radial ornament. The most characteristic feature of the latter is the presence of strong posterior radials, which is the distinguishing feature of HEINZ's variety *michaeli* of *Cl. undulatopli-*

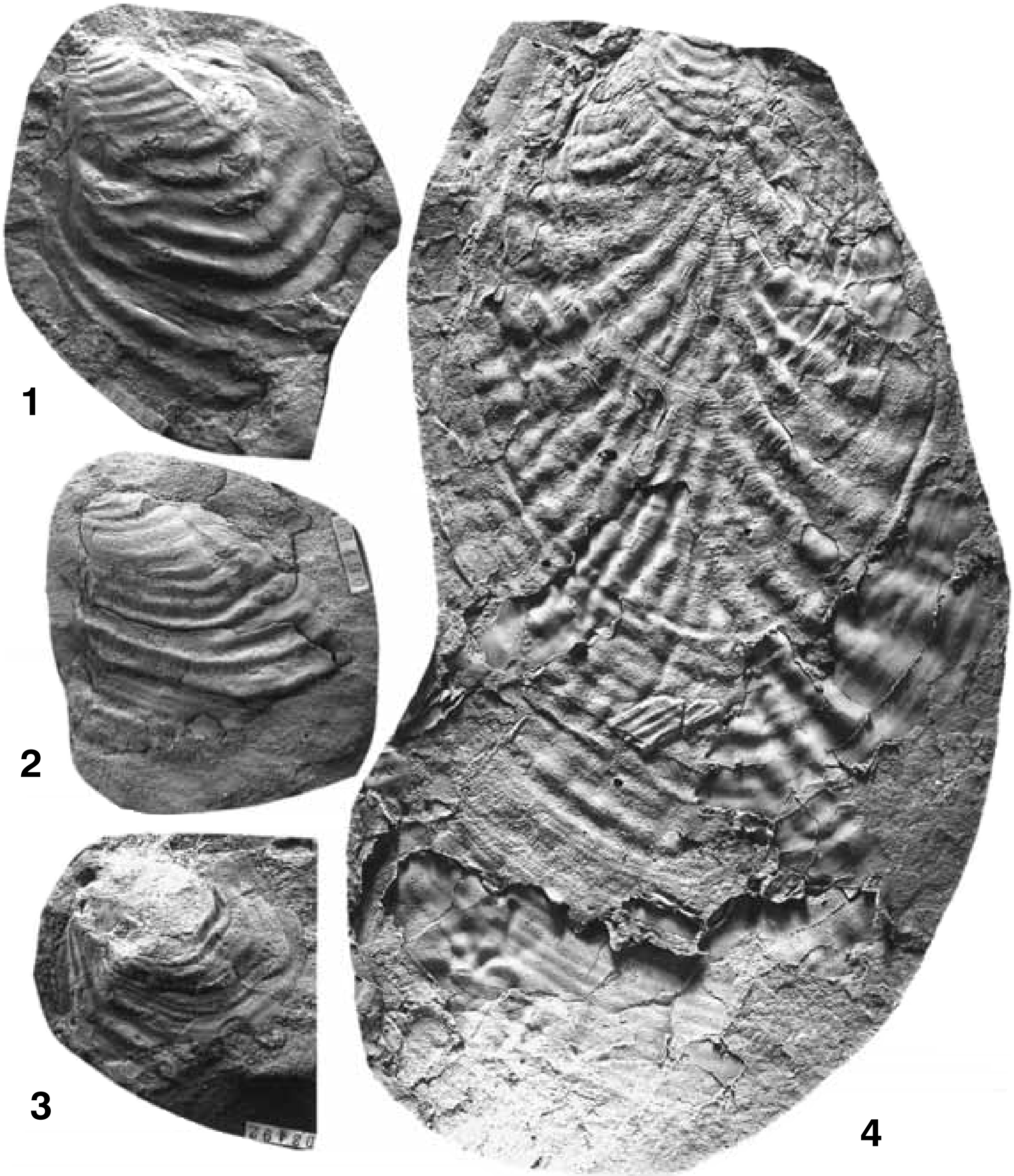

Fig. 40. **1-3** – *Cordiceramus arnoldi* (SEITZ, 1961); 1 – USNM 519930 and 2 – USNM 519931, both from USGS locality D3490; 3 – USNM 519932 from USGS locality D3492; all are × 1. **4** – *Cladoceramus undulatoplicatus* (ROEMER, 1852), USNM 131504 from USGS locality D3490 [original from SCOTT & COBBAN, 1964, pl. 5, fig. 5]; × 0.85

catus. Stronger development of posterior radials is, however, observed in almost any specimen, even in the lectotype, and we regard this feature as being wholly within the range of intraspecific variability (see also discussion by DHONDT & DIENI 1990).

The only complete, albeit juvenile, specimen illustrated by ANDERSON (1958, pl. 22, fig. 4) is quite distinct from *Cl. undulatoplicatus* and belongs to *Sphenoceramus schmidti* (MICHAEL, 1899) (see also NODA & *al*. 1996, NODA 1988). ANDERSON's other specimens (his pl. 43, figs 3-5) are indeterminable fragments.

OCCURRENCE: The species is known from the Lower Santonian throughout the Euramerican biogegraphical region; similar specimens are noted from the Lower Santonian of the East African Province.

Genus *Cordiceramus* HEINZ, 1932

TYPE SPECIES: *Inoceramus cordiformis* SOWERBY (1823).

REMARKS: The genus was discussed at length by SEITZ (1962, pp. 110-114). TSAGARELLI & GAMBASHIDZE's (1984) proposal to separate more '*balticus*' like cordiceramids into a distinct genus *Sornayceramus* seems quite reasonable; however, it requires accepting the view that the pentagonal outline, a characteristic feature of *Cordiceramus*, is polyphyletic.

The genus is well represented in the US Western Interior, with representatives of most of the species known from Europe also represented. *Inoceramus coulthardi* and *Inoceramus pontoni*, two of the species described by MCLEARN (1926) from the Canadian Western Interior, and referred subsequently to *Cordiceramus* (e.g. JELETZKY 1970, COBBAN & *al*. 2005), are very similar morphologically, but their *Cordiceramus* affinity is uncertain. The specimens illustrated by MCLEARN (1926) are small-sized, and they may easily represent juveniles of other posteriorly sulcate forms, such as members of the *Inoceramus gibbosus* group (see WALASZCZYK & WOOD 1999) or early sphenoceramids.

OCCURRENCE: The genus appeared in the Late Coniacian (e.g. NODA 1986) and ranged into the Middle Campanian (SEITZ 1961, 1967; WALASZCZYK & *al*. 2001, WALASZCZYK 2004).

Cordiceramus gilberti (WHITE, 1876)
(Text-figs 41.1, 41.2, 42.1-42.4)

1876. *Inoceramus gilberti* WHITE, p. 113.
1879. *Inoceramus gilberti* WHITE; WHITE, p. 285, pl. 3, fig. 1.
1894. *Inoceramus gilberti* WHITE; STANTON, p. 79, pl. 14, figs 3-4.
1898. *Inoceramus gilberti* WHITE; LOGAN, p. 453, pl. 92, figs 1, 3.
1900a. *Inoceramus gilberti* WHITE; HERRICK & JOHNSON, pl. 37, fig. 3 [reproduction of STANTON's plate 14]
1900b. *Inoceramus gilberti* WHITE; HERRICK & JOHNSON, pl. 11, fig. 3 [reproduction of STANTON's plate 14]
1944. *Inoceramus gilberti* WHITE; SHIMER & SHROCK, p. 389, figs 151.7-151.8.
1977b. *Inoceramus gilberti* WHITE; KAUFFMAN, p. 247, pl. 13, fig. 1.
1978. *Inoceramus gilberti* WHITE; KAUFFMAN & *al*., pl. 17, fig. 1.
1997. *Inoceramus* (*Cordiceramus*) aff. *brancoiformis* SEITZ; LECKIE & *al*., figure 44A, F.

TYPE: The lectotype, herein designated, is USNM 8050a, the original of WHITE (1879, pl. 3, fig. 1c) from near the Last Chance Creek in southern Utah. USNM 8050b, the second specimen of WHITE (1879, pl. 3, fig. 1a-b) is the paralectotype.

MATERIAL: USNM 519974, USNM 519975, USNM 519976 and USNM 519977; all from USGS locality D5308.

DESCRIPTION: The species is of medium to moderately large size, inequilateral, equivalve, with massive appearance. The valve outline varies from rounded subquadrate to obliquely subovate. The umbo is moderately massive, with the beak projecting distinctly above the hinge line. The anterior margin is relatively short, passing into the broadly rounded antero-ventral margin, and thence into the weakly rounded to almost straight ventral margin. The posterior margin is broadly rounded. The hinge line is relatively short, straight. The valve is distinctly divided into the moderately inflated disc, with its maximum inflation in the dorsal part, and the small, subtriangular posterior auricle. The anterior wall is steep, almost perpendicular to the commissure. In the axial part of the disc runs the weakly to moderately well developed radial sulcus, which starts ventrally of the umbonal part.

The valves are covered with relatively strong, irregular to subregular concentric rugae, which, besides those on the posterior auricle, are of similar strength. Superimposed on the rugae are raised growth lines that are best developed in the umbonal and middle part of the valve. The rugae cross the radial sulcus without or only with slight weakening.

REMARKS: The subpentagonal valve outline and the radial sulcus in the axial part of the disc place *Inoceramus gilberti* in the genus *Cordiceramus* and, moreover, into the group of *Cordiceramus muelleri*. From all other members of the group, it differs in its massive appearance and much less regular rugae. The juveniles, however, may hardly be distinguished.

Conspecific with *Cordiceramus gilberti* is *Inoceramus* (*Cordiceramus*) aff. *brancoiformis* SEITZ, illustrated by LECKIE & *al*. (1997, figs 44A, F). Both figured specimens are characterised by a massive

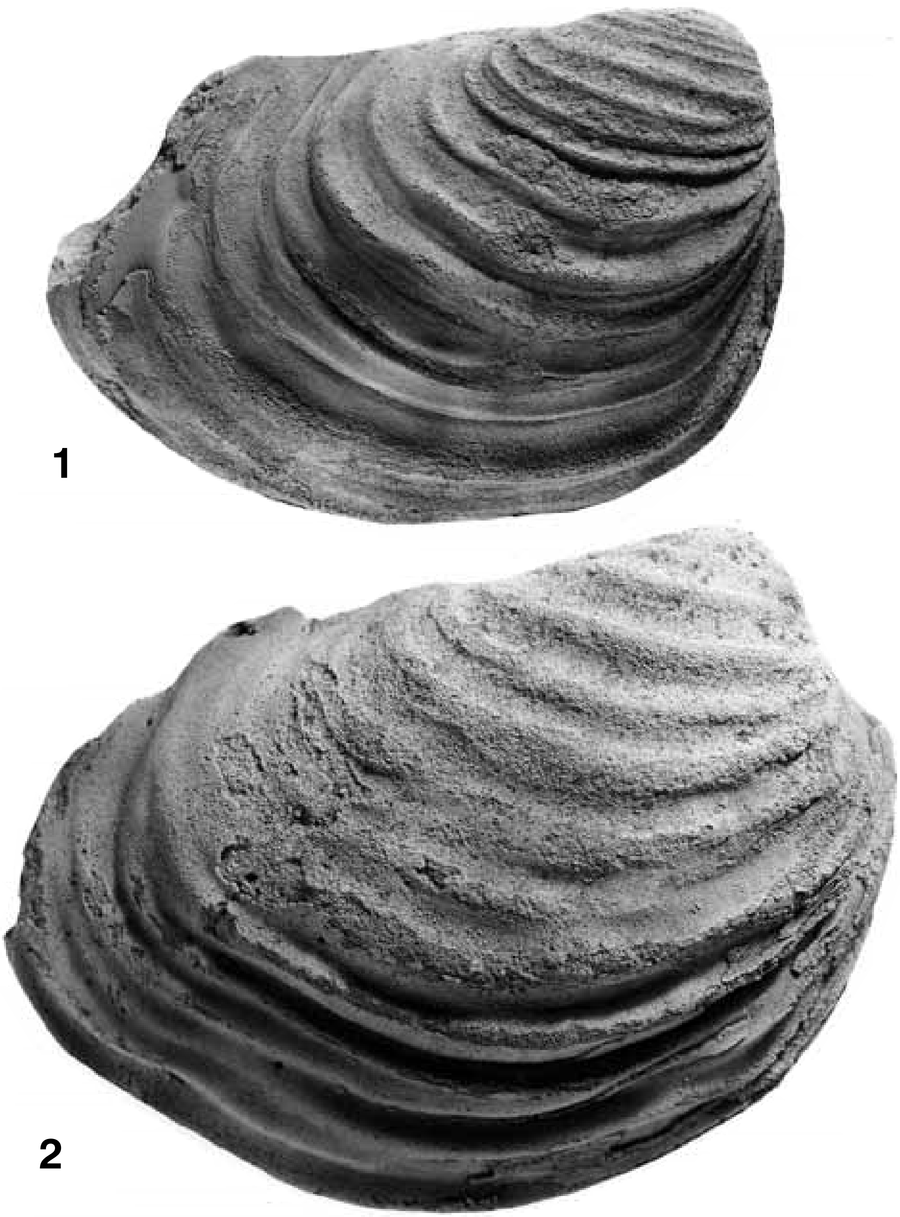

Fig. 41. **1-2** – *Cordiceramus gilberti* (WHITE, 1876), 1 – USNM 519974 and 2 – USNM 519975, both from USGS locality D5308; × 0.8

umbo, projecting well above the hinge line, and strong, rounded, markedly irregular concentric rugae. *Cordiceramus brancoiformis* is a form with two distinct growth stages (with more or less prominent geniculation), is less oblique and with more delicate and regular rugae.

Very similar to *C. gilberti* is *Cordiceramus koeplitzi* described from Germany (SEITZ 1961). Both taxa are posteriorly elongated and strongly inflated. Further material of the German species may show it to be conspecific with the American form.

