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Suture ontogeny in *Ptychoceras* D'ORBIGNY and its implications for the systematics of Cretaceous heteromorphs

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With 11 figures in the text

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Abstract: Shell ontogeny of *Ptychoceras* starts with a spirally coiled initial whorl. After the nepionic constriction (1) the whorl section looses the dorsal concavity, which is reintroduced when the second shaft grows along the primary one, (2) the originally quinquelobate suture (ELU_2U_1I = VLUID) looses U_2 and remains quadrilobate for the rest of ontogeny, even if a concave dorsum reappears. This confirms observations made in most groups of recoiled Ancyloceratina. Problems of defining the Ancyloceratina WIEDMANN by a quadrilobate suture line and the taxonomic value of bifid versus trifid lobes are discussed.

Zusammenfassung: Die Ontogenese des *Ptychoceras*-Gehäuses beginnt mit einer spiral aufgerollten Anfangswindung. Nach der primären Einschnürung am Ende des Ammonitella-Stadiums treten folgende Veränderungen auf: (1) Die dorsale konkave Windungszone verschwindet, um allerdings später – sobald der 2. gerade Arm sich an den 1. Arm anlegt – erneut zu erscheinen; (2) die zunächst quinquelobate Lobenlinie (ELU_2U_1I = VLUID) verliert das Element U_2 und bleibt nun für den Rest der Ontogenese quadrilobat, auch beim erneuten Auftreten der dorsalen konkaven Windungszone. Damit bestätigen sich Beobachtungen, die bei fast allen wieder aufgerollten Ancyloceratina gemacht werden können. Probleme, die sich aus der Definition der Ancyloceratina durch eine quadrilobate Lobenlinie ergeben, werden ebenso wie die taxonomische Bedeutung von bifiden bzw. trifiden Loben erörtert.

1. Introduction

The holotype of the type species of genus *Ptychoceras*, *P. emericianum* D'ORB. (D'ORBIGNY 1842: 579, pl. 137, figs. 1–4), is incomplete; it consists of two closely attached straight shafts. The existence of an innermost third shaft, the initial coil, and the protoconch were unknown at that time. Additional data were contributed by C. W. WRIGHT (1957), noting that the *Ptychoceras* shell – like in *Euptychoceras* – consists of three closely touched shafts.

Later on, EGOIAN (1968, 1969), HOLLIS (1971), and MICHAILOVA (1974) investigated the morphology of the *Ptychoceras* shell. The most important contribution was made by DRUSHCHITS & DOGUZHAEVA (1976, 1981), who pointed

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out that the early ontogenetic stage of *Ptychoceras* is planospiral followed by the straight first shaft.

WIEDMANN (1962a) discussed the relationship between suture ontogeny and changing whorl sections.

I. MICHAILOVA (1974, 1983), who studied the suture ontogeny beginning from the first shaft, noted that in the early stage the suture line consists of four undifferentiated lobes. Later, the ventral lobe E (V)[1], as well as the lateral and umbilical lobes L and U (U and I), become bifurcate, while the dorsal lobe I (D) becomes trifid. It was also mentioned that in some species, i.e. *P. puzosianum* D'ORB., the umbilical lobe is trifid. SHARIKADZE (1986) investigated the whole ontogeny of the suture line of *Ptychoceras* and recognized that the primary suture consists of five lobes. The lobe reduction on the saddle L/U takes place at the end of the planispiral coil, and the resulting quadrilobate suture line ELUI (VLID) is maintained up to the end.

There are still different points of view about the systematic position of *Ptychoceras*. According to WRIGHT (1957), the family Ptychoceratidae MEEK includes the genera *Ptychoceras* D'ORBIGNY 1842, *Anahamulina* HYATT 1900, *Hamulina* D'ORBIGNY 1843, *Hamulinites* PAQUIER 1900, and *Euptychoceras* BREISTROFFER 1952, and is attributed to the superfamily Turrilitaceae MEEK (suborder Lytoceratina). DRUSHCHITS & LUPPOV (1958) included the genus *Ptychoceras* in the family Hamitidae HYATT (superfamily Turrilitaceae, suborder Lytoceratina). CASEY (1960) attributed the genus *Ptychoceras* to the superfamily Ancylocerataceae. SCHINDEWOLF (1968) and WIEDMANN (1969) considered all Cretaceous heteromorph ammonites (including *Ptychoceras*) to belong to the suborder Ancyloceratina WIEDMANN 1966. DRUSHCHITS & I. MICHAILOVA (1974) suggested, however, that heteromorphic ammonites with bifid lateral lobe belong to the Lytoceratida (the superfamilies Turrilitaceae and Scaphitaceae), while the ones with trifid lateral lobe must be attributed to the Ammonitida (superfamily Ancylocerataceae). Later on, BEZNOSOV & I. MICHAILOVA (1983) regarded Turrilitaceae (including *Ptychoceras*) and Ancylocerataceae as independend suborders: 1. Turrilitina BEZNOSOV & I. MICHAILOVA and 2. Ancyloceratina WIEDMANN.

