

Hoplitoplacenticeras (H.) *howarthi* Collignon, 1970 (Cephalopoda: Ammonoidea) from KwaZulu-Natal, South Africa and Madagascar; intraspecific variation, dimorphism and affinities

Herbert Christian Klinger

Natural History Collections Department, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa
E-mail: hklinger@iziko.org.za

&

William James Kennedy

Department of Earth Sciences, Oxford University, South Parks Road, Oxford OX1 3AN, U.K.
E-mail: jim.kennedy@oum.ox.ac.uk

(with 15 figures)

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Additional specimens of the Campanian ammonite *Hoplitoplacenticeras* (H.) *howarthi* Collignon, 1970, as well as examination of Collignon's (1970) Madagascan specimens of *Hoplitoplacenticeras* allow us to discuss the intraspecific variation, probable dimorphism and affinities of the species.

Key words: ammonites, *Hoplitoplacenticeras*; Upper Campanian, intraspecific variation, dimorphism, affinities, Madagascar, KwaZulu-Natal, South Africa.

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INTRODUCTION

In September 2007 one of us (H.C.K.) collected several specimens of the Campanian ammonite *Hoplitoplacenticeras* (H.) *howarthi* Collignon, 1970 from the Nibela Peninsula in KwaZulu-Natal, South Africa. These specimens add to the previous description of the species from the same locality by Klinger & Kennedy (1989), subsurface material from Durban (Kennedy & Klinger 1973) and Madagascar (Collignon 1970). This species is extremely variable as far as ornamentation and relative proportions are concerned. We were able to examine the holotype and other representatives of the subgenus from Madagascar and compare these with some of the better-known representatives of the subgenus from other geographic regions. In addition we can recognize the probable nature of dimorphism in *Hoplitoplacenticeras* (H.) *howarthi*.

LOCALITY DATA, REPOSITORIES AND CONVENTIONS

Details of localities in KwaZulu-Natal, South Africa are given in Kennedy & Klinger (1975).

The following abbreviations are used to indicate the repository of specimens:

SAM: Natural History Collections Department, Iziko South African Museum, Cape Town.

GPIB: Institut für Paläontologie der Rheinischen Friedrich-Wilhelms-Universität, Bonn.

GPIG: Geologisch-Paläontologisches Institut und Museum der Georg-August Universität, Göttingen

NMB: National Museum, Bloemfontein (on permanent loan to SAM)

UBGD: UFR Sciences de la Terre, Université de Bourgogne, Dijon (Collignon Collection)

SP: Sorbonne Collections, Paris.

EMP: Ecole National Supérieur des Mines Collections, now housed in the Université de Lyon, Villeurbanne.

OUM: Oxford University Museum of Natural History, Oxford.

Dimensions are given in millimetres; numbers in brackets indicate a percentage of the measured diameter. D = diameter; Wb = whorl breadth, Wh = whorl height, Wb:Wh = ratio of whorl breadth to whorl height; U = umbilical diameter. Ut and Vt refer to the number of umbilical and ventrolateral tubercles respectively. Numbers followed by 'x' indicate tubercles per half whorl.

SYSTEMATIC PALAEONTOLOGY

Order **AMMONOIDEA** Zittel, 1884
 Suborder **AMMONITINA** Hyatt, 1889
 Superfamily **HOPLITOIDEA** Douvillé, 1890
 Family **PLACENTICERATIDAE** Meek, 1876

Genus **Hoplitoplacenticer** Paulcke, 1907
 (ICZN name No. 1348)
 (= *Dechenoceras* Kayser, 1924)

Subgenus **Hoplitoplacenticer** (*Hoplitoplacenticer*)
 Paulcke, 1907.

Type species

Hoplites-Placenticer *plasticus* Paulcke, 1907, p. 186, ICZN Opinion 554, 1959, Name No. 1629).

For an extensive review and discussion of the genus *Hoplitoplacenticer* see Kennedy (1986, p. 63) and description of the European, specifically the German representatives of the genus see Kaplan *et al.* (1996, 2005) and Kennedy & Kaplan (1997). *Hoplitoplacenticer* differs from other genera referred to the family Placenticeratidae Meek, 1876 (see e.g. Kennedy & Wright 1983 and Klinger & Kennedy 1989) mainly by the ontogenetic change in ornament from the phragmocone to the body chamber, especially on the later part of the latter towards the aperture. The ontogenetic changes include weakening of tuberculation and ribbing, leaving ultimately a body chamber covered in dense lirae and striae only or with near-effaced tubercles.

Hoplitoplacenticer* (*Hoplitoplacenticer*) *howarthi
 Collignon, 1970

Figs 1–6

- 1931 *Hoplites Vari* Schlüter; Basse p. 35, pl. 5, figs 1–3; pl. 12, fig. 2; pl. 13, fig. 1.
 1970 *Hoplitoplacenticer* *marroti* Coquand (= *H. vari* Schlüter); Collignon, p. 75, pl. 638, figs 2342–2343.
 1970 *Hoplitoplacenticer* sp. aff. *marroti* Coquand; Collignon, p. 80, pl. 639, fig. 2353.
 1970 *Hoplitoplacenticer* sp. aff. *plasticum-crassum* Paulcke; Collignon, p. 75, pl. 638, fig. 2344; p. 80, pl. 639, fig. 2352.
 1970 *Hoplitoplacenticer* cf. *dolbergense* Schlüter; Collignon, p. 75, pl. 638, fig. 2345.
 1970 *Hoplitoplacenticer* cf. *costulosum* Schlüter; Collignon, p. 76, pl. 638, fig. 2346.
 ?1970 *Hoplitoplacenticer* *trangahyense* Collignon, p. 76, pl. 638, fig. 2347.
 1970 *Hoplitoplacenticer* *antokazoense* Collignon, p. 76, pl. 638, fig. 2348; p. 80, pl. 639, fig. 2354.
 1970 *Hoplitoplacenticer* *besairiei* Collignon, p. 77, pl. 638, figs 2349–2350.
 1970 *Hoplitoplacenticer* *howarthi* Collignon, p. 80, pl. 639, fig. 2351.
 1973 *Hoplitoplacenticer* *plasticum plasticum* Paulcke; Kennedy & Klinger, p. 102, pl. 5, figs 4a–e.
 1989 *Hoplitoplacenticer* *howarthi* Collignon; Klinger & Kennedy, p. 358, figs 14b, 108–109.

Name of the species

As first revising authors we select *howarthi* as the name of the species

Type

Holotype by monotypy is the original of Collignon (1970, p. 80, pl. 639, fig. 2351 UBGD12351 (Fig. 8G–I) housed in the collections of the UFR Sciences de la Terre, Université de Bourgogne, Dijon, from the Upper Campanian of Gisement 227–2, Mokotibe (Antsalova), Madagascar.

Material

SAM-PCZ6586–6587, PCZ7421, 7711, 7719, PCZ18308 (ex NMB-D1314) PCZ18309, PCZ14268, PCZ22138–22145, OUM KX8284–6, all from locality 110, cliff and foreshore sections at the southwestern tip of the Nibela Peninsula, and SAM-PCZ20172, from locality 109F, to the west of the former locality in foreshore exposures; both St Lucia Formation, Campanian III. A single specimen is from excavations at Somtseu Road, Durban in the collections of the Geology Department, University of Natal, Mzamba Formation, Campanian II?

Dimensions

Specimen	D	Wb	Wh	Wb:Wh	U	Ut	Vt
PCZ18309	–	23	28	0.82			
PCZ22138	–	24	28	0.86			
PCZ6587	50	17 (34)	25 (50)	0.68	13 (26)	5 × 2	9 × 2
PCZ20172	64	25 (39.1)	32 (50)	0.78	–	4 × 2	10 × 2
PCZ22139	64	20 (31.3)	23.8 (44.2)	0.84	–	5 × 2	10 × 2
PCZ7719	67	23 (34.2)	32 (47.8)	0.72	11 (16.4)	–	–
PCZ18308	68	–	28.3 (41.6)	–	18 (26)	8	10 × 2
PCZ22141	72	32 (44.4)	34 (47.2)	0.94	–	6 × 2	14 × 2
PCZ22137	80	32 (40)	33 (41.3)	0.97	17.2 (21.5)	9	13 × 2
PCZ14268	80	32.9 (40)	36 (45)	0.89	20 (25)	5 × 2	10 × 2
PCZ22145	–	34	29	1.2			
PCZ6586	107	38 (35.5)	51 (47.7)	0.75	24 (22.4)	12	12 × 2

Description

As is the case in the family Placenticeratidae in general, (see e.g. Klinger & Kennedy 1989), but specifically in the genus *Hoplitoplacenticer*, the material is extremely vari-

able, both in terms of strength and density of lateral ornament and relative proportions of the shell. This is further complicated by the extreme changes in ornament in the transition from the phragmocone to the body chamber, as well as the effects of dimorphism.

Despite this wide variation in morphology, the following general diagnosis applies to *H. (H.) howarthi* from KwaZulu-Natal:

Narrowly umbilicate, umbilical wall on phragmocone near-vertical, whorl section trapezoidal, generally higher than wide, ornament consists of prominent, conical umbilical tubercles, connected to bifurcating, prorsiradiate sinusoidal ribs with inner and forwardly displaced outer ventro-lateral tubercles. On body chamber ornament changes, with ribbing becoming closer spaced, less prominent, and weaker. The whorl section becomes more rounded, and the umbilical wall tends to slope outwards. Adult size varies considerably, probable microconchs and macroconchs can be distinguished, but relative proportions between these overlap considerably. Complete apertures are unknown.

Early ontogeny

The early ontogenetic stage is partially visible on the inner whorls of PCZ22145 (Fig. 5A–C) and preserved as an impression on PCZ22141 (Fig. 2A–C). It is best seen on the juvenile specimen from Somtseu Road in Durban figured by Kennedy & Klinger (1973, pl. 5, fig. 4a–c) where the dominant ornament consists of numerous, minute, spirally elongated outer ventrolateral, and larger, less numerous inner ventrolateral tubercles. At a diameter of about 20 mm in the small figured specimen, the prominent umbilical tubercles are already visible, but the lateral ribbing is poorly developed.