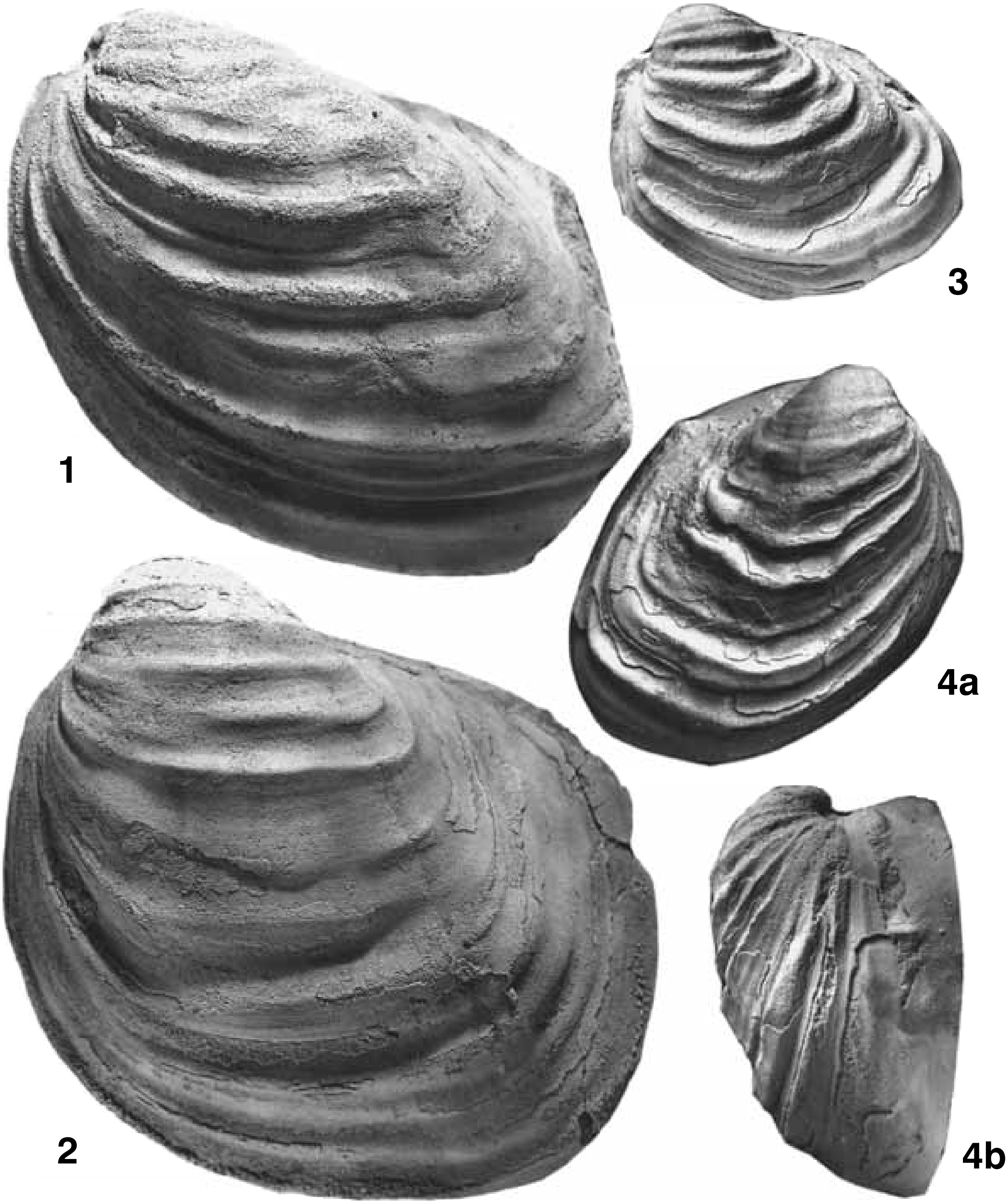

Fig. 42. **1-4** – *Cordiceramus gilberti* (WHITE, 1876); 1 – USNM 519976 from USGS locality D5308; 2 – USNM 519977 from USGS locality D5308; 3 – **lectotype**, USNM 8050; original of WHITE, 1879, pl. 3, fig. 1c; 4 – **paralectotype**, USNM 8050; original of WHITE 1879, pl. 3, figs 1a-b; All are × 0.8

OCCURRENCE: WHITE's original material is difficult to date; the rest of the material comes from the upper part of the Santonian. Well dated specimens from the Mancos Shale at Mesa Verde, [reported as *Inoceramus* (*Cordiceramus*) aff. *brancoiformis* SEITZ] by LECKIE & *al*. (1997, figs 44A, F), are from the basal Upper Santonian [*Clioscaphites choteauensis* ammonite Zone].

Cordiceramus recklingensis (SEITZ, 1961)
not illustrated herein [see SCOTT & COBBAN 1964, pl. 10, fig. 1]

pars 1931. *Endcocostea typica* WHITFIELD; RIEDEL, p. 664, pl. 75, fig. 2 [only]
1931. *Endocostea typica* WHITFIELD var. *cycloidea* RIEDEL, p. 665, pl. 76, fig. 2.
1961. *Inoceramus* (*Cordiceramus*) *mülleri recklingensis* SEITZ, p. 137, pl. 8, figs 2, 4; pl. 15, fig. 2.
part 1964. *Inoceramus simpsoni* MEEK; SCOTT & COBBAN, pl. 10. fig. 1 [non pl. 11, fig. 5 = *Cordiceramus muelleri* (PETRASCHECK)].
1967. *Inoceramus* (*Cordiceramus*) *muelleri recklingensis* SEITZ; SEITZ, p. 127.
1982. *Inoceramus recklingensis* SEITZ; SORNAY, pl. 1, fig. 1.
1986. *Inoceramus* (*Endocostea*) *balticus* BÖHM; SCOTT & *al*., figure 12h.

TYPE: The holotype, by original designation, is S 329 Wb, the original of SEITZ (1961, pl. 8, fig. 2) from the Upper Santonian of the the General Blumenthal mine, shaft number 8, depth 3.5 m, Westphalia, Germany

MATERIAL: USNM 131523 from USGS locality D3505; USNM 388286 from USGS locality D11425.

DESCRIPTION: The species is of medium size for the genus, inequilateral, equivalve. The valve is weakly to moderately inflated, with a rounded to pentagonal outline. The anterior margin is short and convex, passing into the long, broadly convex antero-ventral and thence ventral margins. The posterior margin is again short and weakly convex. The hinge line is relatively long and straight. The posterior auricle is not separated from the disc. The umbo is small, not inflated and not projecting above the hinge line. The radial sulcus is weakly to moderately developed.

The ornament consists of very regular, relatively widely-spaced, almost symmetrical sharp-edged rugae. The interspaces are flat floored. In the anterior and antero-ventral parts the rugae are discontinuous, caused mostly by their obliquity to the growth lines.

REMARKS: *Cordiceramus recklingensis* (SEITZ) differs from all other members of the *C. muelleri* group through the weak to moderate and uniform inflation, and the rounded to slightly subpentagonal outline. The specimens studied resemble the most one of the paratypes, namely SEITZ' (1961, pl. 8, fig. 4), which is less oblique and more subquadrate in outline. This morphotype resembles very closely *Cordiceramus paraheberti* (SORNAY) from the topmost Santonian to Lower Campanian of Madagascar (see SORNAY 1968, p. 38, pl. G and pl. H, figs 1-2). The relationship remains unclear between *C. recklingensis* – *C. paraheberti* and other morphologically very close cordiceramid species, such as *Cordiceramus heberti* (FALLOT) (see illustration in SORNAY 1968, pl. H, fig. 3) or *C. pseudoregularis* (SORNAY) (see SORNAY, 1962, p. 118, pl. 7, fig. 1 and SORNAY 1968, pl. D, figs 1-2). A recently undertaken bed-by-bed study of the Madagascan cordiceramids should help in resolving this question.

The specimens of *C. recklingensis* with a very weakly developed radial sulcus and finer rugae may be difficult to separate from *Cataceramus balticus* (BÖHM). However, the interspaces are usually markedly wider in the latter species. The specimens studied herein, from the lower Upper Santonian of the Pueblo section (see SCOTT & COBBAN 1964, pl. 10, fig. 1), agree well with the characteristic features of *C. recklingensis*.

OCCURRENCE: The species is known from the Upper Santonian and Lower Campanian of Europe, North America, and possibly from Madagascar and Zululand.

Cordiceramus germanicus (HEINZ, 1933)
(Text-figs 43.1, 43.2)

1928d. *Inoceramus germanicus* HEINZ, p. 82.
pars 1931. *Endocostea typica* WHITFIELD; RIEDEL, p. 664, pl. 75, figs 3-4 [only]

1932. *Germanoceramus nigrita* HEINZ; RIEDEL, pl. 9, fig. 2.
1932. *Germanoceramus nigrita* HEINZ, p. 12
part 1933. *Germanoceramus germanicus* HEINZ; HEINZ, p. 250, pl. 21, fig. 2 [only]
1961. *Inoceramus* (*Cordiceramus*) *mülleri germanicus* HEINZ; SEITZ, p. 131, pl. 7, fig. 6; pl. 8, figs 1, 6, 7; pl. 15, fig. 1.
1964. *Inoceramus* (*Germanoceramus*) *germanicus* HEINZ; ARZUMANOVA, p. 108, pl. 1, fig. 4.
?pars 1964. *Inoceramus simpsoni* MEEK; SCOTT & COBBAN, pl. 11, fig. 5 [non pl. 10, fig. 1 = *Cordiceramus recklingensis* (SEITZ)]
1967. *Inoceramus* (*Cordiceramus*) *mülleri germanicus* HEINZ; SEITZ, p. 129, pl. 23, fig. 3; pl. 26, figs 4-5, pl. 27, figs 1, 4, 6.
1982. *Inoceramus germanicus* HEINZ; SORNAY, pl. 1, fig. 2.
1986. *Inoceramus* (*Cordiceramus*) *muelleri* PETRASCHECK; SCOTT & *al*., figs 13a, 15c.
pars 1997. *Inoceramus* (*Cordiceramus*) *mülleri germanicus* HEINZ; LECKIE & *al*., figure 42.F [non figure 42.B = *Cordiceramus bueltenensis* (SEITZ)].

TYPE: The holotype, by original designation, is Hg 57, the original of HEINZ (1933, pl. 21, fig. 2), from the Upper Santonian of Groß-Bülten near Braunschweig, Lower Saxony, Germany.

MATERIAL: USNM 519972 and USNM 519973 from USGS locality D3505; numerous uncatalogued specimens in the US Geological Survey in Denver.

DESCRIPTION: The species is of small to medium size for the genus, inequivalve, inequilateral. The valve is weakly to moderately inflated. The anterior margin is moderately long and very weakly convex or straight, passing into the long, broadly convex antero-ventral margin. The ventral margin is straight or concave. The hinge line is long and straight. The posterior auricle is subtriangular in outline, well separated from the disc, and relatively large. The umbo is small, not projecting or only projecting slightly above the hinge line. The radial sulcus is located along the growth axis and is usually clearly visible.

The valve is ornamented with regular to subregular concentric rugae which pass onto the posterior auricle. The rugae are oblique to the growth lines.

REMARKS: *Cordiceramus germanicus* (HEINZ) differs from *C. recklingensis* in being distinctly more oblique, in its elongated, subtriangular outline, and in the posterior auricle being clearly separated from the disc. It also usually possesses a much better developed radial sulcus.

C. germanicus is very close morphologically to *Cordiceramus brancoiformis* and *C. bueltenensis*. The former differs in the possession of two growth stages with step-wise change in the ornament, whereas the latter possesses less regular ornament. In both cases the small and/or poorly preserved specimens may hardly be separated.

To *C. germanicus* belongs most probably a large adult fragment from the Pueblo section illustrated by SCOTT & COBBAN (1964, pl. 11, fig. 5) and referred to *Inoceramus simpsoni* MEEK. MEEK's species is markedly less oblique in the adult part and the radial sulcus is limited only to the adult stage. The specimen is similar to a large specimen from USGS locality D10840 illustrated by WALASZCZYK & *al*. (2001, pl. 1, fig. 2).

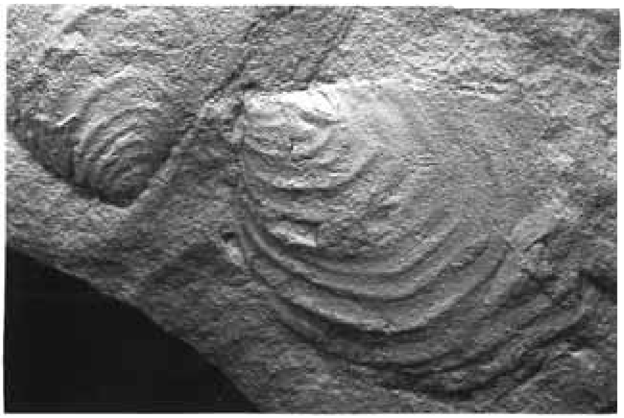

Fig. 43. **1-2** – *Cordiceramus germanicus* (HEINZ, 1933); 1 – USNM 519972 and 2 – USNM 519973, both from USGS locality D3505; both specimens are × 0.6

OCCURRENCE: *Cordiceramus germanicus* (HEINZ) is known from the Upper Santonian and Lower Campanian of Europe, Africa, and North America.

Cordiceramus ex gr. *cordiformis* (J. de C. SOWERBY, 1823) (Text-figs 44.3, 47.2, 48.8)

1823. *Inoceramus cordiformis* J. de C. SOWERBY, p. 61, pl. 44.
1836. *Inoceramus cordiformis* SOWERBY; GOLDFUSS, p. 113, pl. 110, fig. 6b [only].
pars 1898. *Inoceramus Haenleini* G. MÜLLER, p. 41, pl. 5, fig. 7 [only].
1900. *Inoceramus J. Böhmi* G. MÜLLER, p. 39 [footnote].
non 1904. *Inoceramus cordiformis* SOWERBY; AIRAGHI, pp. 184, 189, text-fig. 4; pl. 4, figs 6-9.
non 1911. *Inoceramus cordiformis* SOWERBY; ROGALA, p. 170, pl. 4, fig. 2.
1912a. *Inoceramus cordiformis* SOWERBY; WOODS, p. 334, pl. 53, fig. 8; pl. 54, figs 2-4.
non 1921. *Inoceramus cordiformis* SOWERBY; RAVN, p. 19, pl. 2, fig. 2 [= *Sphenoceramus pachti* (ARKHANGELSKY, 1912)].
1931. *Inoceramus cordiformis* SOWERBY; RIEDEL, p. 651, pl. 73, fig. 4.
?non 1959. *Inoceramus cordiformis* SOWERBY; DOBROV & PAVLOVA, p. 146, pl. 12, fig. 1.
1961. *Inoceramus* (*Cordiceramus*) *cordiformis* SOW.; SEITZ, pp. 110-114.
1961. *Inoceramus* (*Cordiceramus*) *cordiformis cordiformis* SOW.; SEITZ, p. 114, text-fig. 26a, b.
1961. *Inoceramus* (*Cordiceramus*) *cordiformis j.-böhmi* G. MÜLLER; SEITZ, p. 116, pl. 6, figs 1, 6; text-fig. 26c, d.
1961. *Inoceramus* (*Cordiceramus*) *cordiformis purus* n. subsp.; SEITZ, p. 118, pl. 6, figs 3, 4, 7; pl. 10, fig. 9; text-fig. 26e, f.
1961. *Inoceramus* (*Cordiceramus*) *cordiformis* subsp. indet.; SEITZ, p. 120, pl. 7, figs 1, 4, 7; pl. 8, fig. 5.
?1986. *Inoceramus* (*Cordiceramus*) *cordiformis* SOWERBY; SCOTT & *al.*, fig. 12c.

TYPE: The holotype is the original of J. de C. SOWERBY (1823, pl. 440), from the (inferred) Santonian of Gravesend, England.

MATERIAL: USNM 519936 from USGS locality D3499; USNM 519938 from USGS locality 21425; USNM 519954 from USGS locality 21425.

DESCRIPTION: The species is represented by three specimens and another referred to herein as *C.* cf. *cordiformis* (see Text-fig. 48.9). Two further specimens were illustrated by SCOTT & COBBAN (1964, pl. pl. 7, figs 1-2).

USNM 519938 (Text-fig. 47.2) is a double-valved specimen of moderate size, preserved mostly as an internal mould, with small shell fragments on the posterior auricle. It is an equivalve specimen, moderately inflated, higher than long. The umbo is pointed, ranging above the hinge line. The specimen shows a moderately well developed posterior radial sulcus and a rather weakly developed anterior radial sulcus. The anterior wall is steep; no distinct anterior '*Schalenkante*' is developed. The ornament is regular, moderately strong. It is a typical *C. cordiformis*.