The main differences in interpreting the Cretaceous heteromorphs were based on the two suppositions that

a) all heteromorphs have a quadrilobate primary suture and thus a monophyletic origin, while the bifid or trifid shape of L is regarded as insignificant (WIEDMANN 1966, SCHINDEWOLF 1967, 1968); or
b) the heteromorphs with bifid L have to be considered descendants of lytoceratids, while those having a trifid L arose from some member of Ammonitina (DRUSHCHITS & LUPPOV 1958).

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[1] Suture terminology by Soviet authors is given in brackets ( )

2. Morphogenetic investigations

The morphogeny of the *Ptychoceras* shell and suture line is reinvestigated based on about 100 specimens[2] from the Middle to Upper Aptian of the northwestern Caucasus and Dagestan. Investigated are specimens of *P. minimum* ROUCH., *P.* aff. *minimum* ROUCH., *P. renngarteni* EG., *P. levigatum* EG., *P.* sp. juv., and *P.* spp. The most interesting species is *Ptychoceras minimum* ROUCH., which is at the same time the most frequent one (about 50 specimens).

It is remarkable that the majority of specimens has a suture line with bifid L [L][3] (Fig. 1), as was also shown by I. MICHAILOVA (1974) and SHARIKADZE (1986). Six specimens, however, exhibit essential differences (Figs. 2–6):

As is seen in these specimens (Figs. 2 and 3), the element L [L] becomes and remains trifid from the beginning up to the adult stage. All other morphological features are undistinguishable from those of bifid specimens, i.e. adult shell morphology (Fig. 4) and development of the coiled portion (Figs. 5 and 6). The early part of the shell consists of the protoconch and of one planispiral whorl (Figs 5B and 10B). The protoconch (Fig. 6a–c) is spherical and somewhat wider (0.39 mm) than high (0.35 mm); the ammonitella has a diameter of 0.62 mm. Interesting is an early flattening of the ammonitella (Fig. 5B) heralding the straightening of the shell. At the beginning of the planispiral whorl, the section is semilunar (Figs. 5A, C, D, 6e, f, 8e) and considerably wider than high. Beyond the "nepionic", primary constriction the shell straightens (Fig. 6d), while the cross-section rapidly increases in height. It is changing from oval (Figs. 6g, 8f) to circular (Figs. 6h, 8g), to become oval again at the end of the first shaft (Fig. 6i). The second shaft is developing a concave dorsum embracing the first shaft with ammonitella (Figs. 6j, 10a).

The suture line of bifid and trifid forms (Figs. 1, 2, 3, 7 and 8) is characterized by a small number of elements. The prosuture is angustisellate with two lobes (Figs. 1a, 2a, 7a). The primary suture consists of five lobes: ELU_2U_1I [VLUID] (Figs. 1b, 2b, 7b). These five lobes are preserved throughout the ammonitella stage, i.e. for seven to nine chambers (Fig. 8a). The element U_2 [U] is very small; it is placed dorsally of the umbilical seam and is of asymmetric size on both sides (Fig. 5C–G). It is much reduced in the 8th suture line (Fig. 5C) and disappears totally from the 9th on. The ventral lobe E [V] becomes subdivided as late as with the 17th suture line (Fig. 8d). In typical *P. minimum,* all other lobes also become bifid after 1/3 of the 1st shaft (Fig. 1i), while the specimens described herein de-

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[2] This collection is kept in the G. Kharatishvili Paleontological Museum of Georgian Polytechnical Institute Tbilisi, collection no. 8.

[3] Reinterpretation of Soviet suture terminology by SHARIKADZE et al. (1989) in brackets [ ]

