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# Significance of intermediate forms in phyletic reconstruction of ammonites: Early Jurassic *Phricodoceras* case study

JEAN-LOUIS DOMMERGUES and CHRISTIAN MEISTER



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This paper discusses the phyletic interpretation of the genus *Phricodoceras* and its taxonomic classification at the subfamily, family, and superfamily levels from an historical and critical perspective. First a review of the latest findings on this taxon is presented and the grounds for the attribution of *Phricodoceras* to the Schlotheimiidae (Psiloceratoidea) are summarized and illustrated. This review is a synthesis grounded on evolutionary (e.g., heterochronies, innovations), eco-ethological (e.g., assumed shell hydrodynamic capacities) and spatio-temporal patterns (e.g., bio-chronostratigraphy, palaeobiogeography). Then, the main stages of understanding the taxonomy of *Phricodoceras* since the early nineteenth century are reviewed. Two main taxonomic concepts alternate over time. The first is based on the “overall resemblance” of *Phricodoceras* to some coeval Eoderoceratoidea leading to the genus being included in its own family or subfamily (e.g., Phricodoceratinae) among the Eoderoceratoidea. The second hypothesis, recently confirmed by the discovery of an intermediate form (i.e., *Angulaticeras spinosus*), clearly includes *Phricodoceras* within the Schlotheimiidae (Psiloceratoidea). Comparison of these two very different conceptions reveals how “overall resemblance” can be misleading and shows that the discovery of intermediate forms is often the key to phyletic reconstructions in ammonites.

**Key words:** Cephalopoda, Ammonoidea, stratigraphy, paleobiogeography, taxonomy, character, homology, ontogeny, adaptation, Jurassic.

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## Introduction

*Phricodoceras* is a homogeneous and unambiguously defined group among the late Sinemurian and Pliensbachian ammonites. Although generally scarce, *Phricodoceras* has been actively collected and studied since the early nineteenth century because of its attractive and unusual tuberculate ornamental pattern. As a result, despite its rarity, it is discussed in a hundred or so publications. It is surprising therefore that its relationships and consequently its taxonomic attribution should recently have been seriously questioned (Dommergues 1993, 2003; Dommergues and Meister 1999; Meister 2007; Dommergues et al. 2008) and finally reconsidered at the superfamily level (Edmunds et al. 2003; Meister et al. 2010, 2011; Blau and Meister 2011). This edifying late taxonomic revision illustrates the surprising immovability of questionable practices in ammonite taxonomy. The aim of this work is, first, to summarize the

latest discoveries and their taxonomic implications; second, to recapitulate the main steps of the taxonomic practices involving *Phricodoceras* since the early nineteenth century; and third, to examine the grounds for the major changes in the interpretation of the relationships of *Phricodoceras* among the Sinemurian and Pliensbachian ammonites. Special attention is also paid to why the misleading phyletic hypothesis by which the genus *Phricodoceras* was ascribed to the Eoderoceratoidea should have proved so resilient in the literature. The case of *Phricodoceras* is discussed here to exemplify what is a common bias in ammonite taxonomic practices. Taxonomic groupings grounded on some “overall resemblance” combined with stratigraphic control are usually evidence. Unfortunately, later this may become “coarse” evidence and/or may be found to be homeomorphy, as is shown here for *Phricodoceras*. The importance of transitional forms in convincingly defining the primary homologies is also clearly illustrated in the example

studied. Thus, beyond *Phricodoceras*, the present work can be viewed as a “case study” and a possible source of ideas for ammonite taxonomy.

*Institutional abbreviations.*—UBGD, University of Burgundy.

*Other abbreviations.*—M, macroconch; m, microconch; t1, latero-umbilical position; t2, latero-ventral position; t3, perisiponal position; us, umbilical seam; vb, ventral band (see also Fig. 4).

## Stratigraphic and geographic settings

The stratigraphic and paleobiogeographic frameworks of the genus *Phricodoceras* have been extensively and accurately described by Meister (2007: figs. 12, 14, 16, 17). The results of that key work are summarized here and supplemented schematically by more recently published data (Figs. 1, 2). The stratigraphic range of *Phricodoceras* is objectively documented from the base of the *Echioceras raricostatum* Chronozone (*Cruciloboceras densinodulum* Subchronozone) to the top of the *Pleuroceras spinatum* Chronozone (*Pleuroceras hawkskerense* Subchronozone). In the Mediterranean Tethys the last *Phricodoceras* (*Phricodoceras* aff. *cantaluppii* Fantini Sestini, 1978) are associated with *Emaciaticeras* (Meister et al. 2010). The earliest representatives of the genus *Phricodoceras* (*Echioceras raricostatum* Chronozone) belong to the group of *Phricodoceras* gr. *taylori* (Sowerby, 1826)–*P. lamellosum* (Orbigny, 1844). They exhibit from the outset all of the impressive diagnostic features of the genus. Convincingly, *Phricodoceras* roots among the genus *Angulaticeras* and *A. (Angulaticeras) spinosus* Meister, Schlögl, and Rakús, 2010, a recently discovered species with a *Phricodoceras*-like juvenile stage, comes from a condensed Carpathian fauna suggesting a period from the *Arietites bucklandi* to the *Caenisites turneri* chronozones (Meister et al. 2010). The condensed context of this unusual fossiliferous locality must be underlined because the sedimentary processes often associated with condensation can explain the presence of an episode that is usually missing at the regional level (e.g., long lasting submarine exposure and/or erosion) (Olóriz 2000; Cecca 2002; Olóriz and Villaseñor 2010). Even if an age somewhere in the *Caenisites turneri* Chronozone is plausible for *A. (A.) spinosus* (Fig. 1), there remains an undocumented stratigraphic gap in *Phricodoceras* history corresponding approximately to the duration of the *Asteroceras obtusum*–*Oxyntoceras oxynotum* Chronozones. Fig. 1 shows that *Phricodoceras* is clearly the longest-surviving genus of the Family Schlotheimiidae. In point of fact, the genus durations have a propensity to increase throughout the history of the family, and this tendency apparently peaks with *Phricodoceras*. Obviously, like all taxonomic groupings, genera are partly subjective and their duration may be influenced by taxonomic practice, which widely depends on human perception. Thus the long duration of

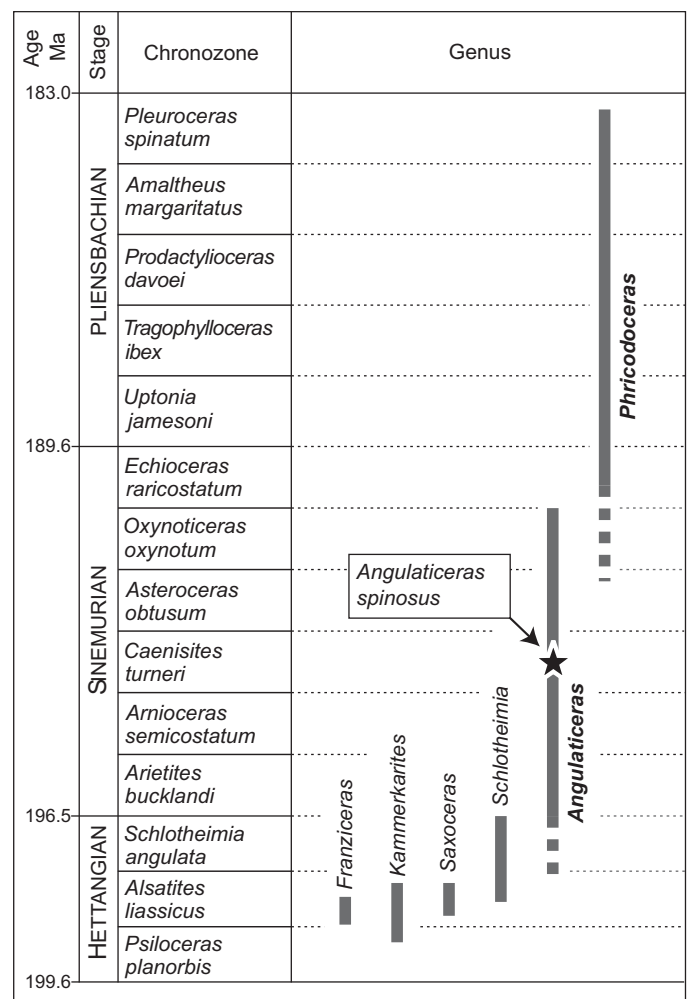


Fig. 1. Bio-chronostratigraphic framework of the six genera belonging to the Schlotheimiidae as this family is understood in the present paper. The ranges are referred to the standard chronostratigraphic scale (stages and chronozones) so that relevant global comparisons can be made. The probable age of *Angulaticeras spinosus* is starred. Radiochronologic ages of the stage boundaries from Ogg et al. (2008). The height of the chronozone boxes varies with the stage duration in Myr.

*Phricodoceras* obviously reflects the persistence of only a few but striking ornamental diagnostic traits (autapomorphies). On the contrary, such flagrant features are missing among the earliest representatives of the family and the genus diagnoses are clearly less constrained as a result. So comparisons of genus durations are perhaps weakly significant in evolutionary words.

In paleobiogeographic terms *Phricodoceras* is a taxon chiefly known in the Mediterranean and NW European confines of the Western Tethys (Fig. 2). Thus, of the just over one hundred publications featuring, to some extent, the genus *Phricodoceras*, 37 concern the Mediterranean faunas (including the Pontides, Northern Turkey), 41 discuss the NW European faunas, and only 7 refer to other parts of the world. In fact, very few specimens are cited outside the Mediterranean Tethys, NW Europe and the Pontides (Fig. 2). Moreover, the