USNM 519936 (Text-fig. 44.3) and USNM 519954 (Text-fig. 48.8) are a single RV and a single LV respectively, fragmentarily preserved. Both specimens have a rather moderately to weakly developed posterior radial sulcus and lack the anterior sulcus; the valve ornament is weak. They resemble the *purus* morphotype of SEITZ (1961).

USNM 131513 and USNM 131514 are two specimens from the Pueblo section illustrated by SCOTT & COBBAN (1964, pl. 7, fig. 1-2). They are well preserved single valve specimens represented by a RV and LV respectively. The latter specimen is characterised by vigorous ornament, which is characteristic of the *j.-boehmi* morphotype of SEITZ 1961 (see also remarks in SEITZ 1965, p. 131), however, it differs in its anterior margin, which is much less distinct. The second specimen possesses a very distinct anterior '*Schalenkante*', typical of the *j.-boehmi* morphotype, but its ornament is very weak, as in the *purus* morphotype.

REMARKS: *Cordiceramus cordiformis* belongs to one of the most variable inoceramid groups, with the variability concerning mostly the general outline and shell ornament. HEINZ (1928a) subdivided the species into a number of varieties based on the relative development of the anterior and posterior radial sulci, one of the main features of SOWERBY's species. The nominal variety was characterised by two sulci that were well developed throughout ontogeny; the morphotype with only the posterior sulcus preserved, he referred to the variety *haenleini*; the variety *sudmerbergensis* was characterised by both sulci being developed only in the juvenile stage, and, finally, the variety *lueneburgensis*, with no radial sulci. Subsequently, HEINZ (1928b) distinguished another variety – *westfalica* – characterised by a single posterior sulcus preserved only on the left valve. HEINZ' (1928b) system was criticised by RIEDEL (1937) and SEITZ (1961), who pointed out that even in SOWERBY's type the sulci were variable and not constantly developed, and suggested that this feature had no taxonomic value. RIEDEL never proposed his own classification, but SEITZ (1961, 1967) discussed the group in great detail and subdivided it based on shell outline and ornament, distinguishing a number of subspecies. The knowledge of the stratigraphical pattern, evolutionary significance, and consequently of the taxonomic status of particular SEITZ' morphotypes is far from sufficient, and his *cordiformis* subspecies –

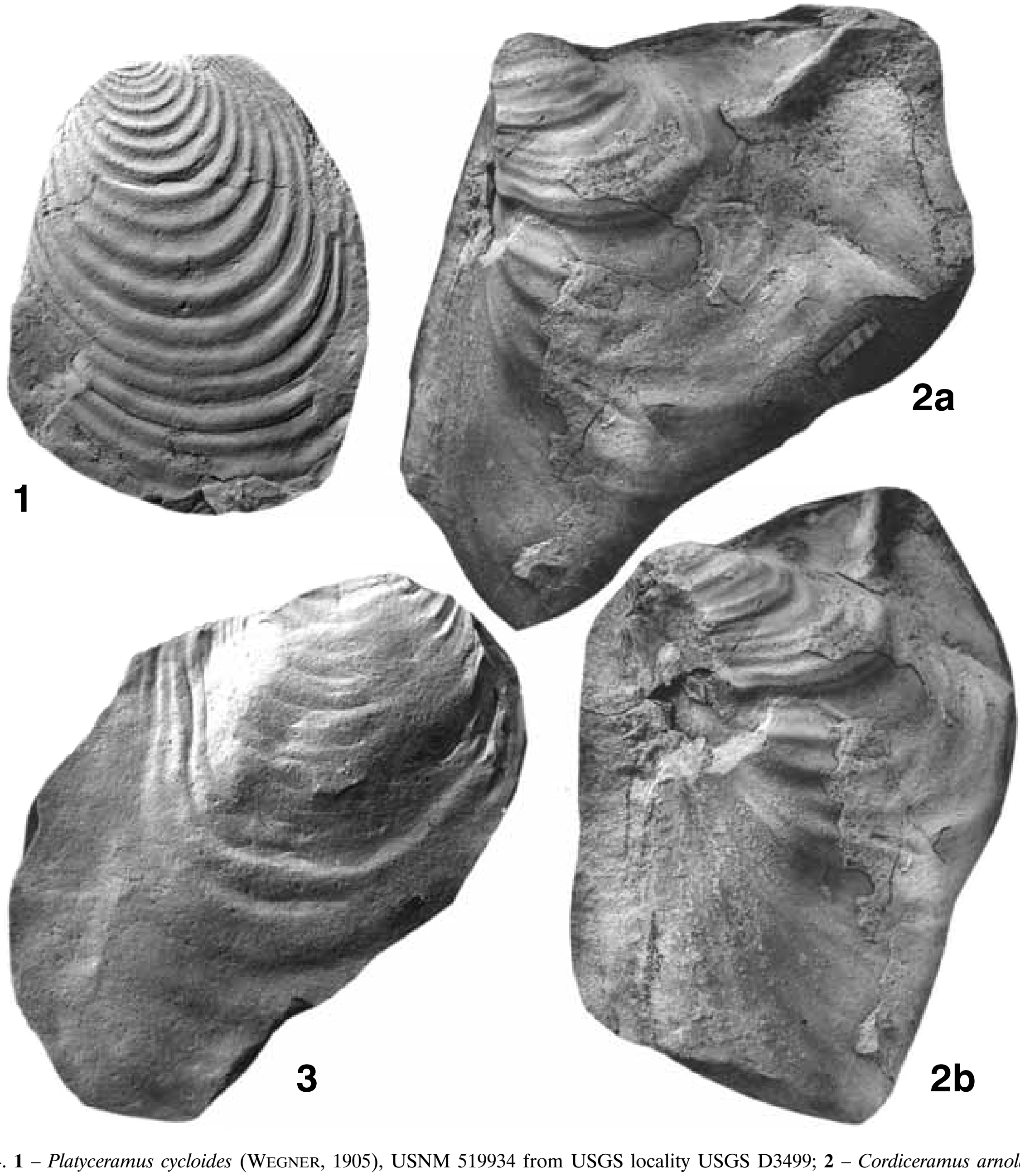

Fig. 44. **1** – *Platyceramus cycloides* (WEGNER, 1905), USNM 519934 from USGS locality USGS D3499; **2** – *Cordiceramus arnoldi* (SEITZ, 1961), USNM 519935 from USGS locality D3495; **3** – *Cordiceramus* ex gr. *cordiformis* (J. DE C. SOWERBY, 1829), USNM 519936 from USGS locality D3499; All specimens are × 1

when used – should be treated for the moment as typologic units.

In our opinion, at least three of SEITZ' subspecies, namely, *j.-boehmi*, *purus*, and the nominative one are so close morphologically (and stratigraphically) that they can be regarded as conspecific, and referred herein to *Cordiceramus cordiformis*. Particular names applied by SEITZ may be used in purely descriptive terms. Into the synonymy of the nominative subspecies, we also included forms referred to by SEITZ (1961, p. 120) as *Inoceramus* (*Cordiceramus*) *cordiformis* subsp. indet.

Although the available *C. cordiformis* material from the US Western Interior is not particularly rich, and is well represented only by the Early and Middle Santonian representatives, it suggests the presence of a uniformly variable species throughout the Euramerican biogeographical region.

OCCURRENCE: The specimens studied of *Cordiceramus cordiformis* are all from the Lower and Middle Santonian. SEITZ (1961, 1967) reported the species from the Lower, Middle and lower Upper Santonian. The species is known from throughout the Euramerican biogeographical region.

Cordiceramus bueltenensis (SEITZ, 1961)
(Text-figs 45.1-45.3, 45.6, 46.1)

pars 1961. *Inoceramus* (*Cordiceramus*) *bueltenensis* SEITZ, p. 142, pl. 9, figs 1, 2, 5-6 [non pl. 9, fig. 4 = *Cordiceramus brancoiformis* (SEITZ, 1967)]

1961. *Inoceramus* (*Cordiceramus*) *bueltenensis wolanskyae* SEITZ, p. 144, pl. 9, fig. 3; pl. 10, figs 3-6.

1964. *Inoceramus* sp.; SCOTT & COBBAN, pl. 10, fig. 3.

?pars 1967. *Inoceramus* (*Cordiceramus*) *bueltenensis bueltenensis* SEITZ; SEITZ, p. 132, ?pl. 23, fig. 2; ?pl. 26, fig. 2; pl. 27, fig. 5.

non 1970. *Inoceramus* (*Cordiceramus*) *bueltenensis* cf. *bueltenensis* SEITZ; KAUFFMAN, pl. 1, fig. 18 [the specimen reillustrated from SEITZ, 1961, pl. 9, fig. 4].

?pars 1974. *Inoceramus* (*Cordiceramus*) *bueltenensis* SEITZ; LUPU, p. 76, pl. 2, fig. 2; pl. 3, fig. 1.

? 1992c. *Inoceramus* (*Cordiceramus*) *bueltenensis bueltenensis* SEITZ; LOPEZ, p. 845, pl. 1, fig. 5.

1997. *Inoceramus* (*Platyceramus*) *platinus* LOGAN; LECKIE & *al*., fig. 41A, B.

TYPE: The holotype by original designation is Cl 5, the original of SEITZ (1965, pl. 9, fig. 1) from the Middle/Upper Santonian of Groß-Bülten, Lower Saxony, Germany.

MATERIAL: USNM 519958 from USGS locality D 3501; USNM 519960 from D3501; USNM 519959 from USGS locality D3501; USNM 519963 from USGS locality D 3501; USNM 519964 from USGS locality D 3504; ?USNM 519961 from USGS locality D3501.

DESCRIPTION: The species is small to medium sized, prosocline, weakly inflated. The valve is subpentagonal in outline, moderately inflated. The beak is small, not projecting or only weakly projecting above the hinge line. Sometimes the juvenile part is markedly inflated, forming an element that is raised distinctly above the rest of the valve. The hinge line is straight, moderately long. The anterior margin is long, broadly convex, passing into the rounded ventral margin and thence into the almost straight posterior margin. The anterior side is slightly higher, all other sides are flattened. The disc is broad, flat, with a variably developed radial sulcus, with its axis running along growth axis. The posterior auricle is small, subtriangular, and weakly separated from the disc.

The valve surface is covered with concentric rugae. Besides the juvenile part, where the rugae are regular, they are subregularly to irregularly spaced toward the venter, usually asymmetrical in cross section with their leading sides distinctly steeper. In the adult part the rugae branch into two on the antero-ventral side of the valve. The rugae become more regular and less distinct on the posterior auricle.

REMARKS: In the concept applied herein *Cordiceramus bueltenensis* comprises forms referred by SEITZ (1961) to *C. bueltenensis bueltenensis* and *C. bueltenensis wolanskyae*. All the features that distinguish the subspecies *wolanskyae* from *bueltenensis* as listed by SEITZ (1961, p. 144), i.e. larger adult size, larger adult interrugae spaces, and longer anterior margin, are interrelated and size-dependent, and consequently should not be regarded as taxonomically important. One other feature, i.e. the different position of the maximum inflation in the subspecies *wolanskyae* (in the adult part instead of in the juvenile part as

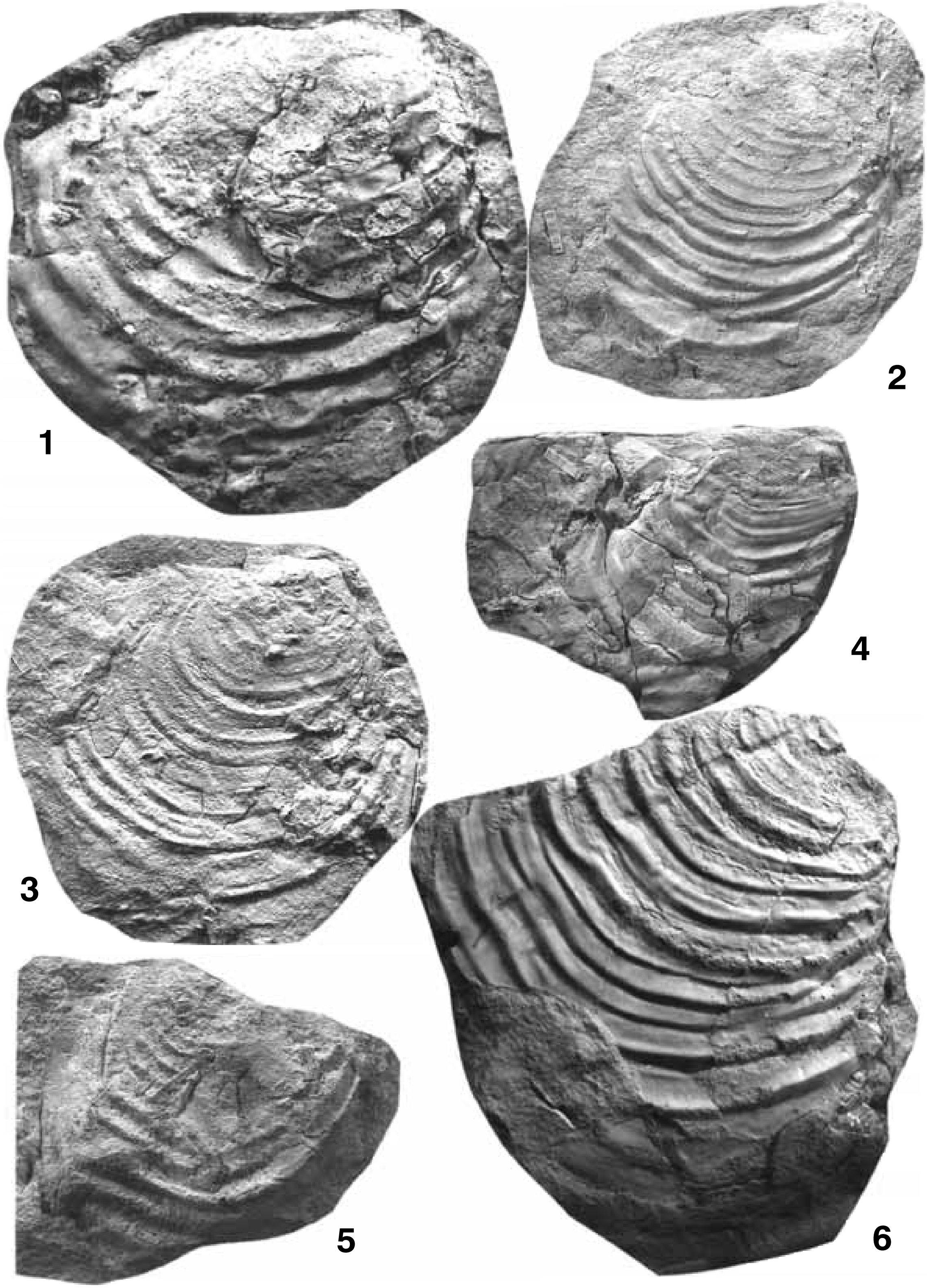

Fig. 45. **1-3, 6** – *Cordiceramus bueltenensis* (SEITZ, 1961); 1 – USNM 519958 from USGS locality D3501; × 0.7; 2 – USNM 519859 from USGS locality D3501; × 0.7; 3 – USNM 519960 from USGS locality D3501; × 0.7; 6 – USNM 519963 from USGS locality D3501; × 0.8. **4** – *Cordiceramus* sp. cf. *bultenensis* (SEITZ, 1961); USNM 519961 from USGS locality D3501; × 0.7; **5** – Cordiceramus sp.; USNM 519962 from USGS locality D3501; × 0.5

Fig. 46. **1** – *Cordiceramus bueltenensis* (SEITZ, 1961); USNM 519964 from USGS locality D3504; × 0.6. **2** – *Cordiceramus* sp., USNM 519965 from USGS locality D3501; × 0.75. **3** – *Cataceramus gladbeckensis* (SEITZ, 1967), USNM 519966 from USGS locality D3503; × 0.6

in *bueltenensis*) is, on the one hand, seen only in its type specimen, and, on the other hand, is also seen in some forms referred by SEITZ to the subspecies *bueltenensis*. Thus this feature does not seem to be constant.