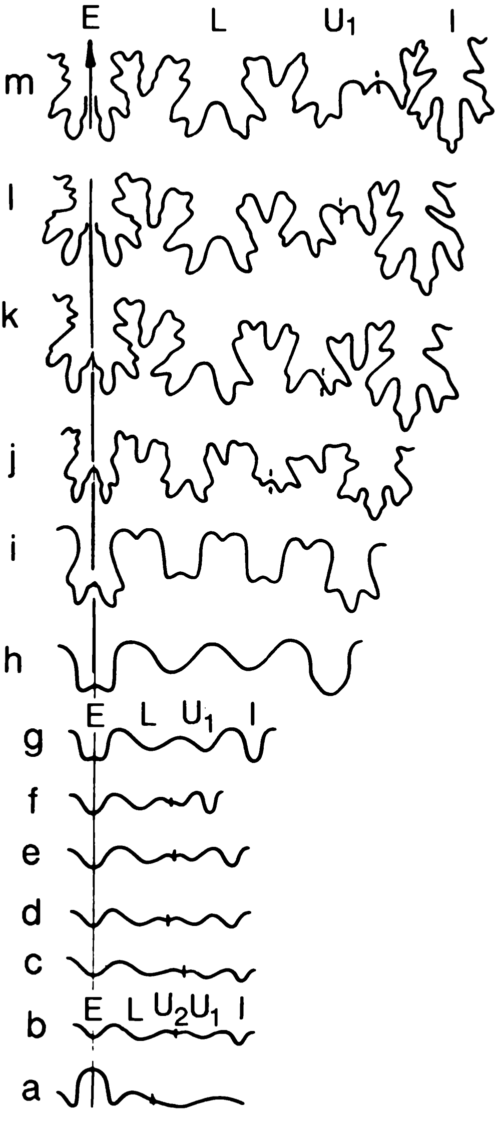

Fig. 1. Suture line ontogeny of *Ptychoceras minimum* ROUCH. f. *typica*. – a–h: 1st, 2nd, 3rd, 7th, 10th, 12th, 19th and 25th suture lines (× 35), specimen No 8-403/9; i: 1/3 of the first shaft (× 25), specimen No 8-403/11; j: end of the first shaft (× 10); k: beginning of the second shaft (× 10); l: 1/4 of the second shaft (× 10); m: middle of the second shaft (× 10); j–m: specimen No 8-403/15. All specimens from late Aptian (Clansayesian), Pshekha River, NW Caucasus.

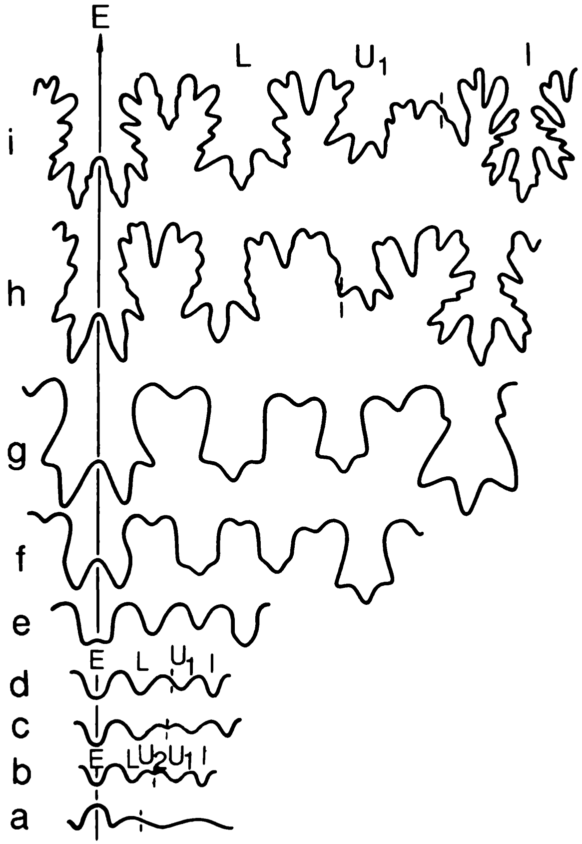

Fig. 2. Suture line ontogeny of *Ptychoceras minimum* ROUCH. f. *trifida*. Specimen No 8-401/57. Clansayesian, Khokodz River, NW Caucasus. – a–c: 1st, 2nd, 6th suture lines (× 35); d: 10th suture line (end of the planispiral whorl) (× 35); e: 18th suture line (the beginning part of the first shaft, × 35); g: 40th suture line (middle of the first shaft, × 35); h: 50th suture line (end of the first shaft, × 20); i: last, 59th suture line (middle of the second shaft, × 15).

velop trifid lobes (Figs. 2f, 3A, 3B, 8d) at the same time. As soon as the concave dorsum appears on the 2nd shaft, U_1 [I] as well as the saddle U_1/I develop asymmetrically (Figs. 2h, i, 3Ac and 3Bc). Accordingly, the trifid L [L] may develop symmetrically (Figs. 2 and 3A) or asymmetrically (Fig. 3B).