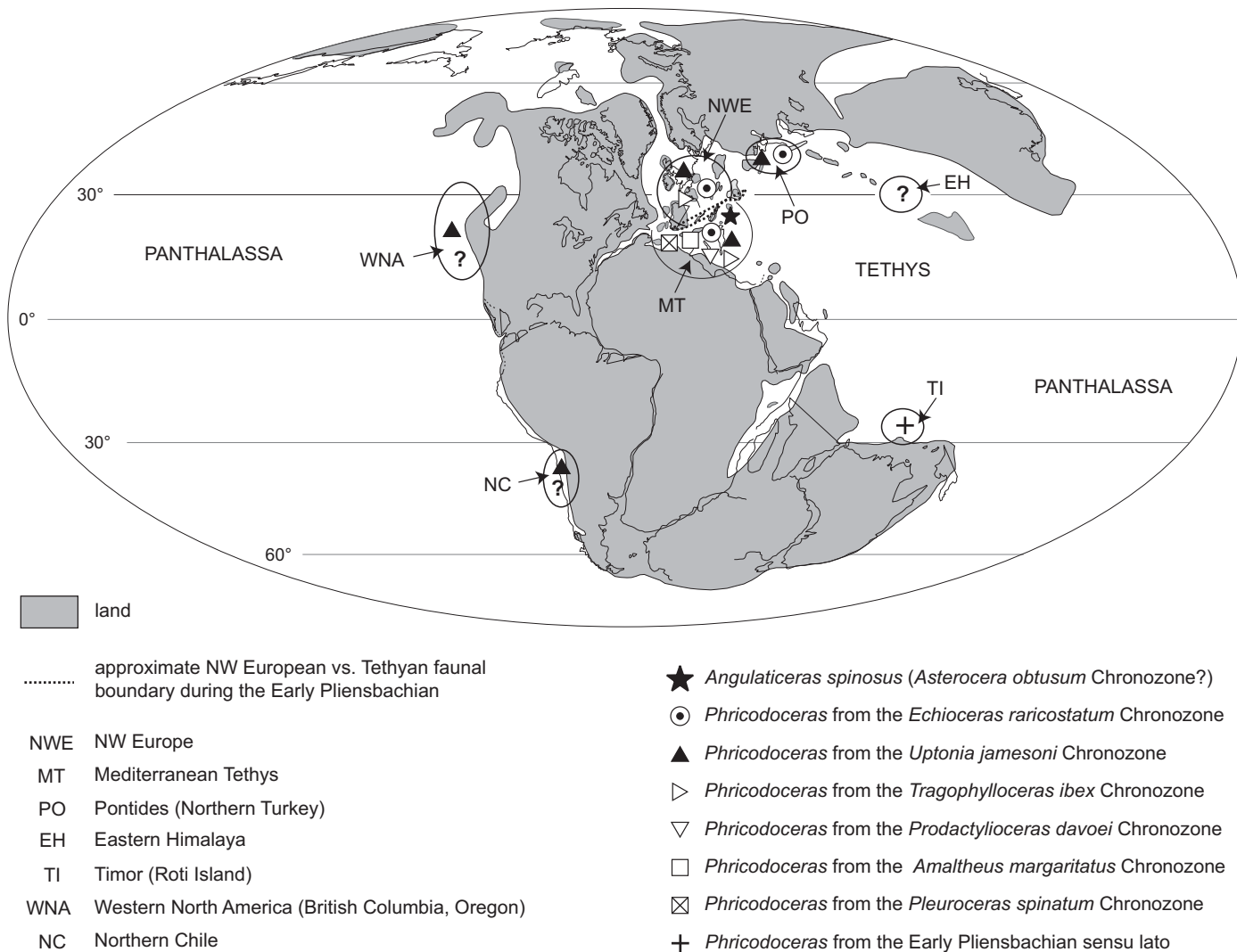


Fig. 2. Schematic distribution of *Angulaticeras spinosus* Meister, Schlögl, and Rakús, 2010 and *Phricodoceras* at the global scale. The approximate boundary between the NW European and Tethyan (Mediterranean) faunas is suggested by a dotted line. Paleogeographical reconstruction from Vrielynck and Bouysse (2001), modified.

specimens from Western North America, Northern Chile and the Eastern Himalayas are unconvincing or questionable. The only reliable representative of the genus *Phricodoceras* from outside the Mediterranean and NW European confines of the Western Tethys is a finely preserved specimen from the Timor area close to the Australian Tethyan margin (Krumbeck 1922). Ideally, it would be best to consider the stratigraphic sensu lato and sedimentological frameworks so as to counterbalance this crude palaeobiogeographical data, which can yield a partly biased picture of reality. Unfortunately, though, the present synthesis is grounded on such heterogeneous literature that the consideration of stratigraphic and sedimentological data is no more than an ideal. Nevertheless—as previously demonstrated for the Early Pliensbachian by Dommergues et al. (2009: fig. 6)—despite a similar study effort (at least in terms of number of publications), the Mediterranean Tethys palaeobiodiversity is clearly richer than that of NW Europe, although it is still undersampled in comparison.

More generally, the Mediterranean Tethys seems to be the only known sustained “hot spot” of *Phricodoceras* diversity. By contrast, only a few species related to the group of *P. taylori* sensu lato are known in NW Europe and almost all of the many specimens known in this area are associated with a brief dramatic acme in the lower part of the *Uptonia jamesoni* Chronozone. Paradoxically, the *Phricodoceras* are never common in the Mediterranean Tethys but both their taxonomic diversity and their morphological disparity remain persistently high in this area where the genus is recurrently observed from the *Echioceras raricostatum* Chronozone to the base of the *Pleuroceras spinatum* Chronozone (Figs. 1, 2). We must also emphasize that *Angulaticeras* (*Angulaticeras*) *spinus*, a possible ancestor of *Phricodoceras*, is to date only known in the Mediterranean Tethys (i.e., Austroalpine). In terms of diversity (i.e., comparison of the number of species during the *Echioceras raricostatum* and *Uptonia jamesoni* chronozones) the

Pontides area occupies an intermediate position between the Mediterranean Tethys and NW Europe.

In this paper, the binominal italicized names of chronozones result from the policy of the journal that any names derivative of biological species should be written in this way.

## Morphology, dimorphism, ontogeny, and adaptation

The diagnostic features of *Phricodoceras* and especially the “juvenile” ornamental features are very unusual for Early Jurassic ammonites and the genus has always been regarded as forming both a highly distinctive and a homogeneous taxon. Even the most morphologically derived forms (e.g., tiny Late Pliensbachian microconchs or large Early Pliensbachian macroconchs) can be fairly easily attributed to the genus. As a result, the synonymy of the genus is limited to a single taxon (i.e., *Hemiparinodoceras* Géczy, 1959) and there is no subgenus to suggest possible groupings within the twenty or so nominal species. Despite its apparent homogeneity, the genus *Phricodoceras* is not a simple lineage but, as evidenced by Meister (2007: fig. 15), a clade with a rather complex internal structure. The concept of “species complex” might be helpful in putting the clade topology into words. Even if the phenomenon tends to decrease with time, a usually obvious microconch (m)/macroconch (M) dimorphism characterizes the *Phricodoceras* as exemplified by the pair of nominal species *P. taylori* (m)–*P. lamellosum* (M) in Fig. 3. Dimorphism seems to have peaked in this group close to the base of the Early Pliensbachian in NW Europe and therefore in a palaeobiogeographical context suggesting a briefly successful northward faunal ingressions. The extent of this striking dimorphism is difficult to quantify because the largest known *P. lamellosum* (M) are all incomplete phragmocones (e.g., Fig. 3A), and their adult body chambers are unknown. However, a ratio of about one to ten in diameter can be reasonably suspected. The intermediate and outer whorls of the large macroconch forms have rather involute and compressed shells with slightly curved flanks and a rounded ventral area. The transition between the umbilical area and the base of the flanks is rounded without shoulders, although faint peri-siphonal shoulders (s3), inherited from juvenile peri-siphonal tubercles (t3), may persist at relatively large diameters (e.g., Fig. 3A, B). The ornamentation of crowded, fine, subdivided and slightly flexuous ribs is rather discreet and often somewhat irregular (e.g., Fig. 3A). At large diameters the ribs may cross the ventral area. Thus, the pre-adult and probably also the adult (body chamber) habitus of the macroconch is coarsely comparable, at the same diameter, to that of *Angulaticeras*. Actually, at large diameters *Phricodoceras lamellosum* (M) looks similar to *Angulaticeras* although with a less compressed shell and a wider and more rounded ventral area. In contradistinction, the traits of the in-

ner whorls of the macroconch and microconch at all ontogenetic stages (e.g., *P. taylori*) are quite distinctive and preclude any confusion. At small diameters *Phricodoceras* may display one of the most impressively tuberculate ornamentations among the Early Jurassic ammonites, notably an exceptional peri-siphonal (t3) row of tubercles or spines (Figs. 4, 5). The inner mould of the phragmocones exhibits only the bases of the spines, which in this case look like truncated tubercles or bullae (Fig. 4), but some well-preserved specimens display prominent spines especially in peri-siphonal (t3) and latero-ventral (t2) positions (e.g., Buckman 1911: pl. 33; Hoffmann 1982: pl. 14: 3; Edmunds et al. 2003: fig. 20.5) (Fig. 5E). Within the groups of *P. taylori* (m)–*P. lamellosum* (M) and of *P. bettoni* (m) Géczy, 1976–*P. urkuticum* (M) (Géczy, 1959) at least, up to three rows of tubercles can be observed, though briefly, during the most strongly ornamented growth stage (Meister 2007: fig. 11). The positions of these three rows of tubercles are indicated in Fig. 4. Among the genus *Phricodoceras* the latero-umbilical (t1) row of tubercles is often missing and the latero-ventral (t2) row is sometimes absent, even in the group of *P. taylori* (m)–*P. lamellosum* (M) (e.g., *Phricodoceras* aff. *cornutum* [Simpson, 1843]) (Fig. 3D). Conversely the peri-siphonal (t3) row of tubercles remains visible, during a brief growth stage at least. The permanence of this trait is strong evidence that the peri-siphonal tubercles or shoulder (t3 or s3) of *Phricodoceras* are homologous with the sudden peri-siphonal interruption of the ribs or shoulders (s3) of *Angulaticeras*, which is also a very permanent juvenile trait (Figs. 4–6). Although less distinctive, the suture lines of *Phricodoceras* also have informative features which can be contrasted with *Angulaticeras* on the basis of a comparative study of septal suture ontogenies. The pointed, often slender and trifid (sometimes sub-triangular) lateral lobe of *Phricodoceras* is the most obvious similarity (Fig. 7), and despite many apparent differences, the suture line of *Phricodoceras* can be understood as a simplified version of that observable in *Angulaticeras* with wider saddles and chiefly without any clear retracted suspensive lobe, as is usual in *Angulaticeras*. Many of these differences and especially the lack of an obvious suspensive lobe are probably partially correlated with different shell morphologies. At the same diameters, shells are clearly more involute and compressed in *Angulaticeras* than in *Phricodoceras* whose inner whorls, at least, often have sub-circular sections and barely overlap the successive whorls, thus providing less space for the retraction of the umbilical lobes. Conversely, the suture lines of *Phricodoceras* are very different from those of both the Lytoceratoidea and Eodoceratoidea whose bifid or trifid lateral lobes are invariably apically broad but abapically often narrow (Fig. 8).