Variation

In our material, extreme forms in ornament, size and whorl section in the later part of the phragmocone can be distinguished, but these features overlap to such an extent that they have to be considered as part of the intraspecific variation.

Specimens with fine, dense ribbing include PCZ22140 (Fig. 4F) and PCZ7719 (Fig. 4A–C), and those with extremely coarse ribbing, e.g. PCZ20172 (Fig. 3D,G), PCZ7711 (Fig. 3C,H) and PCZ18308 (Fig. 6A–B). Specimens with compressed whorl sections include PCZ22141 (Fig. 2A–C), PCZ22143 (Fig. 3E–F) while PCZ22145 (Fig. 5A–C) has an extremely wide whorl section. Specimens like PCZ22137 (Fig. 1A–E) are intermediate with a more rounded whorl section. Small specimens with distinct body chamber modifications such as PCZ7719 (Fig. 4A–C) may be regarded as microconchs, and large specimens, e.g. PCZ6586 (Fig. 6C–D) macroconchs, but specimens with dimensions which fall between these, though apparently near-adult, e.g. PCZ22141 (Fig. 2A–C), PCZ22140 (Fig. 4F) and PCZ18308 (Fig. 6A–B) cannot unequivocally be designated as either macro- or microconchs. As to be discussed below, we suspect that there may be a correlation between absolute size and whorl section; those specimens with compressed whorl sections becoming adult at smaller diameters than those with wider, more inflated whorl sections.

Discussion

Aperture

Despite the abundance of specimens available, complete apertures in the genus (and in the family Placenticeratidae) are a rarity. A complete body chamber and aperture were recorded in *H. (H.) preyi* (Kennedy & Summesberger 1999, p. 25, pl. 3, figs 1, 4) and another possibly in *Hoplitoplacenticer* (*Lemfoerdicer*) *lemfoerdense* from Poland by Machalski *et al.* (2004, p. 458, pl. 5, fig. 2). Numerous specimens of *Hoplitoplacenticer* from Germany described by Kaplan *et al.* (1996) appear to have parts of the aperture preserved in which the shape of the aperture seems to follow that of the growth lines on the body chamber. PCZ22137 (Fig. 1A–E) appears to have lateral sinuses and a ventral rostrum. The former, however, are asymmetric on either side, and truncate, rather than follow the general direction of the lateral ornament (Fig. 1A,B); the latter (Fig. 1E) also appears to truncate the ventral ribbing. Because of this, we have to interpret the apparent lateral sinuses and ventral rostrum in PCZ22137 (Fig. 1A–E) as probably due to biological (arthropod?) or mechanical damage to the body chamber rather than as indications of a complete aperture.

Dimorphism

In discussions on the family Placenticeratidae, and specifically the genus *Hoplitoplacenticer* several references have been made to dimorphism. The earliest reference to the presence of possible dimorphism in the genus was already made by Paulcke (1907 p. 52[218] in his discussion of *H. (H.) plasticus*. He suggested that the *crassus*-types, i.e. the inflated forms were females (macroconchs) and the compressed *laevis*-forms, male (i.e. microconchs). Subsequent references to dimorphism made mainly on differences in size (in *Hoplitoplacenticer*) are found in e.g. Kennedy & Wright (1983, p. 868); Kennedy 1986, p. 63; Klinger & Kennedy (1989); Cobban & Kennedy (1993, p. 73); Kaplan *et al.* 1996) and Kaplan *et al.* (2005)

We suggest that compressed forms mature at smaller diameters than forms with quadrate whorl sections, and are consequently tentatively referred to as micro- and macroconchs respectively.

Comparison with other species

To date, the following species in chronological order have been referred to the genus *Hoplitoplacenticer* *s.l.*:

Hoplitoplacenticer (*H.*) *lafresnayanum* (d'Orbigny, 1841)

H. (H.) marroti (Coquand, 1859)

H. (H.) vancouverense (Meek, 1862)

H. (H.) coesfeldiense (Schlüter, 1867)

H. (H.) costulosum (Schlüter, 1867)

H. (L.) lemfoerdense (Schlüter, 1872)

(= *Ammonites scaphitoides* Schlüter, 1872)

H. (H.) vari (Schlüter, 1872)

(= *Ammonites striatocostatus* Schlüter, 1872)

H. (H.) dolbergense (Schlüter, 1876)

H. (H.) rejaudryi (de Grossouvre, 1894)

H. (H.) gosseleti (de Grossouvre, 1894)

H. (H.) marroti praematura (Imkeller, 1901)

H. (H.) plasticus Paulcke, 1907.
H. (H.) coesfeldiense var. *schlueteri* Mikhailov, 1951
H. (H.) vari var. nov. ind. Mikhailov, 1951
H. (H.) trangahyense Collignon, 1970
H. (H.) antokazoense Collignon, 1970
H. (H.) besairiei Collignon, 1970
H. (H.) howarthi Collignon, 1970
H. (H.) rarecostatum Khakimov, 1976
H. (H.) monju Matsumoto, 1982
H. (H.) fugen Matsumoto, 1984
H. (H.) minor Cobban & Kennedy, 1993
H. (H.) preyi Kennedy & Summesberger, 1999

Doubtful contenders that have been referred to the genus include:

(?) *Scaphites kambysis* Zittel in: Quaas, 1902
Hoplitoplacenticerias awadi Hassan, 1971.

According to Kennedy (1986, pp. 68–70) these latter two are possibly scaphitine homoeomorphs of *Hoplitoplacenticerias*, and may, for the present, be disregarded in the discussion. Also, *H. lemfoerdense* and *H. lafresnayum* (the latter from the Maastrichtian), differ from other *Hoplitoplacenticerias* by the presence of an additional set of ventral tubercles, and are referred to the subgenus *H. (Lemfoerdicerias)* Kennedy, 1986.

Because of the extreme variation, not only in our material, but in the subgenus *Hoplitoplacenticerias* in general, it is difficult to give precise differences between all these species that have been referred to the subgenus.

Our first record of *Hoplitoplacenticerias* from subsurface exposures at Somtseu Road, Durban, was identified as *H. plasticum plasticum* (Kennedy & Klinger 1973, p. 102).

When we first discovered specimens of *H. (Hoplitoplacenticerias)* at locality 110 on the Nibela Peninsula, *H. (H.) howarthi* Collignon (1970, 80, pl. 639, fig. 2351) from the Upper Campanian of Madagascar appeared to be the closest match, and the present material seems to confirm this, especially as far as the whorl section and prominent umbilical tubercles are concerned. The affinities of the other species of *Hoplitoplacenticerias* described by Collignon from only two Upper Campanian localities are more difficult to resolve. Collignon described specimens from the *Hoplitoplacenticerias marrotti* Zone at Gisement 240 'de la 2° Butte-témoin de la piste Trangahy-Antokazo (Antsalova)' as *H. marrotti* Coquand (= *H. vari* Schlüter) (Collignon 1970, p. 75, pl. 638, figs 2342–3) (Fig. 7A–B, C–D); *H. sp. aff. plasticum-crassum* Paulcke (Collignon 1970, p. 75, pl. 638, fig. 2344) (Fig. 7E–F); *H. cf. dolbergense* Schlüter (Collignon 1970, p. 75, pl. 638, fig. 2345) (Fig. 7G–H); *H. cf. costulosum* Schlüter (Collignon 1970, p. 76, pl. 638, fig. 2346) (Fig. 7I–K); *H. trangahyense* Collignon (1970, p. 76, pl. 638, fig. 2347) (Fig. 8A–C); *H. antokazoense* Collignon (1970, p. 76, pl. 638, fig. 2348) (Fig. 8D–F) and *H. besairiei* Collignon (1970, p. 77, pl. 638, figs 2349–50) (Fig. 7L–N, 9H–I) and from the same zone, at gisement 227–2 Mokotibe (Antsalova) *H. howarthi* (Collignon 1970, p. 80, pl. 639, fig. 2351) (Fig. 8G–I); *H. sp. aff. plasticum-crassum* Paulcke (Collignon 1970, p. 80, pl. 639, fig. 2352) (Fig. 9C–D); *H. sp. aff. marrotti* Coquand (Collignon 1970, p. 80, pl. 639, fig. 2353) (Fig. 9E–G) and

H. antokazoense Collignon (1970, p. 80, pl. 639, fig. 2354) (Fig. 9A–B).

We suspect that all these 'species' fall within the variation of *H. (H.) howarthi* (see Klinger & Kennedy 1989, p. 360). *H. marrotti*, *H. cf. costulosum* and *H. besairiei* of Collignon can be compared with the KwaZulu specimens with a compressed whorl section; *H. cf. dolbergense*, *H. trangahyense* and *H. antokazoense* of Collignon correspond to the specimens with a quadrate whorl section, whereas the remaining Madagascan 'species' can be referred to those specimens with 'intermediate', slightly rounded whorl sections. As first revising authors, we choose the name *H. (H.) howarthi* Collignon for this variable Afro-Malagassy species.

Basse (1931, p. 35, pl. 5, figs 1–3; pl. 12, fig. 2; pl. 13, fig. 1) had previously described *Hoplites Vari* Schlüter from '8 km. au Nord de Trangahy, sur la route d'Antsalova, dans les calcaires subcrayeux du Niveau 10'. These specimens have the same general ornament as compressed varieties of *H. (H.) howarthi*, and undoubtedly belong to this species. The other species described by Basse (1931, p. 36, pl. 4, figs 5–6; pl. 13, fig. 3 as *Hoplites (Hoplitoplacenticerias) plasticus* from 'Entre Mokotibe et la forêt située à l'Ouest de ce village Niveau 10', was referred by Collignon (1970, p. 76, pl. 638, fig. 2346) to *Hoplitoplacenticerias cf. costulosum* Schlüter. This is a very compressed form with hardly any lateral ornament, and probably is only an extremely compressed and smooth variety of *H. (H.) howarthi*.