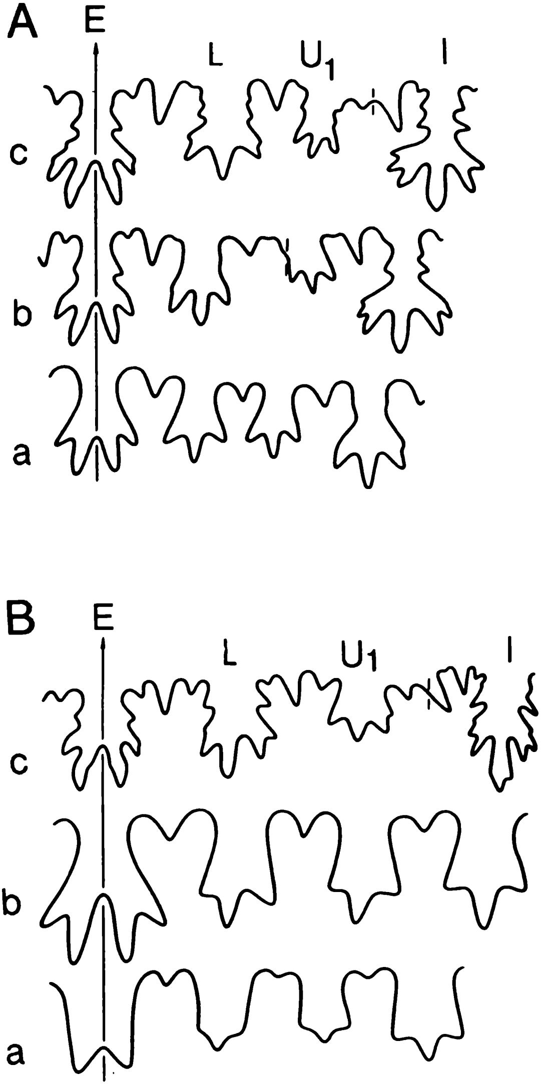

Fig. 3. Suture line ontogeny of *Ptychoceras minimum* ROUCH. f. *trifida*. A: Specimen No 8-401/113. – a: 1/3 of the 1st shaft (× 15); b: end of the 1st shaft (× 12); c: middle part of the 2nd shaft (× 10). B: Specimen No 8-401/145. – a: 1/3 of the 1st shaft (× 25); b: beginning of the 2nd half of the 1st shaft (× 18); c: beginning of the 2nd half of the 2nd shaft (× 10). Both specimens from the Clansayesian, Khokodz River, NW Caucasus.

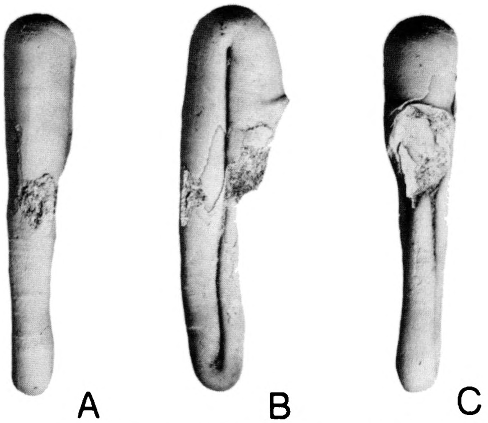

Fig. 4. *Ptychoceras minimum* ROUCH. f. *trifida*. Specimen No 8-401/57. Clansayesian, Khokodz River, NW Caucasus. – A: Ventral view 1st shaft; B: Lateral view; C: Ventral view 3rd shaft (× 2).

3. Systematic conclusions

In view of the high taxonomic value of the bifid vs. trifid shape of L[4] in traditional heteromorph systematics, the importance of these observations is obvious.

Since the described forms with trifid L agree in all other morphological features with the true *Ptychoceras minimum*, since they were found in the same beds[5], and since, obviously, we are not confronted with the initial point and deviation of a new phyletic lineage, we are obliged to conclude that both lobe forms fall into the variability of one species. There is no way of specific separation.

To facilitate discussion, the trifid forms may be considered to constitute a forma *trifida* in contrast to the bifid forma *typica*. The specimens described and figured of f. *trifida* are of Clansayesian age and were collected at Pshekha and Khokodz rivers, NW Caucasus.

At the same time, the generic diagnosis of the genus *Ptychoceras* can be completed: *Ptychoceras* comprises those forms having a spiral first whorl followed by three shafts in contact. The initial (first) shaft is pressed into the dorsum of the 2nd shaft, while the 3rd shaft is in contact with the 1st and 2nd ones simultane-