The evolution of *Phricodoceras* is, as demonstrated by Meister (2007: fig. 11), basically controlled by ontogenetic heterochronies in the “size-based” or “allometric” and not “age-based” sense of the term. Fig. 9 summarizes and simplifies the model proposed by Meister (2007) for *Phricodoceras* and extends it to a broader taxonomic framework

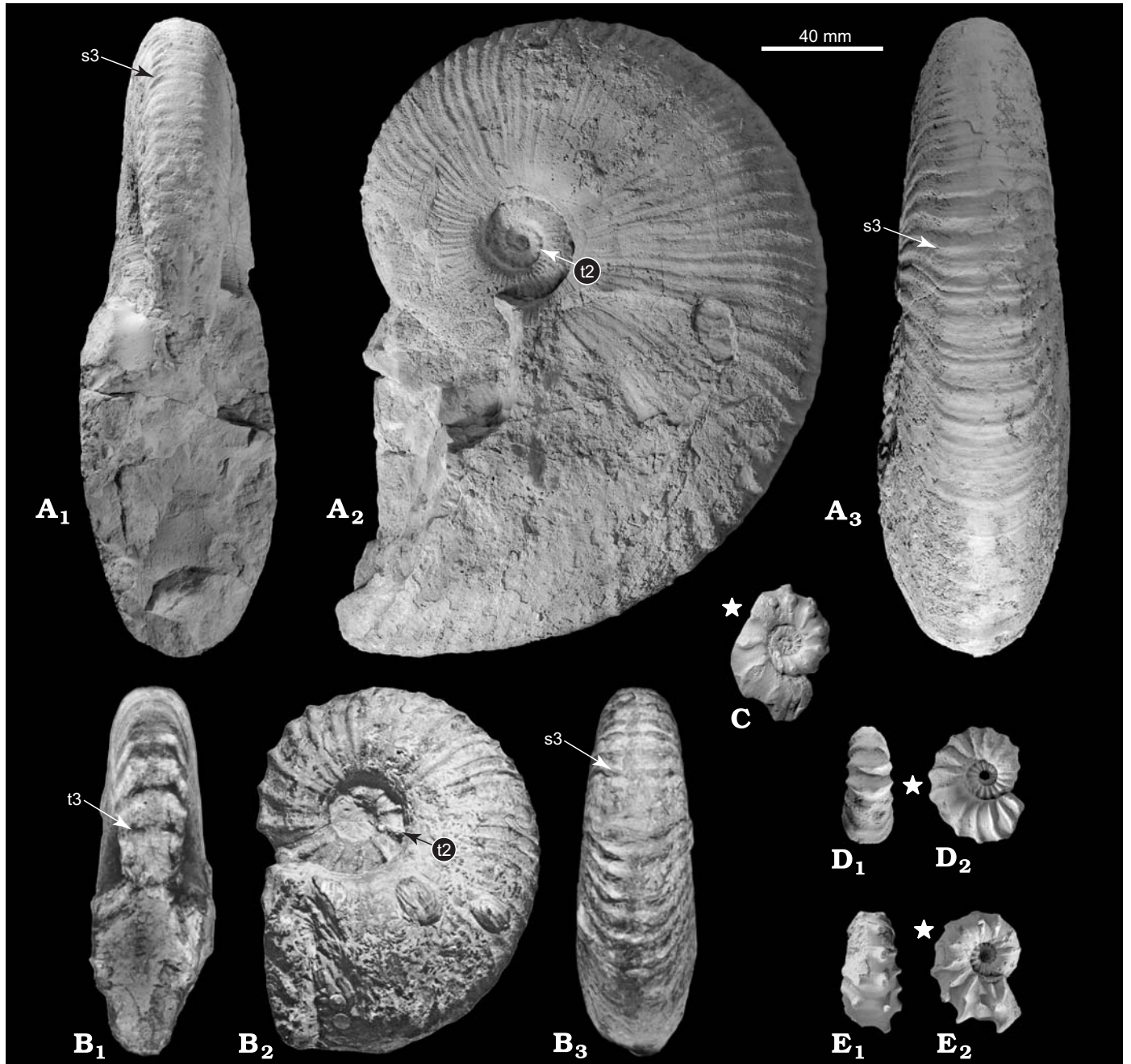


Fig. 3. Microconch (m) / macroconch (M) dimorphism expressed by scholtheimiid ammonoid *Phricodoceras* exemplified by the NW Europe forms in the *Uptonia jamesoni* to *Tragophylloceras ibex* chronozones. **A.** *Phricodoceras lamellosum* (Orbigny, 1844) (M), UBGD 277451, Mazenay, Saône et Loire, France, probably early *Uptonia jamesoni* Chronozone, in apertural (A<sub>1</sub>), lateral (A<sub>2</sub>), and ventral (A<sub>3</sub>) views. **B.** *Phricodoceras lamellosum* (M), Kircheim unter Teck, Baden-Württemberg, Germany, Early Pliensbachian (from Schlegelmilch 1976: pl. 27: 4, modified; original from Quenstedt 1884: pl. 28: 24), in apertural (B<sub>1</sub>), lateral (B<sub>2</sub>), and ventral (B<sub>3</sub>) views. **C.** *Phricodoceras taylori* (Sowerby, 1826) (m), Corbigny, Nièvre, France, *Uptonia jamesoni* Chronozone, *Phricodoceras taylori* Subchronozone (from Dommergues 2003: pl. 1: 4), in lateral view. **D.** *Phricodoceras* aff. *cornutum* (Simpson, 1843) (m), Fresnay-le-Puceux, Calvados, France, Early Pliensbachian (from Dommergues et al. 2008: pl. 3: 6, modified), in ventral (D<sub>1</sub>) and lateral (D<sub>2</sub>) views. **E.** *Phricodoceras taylori* (m), Fresnay-le-Puceux, Calvados, France, Early Pliensbachian (from Dommergues et al. 2008: pl. 3: 5, modified), in ventral (E<sub>1</sub>) and lateral (E<sub>2</sub>) views. The two specimens corresponding to A, B are incomplete phragmocones (juvenile or immature shells) but the three corresponding to C–E are adult microconchs with the major part of the body chamber. The end of the phragmocone is starred. Notice the progressive ontogenetic transformation from tubercle (t3) to faint shoulder (s3) in specimen B. Abbreviations: t2, tubercle in latero-ventral position; t3, tubercle in peri-siphonal position; s3, shoulder peri-siphonal position.

including *Angulaticeras*, with *A. boucaultianum* (Orbigny, 1844) (Early Sinemurian) for comparison and *A. spinosus* (Late Sinemurian) as a possible ancestor or at least the sister group of *Phricodoceras* (Late Sinemurian to Late Pliens-

bachian). The first step (*A. boucaultianum* to *A. spinosus*) involves a “juvenile innovation” sensu Dommergues et al. (1986) and Dommergues (1987), a phenomenon that is not a heterochony sensu stricto but which immediately precedes

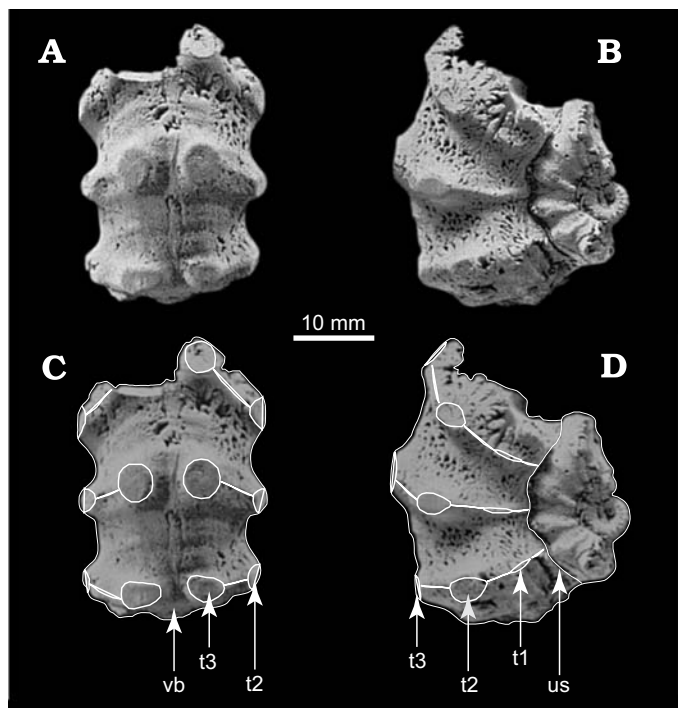


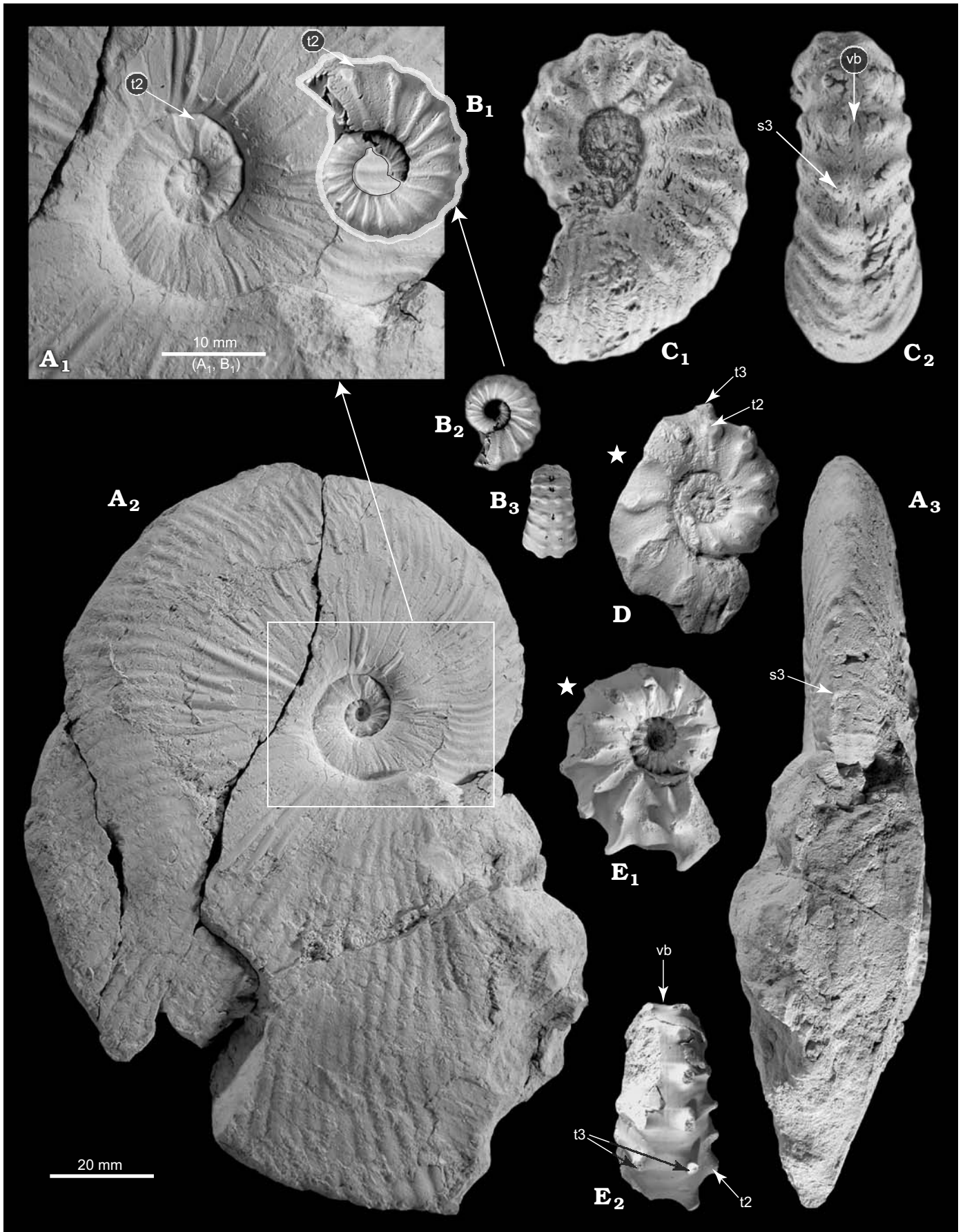
Fig. 4. Position and terminology of the tubercles, spines and/or bullae on *Phricodoceras* shells (juvenile and/or microconch. **A, B.** Normal view. **C, D.** Shaded view with indication of the main ornamental structure outlines (white lines). Abbreviations: t1, latero-umbilical position; t2, latero-ventral position; t3, peri-siphonal position; us, umbilical seam; vb, ventral band.