As far as the strong ornamentation is concerned, *H. (H.) howarthi* bears some similarity to *H. (H.) plasticus* (Paulcke, 1907) and its 'varieties' (Untergruppen) *Hauthali*, *crassus*, *costatus*, *semicostatus* and *laevis* (see Paulcke 1907, p. 20[186]–54[220]. Pls 10(1)–15(6), figs 1–3; Riccardi 1988, pl. 16, figs 4–6 and herein Fig. 10A–G). Paulcke (1907) listed 48 specimens which he referred to five morphological groups ('Untergruppen'), *Hauthali*, *crassus*, *costatus*, *semicostatus* and *laevis*, based more or less on decreasing whorl breadth and strength of ornamentation, though realizing he was probably dealing with a single, variable species. Despite the extreme variation in that species, the umbilical tubercles are never as spinose as in *H. (H.) howarthi*, but are elongated obliquely radial, and the umbilical wall slants outwards rather than being vertical as in the latter. (see Fig. 10A–G) Also, none of our specimens has as rounded and inflated a whorl section as the '*Hauthali*' variety (Fig. 10D–E) of the latter species. Thus as here interpreted, none of the Madagascan specimens referred in open nomenclature to *H. plasticus* by Collignon belong to that species.

Of the predominantly European species, only *H. (H.) dolbergense* (Schlüter, 1876) (1876, p. 159, pl. 44, figs 1–4), comprehensively revised by Kaplan *et al.* (1996, p. 39, pl. 25, figs 3–4; pl. 26, fig. 5; pl. 27, figs 3–4; pl. 28, figs 1–5; pl. 29, figs 1–4; pl. 30, figs 1–5; pl. 31, figs 1–9; pl. 32, figs 4–5) and mentioned subsequently (Kaplan *et al.* 2005, p. 100) (see also Figs 11G–K, 13A–B) is close to *H. (H.) howarthi* as far as strength of ornament is concerned. It lacks the strong umbilical tubercles of *H. (H.) howarthi*, and tends to form looped ribbing on the flanks; a feature not present in the latter. Only the holotype (by monotypy) of *H. (H.) trangahyense* (Fig. 8A–C) has weakly looped ribbing, similar to that of *H. (H.) dolbergense*, as noted by Collignon (1970, p. 76) and Kennedy (1986, p. 66) and may either be regarded

as an atypical variant of *H. (H.) howarthi*, or as belonging to a different species; on the basis of a single specimen we cannot be more definite. The specimen referred to *H. cf. dolbergense* by Collignon (1970, p. 75, pl. 638, fig. 2345) (here Fig. 7G,H) lacks the looped ribbing of typical *H. (H.) dolbergense* and may best be regarded as an inflated form of *H. (H.) howarthi* with a rounded whorl section.

All the other European species revised by Mikhailov (1951), Kennedy (1986), Kaplan *et al.* (1996, 2005, 2006), Kennedy & Kaplan (1997), e.g. *H. (H.) vari* (Schlüter, 1876), (here Figs 12, 14A), *H. (H.) costulosum* (Schlüter, 1867) (here Figs 11B–F; 14B–E) and *H. (H.) coesfeldiense* (Schlüter, 1867) (here Figs 11A, 13C–F) have much finer and denser ribbing than *H. (H.) howarthi* and lack the prominent umbilical tubercles.

Ornament on the body chamber of the macroconch of *H. (H.) howarthi* (Fig. 6C–D) from KwaZulu superficially resembles that of *H. (H.) coesfeldiense*, but ornament on the inner, phragmocone whorls is totally different.

The specimen referred to *H. cf. costulosum* by Collignon (1970, p. 76, pl. 638, fig. 2345) (here Fig. 7I–K) has the strong umbilical tubercles typical of *H. (H.) howarthi*; it is here merely regarded as a compressed and weakly ornamented form of the latter species.

H. (H.) marroti (Coquand, 1859) (see Kennedy 1986, p. 70, pl. 2, figs 3–4; pl. 9, figs 1–8, 11–12; pl. 10, figs 1–12; pl. 12, figs 1–2) (here Fig. 15) has similar, though apparently denser lateral ornament than *H. (H.) howarthi* and differences between the two species are difficult to formulate. None of the known specimens of *H. (H.) marroti* are known to have as coarse ornament as some *H. (H.) howarthi*, (e.g. Figs 3D,G; 6A–B), or to grow to such large size, but some of the Madagascar specimens, e.g. Collignon's (1970, p. 75, pl. 638, fig. 2342) (here Fig. 7A–B) or *H. (H.) besairiei* (Collignon 1970, p. 77, pl. 638, fig. 2349) (lectotype here designated; Fig. 7L–N) are impossible to distinguish from the French specimens of *H. (H.) marroti* figured by Kennedy (1986). It is possible that, given more material, *H. (H.) howarthi* may eventually be merely regarded as a larger, more coarsely ornamented, South African-Malagassy subspecies of *H. (H.) marroti*.

H. (H.) rejaudryi (de Grossouvre, 1894) (see Kennedy 1986, p. 78, pl. 7, figs 1–5; pl. 14, figs 6–7) is consistently much finer ribbed than *H. (H.) howarthi*.

H. (H.) preyi Kennedy & Summesberger (1999, p. 25, pl. 3, figs 1, 4) from the Late Campanian of the Gschliefgraben, Austria, is monotypical and crushed. It differs from *H. (H.) howarthi* in its finer ribbing and complete absence of conspicuous umbilical tubercles of the latter species. Differences with other species are summarized by Kennedy & Summesberger (1999, p. 25–26).

H. (H.) rarecostatum Khakimov (Khakimov in: Atabekian & Khakimov 1976, p. 88, pl. 10, fig. 5) is difficult to interpret. The figured holotype is similar to inflated variants of *H. (H.) howarthi* and has similar strong ornamentation; given more material more precise differences may be determined.

H. (H.) minor Cobban & Kennedy (1993, p. 73, figs 4.1–4.28) from the Middle Campanian Wolfe City Sand in north-eastern Texas lacks the strong umbilical tubercles of *H. (H.) howarthi* and has very dense, thread-like ribbing on the body chamber.

H. (H.) monju Matsumoto, 1982 (1982, p. 244, figs 1–2; 1984, p. 24, pl. 7, fig. 5; pl. 8, fig. 6) was compared by Matsumoto (1984, p. 25) to *H. (H.) trangahyense* Collignon; we regard the latter as a synonym of *H. (H.) howarthi*. They overlap in some morphological features, but *H. (H.) monju* lacks the strong umbilical tuberculation of typical *H. (H.) howarthi*, as does *H. (H.) fugen* Matsumoto (1984, p. 25, pl. 8, fig. 5).

H. cf. marroti (Coquand) described from Angola by Howarth (1965, p. 391, pl. 12, fig. 3; pl. 13, fig. 3) has lateral ornament very similar if not identical to that of *H. (H.) howarthi*.

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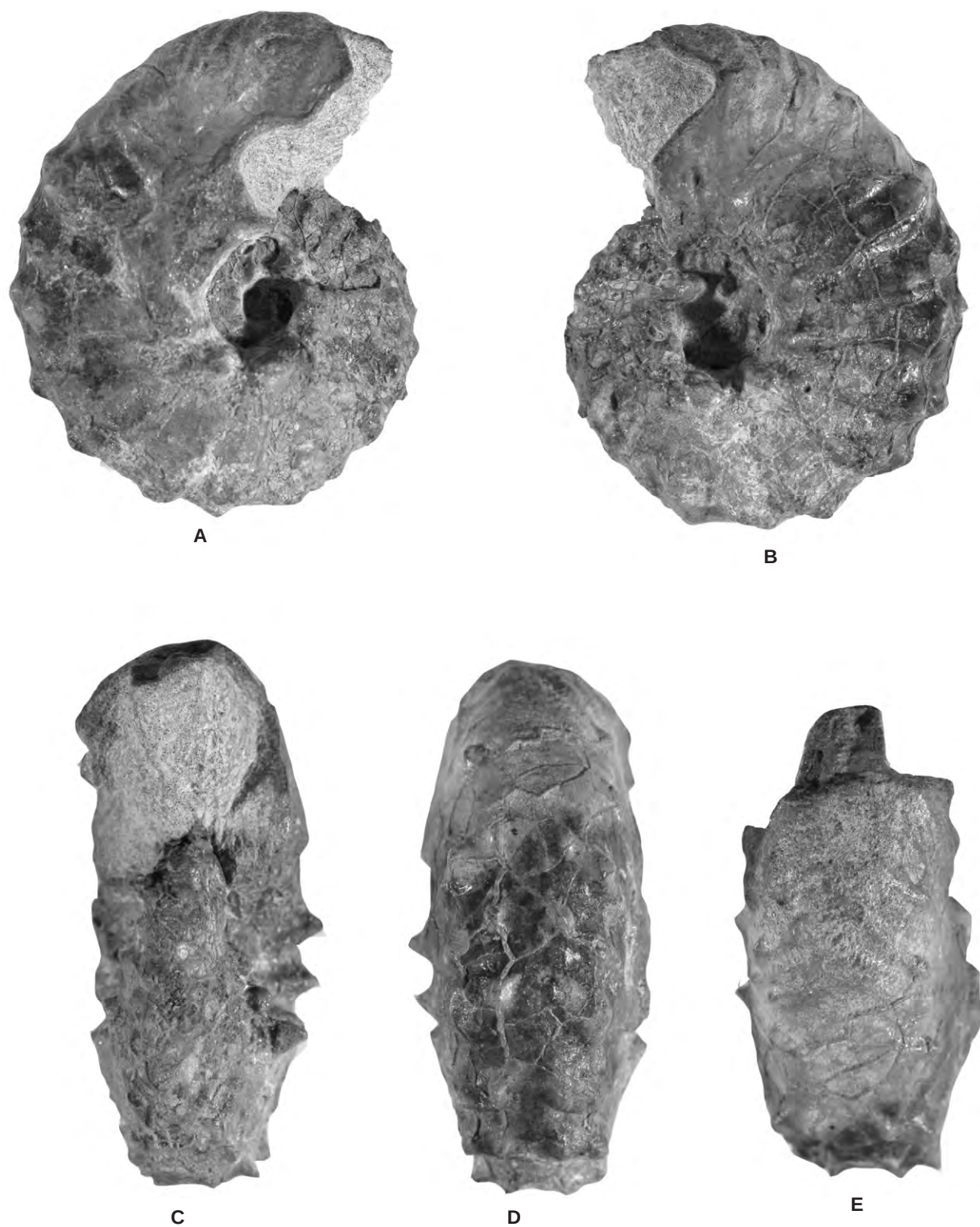


Fig. 1. *Hoplitoplacenticeras (H.) howarthi* Collignon, 1970. SAM-PCZ22137. Specimen with structures on the body chamber suggesting lateral sinuses and ventral rostrum, but due to asymmetry of these, probably due to biological and/or mechanical damage rather than showing the shape of the adult apertural margin. From locality 110, Nibela Peninsula, KwaZulu-Natal, St Lucia Formation, Campanian III. $\times 1$.