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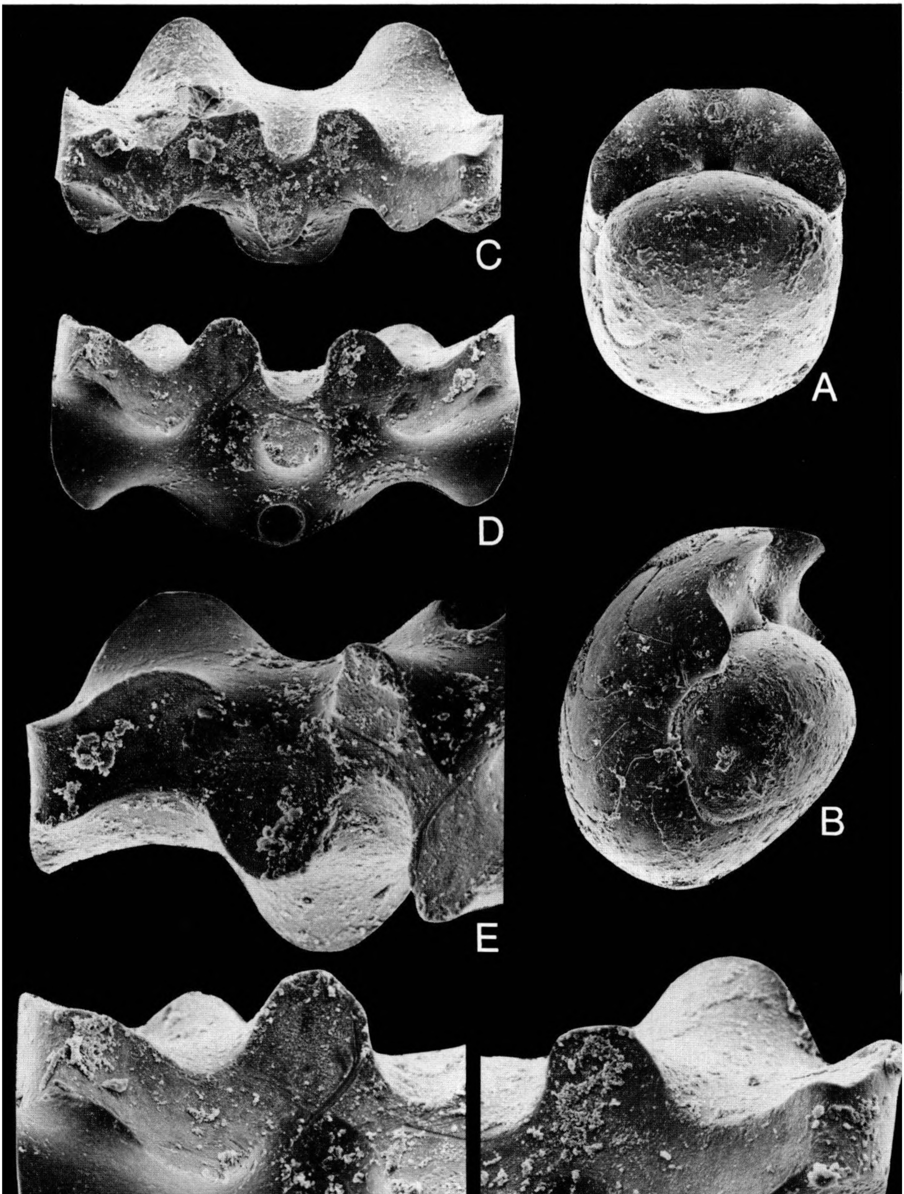
[4] The bifid/trifid shape of the lobe L was introduced for ammonite classification by PERVINQUIÈRE (1907) and used by many authors from NOWAK (1911, 1915) to DRUSHCHITS & LUPPOV (1958) or EGOIAN (1974).

[5] It needs mentioning that these Clansayesian beds are condensed; synchroneity of both forms has, nevertheless, a high degree of probability.


C
A
D
B
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G

ously. The initial shaft has – except for the initial coil – a rounded whorl section, while the 2nd and 3rd shafts have a flat or concave dorsum as far as the initial shaft together with the planospiral initial coil are inserted. The suture line is characterized by a quinquelobate primary suture. These lobes remain undivided

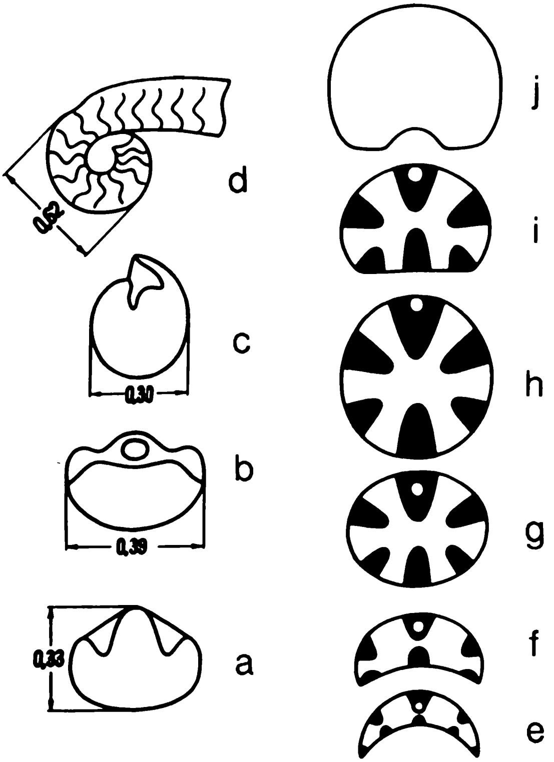

Fig. 6. *Ptychoceras minimum* Rouch. f. *trifida*. Early ontogeny of the specimen No 8-401/58; Clansayesian, Pshekha River, NW Caucasus. – a–c: protoconch (× 40); d: initial whorl and beginning of the 1st shaft (× 26); e–j: cross sections and septal surfaces; e: at the 4th suture (× 36); f: at the 11th suture (end of the spiral coil, × 36); g: at the 17th suture (beginning of the 1st shaft, × 40); h: at the 34th suture (middle of the 1st shaft, × 28); i: at the 1st bend, × 10); j: middle of the 2nd shaft (× 6).