The third subspecies of *C. bueltenensis* distinguished by SEITZ (1961), i.e. *C. bueltenensis arnoldi*, differs from the two others in the markedly inflated juvenile part and the lower h/l ratio at this stage of growth. Although there are species in which a raised juvenile part occurs due to ecological factors (see e.g. TRÖGER 1981a), in the case of *C. arnoldi* a genetic origin for this character cannot be excluded, and consequently this taxon is treated here as a separate species, *Cordiceramus arnoldi* (SEITZ, 1961) (see also the remarks below).

Very close to *C. bueltenensis* are *Cordiceramus brancoiformis* (SEITZ, 1961) and *Cordiceramus germanicus* (HEINZ, 1933). The latter differs from *C. bueltenensis* in the shorter and regularly convex anterior margin, slender disc (higher h/l ratio), more regular ornament, with gradual, ventralward increase of interspaces, and in stronger adult ornament. Moreover, in *C. germanicus* the rugae in the adult part are oblique, whereas they are parallel to growth lines throughout ontogeny in *C. bueltenensis*. *C. brancoiformis* differs from *C. bueltenensis* in possessing two distinct growth stages; the juvenile, with fine, closely-spaced rugae, and the adult, usually geniculated against the juvenile, with stepwise increase of interrugae spaces. To *C. brancoiformis* we refer SEITZ' specimen Ko466 (SEITZ 1961, pl. 9, fig. 4) determined by him as *C. bueltenensis* cf. *bueltenensis*; it clearly possesses two ornament stages and a broadly convex antero-ventral margin, more characteristic of *C. brancoiformis*.

To *C. bueltenensis* belongs *Inoceramus* sp. from USGS locality D3501 of the Pueblo section illustrated by SCOTT & COBBAN (1964, pl. 10, fig. 3). The specimen is represented by an incomplete adult part with characteristic cordiceramid outline and *bueltenensis* ornament.

Of the two specimens illustrated by LUPU (1974, pl. 2, fig. 2 and pl. 3, fig. 1), the smaller specimen is an indeterminable, very incomplete juvenile. The larger specimen shows the *bueltenensis* outline but the preserved part does not allow unequivocal determination.

Two quite complete specimens of *C. bueltenensis* were illustrated by LECKIE & *al*. (1997) from the Upper Santonian and referred to as *Inoceramus* (*Platyceramus*) *platinus* LOGAN. Both specimens show well the obliquely subquadrate outline, irregular ornament and, albeit weak, the radial cordiceramid sulcus (it is very weakly developed in MEVE 74434).

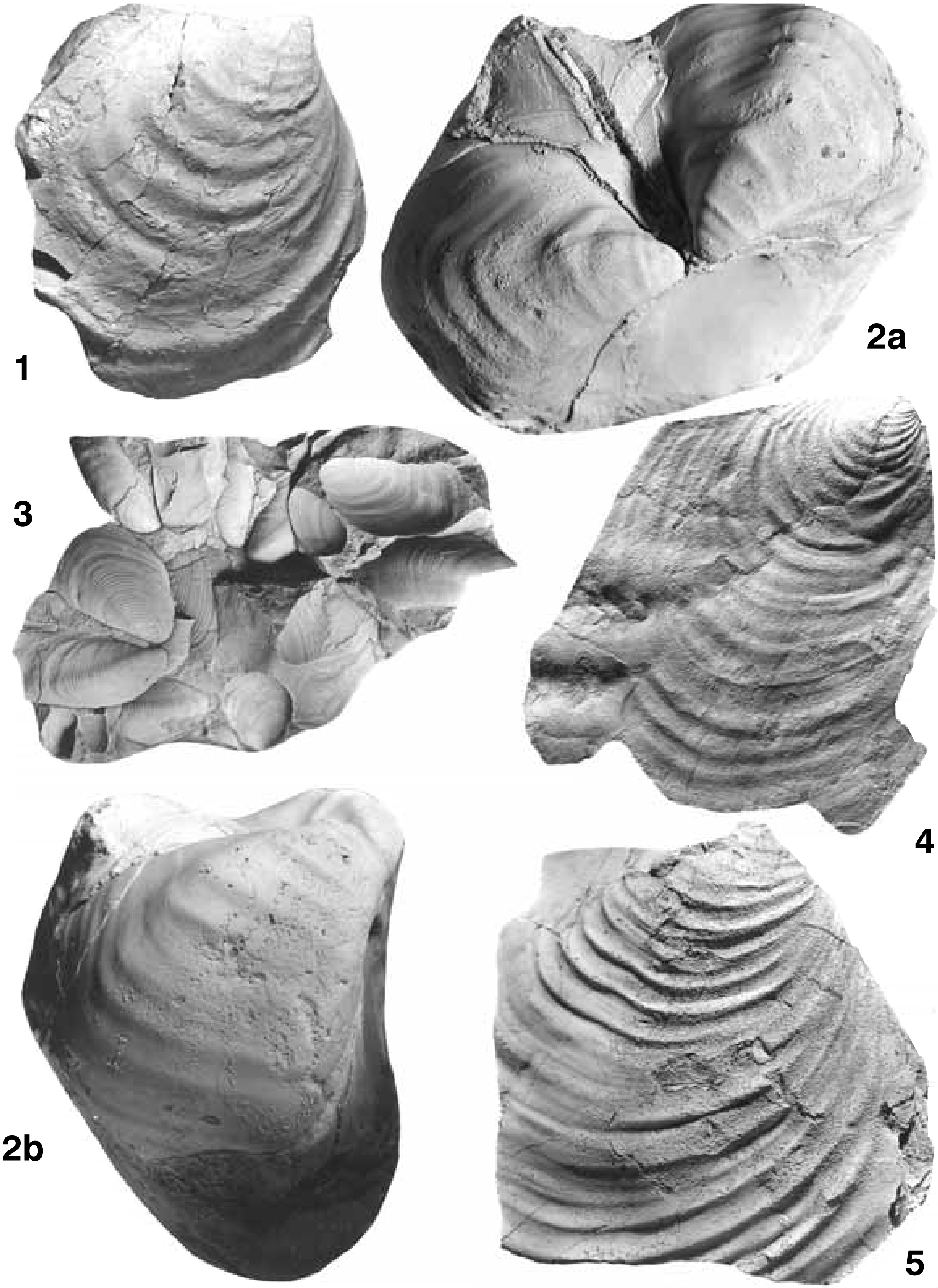

Fig. 47. **1** – *Platyceramus* ex gr. *ezoensis* (YOKOYAMA, 1890), USNM 519937 from USGS locality D3648. **2** – *Cordiceramus* ex gr. *cordiformis* (J. DE C. SOWERBY, 1829), USNM 519938 from USGS locality 21425. **3** – *Cordiceramus lesginensis* (DORBOV & PAVLOVA, 1959), USNM 519939 from USGS locality 21425. **4** – *Platyceramus heinei* (SEITZ, 1961), USNM 519940 from USGS locality D3645. **5** – *Cordiceramus arnoldi* (SEITZ, 1961), USNM 519941 from USGS locality D4371. All specimens are × 0.85

OCCURRENCE: In the collection studied *Cordiceramus bueltenensis* is known exclusively from the material of the Pueblo section, Colorado, where it ranges from D 3501 up through D 3504 (see Text-fig. 2); it is also known from the Mesa Verde section, SW Colorado. In Europe it is reported from the Santonian of Germany, Poland, Spain, and ?Romania.

Cordiceramus arnoldi (SEITZ, 1961)
(Text-figs 40.1-40.3, 44.2, 47.5)

1953. *Inoceramus cycloides* WEGNER; ØDUM, p. 14, pl. 2, fig. 6.
1961. *Inoceramus* (*Cordiceramus*) *bueltenensis arnoldi* SEITZ, p. 147, pl. 11, figs 1-4, 7; pl. 13, fig. 2.
pars 1961. *Inoceramus* (*Cordiceramus*) *brancoiformis* SEITZ, p. 159, pl. 14, fig. 3 [only]
1992c. *Inoceramus* (*Cordiceramus*) bu*eltenensis arnoldi* SEITZ; LOPEZ, p. 847, pl. 1, fig. 4.

TYPE: The holotype, by original designation, is Ko 456, the original of SEITZ (1961, pl. 11, fig. 2) from the Lower Santonian of shaft 8 of the Hugo mine, Westphalia, Germany.

MATERIAL: USNM 519930 and USNM 519931 from USGS locality D3490; USNM 519935 from USGS locality D3495, and USNM 519941 from D4371.

DESCRIPTION: The species is of medium size, inequilateral, equivalve. The valve is subpentagonal in outline, with moderate obliquity, weakly inflated, apart from the juvenile part, which is moderately to strongly inflated. The beak is small, projecting slightly above the hinge line. The anterior margin is moderately long, concave in the juvenile part, then broadly convex, passing into the rounded ventral margin. The posterior margin is almost straight. The hinge line is straight and of moderate length. The anterior face ranges from moderately steep to perpendicular to the sagittal plane. The posterior auricle is relatively small, triangular, and poorly separated from the disc. The shallow radial sulcus runs parallel to the growth axis; it starts at the ventral margin of the juvenile part. The subcontinuous *Hohlkehle* occurs along the axis of the radial sulcus; it begins in the juvenile part.

The ornament is composed of comarginal rugae, subregular to regular in the juvenile and irregular in the adult part. The rugae are distinctly weaker when passing onto the posterior auricle.

REMARKS: *Cordiceramus arnoldi* is very close to *C. bueltenensis*, from which it differs only in the markedly inflated juvenile part. A raised juvenile part is not a unique feature and was observed in some other species, and interpreted as ecologically induced (see e.g. TRÖGER 1981a). An almost identical morphotype appears e.g. in *Platyceramus mantelli* (DE MERCEY), referred by SEITZ (1962, 1965) to a separate subspecies *Platyceramus mantelli beyenburgi* (= *Pl. mantelli angustus* SEITZ, 1962). The morphotype with a raised juvenile part, is also known in material of the Cenomanian "*Inoceramus*" *crippsi* MANTELL, 1822, from Mangyshlak, western Kazakhstan (TRÖGER 1981a; and personal observation), where there is little doubt that this feature is due to environmental factors. Consequently, it is also probable that *C. arnoldi* is only an ecophenotype of the species *C. bueltenensis* and should be put into its synonymy. However, in contrast to "*I.*" *crippsi*, where the morphotype with a raised juvenile stage is limited to a single region, *C. bueltenensis* and *C. arnoldi* seem to have a regular distribution and even a similar mutual frequency both in Europe and N. America. Summing up, although we cannot exclude the interpretation that *C. arnoldi* represents only an environmentally induced morphotype of *C. bueltenensis*, the raised juvenile stage here may also be of genetic origin. Consequently, both are treated herein as separate taxa because their interpretation as two subspecies of *C. bueltenensis*, as suggested originally by SEITZ (1961) would be difficult to accept.

OCCURRENCE: In the material studied, the species is known from the lower Santonian of the Pueblo section (starting at D3490 and ranging up to D3495); it is also known from the lower Santonian (*Clioscaphites saxitonianus* ammonite Zone) of the Cody Shale, Carbon County, Montana.

Cordiceramus brancoiformis (SEITZ, 1961)
not illustrated here [see SCOTT & COBBAN, 1964, pl. 10, fig. 5]

pars 1961. *Inoceramus* (*Cordiceramus*) *brancoiformis* SEITZ, p. 159, pl. 13, figs 1, 4 [non pl. 14, fig.

1 = *Cordiceramus cordiinitialis* (SEITZ); non pl. 14, fig. 2 = *Cordiceramus bueltenensis* (Seitz) or *C. germanicus* (HEINZ); non pl. 14, fig. 3 = *Cordiceramus arnoldi* (SEITZ)]

pars 1961. *Inoceramus* (*Cordiceramus*) *bueltenensis* cf. *bueltenensis* SEITZ, p. 142, pl. 9, fig. 4 [only]

pars 1961. *Inoceramus* (*Cordiceramus*) *bueltenensis bueltenensis* SEITZ, p. 142, pl. 9, fig. 5 (only).

?pars 1961. *Inoceramus* (*Cordiceramus*) *bueltenensis arnoldi* SEITZ, p. 147, pl. 11, fig. 7 [only].

?1967. *Inoceramus* (*Cordiceramus*) *brancoiformis* SEITZ; SEITZ, p. 138, pl. 22, fig. 3; pl. 26, figs 1, 3.

pars 1970. *Inoceramus* (*Cordiceramus*) *brancoiformis* SEITZ; KAUFFMAN, pl. 1, fig. 11 [non pl. 1, fig. 13 = *Cataceramus* ex gr. *balticus* (BÖHM)]

1970. *Inoceramus* (*Cordiceramus*) *bueltenensis* cf. *bueltenensis* SEITZ; KAUFFMAN, pl. 1, fig. 18 [reillustration of SEITZ' original from pl. 9, fig. 4]

?1974. *Inoceramus* (*Cordiceramus*) *brancoiformis* SEITZ; LUPU, p. 77, pl. 3, fig. 3.

?1992c. *Inoceramus* (*Cordiceramus*) *brancoiformis* SEITZ; LOPEZ, p. 858, pl. 2, fig. 4.

non 1997. *Inoceramus* (*Cordiceramus*) aff. *brancoiformis* SEITZ; LECKIE & *al*., fig. 44A, F [= *Cordiceramus gilberti* (WHITE)]

TYPE: The holotype, by original designation, is Ko460, the original of SEITZ (1961, pl. 13, fig. 4), from the Upper Santonian of the Hermannshütte brickyard, near Recklinghausen, Westphalia, Germany.

MATERIAL: USNM 131527 from USGS locality D3501.

DESCRIPTION: USNM 131527 is a mould of a single relatively well preserved, laterally compressed RV. The valve outline is subpentagonal. The hinge line is moderately long, straight. The anterior margin is not particularly well preserved, but is most probably broadly convex, moderately long, passing into the broadly rounded antero-ventral margin and thence into the straight ventral margin. The posterior margin is almost straight. The valve is clearly divided into juvenile and adult parts, which most probably meet along a geniculation zone, although due to lateral compression this is poorly visible.

The valve is ornamented with co-marginal rugae, which change distinctly between the juvenile and adult parts; the adult rugae are less regular, widely and irregularly spaced. On the posterior auricle, the rugae are markedly weaker and become more regular.