evolutionary phenomena chiefly controlled by heterochronies. In the case of *A. spinosus*, the innovation is the possibly rapid emergence of an obviously tuberculated ornamentation in the innermost whorls only. Conversely, the subsequent and merely ribbed growth stages of this species are usual for *Angulaticeras*. Truncated tubercles in (t2) position are clearly visible up to an umbilical diameter of 11 mm (Fig. 5A<sub>1</sub>, A<sub>2</sub>). They are similar to the tubercles in the same position and at the same diameter in *Phricodoceras* (Fig. 5B<sub>1</sub>) so, and although the ventral area is concealed by whorl overlap, it is plausible that tubercles also exist in peri-siphonal position in the inner whorls of *A. spinosum*. The second step (*A. spinosus* to *P. lamellosum*) is chiefly a paedomorphic pattern of heterochony with an obvious deceleration of growth sensu Reilley et al. (1997). As is often the

case, retardation is accompanied by a dramatic enhancement of the juvenile features and the tuberculated ornamentation reaches a maximum in the group of *P. taylori* (m)–*P. lamellosum* (M). The spines reach outstanding proportions and three rows of tubercles are usual. The third (*P. lamellosum* to *P. urkuticum*) and fourth (*P. urkuticum* to *P. paronai* [Bettoni, 1900]) steps follow a reversal and an increase in complexity of the heterochronic pattern. These last two steps in *Phricodoceras* history witness a sustained contraction and weakening of the juvenile tuberculate stage and a correlative progressive decline in adult size. This complex pattern suggests the combination of two distinct polarities, one peramorphic (by acceleration of growth) and the other paedomorphic (by hypomorphosis), although “phyletic dwarfism” is another possibility because size is not necessarily a proxy of age. In palaeobiogeographical terms the late tiny or at least smallish (possibly dwarf ?) *Phricodoceras* are rare, or even very rare, strictly Tethyan species; however, relations with the palaeoenvironmental conditions remains obscure.

In terms of adaptation and traits of life history only assumptions are possible. Nevertheless, the importance of patterns chiefly related with juvenile stages (i.e., juvenile innovation and paedomorphosis by deceleration) suggests that the evolutionary history of *Phricodoceras* was a phenomenon partly associated with changes in juvenile living conditions (Fig. 10). It seems reasonable to assume that the spectacular tuberculate ornamentation ensured an effective passive protection both for the juvenile macroconchs and for the microconchs throughout their growth. In this sense, the emergence of a tuberculate growth stage in *Phricodoceras*, and therefore within the Schlottheimidae, could be understood as a convergence with the plentiful and diversified Late Sinemurian and Early Pliensbachian tuberculated Eoderoceratoidea (Fig. 11B, C). Conversely, it is possible that the living conditions of the post-juvenile macroconchs of *Phricodoceras* were little changed from those of *Angulaticeras*. Differences in lifestyle between juvenile macroconchs and microconchs (assumed to have been not very mobile but passively protected) and adult macroconchs (assumed to have had better hydrodynamic abilities and mobility, as suggested by the more compressed shell, with weaker and more flexuous ornamentation) are therefore perhaps the key to the spe-

Fig. 5. Comparison of morphological and ornamental patterns of schlottheimiid ammonoid *Angulaticeras spinosus* Meister, Schlögl, and Rakús, 2010 and *Phricodoceras* gr. *taylori* (Sowerby, 1826) (m)–*Phricodoceras lamellosum* (Orbigny, 1844) (M). **A.** *Angulaticeras* (*Angulaticeras*) *spinosus* (M?), holotype, Chtelnica, Male Karpaty Mts., Western Carpathians, Slovakia, Sinemurian condensed bed (from Meister et al. 2010: fig. 34, a, b, modified), in lateral (A<sub>1</sub>, A<sub>2</sub>) and apertural (A<sub>3</sub>) views. **B.** *Phricodoceras taylori* (m?), Corbigny, Nièvre, France, *Uptonia jamesoni* Chronozone, *Phricodoceras taylori* Subchronozone (from Dommergues 2003: pl. 1: 2, modified), in lateral (B<sub>1</sub>, B<sub>2</sub>) and ventral (B<sub>3</sub>) views. **C.** *Phricodoceras lamellosum* (M), Hinterweiler, Baden-Württemberg, Germany, Early Pliensbachian (from Schlatter 1980: pl. 6: 6, modified), incomplete phragmocone showing the transition between the juvenile tuberculate stage and the late merely ribbed stage, in lateral (C<sub>1</sub>) and ventral (C<sub>2</sub>) views. **D.** *Phricodoceras taylori* (m), Corbigny, Nièvre, France, *Uptonia jamesoni* Chronozone, *Phricodoceras taylori* Subchronozone (from Dommergues 2003: pl. 1: 4), in lateral view. **E.** *Phricodoceras taylori* (m), Fresnay-le-Puceux, Calvados, France, Early Pliensbachian (from Dommergues et al. 2008: pl. 3: 5, modified), in lateral (E<sub>1</sub>) and ventral (E<sub>2</sub>) views. To facilitate comparisons at small diameters, A<sub>1</sub> and B<sub>1</sub>, respectively corresponding to A<sub>2</sub> and B<sub>2</sub>, are twice magnified. The three specimens corresponding to A–C are incomplete phragmocones (juvenile or immature shells) but the two specimens corresponding to D, E are adult microconchs with the major part of the body chamber. The end of the phragmocone is indicated by a star. Some noticeable ornamental elements are indicated by arrows: smooth ventral band (vb), tubercle in latero-ventral position (t2), tubercle or shoulder in peri-siphonal position (t3 or s3).





cific features of *Phricodoceras*. This hypothesis, summarized in Fig. 10, is partly speculative, though, because ecological considerations derived from shell type and sculpture with respect to “abilities” for swimming and/or maneuverability are interesting but unfortunately limited for all ectocochleate cephalopods (Westermann and Tsujita 1999).

## Systematic palaeontology

Class Cephalopoda Cuvier, 1798

Subclass Ammonoidea Zittel, 1884

Order Phylloceratida Arkell, 1950  
(sensu Hoffmann 2010)

Suborder Psiloceratina Housa, 1965  
(sensu Guex 1987 = Ammonitina Arkell, 1950,  
sensu Hoffmann 2010)

Superfamily Psiloceratoidea Hyatt, 1867  
(sensu Guex 1995)

Family Schlotheimiidae Spath, 1923

*Remarks.*—In view of the close relationships between *Angulaticeras* and *Phricodoceras* with *A. spinosus* as a convincing intermediate form, it appears convenient to include *Phricodoceras* in the Schlotheimiidae and to abandon the subfamily and family terms Phricodoceratinae and Phricodoceratidae. This classification has already been adopted by Meister et al. (2011). Its main advantage is that it is readily supported by the comparative anatomy within the Psiloceratoidea and is founded on an odd morpho-ornamental feature (i.e., the “*Phricodoceras* habitus”) the complexity of which greatly reduces the risk of convergences.

Genus *Phricodoceras* Hyatt in Zittel, 1900  
= *Hemiparinodiceras* Géczy, 1959

*Type species:* *Ammonites taylori* Sowerby, 1826; Early Pliensbachian, from a boulder in glacial till at Happisburgh, Norfolk, England, by original designation.

*Remarks.*—21 nominal species can be attributed to the genus *Phricodoceras*. Nine of them are based on NW European specimens and 11 on Tethyan sensu lato forms. In a recent revision of the genus, Meister (2007) retains only 11 valid species, three of which are NW European while seven are Tethyan. These proportions are representative of the high diversity of the genus *Phricodoceras* in Tethyan and especially Mediterranean faunas. According to Meister (2007), three m–M pairings can be suspected while four small or tiny species (one NW European and three Mediterranean) cannot readily be considered microconchs despite their small size. In fact, despite its indisputable success in the palaeontological literature, the m–M model is often far from evidence. The possibility of small species without or at least without significant m–M dimorphism is rarely considered as a valuable alternative hypothesis for ammonites (Davis et al.

1996). Such a pattern, however, is not rare among the extant cephalopods.

*Geographic and stratigraphic range.*—Chiefly NW Europe and Mediterranean Tethys including Pontides (Turkey). The presence of *Phricodoceras* is also attested in Timor (Indonesia) but is doubtful in British Columbia (Canada), Oregon (USA), and Chile. *Phricodoceras* ranges from Late Sinemurian to Late Pliensbachian.

## The phylogenetic and taxonomic quest

*Phricodoceras* in the literature.—Since 1826, a hundred or so publications have dealt, at least in part, with *Phricodoceras*. Most of them contain illustrations (drawings or photographs). All these publications are considered in Fig. 12 with a view to summarizing the taxonomic opinions of their authors (Sowerby 1826; Zieten 1830; Orbnigny 1844; Quenstedt 1846, 1849, 1883; Opper 1853, 1856; Hauer 1861; Wright 1880; Fucini 1898, 1908; Bettoni 1900; Del Campana 1900; Hyatt 1900; Buckman 1911, 1921; Krumbeck 1922; Schröder 1927; Höhne 1933; Gérard and Théry 1938; Roman 1938; Spath 1938; Otkun 1942; Venzo 1952; Fantini Sestini and Paganoni 1953; Donovan 1954; Arkell et al. 1957; Géczy 1959, 1979, 1998; Dean et al. 1961; Fantini Sestini 1962, 1978; Schindewolf 1962; Bremer 1965; Cantaluppi and Brambillia 1968; Frebald 1970; Wiedmann 1970; Tintant et al. 1975; Schlegelmilch 1976; Schlatter 1977, 1980, 1990, 1991; Dommergues 1978, 1993, 2003; Dubar and Mouterde 1978; Alkaya 1979; Linares et al. 1979; Wiedenmayer 1980; Donovan et al. 1981; Hoffmann 1982; Venturi 1982; Braga 1983; Mouterde et al. 1983; Büchner et al. 1986; Meister and Sciau 1988; Smith et al. 1988; Dommergues and Meister 1990, 1999; Dommergues et al. 1990, 2000, 2008; Cope 1991; Ferretti 1991; Sciau 1991; Tipper et al. 1991; Page 1993, 2008; Dommergues and Mouterde 1994; Mouterde and Dommergues 1994, Alkaya and Meister 1995; El Hariri et al. 1996; Faraoni et al. 1996; Smith and Tipper 1996; Géczy and Meister 1998, 2007; Rakús 1999; Macchioni 2001; Venturi and Ferri 2001; Howarth 2002; Rakús and Guex 2002; Donovan and Surlyk 2003; Edmunds et al. 2003; Meister et al. 2003, 2010, 2011; Hillebrandt 2006; Meister 2007; Yin et al. 2007; Venturi and Bilotta 2008; Venturi et al. 2010; Blau and Meister 2011).