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Fig. 5. *Ptychoceras minimum* Rouch. f. *trifida*. REM photographs of specimen 8-401/58. Clansayesian, Pshekha River, NW Caucasus. A, B: Frontal and lateral view of spiral coil (protoconch and six chambers). A: × 75; B: × 80; C: 8th chamber, × 130; D: 7th chamber, × 140; E, F: 7th chamber, × 250; G: 8th chamber, × 250.

on the spiral coil. The reduction to four lobes coincides with the straightening of the shell and is connected with the reduction of a concave dorsum. Later in ontogeny, E [V] becomes symmetrically bifid, I [D] trifid, while L [L] and U_2 [I] acquire a bifid or trifid outline. In the 2nd shaft, a concave dorsum becomes developed again in which a part of the first shaft with initial coil is inserted (Figs. 9A and 9B). The umbilical seam is now placed within the element U_1 [I] (Figs. 1j, k and 2h) and moves into the saddle U_1/I which becomes asymmetric (Figs. 1l, m and 2i).

As can be seen from Fig. 9, there is no stability in the final shape of lobes L and U_1. While *Pt. minimum* ROUCH. has either bifid or trifid L and U_1 (Figs. 1, 2), in the figured specimen of *Pt.* cf. *renngarteni* EG. (Fig. 9d) L is trifid, while U remains bifid. In *Pt.* cf. *parvum* EG. (Fig. 9c) and in *Pt.* cf. *levigatum* EG. (Fig. 9b) these two lobes are trifid, while in other specimens of the last mentioned species (Fig. 9a) L might remain bifid in contrast to a trifid U_1.

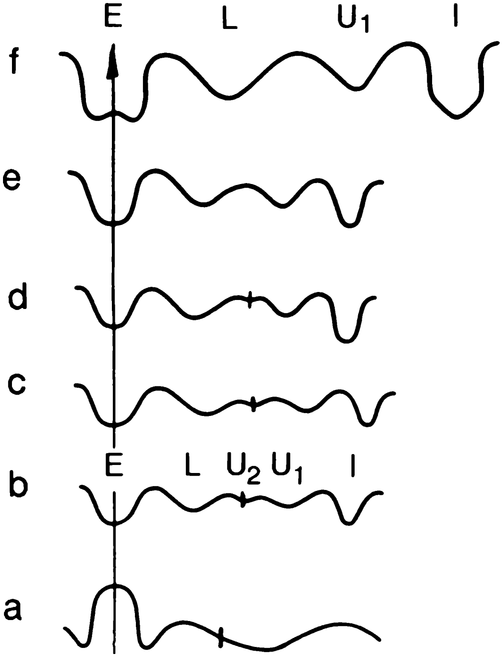

Fig. 7. Suture line ontogeny of *Ptychoceras* sp. juv. Specimen No 8-403/8. Clansayesian, Pshekha River, NW Caucasus. a–f: 1st, 2nd, 4th, 12th, 15th, 22nd suture lines (× 70).

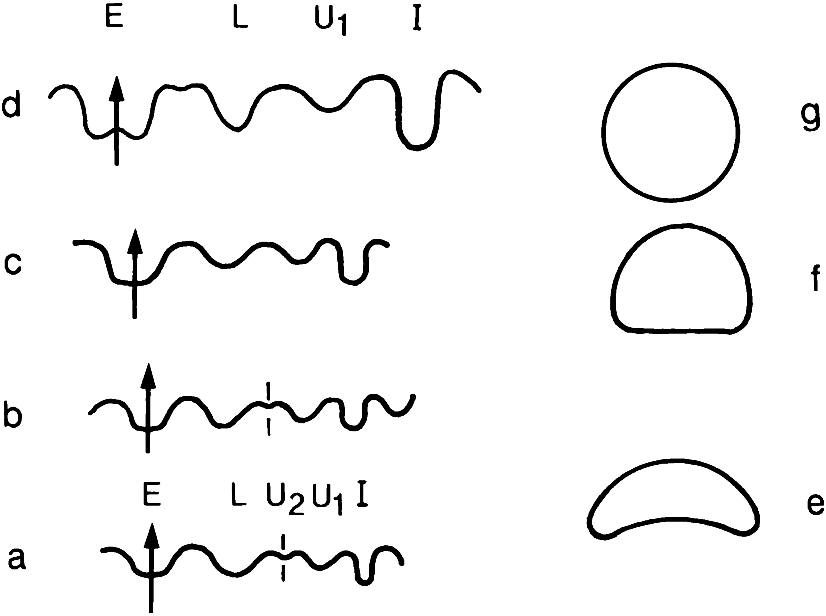

Fig. 8. Suture line ontogeny of *Ptychoceras minimum* ROUCH. f. *trifida*. Specimen No 8-403/14. – a–d: 7th, 9th, 11th, 17th suture lines; e–g: equivalent whorl sections (× 70).