REMARKS: The species is characterised by two distinctly ornamented growth stages which, additionally, are often separated along more or less steep geniculation. The juvenile stage varies in size and is ornamented with fine closely-spaced rugae; the adult stage is covered with moderately regular concentric rugae. The general outline and the type of ornament make the species very close to *Cordiceramus bueltenensis* and to forms from the *C. muelleri* group (particularly to *C. germanicus*). More extensive material may eventually show that the typical *C. brancoiformis* represents only extreme forms of other cordiceramid species.

The American specimen, *Inoceramus* sp. from the Pueblo section (illustrated in SCOTT & COBBAN 1964, pl. 10, fig. 5), although being markedly compressed laterally and with a poorly preserved juvenile stage, shows the main features of *Cordiceramus brancoiformis*. The two specimens illustrated by LECKIE & *al*. (1997, fig. 44A, F) from the Mesa Verde, Colorado, are strongly, uniformly inflated cordiceramids of the species *gilberti*.

OCCURRENCE: According to the European data *C. brancoiformis* is known from the Middle and Upper Santonian; the American specimen comes from the upper Middle Santonian of the Pueblo section.

Cordiceramus? *lesginensis* (DOBROV & PAVLOVA, 1959)
(Text-figs 47.3, 48.1-48.2)

1955. *Inoceramus renngarteni* PAVLOVA, p. 213, pl. 12, figs 1-2.

1959. *Inoceramus lesginensis* DOBROV & PAVLOVA, p. 150, pl. 10, fig. 2; pl. 11, fig. 2.

1968. *Inoceramus lesginensis* DOBROV & PAVLOVA; KUZNETZOV, p. 211, pl. 8, fig. 2-4.

1968. *Inoceramus goldfussi* ORBIGNY; KUZNETZOV, pl. 1, fig. 4.

?1969. *Inoceramus lesginensis lesginensis* PAVLOVA; KHALAFOVA, p. 204, pl. 23, fig. 2.

?1969. *Inoceramus lesginensis madagisensis* KHALAFOVA, p. 206, pl. 23, fig. 3.

1997. *Inoceramus lesginensis* PAVLOVA; ATABEKIAN, p. 66, pl. 25, figs 1-2.

TYPE: The holotype, by original designation, is MGU 103/49 from the 'lower' Santonian of Dhagestan, NE Caucasus, Russia.

MATERIAL: USNM 519939, USNM 519947, USNM 519948, all from USGS Mesozoic locality 21425.

DESCRIPTION: The species is of small to moderate size for the genus, equivalve, inequilateral. The moderately inflated valves are strongly oblique, with δ ranging between 30 and 35°, and axially elongated. The umbo is terminal, curved antero-dorsally, not prejecting above the hinge line. The posterior auricle is very small. The disc is moderately inflated, with maximum inflation in its dorso-central part. A more or less distinct radial sulcus runs over its entire length, posterior to the growth axis. The hinge line is long and straight. The anterior margin is broadly convex, passing gradually into the

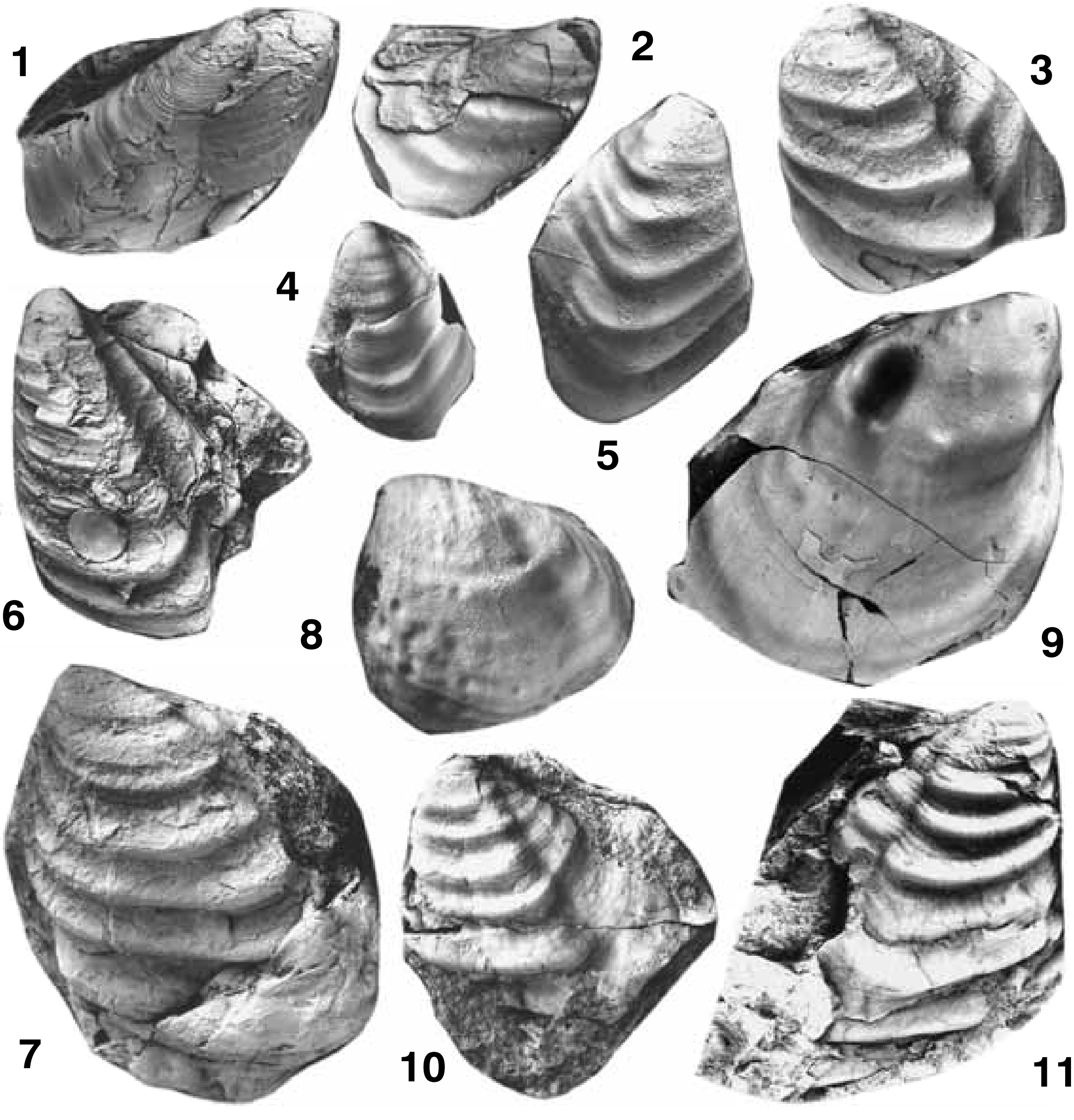

Fig. 48. **1-2** – *Cordiceramus lesginensis* (Dorbov & Pavlova, 1959); 1 – USNM 519947 from USGS locality 21425; × 0.85; 2 – USNM 519948 from USGS locality 21425; × 0.9. **3-6** – *Sphenoceramus* ex gr. *cardissoides* (Goldfuss, 1835); 3 – USNM 519949 from USGS locality 11621; × 0.85; 4 – USNM 519950 from USGS locality 21425; × 0.85; 5 – USNM 519951 from USGS locality 11621; × 0.8; 6 – USNM 519952 from USGS locality 8605; × 0.8. **7, 10-11** – *Sphenoceramus* ex gr. *pachti* (Arkhangelsky, 1912), 7 – USNM 519953 from USGS locality 11621; × 0.8; 10 – USNM 519956 from USGS locality D6075; × 0.8; 11 – USNM 519957 from USGS locality D6075; × 0.8. **8** – *Cordiceramus* ex gr. *cordiformis* (J. de C. Sowerby, 1829); USNM 519954 from USGS locality 21425; × 0.8; **9** – *Cordiceramus* cf, *cordiformis* (J. de C. Sowerby); USNM 519955 from USGS locality 21425; × 0.8

similarly convex antero-ventral margin, and thence into the narrowly rounded ventral margin. The posterior margin is short and rounded.

The valves are covered by regular, raised, slightly asymmetrical growth lines and superimposed rugae, which start to occur regularly at some distance from the beak. The rugae are rounded in cross section and disappear toward the anterior margin.

REMARKS: It is a very characteristic species of the Santonian inoceramid fauna of the Euramerican biogeographic region. It closely resembles the Canadian species *Inoceramus pontoni*, described by McLearn (1926, p. 121, pl. 20, figs 1-2; see also Collom 2001, pl. 12, figs 1-2) from the Bad Heart Formation at Smoky River, Alberta. McLearn's holotype agrees in valve outline, ornament, and in the possession of the posterior radial sulcus. According to Mclearn (1926, p. 121), his species is highly variable, so although the type looks much the same as representatives of the Russian species, more material of the Canadian species is needed before formal proposal of the synonymy of these two species may be made.

OCCURRENCE: The specimens studied are from the Middle Santonian; the species is known from the Santonian of the Caucaus, from the Upper Santonian of the Crimea, Lower Santonian of the Tuarkyr (Turkmenistan), and from the Middle Santonian of northern Germany.

Genus *Sphenoceramus* J. Böhm, 1915

TYPE SPECIES: *Inoceramus cardissoides* Goldfuss.

GENERIC CHARACTERS: The genus comprises weakly to moderately inflated, medium to large-sized, equivalve and inequilateral representatives of the family Inoceramidae. The forms are wedge-shaped in outline, distinctly oblique, and usually possess a large posterior auricle that is clearly separated from the disc. The disc commonly possesses a more or less well developed radial sulcus. The umbo is usually pointed, extending distinctly above the hinge line. The ornament, clearly distinct between the disc and the posterior auricle, is composed mainly of concentric rugae, but in some species the radial elements predominate. Oblique divergent plications occur in some species.

REMARKS: One of the main feature of forms referred herein to the genus *Sphenoceramus* is its twofold character in respect of the valve outline (Seitz 1965, but also Schlüter 1877, Böhm 1915): throughout the entire stratigraphical range every species is composed of two parallel morphotypes: the slender one, with the anterior margin relatively long in relation to the length of the growth axis, and the broad one, with the anterior margin markedly shorter in relation to the length of the respective growth axis. These two groups are as follows (after Seitz 1965): (i) *Sphenoceramus cardissoides – S. martini – S. lundbreckensis* (= *S. angustus*); and (ii) *Sphenoceramus pachti – S. pinniformis – S. cancellatus* (= *S. patootensiformis*). Whether these groups represent two distinct lineages, a dimorphic pair of a single species, or just a single linage with wide morphological variability, is still to be resolved. The last possibility – at least in part – was recently suggested by Khomentovskij (1991). This author, based on a rich sample of Early Santonian sphenoceramids (referred by him to *Sphenoceramus cardissoides*) from the Kustanay County, SW part of Western Siberia, Russia, stated that, based on the ratio between the length of the anterior margin and the length of the growth axis, it was impossible to separate two populations that would be referred to *S. cardissoides* and *S. pachti*, according to standard recent taxonomy. Consequently, he synonymised *S. pachti* (broad morphotype) with *S. cardissoides* (narrow morphotype). Unfortunately, this statement is not clear from his data, which suggest rather the existence of two subgroups; moreover, his suggestion is based on a single sample, representing apparently a tempestitic accumulation, and thus a sample with clear *post mortem* sorting.

Our material does not help greatly in resolution of this question, and, consequently, we applied the standard taxonomic treatment as worked out by Seitz (1965) in his monographic description of sphenoceramids. The points on which we differ are few, and are as follows: (i) sphenoceramids are referred herein to a separate genus *Sphenoceramus* instead of to a subgenus; (ii) *Sphenoceramus patootensiformis* (Seitz, 1965) is regarded as conspecific with *Sphenoceramus cancellatus* (Goldfuss, 1835) and, consequently, is put into the synonymy of the latter; (iii) and finally *Sphenoceramus angustus* (Beyenburg, 1936) is regarded as a synonym of *Sphenoceramus lundbreckensis* (McLearn, 1929). Forms morphologically close to *Sphenoceramus lin-*

gua are left in open nomenclature and referred to *S*. cf. *lingua*; as indicated by SEITZ (1965), GOLDFUSS' name was applied to a juvenile fragment and it cannot be applied to any other specimen but the type specimen. The details of particular points are discussed under the description of the respective taxa.

OCCURRENCE: The genus appeared – as far as we know – in the Late Coniacian (HEINE 1929 – see SEITZ 1962, TRÖGER & CHRISTENSEN 1991, and this paper), and in the Euramerican biogeographical region it ranged up to the mid-Early Campanian. It is a Boreal species, although single occurrences from the Mediterranean area are reported (e.g. TRÖGER & SUMMESBERGER 1994). In the North Pacific region the genus is interpreted to range as late as the Maastrichtian, comprising a series of forms in the Middle Campanian (e.g. MATSUMOTO & *al*. 1982; TOSHIMITSU 1988, NODA 1988) and ending with the species *Sphenoceramus hetonaianus* (MATSUMOTO) being its youngest Early Maastrichtian representative (MATSUMOTO & *al*. 1993). This view, however, is not commonly shared, and Campanian and Maastrichtian *Sphenoceramus*-like forms from that area are referred to other genera (e.g. ZONOVA, 1992, 1993). This sceptic view is supported by recent study of the Santonian inoceramids of the South African Province, and suggests that at least most of the Campanian and early Maastrichtian North Pacific sphenoceramids may indeed represent members or descendants of the genus *Rhyssomytiloides* HESSEL, 1988 (see KENNEDY & *al*. submitted). *Sphenoceramus* is unknown from the Southern Hemisphere. Reports of this genus by HEINZ (1929) or KAUFFMAN (in KENNEDY & *al*. 1973) from South Africa are based on misidentifications, and the specimens illustrated represent various *Cordiceramus* species (see discussion in KENNEDY & *al*. submitted).

Sphenoceramus canaliculatus (HEINE, 1929)
(Text-fig. 22.1)

1929. *Inoceramus canaliculatus* HEINE, p. 80, pl. 12, fig. 53.

TYPE: The holotype, by monotypy, is the original of HEINE (1929, pl. 12, fig. 53) from the Upper Coniacian of the Preussen II mine shaft in Westphalia, Germany (SEITZ 1962, fig. 6).

MATERIAL: Single specimen USNM 519862 from the USGS locality D940.

DESCRIPTION: The species is represented by a single RV of moderate size, with the posterior auricle missing. The valve is moderately and regularly inflated. The disc is subrectangular in outline, height-elongated, markedly higher than long. The anterior margin is long, broadly convex, passing into the regularly rounded ventral margin. The posterior margin is not preserved. What is seen is the posterior part of the disc, which is long and almost straight. The beak and umbo are not well seen, and neither is the hinge line. Posterior to the growth axis is the radial sulcus, which is sharp, narrow, and relatively deep.

The ornament is composed of concentric and radial elements, with the former dominating the latter. The concentric rugae, although irregularly developed in the specimen studied, are clearly twofold, with the smaller, more regularly spaced rugae, and superimposed, low, widely spaced undulations. The radial elements are generally weak, and in the part preserved, always subordinate to the concentric rugae. They are strongest when passing through the interspaces between the strongest concentric rugae. They seem to be limited to the part of the disc anterior to the radial sulcus.