In all, 162 specimens are figured in these publications, including 78 for NW Europe and 84 for the Tethyan realm sensu lato. Compared with other taxa, such a large number of illustrations is not in proportion to the relative scarcity of *Phricodoceras* in the fossil record but partly reflects the special interest shown by authors in this morphologically astonishing and taxonomically challenging group. In fact, the illustrated specimens correspond to a significant portion of the

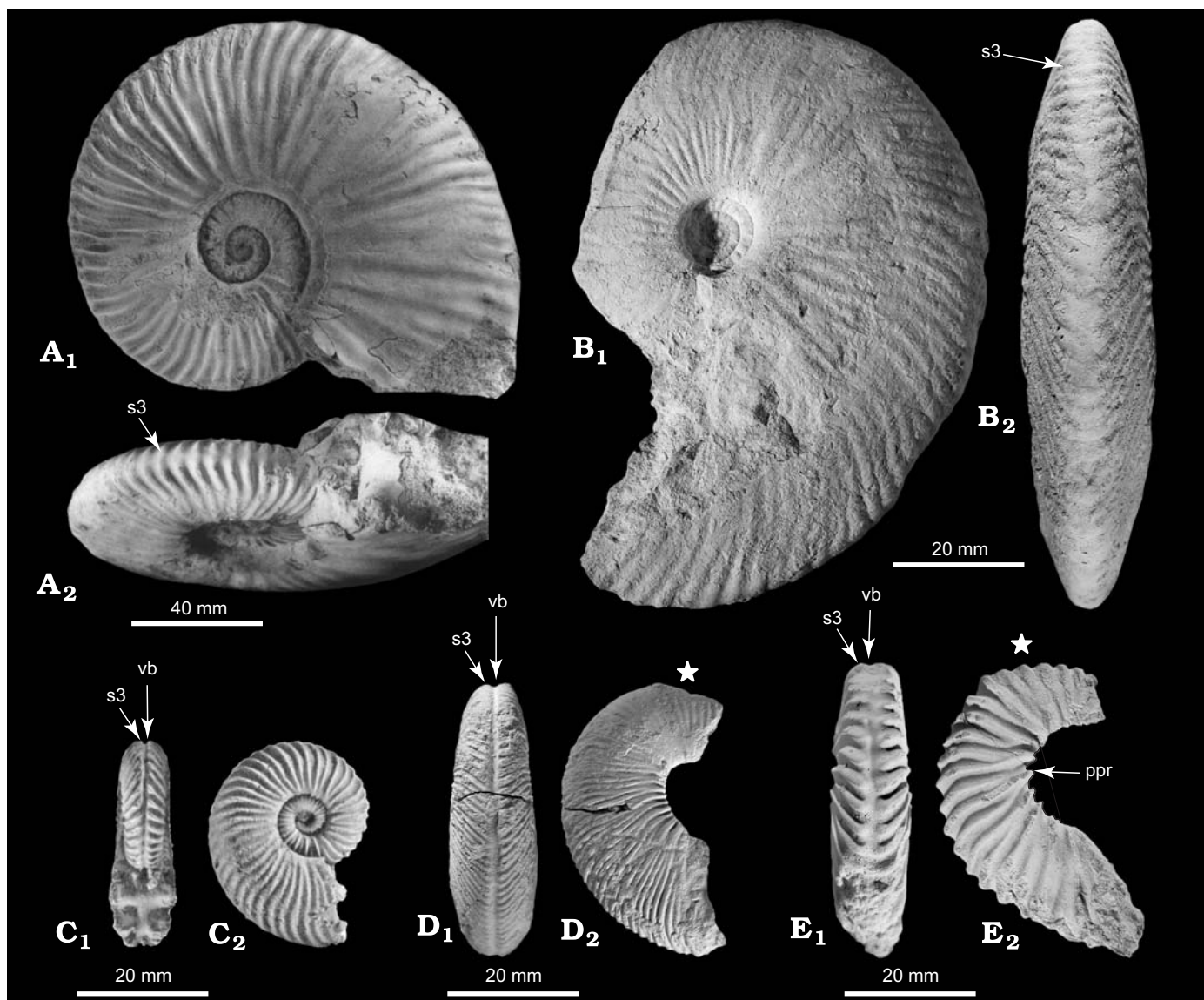


Fig. 6. Habitus of some specimens belonging to scholtheimiid ammonoid *Agulaticeras*, the genus which represents the root of *Phricodoceras*. **A.** *Angulaticeras (Sulciferites) charmassei* (Orbigny, 1844), Stuttgart-Vaihingen, Baden-Württemberg, Germany, *Arietites bucklandi* Chronozone, *Coroniceras rotiforme* Subchronozone (from Bloos 1988: pl. 11, modified), in lateral (A<sub>1</sub>) and apertural (A<sub>2</sub>) views. **B.** *Angulaticeras (Boucaulticeras) boucaultianum* (Orbigny, 1844), Chtelnica, Male Karpaty Mts., Western Carpathians, Slovakia, Sinemurian condensed bed (from Meister et al. 2010: fig. 42f, g, modified), in lateral (B<sub>1</sub>) and ventral (B<sub>2</sub>) views. **C.** *Angulaticeras (Boucaulticeras) gr. deletum* (Canavari, 1882), Jbel Bou Hamid, Central High Atlas (Rich), Morocco, Late Sinemurian (from Guex et al. 2008: pl. 4: 6, modified), in apertural (C<sub>1</sub>) and lateral (C<sub>2</sub>) views. **D.** *Angulaticeras (Boucaulticeras) gr. rumpens* (Oppel, 1862), Chtelnica, Male Karpaty Mts., Western Carpathians, Slovakia, Sinemurian condensed bed (from Meister et al. 2010: fig. 40c, d, modified), in ventral (D<sub>1</sub>) and lateral (D<sub>2</sub>) views. **E.** *Angulaticeras (Sulciferites) chtelnicaense* Meister, Schlögl, and Rakus, 2010, holotype, Chtelnica, Male Karpaty Mts., Western Carpathians, Slovakia, Sinemurian condensed bed (from Meister et al. 2010: fig. 32d, e, modified), in ventral (E<sub>1</sub>) and lateral (E<sub>2</sub>) views. A, C (and possibly B) are incomplete phragmocones (juvenile or immature shells) but the two specimens corresponding to D, E have a significant part of the body chamber intact. The age of D is doubtful but E is probably an adult. The end of the phragmocone is indicated by a star. The ornamentation of *Angulaticeras* is chiefly constituted by usually crowded, fairly flexuous and divided ribs which suddenly break up just before reaching the venter. At least at small diameters (juveniles, microconchs) the ventral area bears a narrow smooth and more or less depressed ventral band (vb). The abrupt endings of the ribs look like shoulders in peri-umbilical position (s3). Shoulders may vanish progressively with growth (B). Moreover, some rare species may exhibit unusual peri-umbilical projections from the ribs (ppr), which partially obstruct the umbilicus (E). Such projections are not true tubercles or spines.

samples collected in the NW European faunas and encompass almost all of the samples recovered in Tethyan *sensu lato* areas. In this context, the literature is probably very representative of the material collected over some two centuries, and largely housed in museums.

**Hypotheses, discussions, and facts.**—From Sowerby (1826) to Hauer (1861), the early authors described and depicted some convincing specimens belonging to the group of *Phricodoceras taylori* under the generic name *Ammonites* without any indication of possible relationships within this huge genus

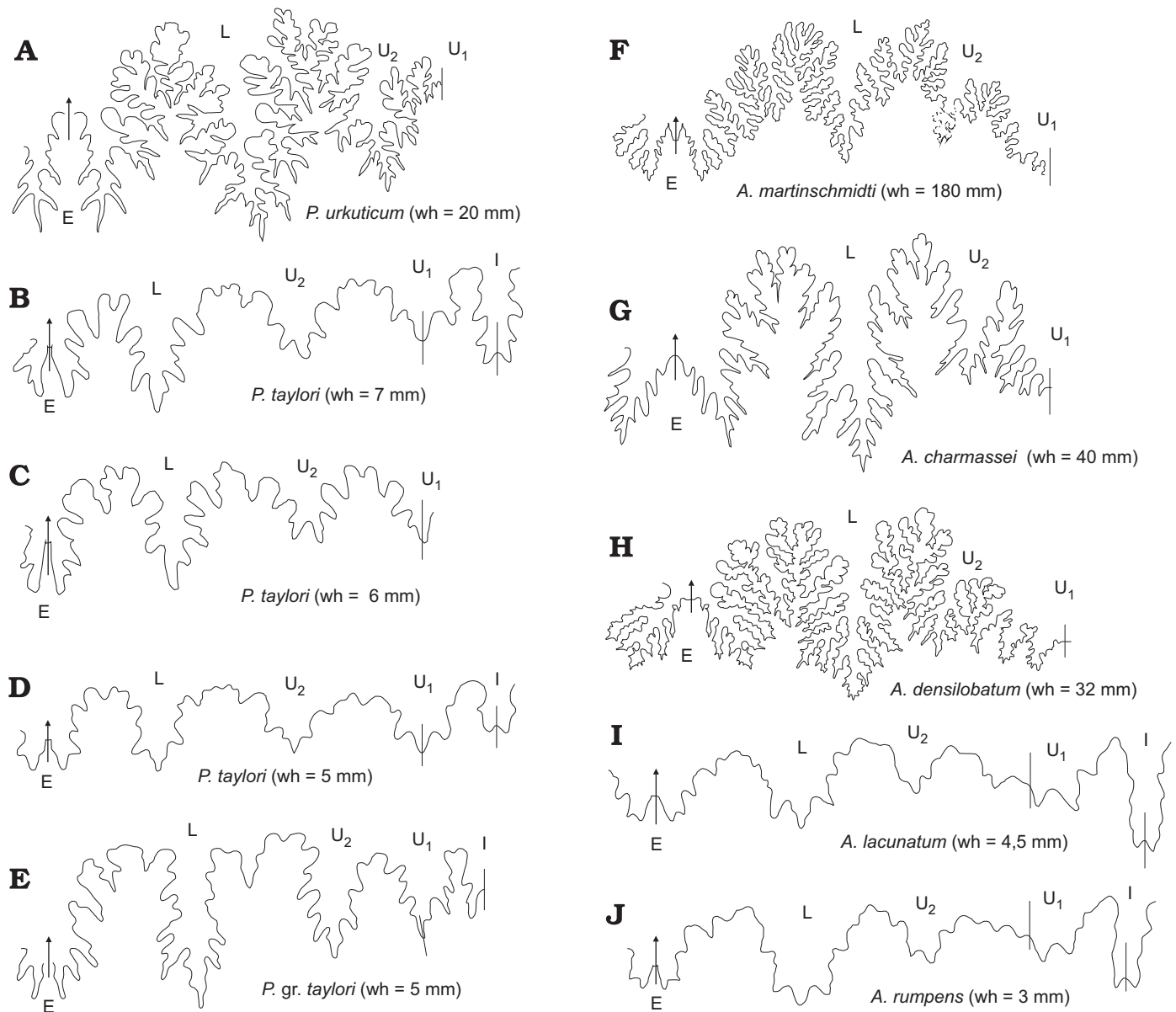


Fig. 7. Septal suture lines of several Schlotheimiidae belonging to the genera *Phricodoceras* (A–E) and *Angulaticeras* (F–J). **A.** *Phricodoceras urkaticum* (Géczy, 1959) (from Géczy 1976: fig. 49, modified). **B.** *Phricodoceras taylori* (Sowerby, 1826) (from Dommergues 2003: fig. 6A, modified). **C.** *Phricodoceras taylori* (from Dommergues 2003: fig. 6B, modified). **D.** *Phricodoceras taylori* (from Schlegelmilch 1976: 61, modified). **E.** *Phricodoceras* gr. *taylori* (Sowerby, 1826) (from Schlatter 1990: fig. 3, modified). **F.** *Angulaticeras martinischmidtii* (Lange, 1951) (from Schlegelmilch 1976: 38, modified). **G.** *Angulaticeras charmassei* (Orbigny, 1844) (from Schlegelmilch 1976: 38, modified). **H.** *Angulaticeras densilobatum* (Pompeckj, 1893) (from Schlegelmilch 1976: 39, modified). **I.** *Angulaticeras lacunatum* (J. Buckman, 1844) (from Schlegelmilch 1976, 38, modified). **J.** *Angulaticeras rumpens* (Opper, 1862) (from Schlegelmilch 1976: 39, modified). For each suture line the whorl height (wh) is indicated, if known. The main elements of the suture line are indicated by following abbreviations: E, external lobe; L, lateral lobe; U<sub>1</sub>, U<sub>2</sub>, umbilical lobes; I, internal lobe.