4. Discussion on suture lines in Cretaceous heteromorphs

A. Trifid vs. bifid lobes

Ptychoceratids are proven to be a good example to demonstrate how consistent the form of the "lateral" lobes L and U_1 [L,I] and the internal lobe I [D] is in heteromorphs. Up to present, both "lateral" lobes were used to define high order taxa (genera to suborders). SPATH (1939) and EGOIAN (1969, 1974) separated anisoceratid genera and even families ("Epacrioceratidae" EGOIAN) based on a bifid or trifid shape of U_1. WIEDMANN & DIENI (1968, text-fig. 85) however, were able to demonstrate that in anisoceratid species U [I] might be bifid on one flank of a specimen, while it is trifid on the other. CASEY (1961) figured a great number of protanisoceratid suture lines having a bifid L (e.g., *P. (P.) cantianum* SPATH) as well as a trifid one (e.g. *P. (P.) coptense* CASEY), a bifid U [I] (e.g., *P. (P.) acteon* (D'ORB.)) as well as a trifid one (e.g., *P. (P.) coptense* CASEY), or a bifid I [D] (e.g., *P. (P.) coptense* CASEY) as well as a trifid one (e.g., *P. (P.) raulinianum* (D'ORB.)). There is little doubt that all these forms belong to the genus and subgenus *Protanisoceras*; further subdivision would be inadequate. Similar observations were made in ancyloceratids. KAKABADZE et al. (1978, text-fig. 4) were able

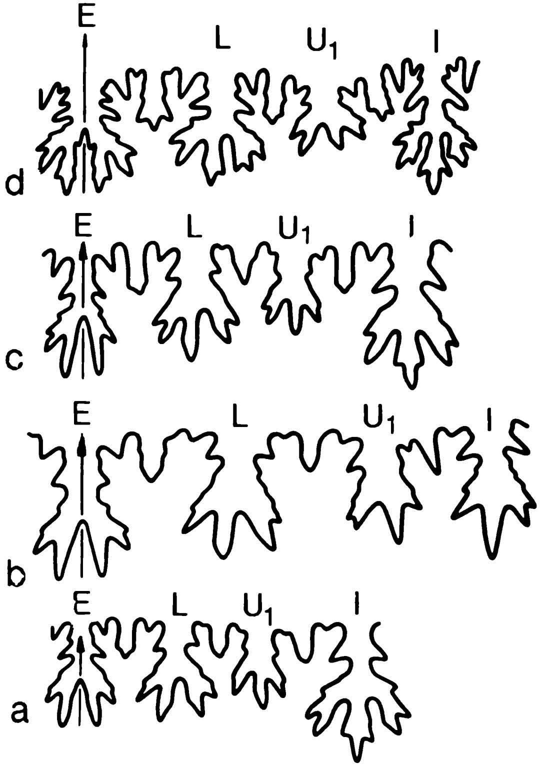

Fig. 9. Suture lines of some representatives of the genus *Ptychoceras* D'ORBIGNY. – a: *Ptychoceras* cf. *levigatum* EGOIAN, specimen No 8-66/2, middle part of the 1st shaft (× 6); b: *Ptychoceras* cf. *levigatum* EGOIAN, specimen No 8-66/3, end of the 1st shaft (× 7); c: *Pt.* cf. *parvum* EGOIAN, specimen No 8-66/1, beginning of the 2nd half of the 1st shaft (× 8); d: *Pt.* cf. *renngarteni* EGOIAN, specimen No 8- 66/4, middle part of the 2nd shaft (× 5).

to show that in *Luppovia adjiderensis* BOGD., KAKAB. & MICH., U_1 [I] has a bifid as well as a trifid shape. Due to SHARIKADZE et al. (1989, text-fig. 2), in *Matheronites ridzewskyi* KARAK. U_1 [I] is also bifid or trifid; in one specimen again, U_1 [I] has a different shape on the two flanks. Moreover, I [D] is either bifid or trifid.

From scaphitids we know that the originally bifid L [L] may become trifid during phylogeny (COBBAN 1958, text- fig. 3) and even during ontogeny (WIEDMANN 1962b, text-fig. 53).

Considering the great number of examples in which the shape of L [L], U_1 [I] and I [D] in Cretaceous heteromorphs alters from bifid to trifid (and vice versa, e.g. anisoceratids), the use of this lobe shape for taxonomy and classification is only very limited.