Only small fragments of the shell are preserved in the postero-ventral and dorsal parts of the valve.

REMARKS: The sharp, deep radial sulcus and the type of the ornament correspond well to the type of the species (HEINE 1929, pl. 12, fig. 53) from the Upper Coniacian of Germany (SEITZ 1962, p. 370). HEINE's specimen possesses stronger radial ornament, but it is larger than the specimen studied herein, and the radial elements tend to become stronger ventralward.

OCCURRENCE: The specimen studied here is the second report of this species besides the German type. Both come from the Upper Coniacian.

Sphenoceramus sp. A.
(Text-fig. 11.2)

pars 2001. *Euryceramus cardissoides* (GOLDFUSS); COLLOM, p. 489, pl. 13, figs ?5, 6 [non pl. 14, figs 1-3 = ?*Sphenoceramus subcardissoides*]

MATERIAL: Single specimen, USNM 519869 from USGS locality D934.

DESCRIPTION: It is a quite well preserved LV composed of a moderately inflated triangular disc and a large posterior auricle, extended postero-dorsally. The posterior margin of the disc is not distinct, with the transition between the disc and the auricle in the form of a moderate bend. The ligamental plate is not preserved. The hinge line is long and straight. The anterior margin is straight, with a low anterior face, and passes into the rounded ventral margin, and thence into the postero-ventral margin, which is characterised by a step at the transition from the disc to the posterior auricle. The radial sulcus, located posterior to the growth axis, is weak and shallow.

The disc is ornamented with regularly spaced rugae with interspaces increasing gradually ventralward. In the juvenile part, raised growth lines are superimposed on the the rugae; these growth lines seem to be the only ornament element in the most juvenile part. In the adult stage the interspaces bear irregularly-spaced ribs. The radial ornament first appears at ca. 40 mm axial length, and is composed of discontinuous radial ribs, which are stronger only at the edges of the concentric rugae. The radial ribs are limited to the axial part of the disc (at least at the preserved length). The concentric rugae become weaker and less regular when passing onto the posterior auricle but they are already weaker when crossing the posterior sulcus. At the junction between the disc and the posterior auricle the rugae form a distinct sulcus and then are curved outwardly – with a sickle-shape pattern – before reaching the hinge line.

REMARKS: The specimen studied differs from other *Sphenoceramus* species first of all in the lack of a distinct posterior margin to the disc and in the sharp change in the ornament. These features are well seen e.g. on the two specimens from the same locality representing *Sphenoceramus canaliculatus* (Text-fig. 22.1) and *S. latisulcatus* (Text-fig. 13.3). Our specimen is very similar to the Canadian specimen from Alberta illustrated recently by COLLOM (2001, pl. 13, fig. 6 and possibly fig. 5; his specimens from pl. 14 have strong radial ornament both anterior and posterior to the radial sulcus and closely resemble SCHLÜTER's species *S. subcardissoides*).

OCCURRENCE: Upper Coniacian of the North American Western Interior.

Sphenoceramus cf. *latisulcatus* (HEINE, 1929)
(Text-fig. 13.3)

Compare:

1929. *Inoceramus latisulcatus* HEINE, p. 82, pl. 13, figs 59-60.

TYPE: The lectotype, here designated, is the original of HEINE (1929, pl. 13, fig. 60) from the Preussen 2 mineshaft, depth 64 m, northern Germany; Upper Coniacian (see SEITZ 1962, p. 370).

MATERIAL: USNM 519897, a single fragmentary specimen from USGS locality D 940.

DESCRIPTION AND REMARKS: The specimen is represented by a fragment of the posterior part of the adult disc; the posterior auricle is not preserved. Despite very fragmentary preservation, the specimen clearly shows the character of the posterior radial sulcus and of the adult ornament. The radial sulcus is wide, shallow, and separates a rather narrow part of the disc lying posterior to the radial sulcus from the remainder of the disc. The ornament is composed of two distinct types of rugae, with one or two smaller rugae between the main rugae. The main rugae are asymmetrical, with their ventral sides much steeper than the dorsal ones. The minor rugae are sharp-edged and slightly asymmetrical.

OCCURRENCE: The species is known from two reports; the original report from the Upper Coniacian of northern Germany and the specimen described here from the Upper Coniacian of Montana.

Sphenoceramus gilli sp. nov.
(Text-fig. 49.1-49.5)

TYPES: The holotype is USNM 519942; USNM 519943, USNM 519944, USNM 519945, and USNM 519946 are paratypes; all from the Upper Santonian Virgette Sandstone, Montana, USGS Mesozoic locality D3629.

MATERIAL: 5 moderately well preserved internal moulds mostly double-valved.

DERIVATION OF NAME: In honour of the late James Rogers GILL, who collected the types and who added much to our knowledge of Western Interior Cretaceous stratigraphy.

DIAGNOSIS: Strongly oblique and moderately-sized *Sphenoceramus* species, with distinct radial sulcus posterior to growth axis and with ornament composed of lamellate growth axis in juvenile and of rugae with superimposed lamellate growth lines in adult.

DESCRIPTION: The species is of small to moderate size, inequilateral, sub- to equivalve. The valves are subtriangular in outline, distinctly elongated parallel to the strongly oblique growth axis, with moderate or weak inflation. The growth axis is curved broadly toward the anterior margin. Usually the valves have a distinct radial sulcus, posterior to the growth axis. The beak is small, prosocline, pointed, curved anteriorly; it projects slightly above the hingeline. The posterior auricle is subtriangular and elongated parallel to the hingeline. It is usually poorly preserved. The anterior margin is broadly convex, moderately long, passing into the rounded ventral margin and thence into the rather short, straight posterior margin. The hingeline is long, apparently straight, although we have no specimen with the ligament preserved.

The juvenile ornament is composed of regularly spaced, lamellate growth lines, which increase ventralward. In the adult stage the ornament is dominated by regular, round-edged rugae, with superimposed growth lines. Toward the ventral margin the

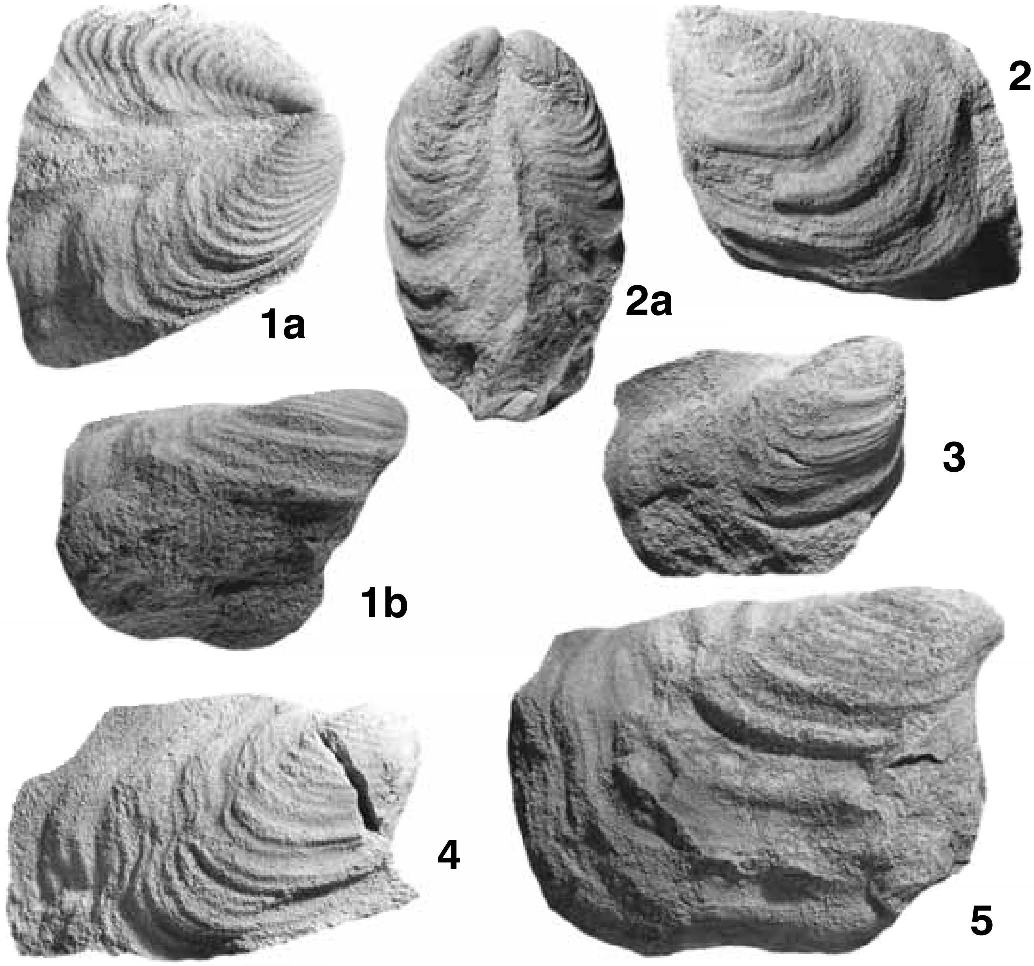

Fig. 49. *Sphenoceramus gilli* sp. nov.; 1 – USNM 519942, 2 – USNM 519943, 3 – USNM 519944, 4 – USNM 519945, and 5 – USNM 519946; all from USGS D3629; all specimens are × 0.8

adult growth lines become gradually less distinct. Both concentric elements pass the radial sulcus with only slight weakening.

REMARKS: In general outline the species resembles Early/Middle Santonian *Cordiceramus lesginensis* (PAVLOVA), from which it differs in much stronger ornament and a stronger radial sulcus. Moreover, the rugae and ribs in *S. gilli* are lamellate in character, whereas they are symmetric in *Cordiceramus lesginensis*.

S. gilli is most similar to North Pacific forms, reported from Sakhalin by PERGAMENT (1974, pl. 2, figs 2-3), and referred by him to *Inoceramus patootensis* aff. *angustus*. A very similar morphotype is also represented by forms referred by that author to the *Inoceramus transpacificus* group (PERGAMENT 1974, pl. 2, fig. 4; pls 3-8; pl. 9, figs 1-2, 6-9), as well as some of the forms referred earlier by him to the *I. lingua* group (e.g. PERGAMENT 1965, pl. 10, fig. 2, 7).

OCCURRENCE: All specimens studied are from the topmost Santonian (*Desmoceras bassleri* ammonite Zone) of the Virgette Sandstone, northwestern Montana.

Sphenoceramus ex gr. *cardissoides* (GOLDFUSS, 1836)
(Text-figs 48.3-48.6)

1965. *Inoceramus cardissoides* subsp. indet.; SEITZ, p. 47, pl. 4, figs 1-4.

MATERIAL: Four specimens; USNM 519952 from the Upper Santonian of USGS locality 8605 (Montana), USNM 519951 and USNM 519949 from the Lower Santonian of USGS locality 11621 (Alberta), and USNM 519950 from the Middle Santonian of USGS locality 21425 (Montana).

DESCRIPTION: USNM 519952 (Text-fig. 48.6) is a well preserved LV, 62 mm in h. It is strongly elongated parallel to valve height and possesses a regularly triangular outline. The specimen possesses a pointed umbo, curved antero-dorsally; a broadly concave anterior margin, a regularly rounded ventral margin and again an almost straight posterior margin. The hinge line is poorly preserved but apparently straight and relatively long. Posterior to the growth axis there is a strong, continuous radial sulcus; the posterior margin of the disc passes into the posterior auricle along a distinct step. The ornament is composed of commarginal rugae, with interspaces growing rapidly ventralward. Radial elements are unrecognisable.

USNM 519951 (Text-fig. 48.5) is an internal mould of a RV; the specimen is slightly deformed, being compressed obliquely toward the posterior margin. The posterior radial sulcus is much weaker than in USNM 519952. The ornament is composed of concentric rugae, characterised by sharp edges and relatively large interspaces.

USNM 519949 (Text-fig. 48.3) is a fragment of the disc of a LV, with the umbonal and ventral parts missing. The relatively narrow part of the disc anterior of the growth lines suggests a relatively long anterior margin, as is characteristic of *S. cardissoides*.

USNM 519950 (Text-fig. 48.4) is a juvenile fragment of a LV, preserved as an internal mould. The specimen is much less oblique than the two other specimens. The ornament is composed of rugae and superimposed, raised growth lines.

REMARKS: All three specimens studied, and particularly USNM 519952, have the typical general outline, shape, and the concentric ornament of *Sphenoceramus cardissoides*. From the typical specimens (see e.g. GOLDFUSS 1835, pl. 110, fig. 2; SEITZ 1965, pl. 1, figs 1-6), they differ only in the lack of the radial ornament, and closely resemble forms referred by SEITZ (1965, p. 47) to *Inoceramus cardissoides* subsp. indet. SEITZ did not name this variety, suggesting that it might comprise only the juvenile stage, not the radially ornamented stage. This cannot be excluded. However, based on the presence of moderately large representatives of *S. pachti* that are devoid of radial ornament, the presence of a *Sphenoceramus cardissoides* variety with exclusively concentric ornament seems probable.

OCCURRENCE: The American specimens comes from the Lower, Middle and Upper Santonian; In Germany this non-radially ornamented variety was reported from the Lower and Middle Santonian.

Sphenoceramus ex gr. *pachti* (ARKHANGELSKY 1912)
(Text-figs 48.7, 48.10, 48.11)

?pars 1965. *Inoceramus pachti* subsp. indet.; SEITZ, p. 62, pl. 9, figs ?1, 3-4.

MATERIAL: Three specimens; all represented by single valves; USNM 519953 from the Lower Santonian of USGS locality 11621 (Alberta); USNM 519956 and USNM 519957 from USGS locality D6075.

DESCRIPTION: USNM 519957 (Text-fig. 48.11) is the best preserved specimen; it is represented by the disc only, the posterior auricle is missing. It is a RV with the postero-dorsal and postero-ventral parts missing, and with the anterior part moderately well exposed. The valve is subquadrate, clearly oblique, 75 mm h long. The anterior margin is moderately long, passing into the broadly convex antero-ventral margin; the postero-ventral margin is not preserved but apparently regularly convex. The umbo is small, pointed, curved antero-dorsally. A characteristic element of the disc is the presence of a distinct, deep, radial sulcus, located posterior to the growth axis. The posterior margin of the disc is distinct. The valve is ornamented with regularly-spaced concentric rugae, with the interspaces increasing regularly ventralward. Moderately raised growth lines are superimposed on the rugae.

USNM 519956 (Text-fig. 48.10) is another specimen from the same locality as USNM 519957 and very similar to it. The specimen, represented by a disc of a LV, is incomplete, with the antero-dorsal and ventral parts missing. The ornament corresponds to that of the other specimens.

USNM 519953 (Text-fig. 48.7) is a disc of a moderately large LV, with hmax = 78 mm. It shows well the anterior margin and anterior face, which is moderately steep; the valve is most probably slightly deformed so the actual steepness of the anterior face was slightly higher than observed. The ornament is the same as in two other specimens.

REMARKS: The specimens studied correspond well to the German specimens referred to *S. pachti* subsp. indet by SEITZ (1965, pl. 9, figs ?1, 3-4), which are characterised by the absence of radial ornament [SEITZ' specimen from his pl. 9, fig. 1 is probably a poorly preserved specimen of the radially ribbed variety]. SEITZ (1965) regarded the possibility that this variety represented juvenile fragments of otherwise typical (i.e. radially ornamented) *Sphenoceramus pachti* and left the morphotype in open nomenclature.