(Fig. 12). Publications during the subsequent period from Wright (1880) to Del Campana (1900) still lack explicit information about the possible relationships of the *Phricodoceras* at the family level. Nevertheless, the arrangement of the illustrated specimens on the plates (e.g., Quenstedt 1883–1885) and/or the use of genus names such as *Aegoceras* or *Dero-ceras* (e.g., Wright 1880; Bettoni 1900) suggest that the authors suspected possible relationships with certain taxa currently attributed to the Eoderoceratoidea (e.g., Liparoceratidae). This pre-family position is clearly supported by the

presence of tubercles and/or spines. At that same time, Hyatt (1900: 586–587) proposed the genus name *Phricodoceras*. Curiously this author included his new taxon in the “Cosmocerotidae” family with some Middle Jurassic forms (i.e., *Kosmoceras* and *Sigaloceras*) and surprisingly, at an informal higher taxonomic level, in the “Cosmocerotida” with some Cretaceous taxa (e.g., *Douvillieceras*). The grouping at family level proposed by Hyatt (1900) is based on obvious ornamental convergences and it is currently rejected as strongly polyphyletic. Only Gérard and Théry (1938) followed Hyatt’s

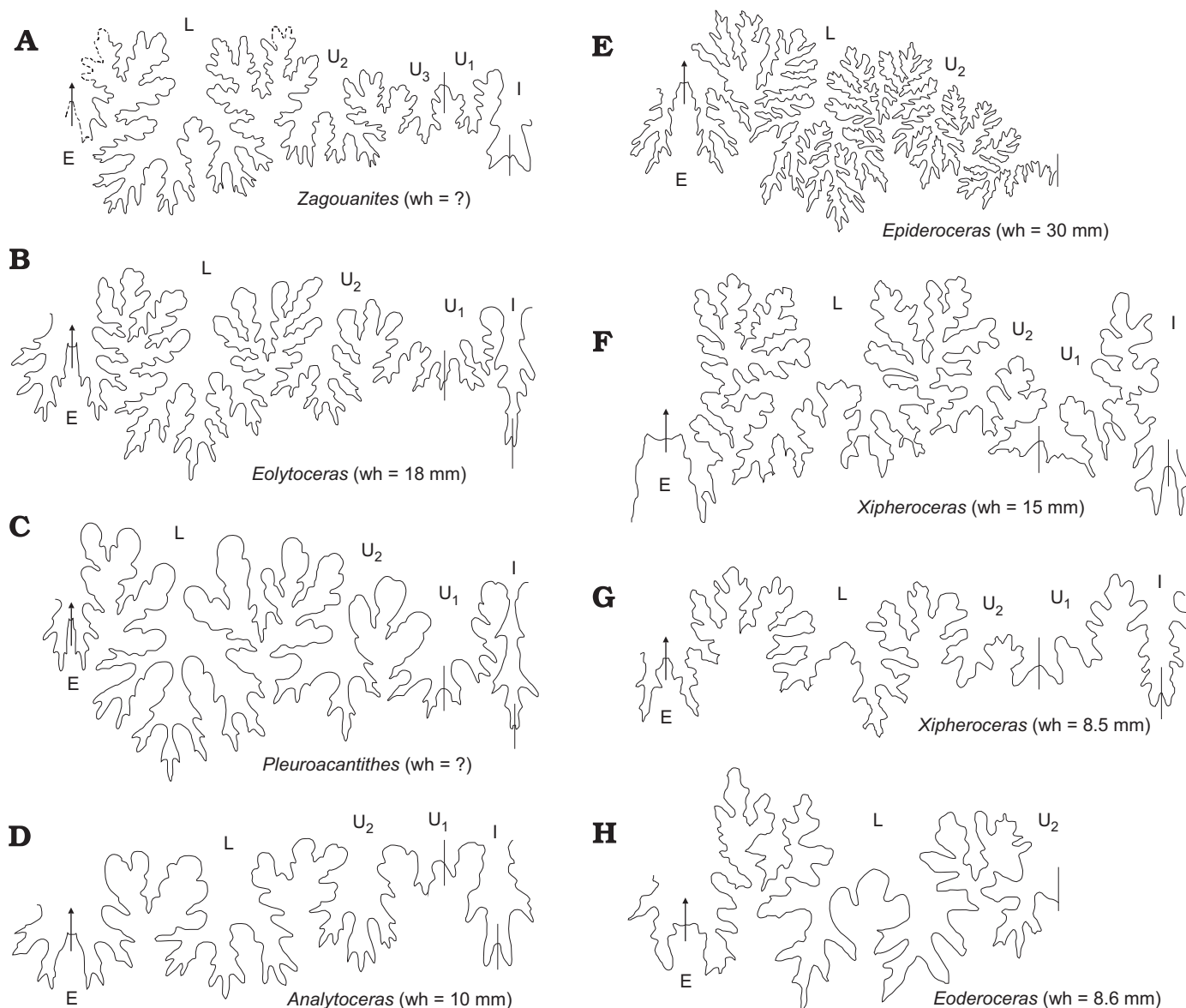


Fig. 8. Septal suture lines of several Lytoceratoidea (A–D) and Eoderoceratoidea (E–H) for comparisons with those of the scholtheimiid ammonoids *Angulaticeras* and *Phricodoceras* (Fig. 7). **A.** *Zagouanites arcanum* (Wiedenmayer, 1977) (from Rakús and Guex 2002: fig. 54e, modified). **B.** *Eolytoceras tasekoi* Frebold, 1967 (from Wiedmann 1970: text-fig. 9c, modified). **C.** *Pleuroacanthites bififormis* (Sowerby in De La Beche, 1831) (from Canavari 1888: text-fig. 2.3, modified). **D.** *Analytoceras* gr. *articulatum* (Sowerby in De La Beche, 1831) (from Wiedmann 1970: text-fig. 8a, modified). **E.** *Epideroceras planarmatum* (Quenstedt, 1856) (from Schlatter 1980: beil. 15a, modified). **F.** *Xipheroceras rasinodum* (Quenstedt, 1884) (from Schlegelmilch 1976: 57, modified). **G.** *Xipheroceras ziphus* (Zieten, 1830) (from Schlegelmilch 1976: 56, modified). **H.** *Eoderoceras bisbinigerum* (Buckman, 1918) (from Schlegelmilch 1992: 62, modified). For each suture line the whorl height (wh) is indicated, if known. The main elements of the suture line are indicated by following abbreviations: E, external lobe; L, lateral lobe; U<sub>1</sub>, U<sub>2</sub>, umbilical lobes; I, internal lobe.

(1900) proposal. On the contrary, Buckman (1911, 1921) explicitly includes *Phricodoceras* within the Liparoceratidae thereby clarifying and formalizing the implicit hypothesis of many previous authors. From that time until fairly recently—even if Spath (1938) creates the subfamily Phricodoceratinae (within the Eoderoceratidae)—*Phricodoceras* was understood, usually unreservedly, as belonging to the Eoderoceratoidea. The single notable exception is Wiedmann (1970: 1002) who proposes that *Phricodoceras* is a possible relative of *Adnethiceras* within the Lytoceratoidea. In fact, at the

superfamily level, the authors tend to conform to the position of Arkell et al. (1957) even if the family and subfamily levels are sometimes challenged. For example, the grouping of *Phricodoceras* and *Epideroceras* within the Phricodoceratinae proposed by Arkell et al. (1957) is abandoned by several authors (e.g., Cope 1991; Schlatter 1991; Dommergues and Meister 1999). Nevertheless, it was not until 1991 that the inclusion of *Phricodoceras* in the Eoderoceratoidea was seriously challenged by Kevin Page (personal communication to Dommergues 1993) and that convincing relationships with the