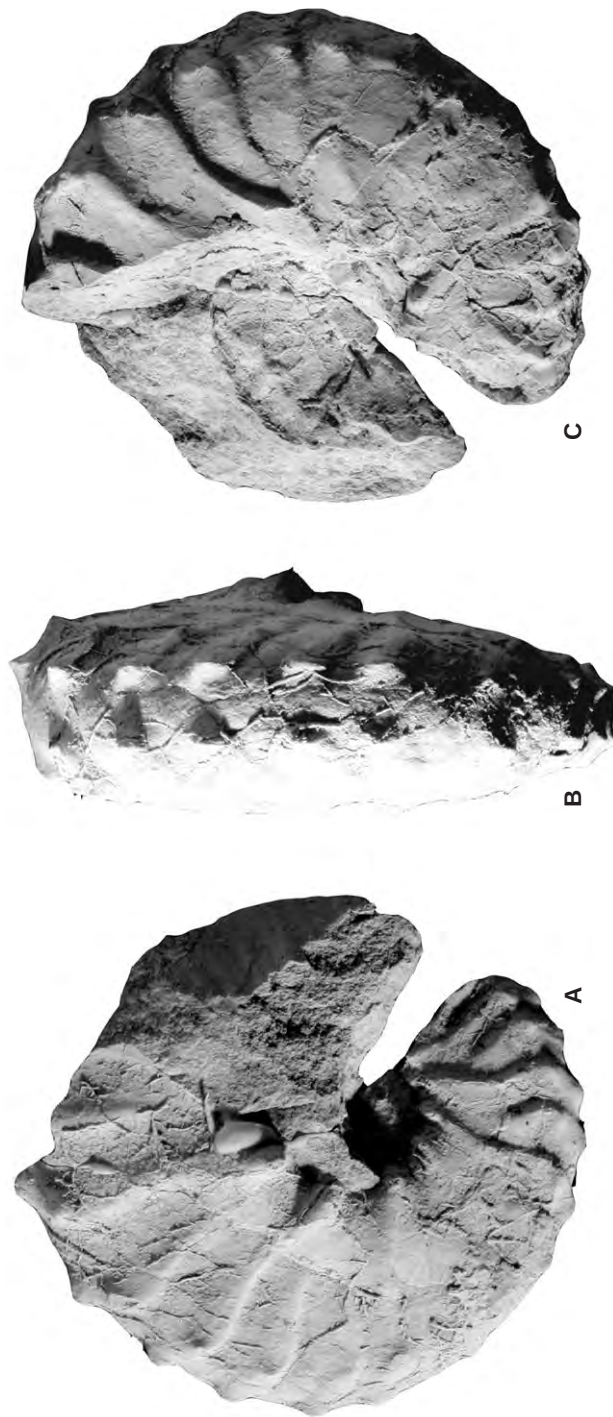


Fig. 2. *Hoplitoplacenticeras (H.) howarthi* Collignon, 1970. SAM-PCZ22141. From locality 110, Nibela Peninsula, KwaZulu-Natal, St Lucia Formation, Campanian III. $\times 1$.

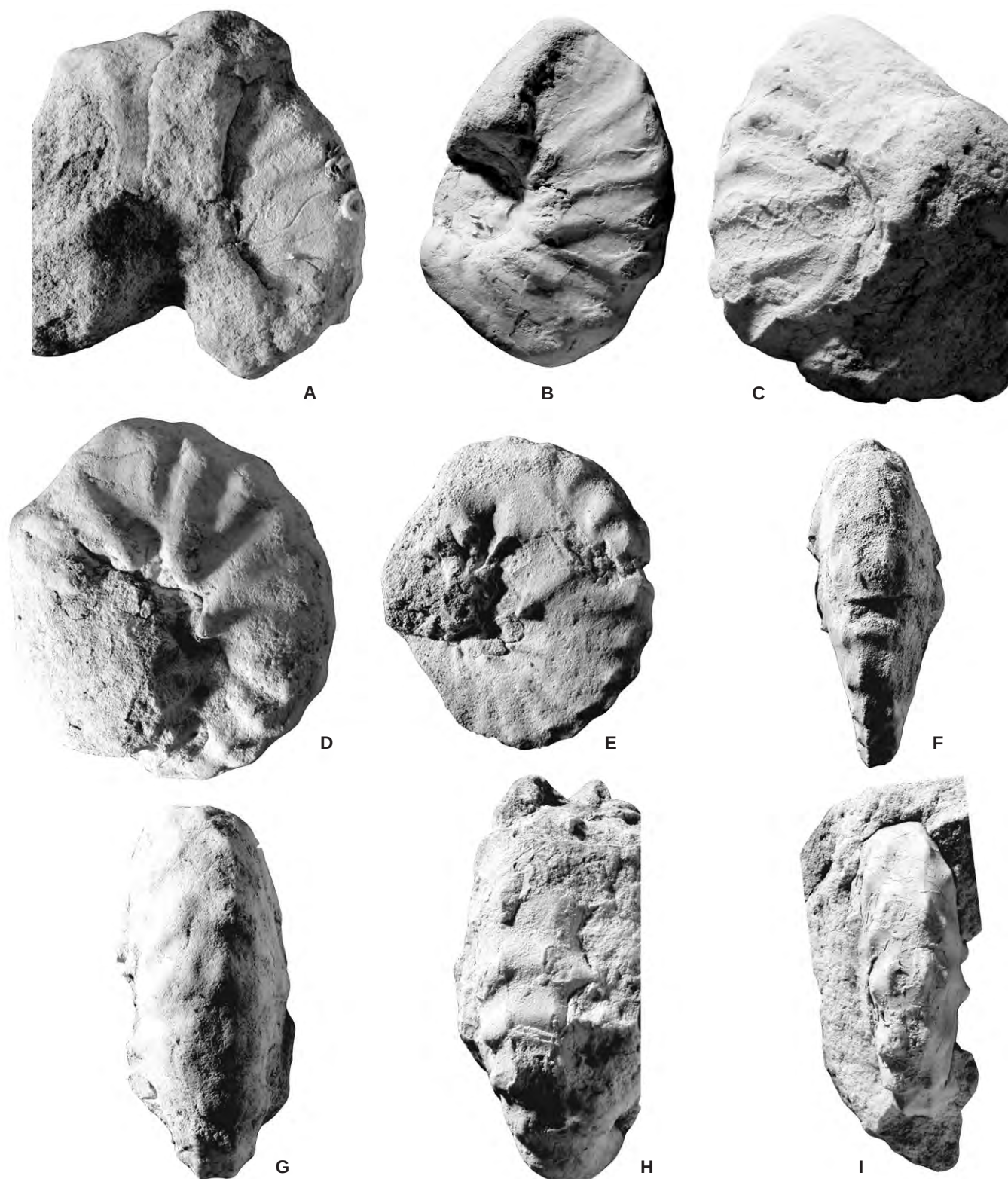


Fig. 3. *Hoplitoplacenticeras (H.) howarthi* Collignon, 1970. **A**, SAM-PCZ22144. **B**, SAM-PCZ18309. **C**, **H**, SAM-PCZ7711. **D**, **G**, SAM-PCZ20172. **E**–**F**, SAM-PCZ22143. **I**, SAM-PCZ6587. All from locality 110, Nibela Peninsula, KwaZulu-Natal, St Lucia Formation, Campanian III. All $\times 1$.