The juvenile parts of *S. pachti* described herein are morphologically very close to the type of *I. pontoni* MCLEARN (1926, pl. 20, fig. 1).

OCCURRENCE: USNM 519953 is from the Lower Santonian of Alberta, Canada. The German specimens are from the Lower and Middle Santonian.

Sphenoceramus lundbreckensis (MCLEARN, 1929)
(Text-figs 50, 51, 52, 53.6, 53.7)

pars 1877. *Inoceramus lobatus* MÜNSTER; SCHLÜTER, p. 275, pl. 39, fig. 2 [non pl. 39, fig. 1 = *Sphenoceramus cancellatus* (GOLDFUSS)]

pars 1929. *Inoceramus lundbreckensis* MCLEARN, p. 77, pl. 15, fig. 4 [non pl. 16, fig. 2 = *Sphenoceramus cancellatus* (GOLDFUSS)]

?1929. *Inoceramus* cf. *lundbreckensis* MCLEARN, p. 78, pl. 17, fig. 1.

1936. *Inoceramus patootensis* DE LORIOL var. n. *angusta* BEYENBURG, p. 110, pl. 25, fig. 4.

1955. *Inoceramus lobatus* GOLDFUSS; COBBAN, p. 207, pl. 4 [illustrated herein in Text-fig. 46]

?1958. *Inoceramus patootensis* LOR. var. *sibirica* DOBR.; BODYLEVSKI, pl. 41, fig. 1.

?1958. *Inoceramus patootensis* LORIOL var. *tanamaensis* nov.; BODYLEVSKI, p. 83, pl. 39, fig. 1.

?1958. *Inoceramus patootensis* LOR. aff. var. *angusta* BEYENB.; BODYLEVSKI, p. 84, pl. 40, fig. 2.

?1958. *Inoceramus alexandrovi* BODYL.; BODYLEVSKI, p. 81, pl. 35, fig. 1.

pars 1960. *Inoceramus* (*Sphenoceramus*) *patootensis* DE LORIOL; JONES & GRYC, p. 161, pl. 22, figs 2-3; ?pl. 23, fig. 3 [non pl. 22, fig. 1 = *Sphenoceramus cancellatus*; non pl. 21, fig. 5 = *Sphenoceramus* sp.]

1965. *Inoceramus* (*Sphenoceramus*) *angustus* BEYENBURG; SEITZ, p. 96, pl. 17, fig. 2; pl. 18, figs 1-2; pl. 19, fig. 1; ?pl. 20, fig. 4; pl. 22, figs 1, 3; pl. 24, fig. 3.

1962. *Inoceramus* (*Sphenoceramus*) m.f. *lingua/cancellatus* GOLDF.; SEITZ, p. 95, pl. 19, fig. 2.

non 1974. *Inoceramus patootensis* aff. *angustus* (BEYENBURG); PERGAMENT, p. 70, pl. 2, figs 2-3.

pars 1986. *Inoceramus* (*Sphenoceramus*) *lundbreckensis* MCLEARN; COBBAN & *al*., fig. 15b [non fig. 14c-d = *Sphenoceramus cancellatus* (GOLDFUSS)]

non 1997. *Inoceramus* (*Sphenoceramus*) *lundbreckensis* MCLEARN; LECKIE & *al*., fig. 43A, D, F [= *Sphenoceramus cancellatus* (GOLDFUSS)]

TYPE: The holotype, by original designation, is NMC 9037, the original of McLearn (1929, pl. 15, fig. 4), from the latest Santonian/earliest Campanian of the topmost part of the Colorado Shale on the north bank of Crowsnest River, 2 miles west of Lundbreck, Blairmore region, Alberta, Canada.

MATERIAL: Plaster cast of the holotype; USNM 128885 from USGS locality 24596; USNM 519983 from USGS locality D690; USNM 519984 from USGS locality D690, and USNM 519995 from USGS locality 9625.

DESCRIPTION: The species is medium-sized to large, triangular in outline, strongly elongated along the growth line. The anterior margin is long, broadly convex to straight, passing into the rounded ventral margin. The posterior margin is straight.

Fig. 50. *Sphenoceramus lundbreckensis* (McLearn, 1929), holotype, NMC 9037, original to McLearn (1929, pl. 15, fig. 4), latest Santonian/earliest Campanian of the topmost part of the Colorado Group on the north bank of Crowsnest River, 2 miles west of Lundbreck, Blairmore region, Alberta, Canada; × 1

The umbo is small, pointed, not projecting above the hinge line. The disc is moderately inflated, mostly in the axial region. Posterior to the growth axis there is a distinct, radial sulcus that broadens gradually. The posterior margin of the disc is straight and long. The posterior auricle is triangular and distinctly separated from the disc.

The disc is covered with two systems of rugae; the main one is composed of widely-spaced rugae, with the interspaces increasing ventralward, up to some centimetres. Superimposed on the main rugae is a second system, comprising distinctly smaller, closely-spaced rugae, with up to 6-7 within a single main ruga. In the adult stage, the main rugae cut the secondary rugae obliquely in the axial part of the disc, and are distinctly raised at the posterior margin, sometimes forming a line of tuberculation.

Fig. 51. *Sphenoceramus lundbreckensis* (McLearn, 1929), USNM 128885 from USGS locality 24596, Telegraph Creek Formation of the Bearpaw Mountains of north-central Montana; *Desmoscaphites erdmanni* ammonite Zone [original of Cobban 1955, pl. 4]; × 0.8

REMARKS: *Sphenoceramus lundbreckensis* is the oldest name available for forms referred hitherto to *Sphenoceramus angustus* (BEYENBURG) as diagnosed by SEITZ (1965). Seitz (1965) listed MCLEARN's Canadian specimens among the incompletely preserved specimens that were unsuitable for specific determination. This is however, not the case. The holotype (MCLEARN 1929, pl. 15, fig. 4; illustrated herein in Text-fig. 50) is quite nicely preserved, with its anterior part, although deformed to some extent, maintaining the original outline well. It is also complete in the umbonal part and shows well the details of the ornament. What is missing is the greater part of the posterior auricle, only the most internal part

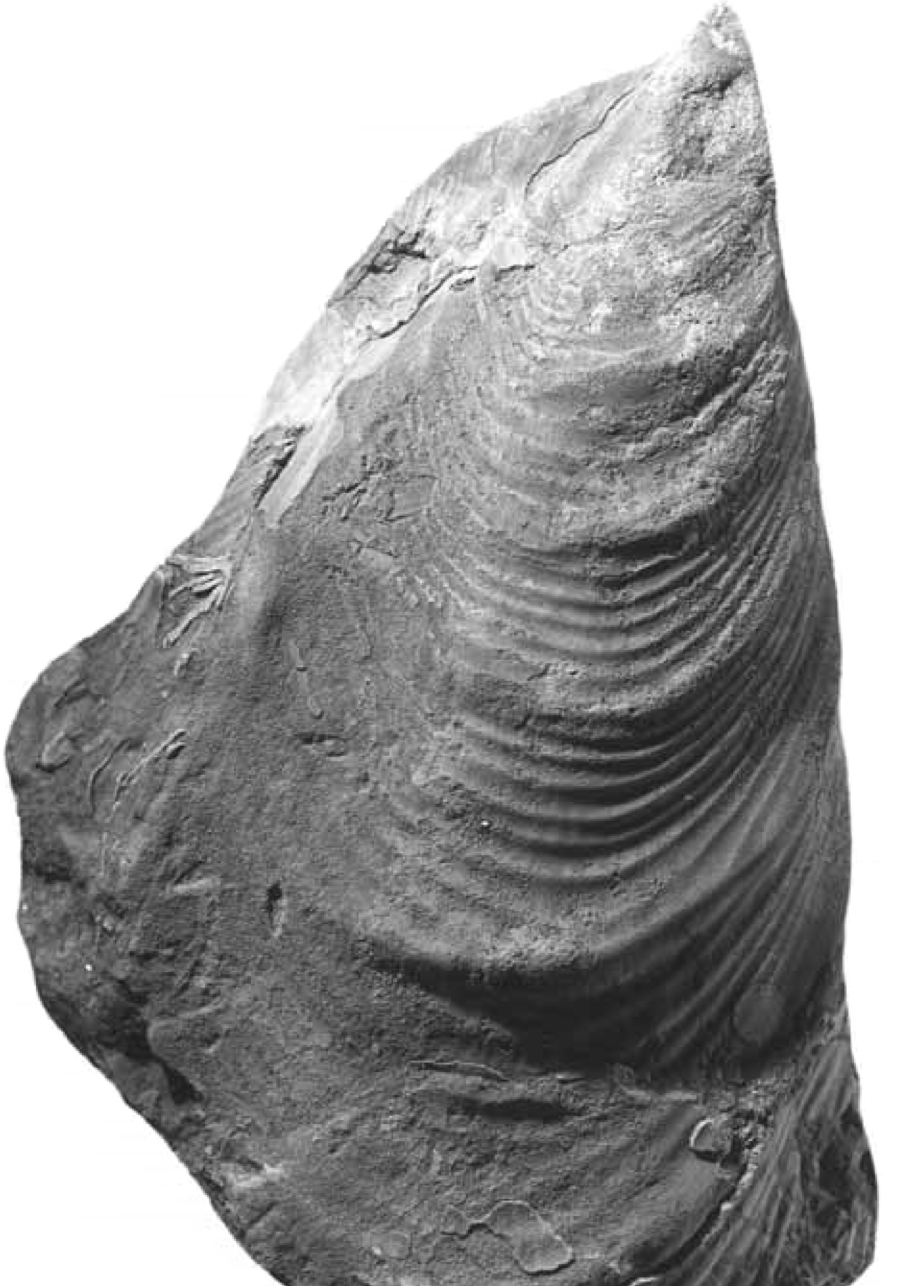

Fig. 52. *Sphenoceramus lundbreckensis* (MCLEARN, 1929), USNM 519995 from USGS locality 9625; × 0.8

being preserved. Much less complete, and possibly belonging to another species, are two other Canadian specimens: a large fragment of a RV (McLearn 1929, pl. 16, fig. 2) most probably represents a fragment of *S. cancellatus*; and the third specimen (McLearn 1929, pl. 17), represented by a relatively large LV, completely lacks the anterior margin, and may either be another specimen of *S. lundbreckensis* or represents *S. cancellatus*.

OCCURRENCE: Upper Santonian and lower Lower Campanian of the Euramerican biogeographical region.

Sphenoceramus cancellatus (Goldfuss, 1835)
(Text-fig. 53.5)

1835. *Inoceramus cancellatus* nobis, Goldfuss, p. 113, pl. 110, fig. 4.
1965. *Inoceramus* (*Sphenoceramus*) *patootensiformis* n.sp., Seitz, p. 107, pl. 02, figs 1-2; pl. 21, fig. 2; pl. 22, fig. 2; pl. 23, figs 2-3; pl. 24, figs 1-2, 4; pl. 25, fig. 2 [and the literature cited therein]

TYPE: The holotype, by monotypy, is the original of Goldfuss (1835, pl. 110, fig. 4), from the Lower Campanian Dülmen-Schichten of Dülmen, Germany.

MATERIAL: One specimen: USNM 519982 from USGS locality 21419.

DESCRIPTION AND REMARKS: The specimen is an incomplete single valve, with its postero-ventral part missing. Its general outline and the type of ornament agree well with the characteristics of *S. cancellatus*.

S. cancellatus is used here as a senior synonym of *S. patootensiformis* (Seitz, 1965), the species to which such forms were commonly referred. Inspection of the type of *S. cancellatus* shows that the Goldfuss original is quite distinctly deformed, with its disc compressed from the anterior toward the posterior. This compression results in its apparent inflation. It is also possible that the anterior radial sulcus observed in the type results from, or at least was markedly strengthened by, this deformation. When restored to its original shape, the outline and inflation of the type agree well with those of typical forms referred commonly to *S. patootensiformis*. Both species also agree completely in the type of ornament; although the concentric rugae in Goldfuss' type are finer than in the type of *S. patootensiformis*, it is still within the range of its variability.

OCCURRENCE: *Sphenoceramus cancellatus* is known from the Euramerican biogeographic region; in Europe it occurs in the upper Upper Santonian and lower Lower Campanian; it appears earlier in the US Western Interior, where it is noted already at the base of the Upper Santonian.

Sphenoceramus cf. *lingua* (Goldfuss, 1836)
(Text-figs 53.1, 53.2, 53.3, 53.4, 54.1, 54.3, 54.5, 54.6, 54.7, 54.8, 54.9)

MATERIAL: USNM 519978 and USNM 519981 from USGS locality 21406; USNM 519979 from USGS locality 21419 (*D. erdmanni* ammonite Zone); USNM 519980 from USGS locality D5636; USNM 519986 from USGS locality 23113 (*S. hippocrepis* ammonite Zone); USNM 519990 and USNM 519992 from USGS locality D666 (*D. bassleri* ammonite Zone); USNM 519991 from USGS locality D694 (*D. erdmanni* ammonite Zone); USNM 519988 from USGS locality 8048; USNM 519993 from USGS locality 23689; USNM 519985 and 519994 from USGS locality 21568.

DESCRIPTION AND REMARKS: We refer here to all forms corresponding to various taxa (or units) compared or referred to *Sphenoceramus lingua*. As pointed out by Seitz (1965), the name *S. lingua* can only be applied to the type specimen; no other specimen can correctly be compared to this juvenile fragment. Commonly, these *lingua*-like forms are either compared in open nomenclature to Goldfuss' species (e.g. Seitz 1965), or separated as distinct varieties or, more formally, subspecies (Beyenburg 1936, Pergament 1965). Our material does not give a chance to clarify the taxonomy of what is referred to here as the *lingua* group, and consequently, no such attempt was undertaken. However, it is important to note the occurrence in the study area of most of the morphological varieties of this group known from Europe or Greenland.