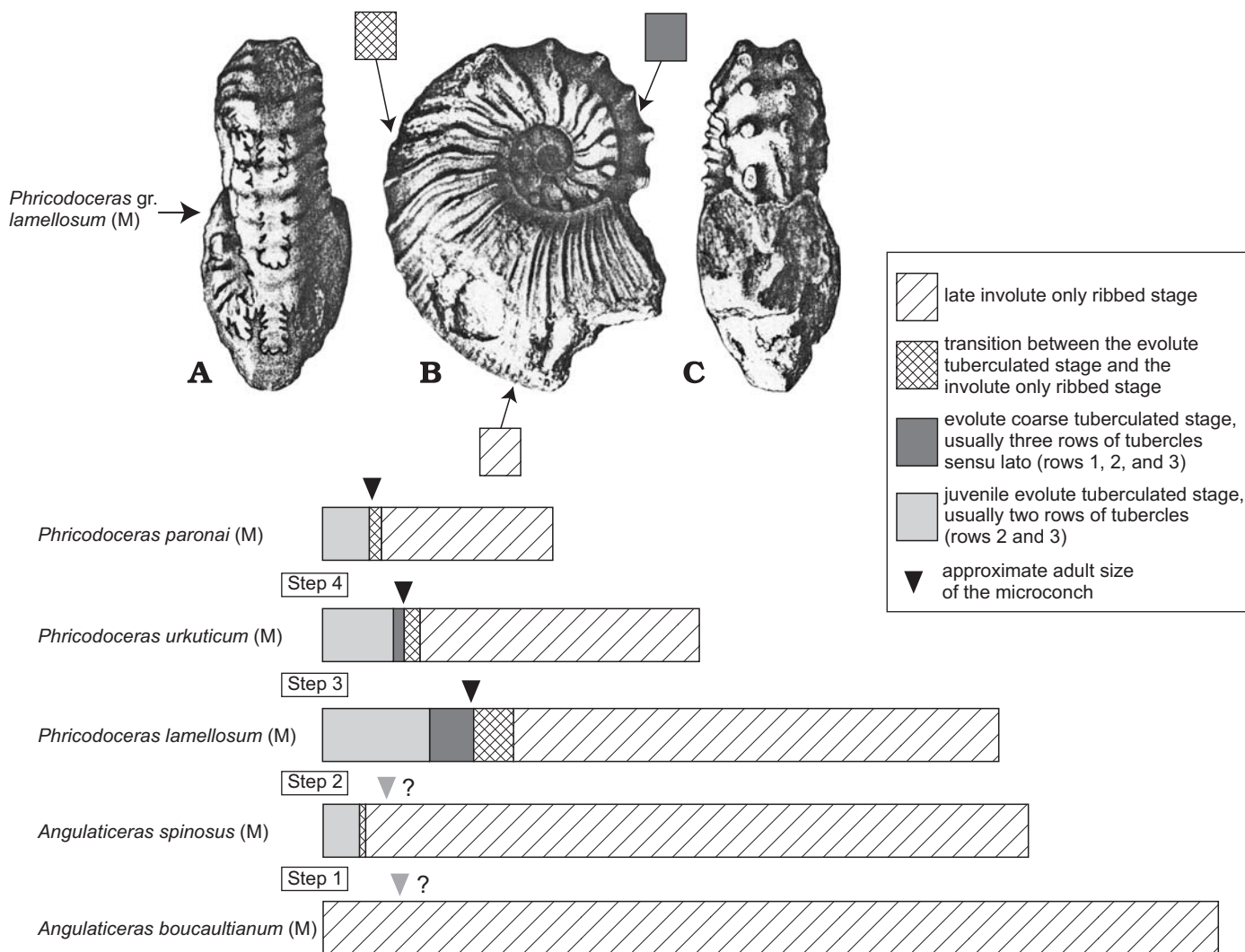


Fig. 9. Some illustrative steps—in terms of morphological ontogeny—in the intricate evolutionary trend from the Sinemurian scholtheimiid genus *Angulaticeras* to the late Pliensbachian *Phricodoceras* (i.e., *Phricodoceras paronai* [Bettoni, 1900]). For simplicity, the complex and more or less gradual ontogenetic transformations are reduced to just four stages (see A–C for an illustration of the last three). The length and the place of a given stage in the ontogenetic cartouches depend on its duration and position during ontogeny. The overall length of the cartouche is proportional to adult size. Ontogenies of the macroconchs (M) alone are depicted in the cartouches and the adult sizes (complete shells) of the microconchs (m) are suggested by black triangles (grey if doubtful). A–C. Scholtheimiid ammonoid *Phricodoceras lamellosum* (Orbigny, 1844), Rote Island, East Nusa Tenggara, Indonesia, probably Early Pliensbachian (from Krumbeck 1922: pl. 17: 5, modified), in ventral (A), lateral (B), and apertural (C) views.

Schlotheimiidae within the Psiloceratoidea were considered for the first time to be at least a plausible hypothesis. Despite this first serious challenge to the traditional taxonomic attribution, most authors until Yin et al. (2007) continued to consider *Phricodoceras* as member of Eoderoceratoidea with no further discussion. In spite of this taxonomic inertia, several publications have understood *Phricodoceras* as an unresolved taxon and two to four credible but rival hypothesis have been suggested (Dommergues 1993, 2003; Dommergues and Meister 1999; Meister 2007; Dommergues et al. 2008). In all these papers, the possibility of the Schlotheimiidae and *Phricodoceras* being closely related is seriously considered but Edmunds et al. (2003) were clearly the first to propose this taxonomic option unreservedly albeit unfortunately without any compelling evidence. Later, Page (2008) took up this position

but with some reservations. Such an alternative was discussed also by Venturi and Bilotta (2008) and Venturi et al. (2010), and their choice of a doubtful superfamily classification for the Phricodoceratidae was due to the lack of decisive data. The proof that *Phricodoceras* belongs to the Schlotheimiidae was ultimately provided by Meister et al. (2010), who described a new *Angulaticeras* (i.e., *A. spinosus*) whose inner whorls are virtually indistinguishable from those of *Phricodoceras* gr. *taylori*–*P. lamellosum* at the same diameter. Since this publication, all subsequent works have placed the *Phricodoceras* within the Psiloceratoidea and close to or within the Schlotheimiidae (Blau and Meister 2011; Meister et al. 2011).

**Characters, assumed relationships, and taxonomic practice.**—The history of taxonomic practice is rarely considered

for itself, especially for ammonites (Donovan 1994). This is regrettable because such historical approaches may help to refine taxonomic practices empirically by highlighting some misleading but consensual traditions. The case of *Phricodoceras* is particularly instructive in this respect because a widely accepted hypothesis, herein rejected, has affected the taxonomic understanding of this remarkable group of ammonites. This confusing but successful hypothesis is based on a dual argument grounded on both the concepts of “overall resemblance” and of “stratigraphic consistency”. Indeed, *Phricodoceras* and especially the emblematic *P. taylori*, which is locally not rare in the *Uptonia jamesoni* and *Tragophylloceras ibex* chronozones (Early Pliensbachian), can be roughly compared with some Late Sinemurian and/or Early Pliensbachian Eoderoceratoidea (e.g., Eoderoceratidae, Polymorphitidae, Liparoceratidae). Some of these more or less markedly tuberculated forms have subplatycone, subplanorbicone or subsphaerocone shells with usually rounded and keelless ventral areas. The habitus of such Early Pliensbachian Eoderoceratoidea (Fig. 11) are not very close to those of *Phricodoceras* (Figs. 3–5) (e.g., lack of peri-siphonal tubercles but usually presence of ventral secondary and intercalary ribs between the ventro-lateral rows of tubercles in Eoderoceratoidea but not in *Phricodoceras*), but all these forms are roughly coeval and the presence of tubercles and/or spines was long regarded as a diagnostic trait confined or pretty much so to the Eoderoceratoidea among the Pliensbachian ammonites. Contrariwise, Schlotheimiidae were understood until recently as forms unable to produce true tubercles and/or spines. Thus, in addition to the age (chiefly Early Pliensbachian), the presence of tubercles, the keelless smooth ventral area and the rather evolute juvenile coiling pattern were all used as arguments (taxonomic shoehorns) for placing *Phricodoceras* within the Eoderoceratoidea. This nearly universally or at least widely accepted argument is in fact circular. It was ultimately overturned by the recent discovery by Meister et al. (2010) of a clearly tuberculate juvenile growth stage in the inner whorls of a typical Schlotheimiidae (i.e., *Angulaticeras spinosus*). From then on, it becomes easy to understand the genus *Phricodoceras* as a close relative of *Angulaticeras* within the Schlotheimiidae and to fundamentally rethink the comparative anatomy of these forms. For example, it becomes possible to prove the peri-siphonal shoulders of the Schlotheimiidae are homologous with the peri-siphonal tubercles of *Phricodoceras*. In fact, the homologies (e.g., shell morphology, ornamentation, suture line if controlled by ontogenesis) with *Angulaticeras* are so numerous and obvious, throughout the growth stages, that it seems unnecessary to use a distinct subfamily or family level name to separate the two genera.

## Conclusions

The history of taxonomic practice with respect to *Phricodoceras* is edifying because it clearly exemplifies the vulnerability of approaches based on “overall similarity” even if

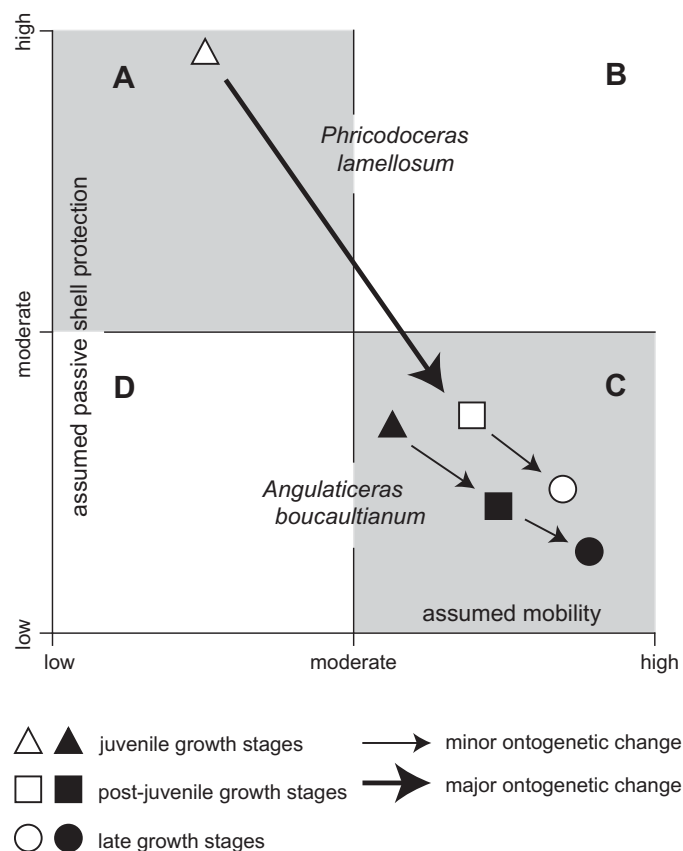


Fig. 10. Schematic representation and comparison of the ontogenies of an *Angulaticeras* macroconch (*A. boucaultianum*) and of a *Phricodoceras* macroconch (*P. lamellosum*) in a simplified diagram taking into account the assumed mobility (x-axis) and the assumed passive shell protection (y-axis). These parameters cannot be fully expressed quantitatively. Mobility depends mainly on hydrodynamic abilities, which are correlated with shell geometry but also with some aspects of ornamentation. Marked ornamental traits may play an important role. For example a keel or a ventral groove may increase the hydrodynamic stability of the shell and thereby facilitate mobility, but prominent tubercles and/or spines may significantly increase hydrodynamic drag thereby reducing mobility. Conversely the prominence of ornamentation (chiefly of tubercles and/or spines) may be an effective passive protection against predators. Although highly schematic and hypothetical, such a diagram can be understood as an approximate representation of an “adaptive landscape” in which successive growth stages can be roughly situated. This “adaptive landscape” can be divided into four quadrants labeled A–D. The two studied species occupy only quadrants A (rather poor mobility but good passive shell protection) and C (good mobility but poor passive shell protection). In fact, only the juvenile growth stages of *Phricodoceras lamellosum* are situated in quadrant A but all the other growth stages, of both species, are in quadrant C. This pattern underlines the adaptive peculiarity of the juvenile growth stages of *Phricodoceras*.

they are stratigraphically well constrained. In addition, it shows how much an allegedly consensus-based formalization such as that proposed in the “Treatise of Invertebrate Paleontology” (Arkell et al. 1957) may become sterilizing for taxonomic research. The present synthesis suggests that the understanding of relationships between ammonites, and particularly between clearly identified and distinct groups, depends largely on the discovery of transitional forms and/or