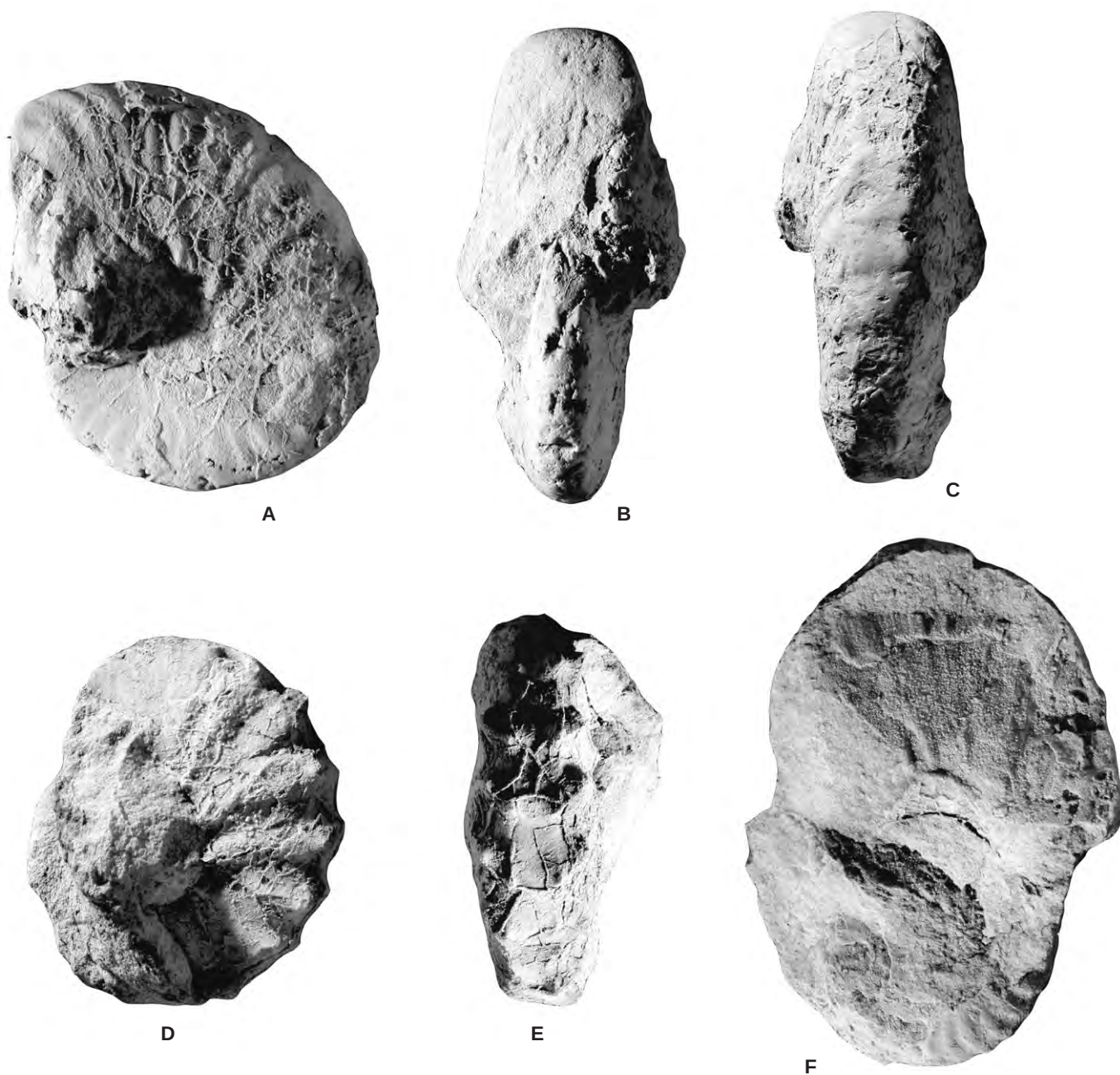
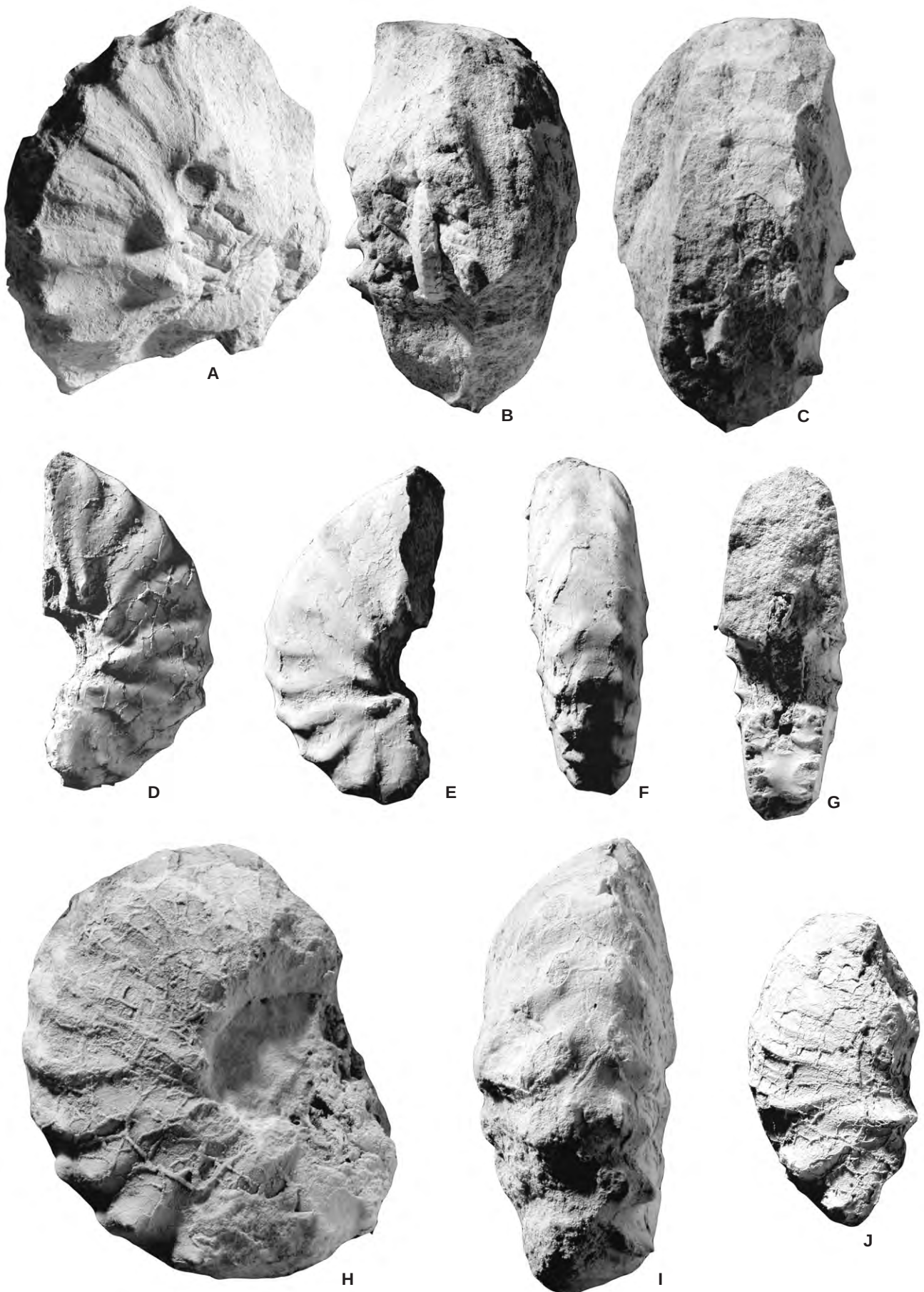


Fig. 4. *Hoplitoplacenticeras (H.) howarthi* Collignon, 1970. **A–C**, SAM-PCZ7719, microconch. **D–E**, SAM-PCZ1142. **F**, SAM-PCZ22140. All from locality 110, Nibela Peninsula, KwaZulu-Natal, St Lucia Formation, Campanian III. All $\times 1$.

Fig. 5. *Hoplitoplacenticeras (H.) howarthi* Collignon, 1970. **A–C**, SAM-PCZ22145. Specimen with quadrate whorl section. **D–G**, SAM-PCZ22139, specimen with compressed whorl section. **H–I**, SAM-PCZ14268, specimen with coarse ornament. **J**, SAM-PCZ22138. All from locality 110, Nibela Peninsula, KwaZulu-Natal, St Lucia Formation, Campanian III. All $\times 1$.



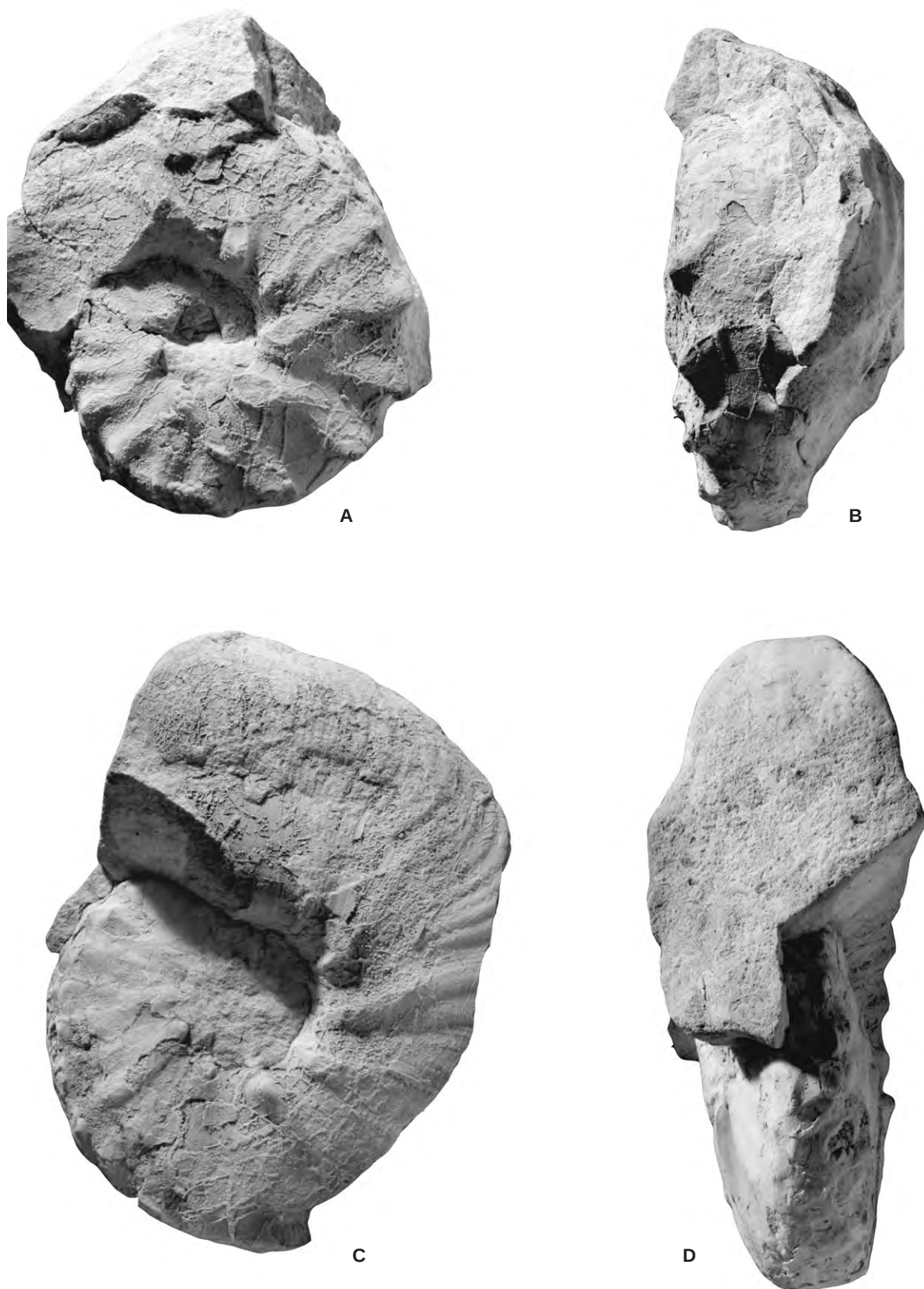


Fig. 6. *Hoplitoplacenticeras* (*H.*) *howarthi* Collignon, 1970. **A–B**, SAM-PCZ18308. **C–D**, SAM-PCZ6586, Macroconch. Both from locality 110, Nibela Peninsula, KwaZulu-Natal, St Lucia Formation, Campanian III. Both $\times 0.9$.