The particular morphotypes differ in respect of valve outline and/or ornament. As far as valve outline is concerned, both the narrow and the broad morphotypes are represented. The specimens

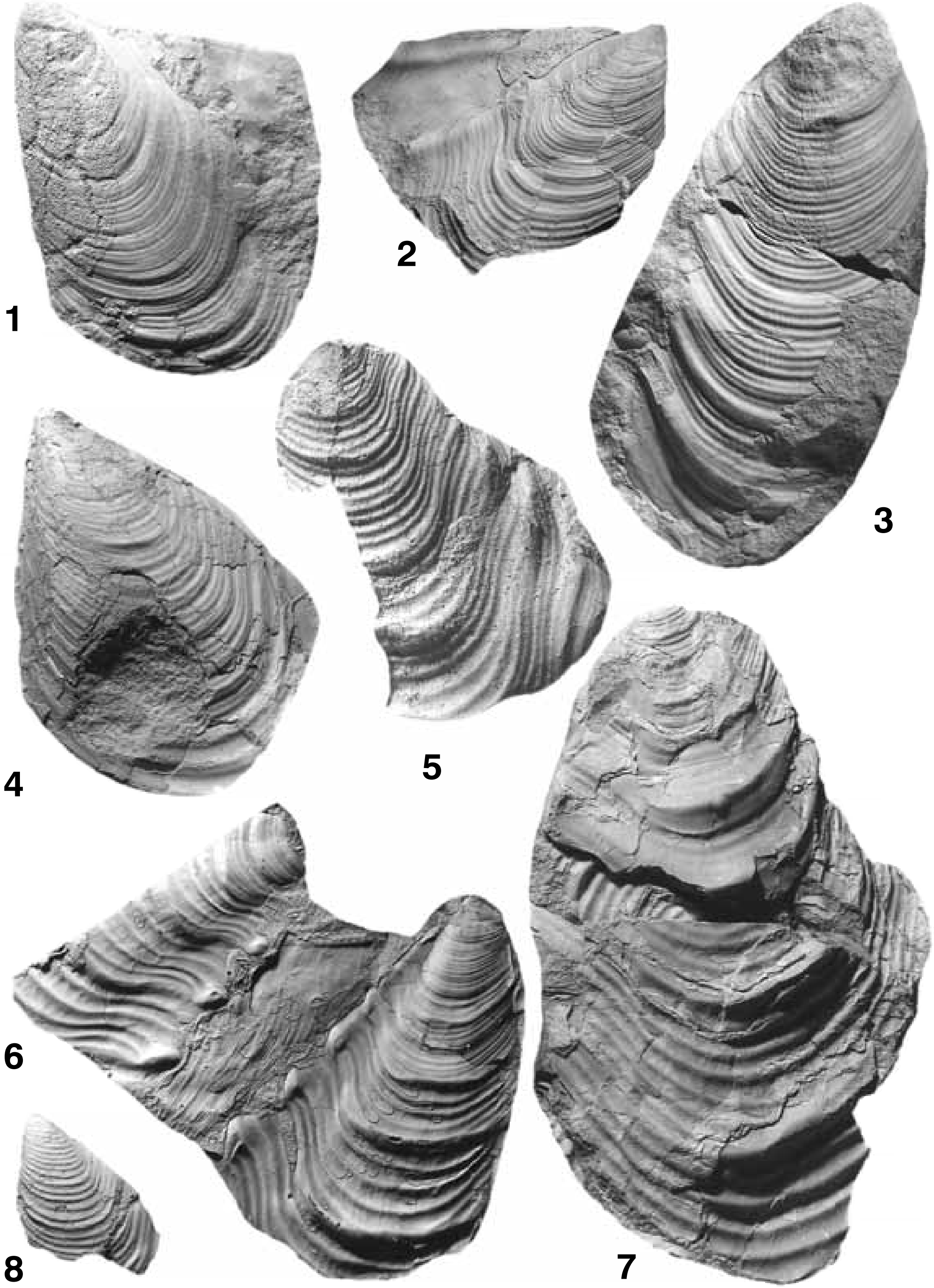

Fig. 53. **1-4, 8** – *Sphenoceramus* cf. *lingua* (GOLDFUSS, 1835); 1 – USNM 519978 from USGS locality 21406; 2 – USNM 519979 from USGS locality 21419; 3 – USNM 519980 from USGS locality D5636; 4 – USNM 519981 from USGS locality 21406; 8 – USNM 519985 from USGS locality 21568. **5** – *Sphenoceramus cancellatus* (GOLDFUSS, 1835); 5 – USNM 519982 from USGS locality 21419. **6-7** – *Sphenoceramus lundbreckensis* (MCLEARN, 1929), 6 – USNM 519983 from USGS locality D690; 7 – USNM 519984 from USGS locality D690. All specimens are × 0.85

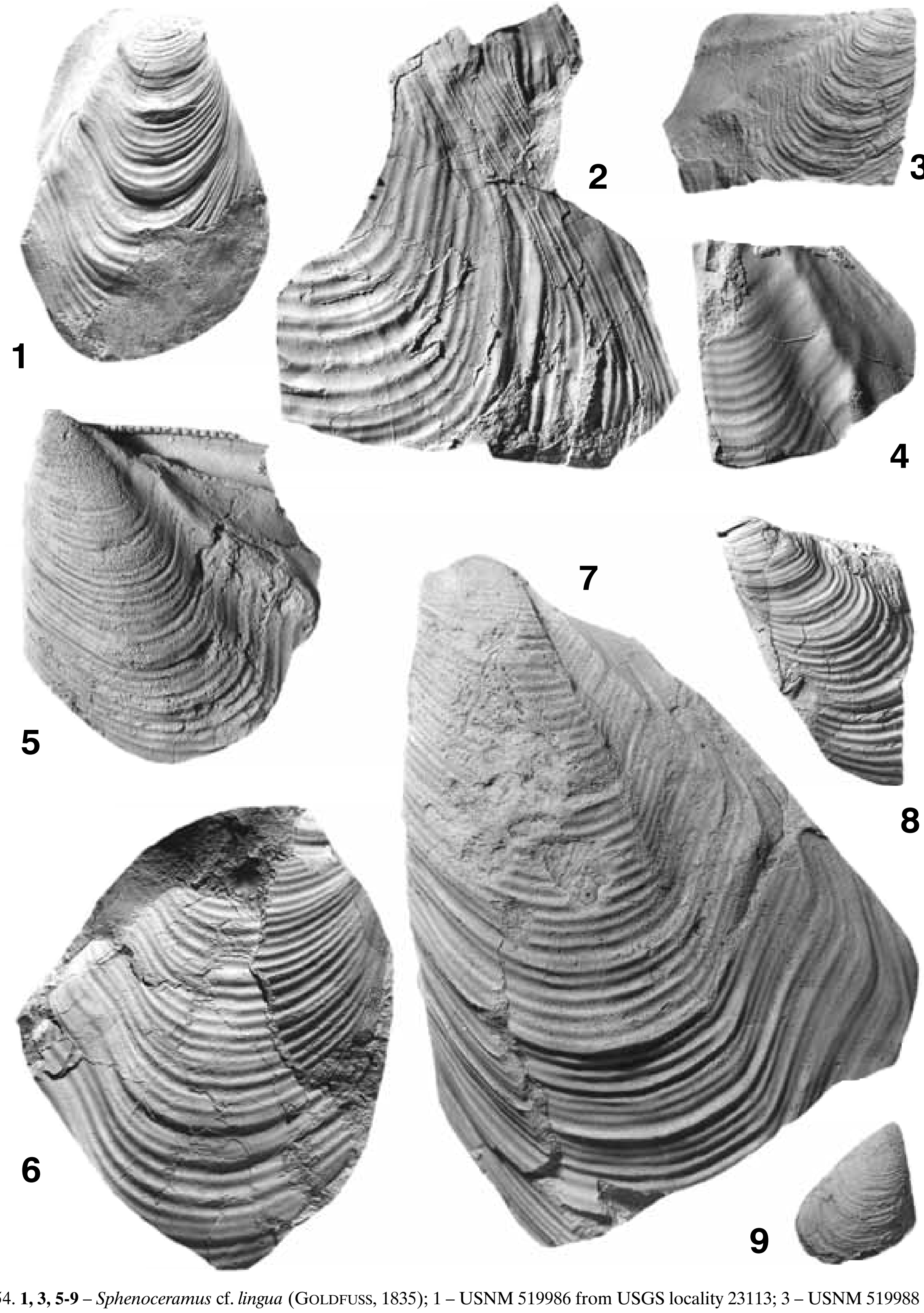

Fig. 54. **1, 3, 5-9** – *Sphenoceramus* cf. *lingua* (GOLDFUSS, 1835); 1 – USNM 519986 from USGS locality 23113; 3 – USNM 519988 from USGS locality 8048; 5 – USNM 519990 from USGS locality D666; 6 – USNM 519993 from USGS locality D694; 7 – USNM 519992 from USGS locality D666; 8 – USNM 519991 from USGS locality 23689; 9 – USNM 519994 from USGS locality 21568. **2** – *Sphenoceramus* ex gr. *cancellatus*/*lundbreckensis*, USNM 519987 from USGS locality D5634. **4** – *Sphenoceramus* sp., USNM 519989 from USGS locality D694; × 0.85

studied range from forms with a more or less uniform ornament (Text-fig. 54.5), regarded as typical of *S. lingua*, to forms with twofold concentric ornament, interpreted as transitional morphotypes to *S. lundbreckensis* (Text-figs 54.7, 54.8) or *S. cancellatus* (Text-figs 54.2, 54.6).

BEYENBURG (1936) referred forms with ornament transitional between those of *S. lingua* and *S. lunbreckensis*/*cancellatus* (=*angustus*/*patootensiformis*) to a separate variety *media*, which he referred to a species *S. patootensis*. BEYENBURG's originals are represented, however, by incomplete

Fig. 55. *Sphenoceramus steenstrupi* DE LORIOL, 1883, NMC 21851, ?Upper Santonian/Lower Campanian of Northwest Territories, Canada [original to JELETZKY, 1970, pl. 27, fig. 8] ; × 0.8

specimens which – particularly in the case of the type of the variety (BEYENBURG 1936, pl. 25, fig. 2) – cannot be referred with confidence either the narrow or the broad form; SEITZ (1965, p. 89) referred them to transitional forms *I.* m.f. *lingua/angustus* and/or *I.* m.f. *lingua/patootensiformis*. A separate taxonomic unit for forms with transitional ornament was also proposed by BODYLEVSKI (1959) and PERGAMENT (1965).

OCCURRENCE: The species occurs in the Upper (uppermost?) Santonian and lowermost Campanian of the Euramerican biogeographical region. The forms referred to this species from the North Pacific Province (LIVEROVSKAYA 1960, PERGAMENT 1965, 1974) are regarded here as representing other species.

Sphenoceramus steenstrupi (DE LORIOL, 1883)
(Text-fig. 55)

1883. *Inoceramus Steenstrupi* DE LORIOL, p. 211.
? 1912. *Inoceramus tuberculatus* sp. nov.; WOODS, p. 302, text-fig. 59, ?pl. 54, fig. 8.
1918. *Inoceramus Steenstrupi* DE LORIOL; RAVN, p. 336, pl. 5, fig. 2.
?1929. *Inoceramus steenstrupi* DE LORIOL; HEINE, p. 9, pl. 10, fig. 46.
non 1930 *Inoceramus Steenstrupi* DE LORIOL; HÄGG, p. 30, pl. 2, fig. 13; pl. 3, figs 2-4
?1931. *Inoceramus steenstrupi* DE LORIOL; RIEDEL, p. 660 [not illustrated]
non 1958. *Inoceramus* aff. *steenstrupi* DE LORIOL; BODYLEVSKI, p. 84, pl. 38, figs 3-4.
non 1960. *Inoceramus* (*Sphenoceramus*) *steenstrupi* DE LORIOL; JONES & GRYC, p. 162, pl. 19, fig. 6; pl. 23, figs 1-2.
non 1965. *Inoceramus* cf. *steenstrupi* DE LORIOL; PERGAMENT,. P. 88, pl. 9, fig. 8
1965. *Inoceramus steenstrupi* DE LORIOL; SEITZ, p. 81, pl. 15, fig. 1 [reillustration of the holotype after RAVN, 1918, pl. 5, fig. 2]
1970. *Inoceramus steenstrupi* DE LORIOL; JELETZKY, pl. 27, fig. 8.

TYPE: The lectotype is the specimen illustrated originally by RAVN (1918, pl. 5, fig. 2) from the topotypic material of DE LORIOL (1883). According to the description of DE LORIOL (1883), at least three other specimens – paralectotypes – were in his original collection. The lectotype is from Patoot b, Greenland, most probably from the Upper Santonian/lowermost Campanian interval.

MATERIAL: Plaster cast of NMC 21851, the original of JELETZKY (1970, pl. 27, fig. 8), from the upper Santonian/lower Campanian of Northwest Territories, Canada.

DESCRIPTION: It is a huge right valve, with incomplete anterior and umbonal parts. The flattened posterior radial sulcus suggests lateral compression of the specimen. The posterior disc margin is well preserved, with a distinct step toward the posterior auricle. The latter is quite well preserved with parts of the shell attached in the middle part.

Up to about 70 mm, the disc is ornamented with quite regularly-spaced first and second order rugae, typical of the *lundbreckensis/cancellatus* group, i.e. with widely-spaced first order rugae, with flat-floor interspaces, on which are superimposed 4 to 7, more closely-spaced second order rugae. The ornament of the rest of the disc is more uniform: the concentric ornament is dominated by second order rugae on which, particularly in the axial part, are superimposed strong radial ribs. More dorsally, only parts of the radial ribs are continuous, with the rest composed rather of rows of tubercles formed at the intersections of the radial and concentric ornament. Ventrally the radial ribs become definitely stronger.

REMARKS: *Inoceramus steenstrupi* is a form similar in general outline to *Sphenoceramus cancellatus* (=*patootensiformis*) but possessing a distinct reticulate ornament. Most of the reports of *S. steenstrupi* are either clearly different forms or specimens that are too incomplete for positive assignment to a species. To *I. steenstrupi* are mostly referred representatives of *S. lunbreckensis* (=*S. angustus*) or *S. cancellatus* with more or less well developed radial ornament, irrespective of its character.

Inoceramus tuberculatus, described from the Lower Campanian of Yorkshire, England by WOODS (1912a, text-fig. 59), is most probably a junior synonym of *S. steenstrupi*. Although WOODS' type specimen is incompletely preserved, it has the general outline and the same type ornament as *S. steenstrupi*.

OCCURRENCE: Most probably *patootensiformis* Zone, dated as Upper Santonian/lowermost Campanian; known from Canada, Greenland, and England; rather rare.

Genus *Cataceramus* HEINZ, 1932

TYPE SPECIES: *Inoceramus balticus* BÖHM, 1907.

Cataceramus gladbeckensis (SEITZ, 1967)
(Text-fig. 46.3)

1967. *Inoceramus* (*Selenoceramus*) *gladbeckensis* n. sp., SEITZ, p. 102, pl. 14, figs 1-4; pl. 15, figs 1-7.

TYPE: The holotype, by original designation, is A 343, illustrated by SEITZ (1967, pl. 14, fig. 1) from the upper Middle Santonian of the Recklinghäuser Sandmergel near Gladbeck, Germany.

MATERIAL: Single specimen, USNM 519966 from USGS locality D3503.

DESCRIPTION AND REMARKS: USNM 519966 is an internal mould of a single LV, of moderate size, typical of the species. The specimen shows well the specific characteristics of *C. gladbeckensis*: posterior elongation of the valve, small umbo not projecting above the hinge line, and fine, closely-spaced concentric ornament. In the adult part the ornament becomes slightly irregular. In the axial part there is a moderately well developed *Holkehle*, which starts some distance from the umbo. The hinge line is only partially preserved.

Based on the general outline and type of ornament, *Inoceramus gladbeckensis* is referred herein to the genus *Cataceramus* HEINZ, 1932, and is believed to represent the earliest representative of that genus. The subgenus *Selenoceramus* SEITZ 1967 (one of HEINZ' 1932 taxa, newly defined), to which *I. gladbeckensis* was originally referred, we regard as a junior synonym of the genus *Cataceramus*. The geniculation and change of growth direction which, according to SEITZ (1967), are diagnostic features of the subgenus *Selenoceramus*, are noted in most species of *Cataceramus*.

OCCURRENCE: The specimen studied is from the Middle Santonian of the Pueblo section; SEITZ (1967) reported the species from the Middle Santonian of Germany.

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