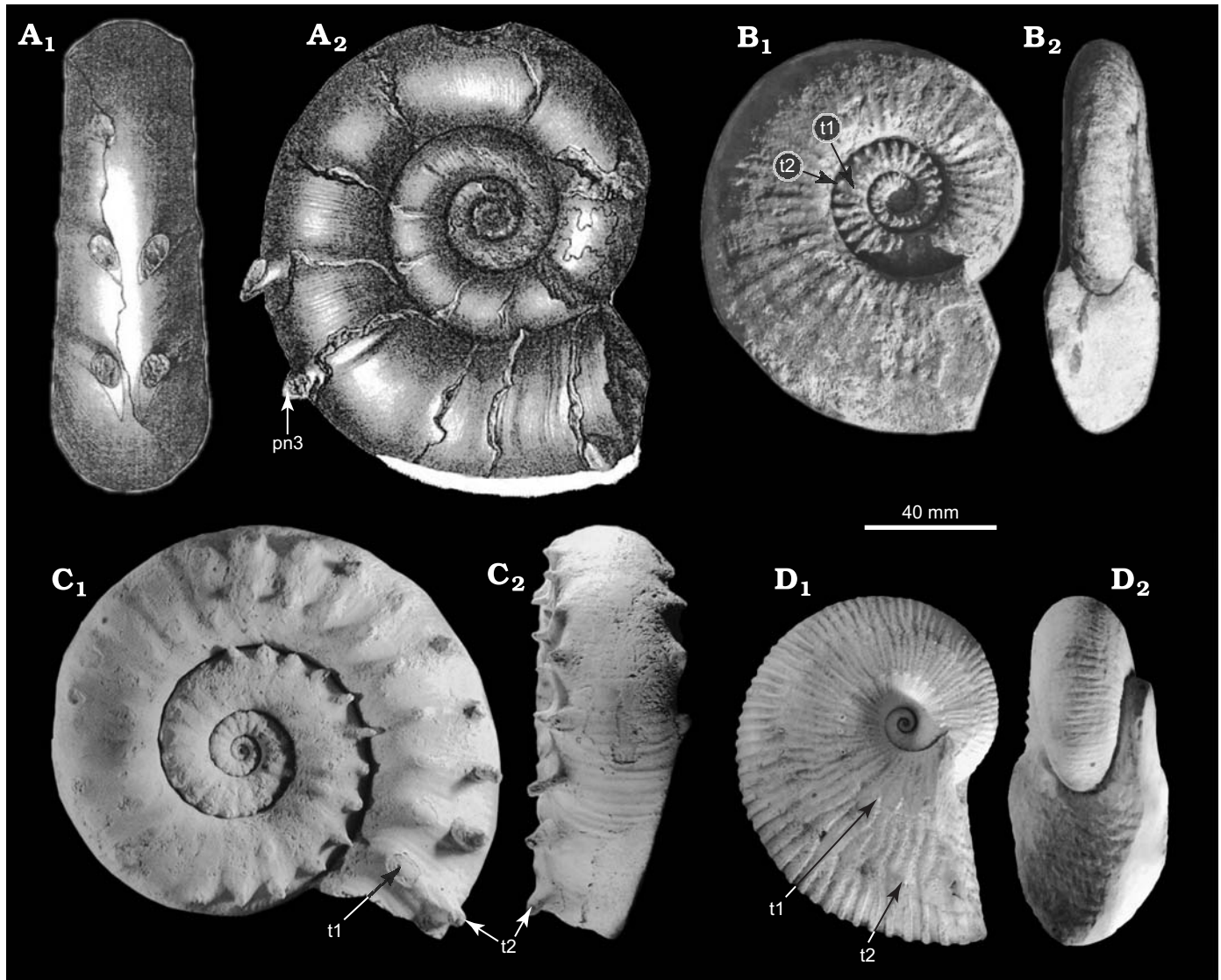


Fig. 11. Habitus of some noded, spined and/or tuberculate Lytoceratoidea (A) and Eoderoceratoidea (B–D). **A.** *Analytoceras hermanni* (Gümbel, 1861), Kammerkaralpe, Waidring, Tyrol, Austria, probably Late Hettangian (from Wähner 1894: pl. 3: 3a, b, modified), in ventral (A<sub>1</sub>) and lateral (A<sub>2</sub>) views. **B.** *Epideroceras lorioli* (Hug, 1899), St Peter's Field, Radstock, Somerset, UK, *Echioceras raricostatum* Chronozone, *Paltechioceras aplanatum* Subchronozone (from Edmunds et al. 2003: fig. 21. 4, modified), in lateral (B<sub>1</sub>) and apertural (B<sub>2</sub>) views. **C.** *Tetraspidoceras repentinum* Edmunds, 2009, St Peter's Field, Radstock, Somerset, UK, *Uptonia jamesoni* Chronozone, *Phricodoceras taylori* Subchronozone (from Edmunds 2009: pl. 32: 1, modified), in lateral (C<sub>1</sub>) and ventral (C<sub>2</sub>) views. **D.** *Becheiceras bechei* (Sowerby, 1821), Golden Cap, Seatown, Dorset, UK, *Prodactylioceras davoei* Chronozone, *Oistoceras figulinum* Subchronozone (from Edmunds 2009: pl. 38: 1, modified), in lateral (D<sub>1</sub>) and apertural (D<sub>2</sub>) views. Tubercles and/or spines in (t1) and/or (t2) positions of the Eoderoceratoidea (B–D) are not homologous with those of *Phricodoceras*, nevertheless this genus was long understood as a (borderline) member of this superfamily. In the case of Lytoceratoidea (A) the ornamental features in peri-siphonal position (pn3) are parabolic nodes which are morphologically clearly distinct from the tubercles or spines of both Eoderoceratoidea and *Phricodoceras*. The growth stage of the specimen is unknown.

series in an acceptable stratigraphic context. If heterochronal processes, possibly associated with innovation, are involved (as is the case for *Phricodoceras*), such transitional forms are often informative and easy to interpret in evolutionary and phylogenetic terms. Unfortunately, intermediate forms between obviously distinct groups are usually very rare and localized. For example, *Angulaticeras spinosus*, the key species for the understanding of the relationship between *Angulaticeras* and *Phricodoceras*, is known by only three specimens (including the holotype) from a single but ex-

tremely rich fossiliferous locality in the western Carpathians, Slovakia (Meister et al. 2010). This locality has yielded several thousand specimens including various *Angulaticeras* so *Angulaticeras spinosus* is obviously extremely rare. The sedimentary context is certainly important. For example, condensed deposits are probably particularly favorable for the search of transitional forms. Nevertheless, and despite the probable scarcity of many transitional forms, field studies still appear to be the most reliable way to resolve many enigmatic taxonomic problems and to clarify our knowledge of

Publications		H?	Eo	Ko	Ly	Ps	La	Publications		H?	Eo	Ko	Ly	Ps	La
Sowerby	1826	×						Hoffmann	1826	•••					
Zieten	1830	×						Venturi	1826	•••					
Orbigny	1844	×						Braga	1826	•••					
Quenstedt	1846	×						Mouterde et al.	1826	•••					
Quenstedt	1849	×						Büchner et al.	1846	×					
Oppel	1853	×						Meister and Sciau	1846	•••					
Oppel	1856	×						Smith et al.	1846	×					
Hauer	1861	×						Dommergues and Meister	1846	•••					
Wright	1880		•					Dommergues et al.	1846	•••					
Quenstedt	1883		•					Schlatter	1846	•••					
Fucini	1898		•					Cope	1846	•••					
Bettoni	1900		•					Ferretti	1846	×					
Del Campana	1900		•					Page (personal commun.)	1846	••			••		
Hyatt	1900			•••				Schlatter	1846	•••					
Fucini	1908	×						Sciau	1846	×					
Buckman	1911		••					Tipper et al.	1846	×					
Buckman	1921		••					Dommergues	1846	••				••	
Krumbeck	1922		•					Page	1846	•••					
Schröder	1927		••					Dommergues and Mouterde	1846	•••					
Höhne	1933		•					Alkaya and Meister	1846	•••					
Gerard and Tetry	1938			•••				El Hariri et al.	1846	•••					
Roman	1938		•••					Faraoni et al.	1846	×					
Spath	1938		•••					Smith and Tipper	1846	•••					
Otkun	1942	×						Geczy	1846	•••					
Venzo	1952	×						Geczy and Meister	1846	•••					
Fantini and Paganoni	1953	×						Dommergues and Meister	1846	••				••	
Donovan	1954		•••					Rakus	1846	•••					
Arkeel et al.	1957		•••					Dommergues et al.	1846	•••					
Geczy	1959	×						Macchioni	1846	•••					
Dean et al.	1961	×						Venturi and Ferri	1846	•••					
Fantini-Sestini	1962	×						Howarth	1846	•••					
Schindewolf	1962		•••					Rakus and Guex	1846	•••					
Bremer	1965		•••					Dommergues	1846	••			••	••	
Cantaluppi and Brambill	1968	×						Donovan and Surlyk	1846	••					
Frebold	1970		•••					Edmunds et al.	1846	•••				•••	
Wiedmann	1970				••			Meister et al.	1846	×					
Tintan et al.	1994		••					Hillebrandt	1846	•••					
Geczy	1976		•••					Geczy and Meister	1846	•••				•	
Schlegelmilch	1976		•••					Meister	1846	••			••	••	••
Schlatter	1977	×						Yin et al.	1846	•••					
Dommergues	1978		•••					Dommergues et al.	1846	••			••	••	
Dubar	1978	×						Page	1846	••				••	
Fantini-Sestini	1978		•••					Venturi and Bilotta	1846	×					
Alkaya	1979		•••					Meister et al.	1846	•••				••••	
Linares et al.	1979	×						Venturi et al.	1846	×					
Schlatter	1980		•••					Blau and Meister	1846	•••				•••	
Wiedenmayer	1980		•••					Meister et al.	1846	•••				••••	
Donovan et al.	1981		•••					this paper	1846	•••				••••	

Fig. 12. Historical synthesis of the taxonomic interpretation for the genus *Phricodoceras* from 1826 until today. Six options are considered: H?, no taxonomic attribution or attribution deliberately left undetermined; Eo, explicit attribution to Eoderoceratoidea or implicit proximity with some ammonites currently attributed to the Eoderoceratidae; Ko, explicit attribution to the Kosmoceratidae; Ly, explicit attribution to the Lytoceratoidea (in the current sense); Ps, explicit attribution to the Psiloceratoidea and proximity with the Schlotheimiidae; La, enigmatic Lazarus taxon. A cross indicates an absence of attribution to a taxon. A single black dot suggests an implicit or explicit but very reserved attribution. Two black dots suggest an explicit but debatable attribution. Three black dots suggest an unconditional explicit attribution. Four black dots suggest an explicit attribution based on ontogenetic evidence. For easy reading, the two columns corresponding to the two most frequent taxonomic interpretations (i.e., Eo and Ps) are shaded.



palaeobiodiversity. In the absence of intermediate forms and/or series, cladistic analysis can be a useful approach in attempting to reconstruct phylogenies, but frequent homoplasies and the weakness of many primary homologies in the absence of transitional forms mean that this type of approach is often quite frustrating and nothing can replace the discovery of a key intermediate form.

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