Fig. 7 A–B, UBGD12342, the original of Collignon 1970, p. 75, pl. 638, fig. 2342 *Hoplitoplacenticeras marroti* Coquand (= *H. vari* Schlüter). C–D, UBGD12343, the original of Collignon 1970, p. 75, pl. 638, fig. 2343 *Hoplitoplacenticeras marroti* Coquand. E–F, UBGD12344, the original of Collignon 1970, p. 75, pl. 638, fig. 2344 *Hoplitoplacenticeras* sp. aff. *plasticum-crassum* Paulcke. G–H, UBGD12345, the original of Collignon 1970, p. 75, pl. 638, fig. 2345 *Hoplitoplacenticeras* cf. *dolbergense* Schlüter. I–K, UBGD12346, the original of Collignon 1970, 76, pl. 638, fig. 2346 *Hoplitoplacenticeras* cf. *costulosum* Schlüter. L–N, UBGD12349, the lectotype of *Hoplitoplacenticeras besairiei* Collignon, the original of Collignon 1970, p. 77, pl. 638, fig. 2349. All figures $\times 1$.

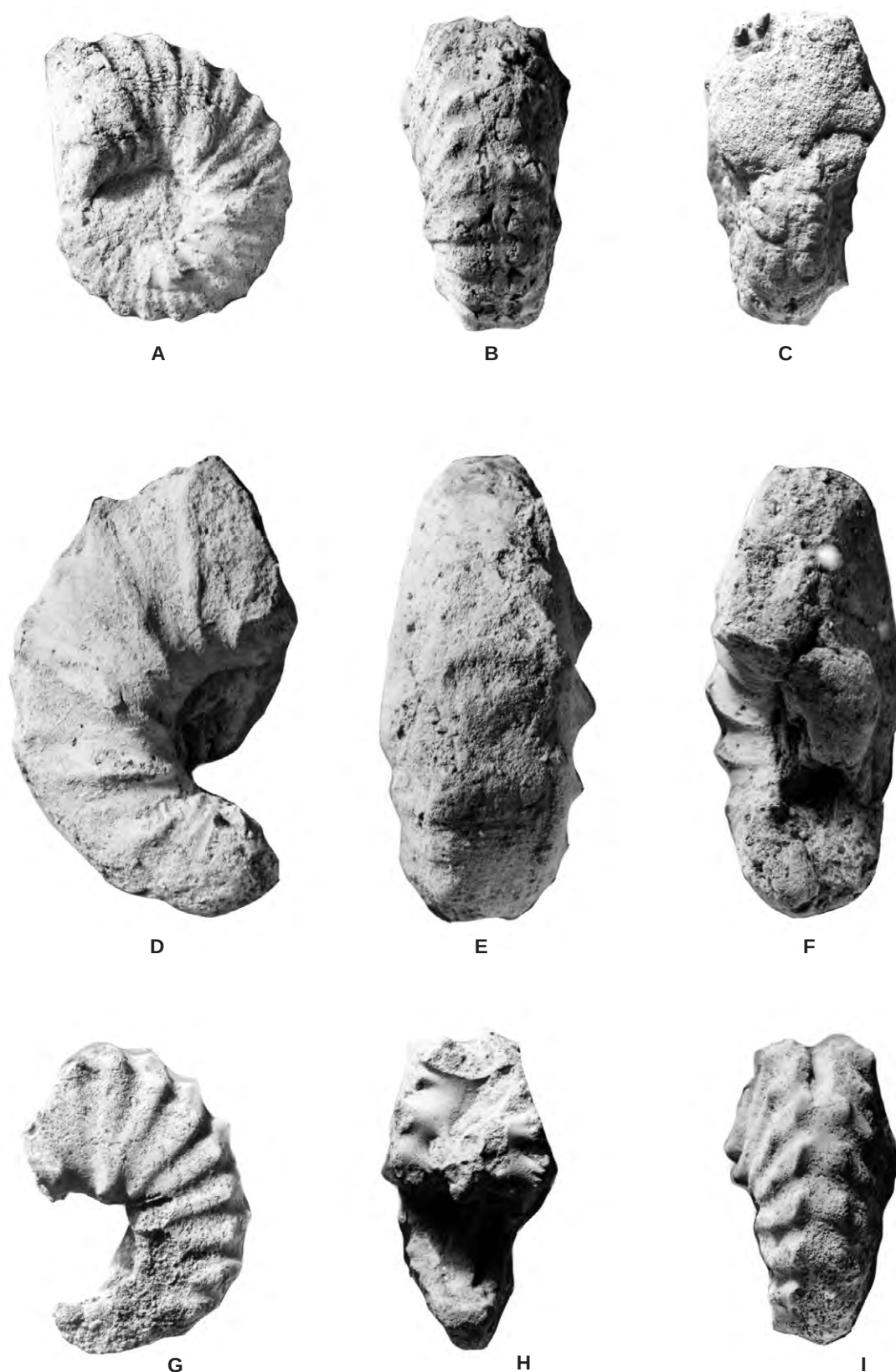


Fig. 8. A–C, UBGD12347, The holotype by monotypy of *Hoplitoplacenticerus trangahyense* Collignon, the original of Collignon 1970, p. 76, pl. 638, fig. 2347. D–F, UBGD12348, the paralectotype of *Hoplitoplacenticerus antokazoense* Collignon, 1970, the original of Collignon 1970, 76, pl. 638, fig. 2348. G–I, UBGD12351, the holotype by monotypy of *Hoplitoplacenticerus howarthi* Collignon, 1970, the original of Collignon 1970, p. 80, pl. 639, fig. 2351. All figures $\times 1$.

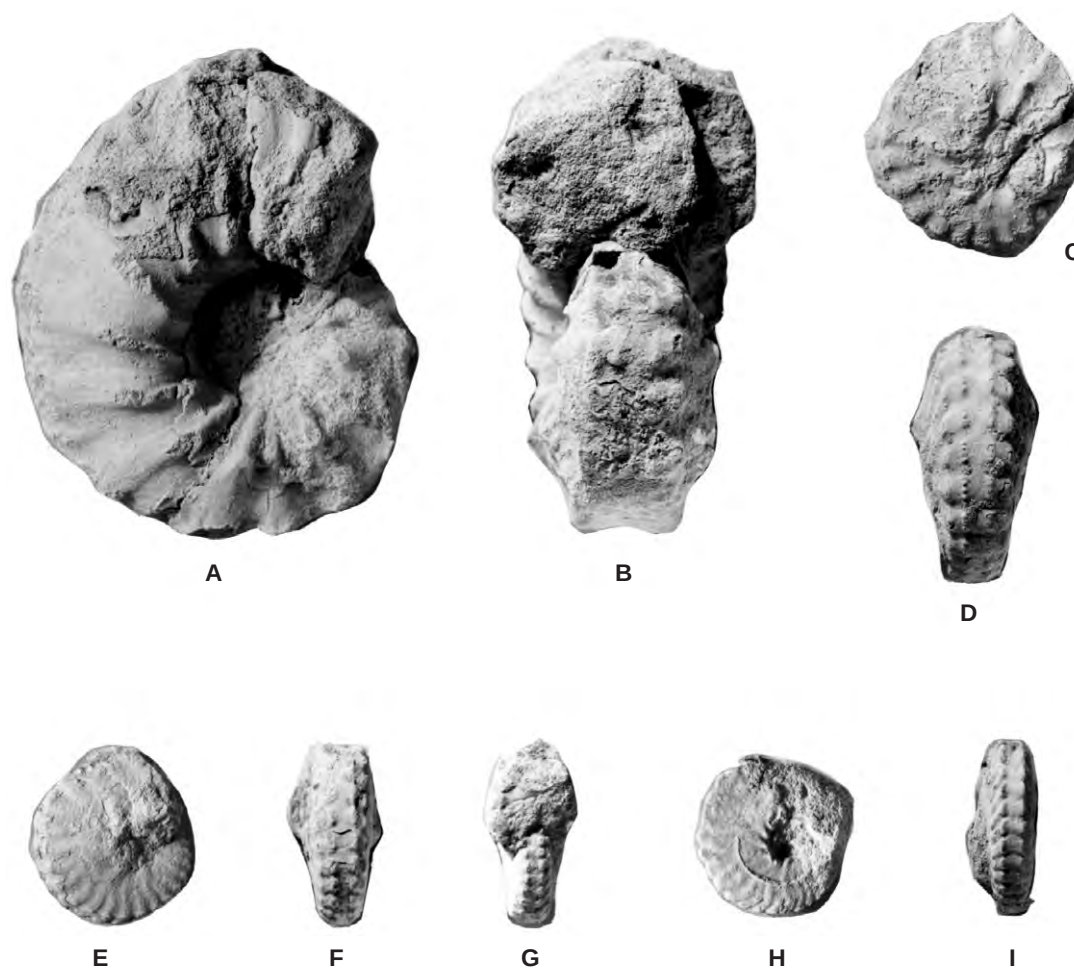
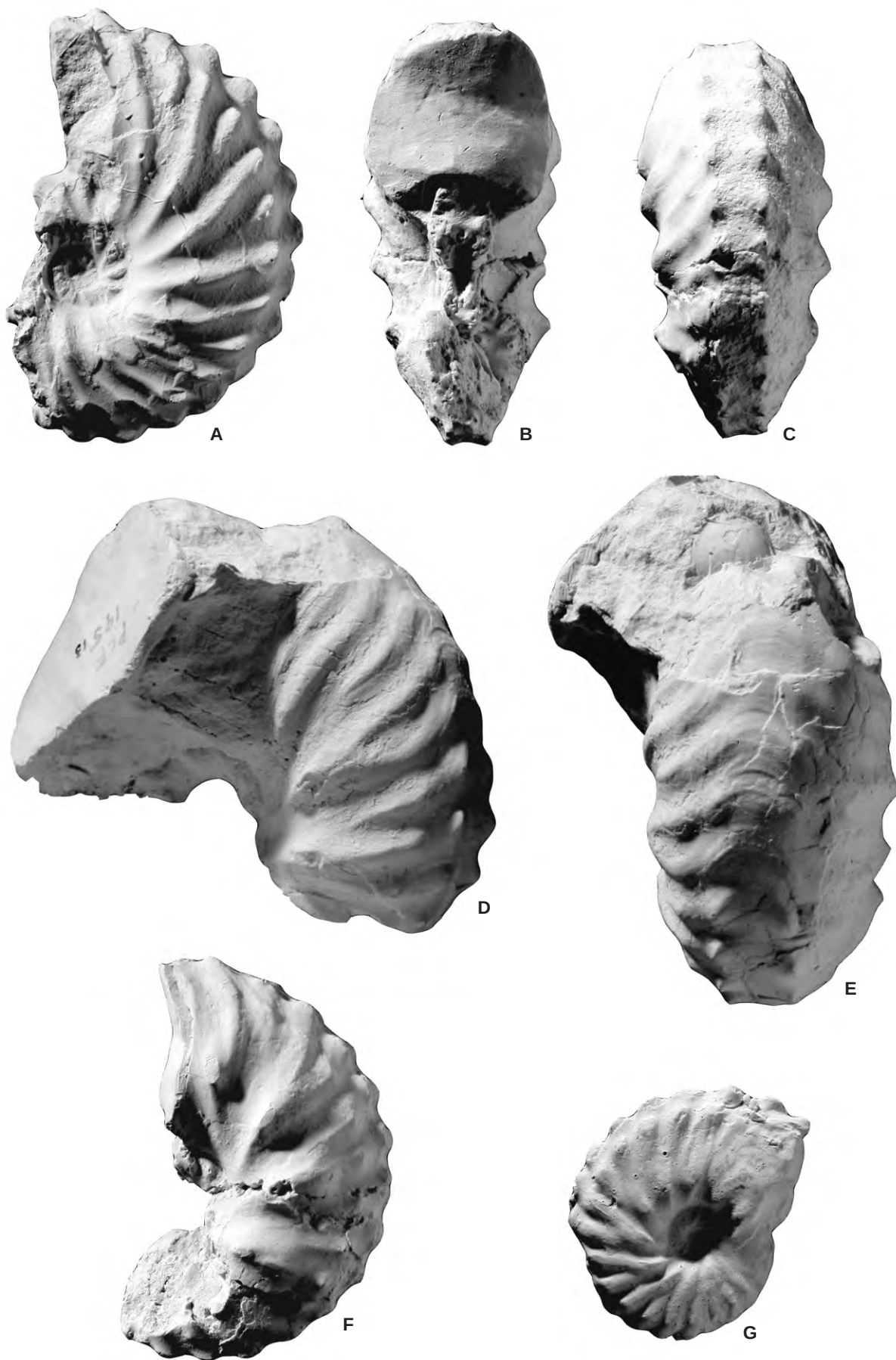


Fig. 9. **A–B**, UBGD12354, the lectotype of *Hoplitoplacenticeras antokazoense* Collignon, 1970, the original of Collignon 1970, p. 80, pl. 639, fig. 2354. **C–D**, UBGD12352, the original of Collignon 1970, p. 80, pl. 639, fig. 2352 *Hoplitoplacenticeras* sp. aff. *plasticum-crassum* Paulcke. **E–G**, UBGD12353, the original of Collignon 1970, p. 80, pl. 639, fig. 2353 *Hoplitoplacenticeras* sp. aff. *marroti* Coquand. **H–I**, UBGD12350, the paralectotype of *Hoplitoplacenticeras besairiei* Collignon, 1970, the original of Collignon 1970, p. 77, pl. 638, fig. 2350. All figures $\times 1$.

Fig. 10. *Hoplitoplacenticeras (H.) plasticum* Paulcke, 1907. **A**, SAM-PCF19516. **B, C, F**, SAM-PCF19514. **D–E**, SAM-PCF19513. **G**, SAM-PCF19515. All plaster casts of specimens from Cerro Cazador, Argentina. Donated by Dra M.B. Aguirre Urreta, Buenos Aires. All $\times 1$.



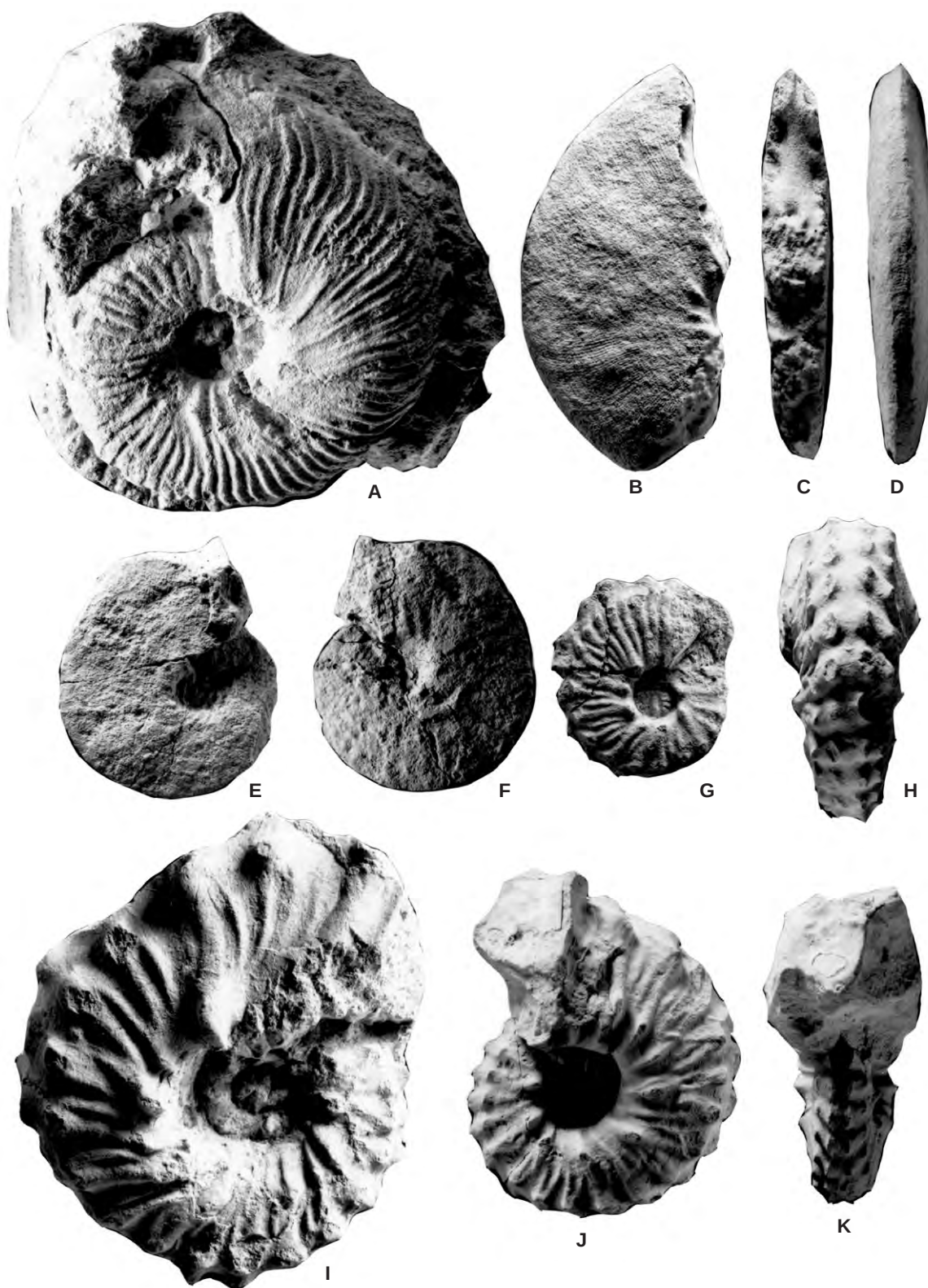


Fig. 11. A, *Hoplitoplacenticerias (H.) coesfeldiense* (Schlüter, 1867). The lectotype, GPIB19d, the original of Schlüter 1867, pl. 1, fig. 1 from Coesfeld. B–F, *Hoplitoplacenticerias (H.) costulosum* (Schlüter, 1867). B–D, Paralectotype GPIB20d, of *Ammonites costulosum* Schlüter, 1867, the original of Schlüter 1867, pl. 2, fig. 3 from Coesfeld. E–F, Paralectotype GPIB20b, the original of Schlüter 1867, pl. 2, fig. 4 also from Coesfeld. G–K: *Hoplitoplacenticerias (H.) dolbergense* (Schlüter, 1876). G, GPIB19c. The original of Schlüter 1872, pl. 17, fig. 3 from Coesfeld. H, J, K, Lectotype GPIB90b, the original of Schlüter, 1876, pl. 44, figs 2–3, ?4 from Dolberg. I, Paralectotype GPIB90a, the original of Schlüter, 1876, pl. 44, fig. 1 from Darup. All $\times 0.9$.



Fig. 12. A–C, *Hoplitoplacenticeras (H.) vari* (Schlüter, 1872). The lectotype, GPIB20a, the original of Schlüter 1867, pl. 2, fig. 1 from Ahlten. $\times 1$.

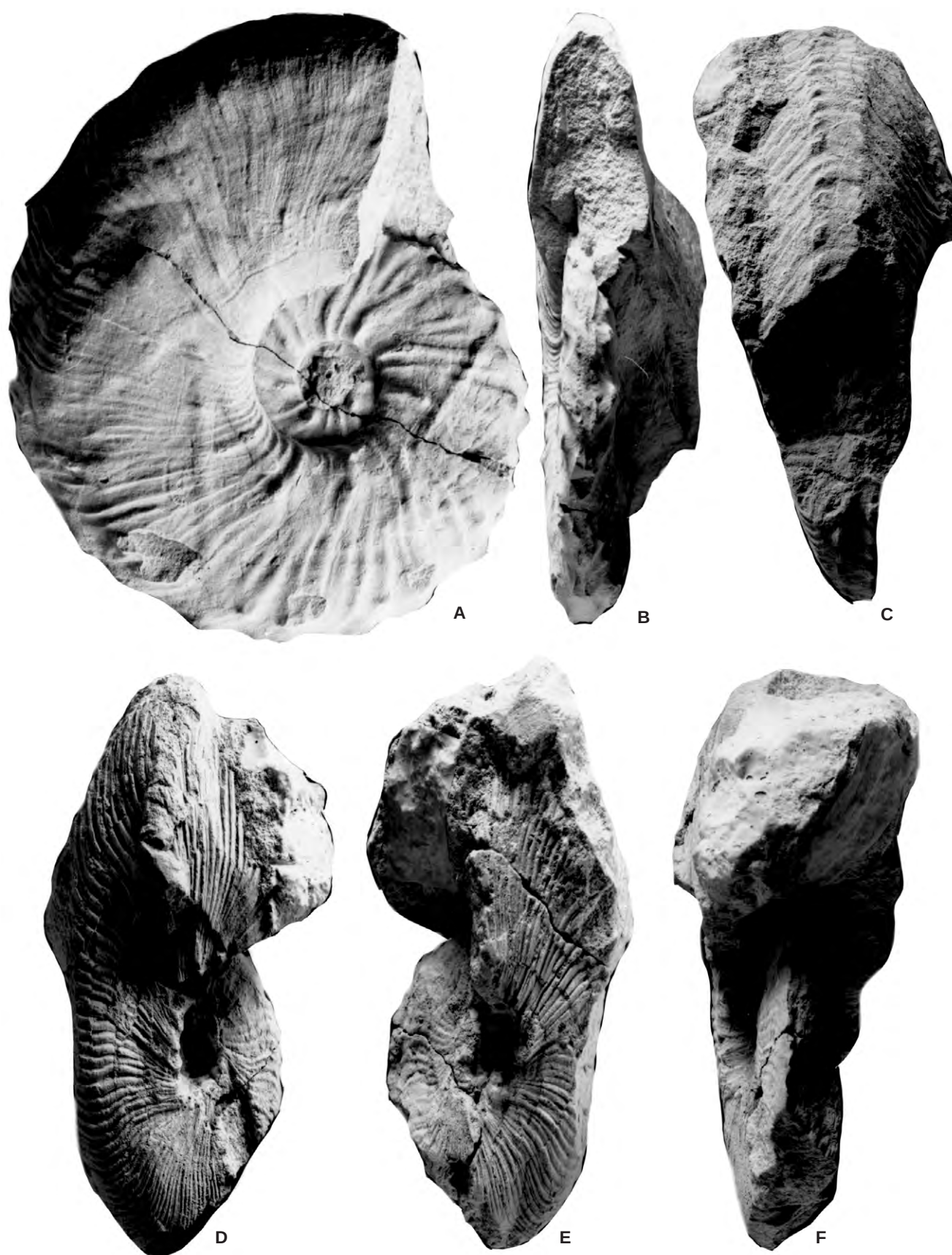


Fig. 13. A–B, *Hoplitoplacenticeras (H.) dolbergense* (Schlüter, 1876). The original of Schlüter 1872, pl. 17, figs 1–2, GPIB unregistered specimen, from between Beckum and Ennigerloh. C–F, *Hoplitoplacenticeras (H.) coesfeldiense* (Schlüter, 1867). Paralectotype GPIB19d, the original of Schlüter 1867, pl. 1, fig. 4 from the vicinity of Coesfeld. All $\times 1$.

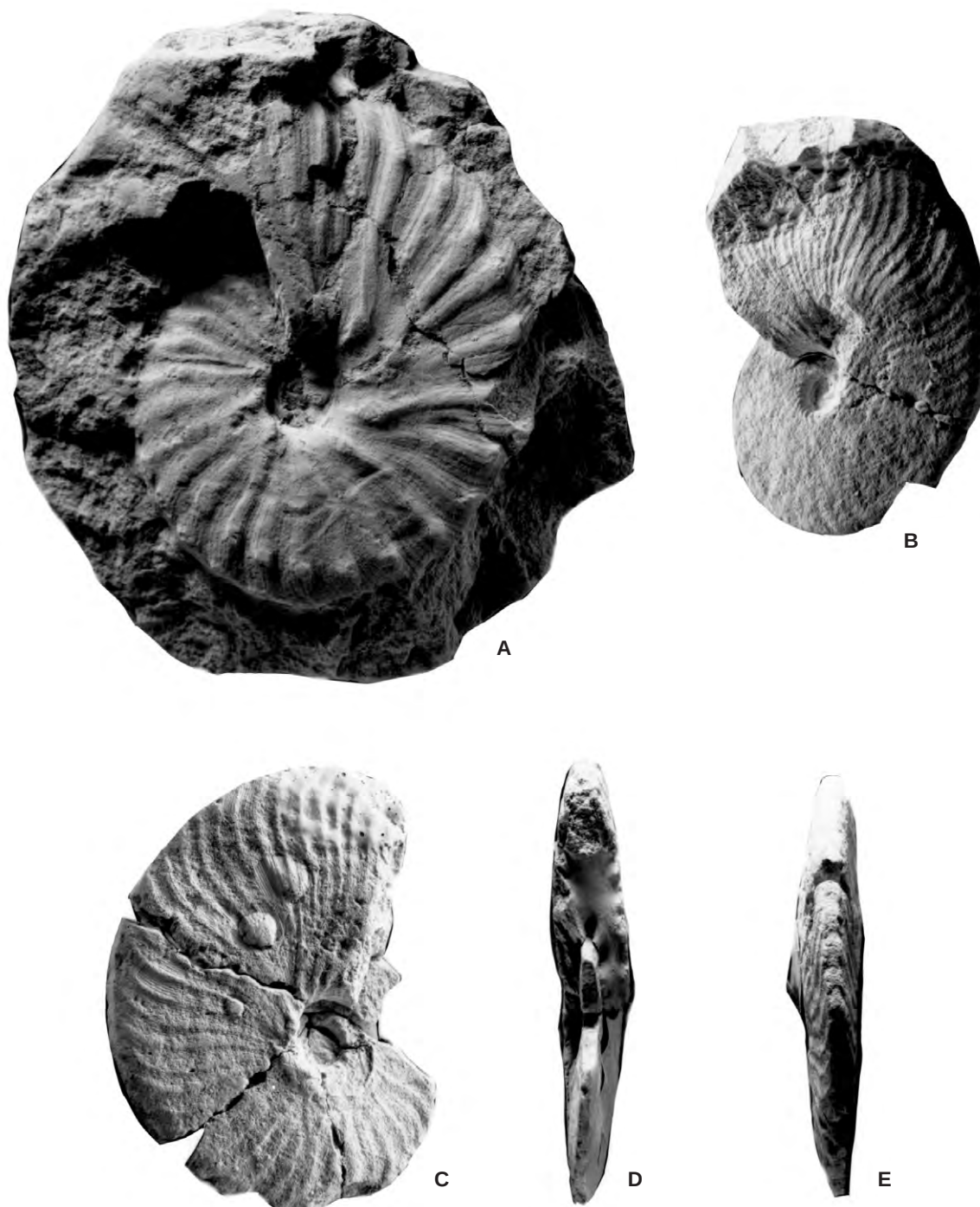


Fig. 14. **A**, *Hoplitoplacenticer* (*H.*) *vari* (Schlüter, 1876). Paralectotype GPIG65–6, the original of Schlüter 1872, pl. 20, figs 1–2 from Haldem. **B–E**: *Hoplitoplacenticer* (*H.*) *costulosum* (Schlüter, 1867). **B**, GPIB51, the original of Schlüter 1872, pl. 20, figs 5–6 from Darup. **C–E**, The lectotype, GPIB20c, the original of Schlüter 1867, pl 2, fig. 2a,b from Coesfeld. All $\times 1$.

Fig. 15. **A–V**, *Hoplitoplacenticer* (*H.*) *marroti* (Coquand, 1859). **A**, **B**, SP Unregistered, ex Arnaud Collection from Assize P³ Bouteille, Dordogne, France; the original of De Grossouvre, 1894, pl. 9, fig. 2. **C**, **D**, SP unregistered, ex Toucas Collection from Montmoreau, Charente, France. **E–I**, all from a private collection, Assize P³ 1.5 km east of St Victoir, Dordogne, France. **J–L**, LG55P118, from Aubeterre-sur-Dronne, Charente, France. **M**, **N**, an adult microconch SP unregistered ex Arnaud Collection from Assize P³, Petingaud, near Montmoreau, Charente, France, the original of De Grossouvre 1894, pl. 9, fig. 3. **O**, **P**, **R**, **S**, both SP unregistered, ex Arnaud Collection, from Assize P³, Chavenat (Charente). **Q**, **V**, the holotype, EMP unregistered, from the environs of Ribérac, Dordogne, France. **T**, **U**, SP unregistered, from Assize P³, Leygonie, near Ribérac, Dordogne. All figures $\times 1$.