B. Quadrilobate vs. quinquelobate

WIEDMANN (1966) and SCHINDEWOLF (1967, 1968) studied the suture ontogeny of different groups of Cretaceous heteromorphs and came to the result that all the studied forms show the reduction of one umbilical lobe (U_2?) starting from the primary quadrilobate suture ELUI up to the adult. WIEDMANN (1966) realized at the same time that some groups of "hoplitid" Ammonitina (e.g. Douvilleicerataceae, Deshayesitaceae) are normally recoiled heteromorphs due to their quadrilobate suture ontogeny, or at least due to their primary suture and early ontogeny (e.g. Deshayesitaceae). He concluded that all uncoiled and recoiled Cretaceous forms – without regard to the shape of L – are one monophyletic unit (Ancyloceratina).

Within the Jurassic heteromorphs (Spiroceratinae, Acuariceratinae), however, a quinquelobate primary suture was recognized (SCHINDEWOLF 1961), followed by ontogenetic size reduction of the two lobes L and U_1 (Fig. 11B). Also the Triassic heteromorphs (Choristoceratidae) are provided with a quadrilobate primary suture (Fig. 11A), but with undivided lobe E.

MICHAILOVA (1976, 1983) contributed an important correction; she observed that in many Cretaceous heteromorphs and descendants the suture ontogeny starts with a quinquelobate primary suture passing into the final quadrilobate one early in ontogeny.

SHARIKADZE (1986) added the early ontogeny of *Ptychoceras minimum* ROUCH. with quinquelobate primary suture.

The investigations on *Ptychoceras minimum* f. *trifida* also improve these observations and clearly show that even in this dwarfed form with a small protoconch (diameter 0.35 mm) a quinquelobate primary suture is present (Fig. 2b) and continues up to the primary constriction (Figs. 2c, 8a, b). The second umbilical lobe U_2 [U] is very small and placed on the umbilical seam of the coiled portion; it is, however, perfectly recognizable in REM-photographs (Fig. 5). As can be seen in Figs. 5C–G, there is some asymmetry in size and position of U_2 [U] on the two sides. It is interesting that, at the same time, the dorsoventral flattening of the protoconch (Fig. 5B) heralds the later uncoiling.

Immediately after the primary constriction, the 5th lobe U_2 [U] disappears together with the onset of uncoiling (Figs. 2d and 8c). There is an obvious correlation between the early quinquelobate stage and the presence of a concave dorsum, and, on the other hand, between lobe reduction, suture line shortening (Figs. 2d, 7e and 8c), and loss of the concave dorsum. It is, however, interesting to note that the later development of a concave dorsum on the second shaft does not allow the reappearance of the lost lobe element. In comparison, recoiling in the douvilleiceratids also does not alter the quadrilobate suture pattern (WIEDMANN 1966, 1969).

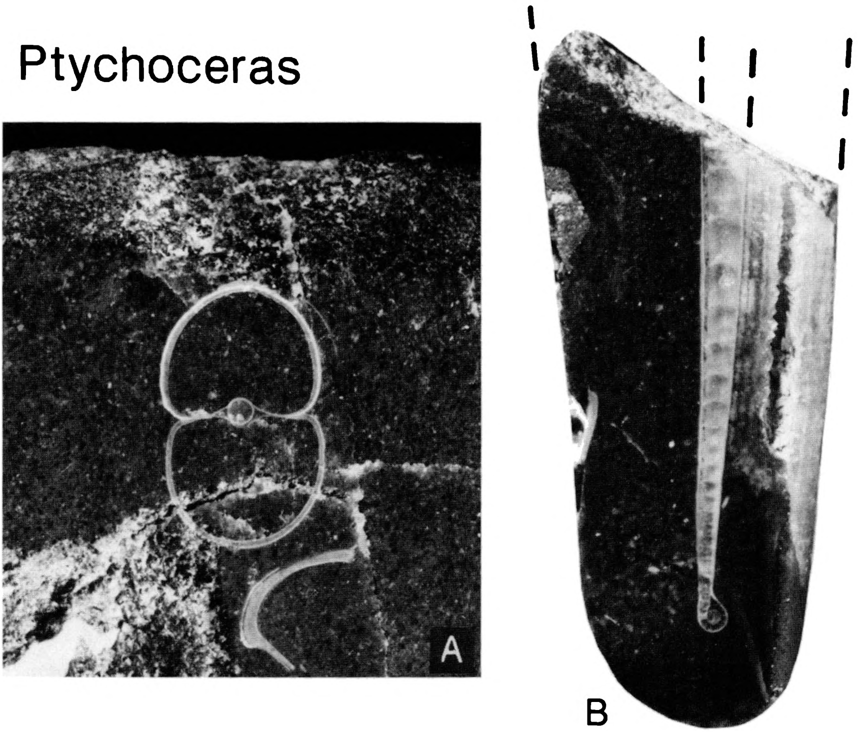

Fig. 10. *Ptychoceras* sp. juv.
A: Cross section through the three shafts and initial coil of specimen No 8-403/79 (× 6).
B: Longitudinal section through the three shafts and initial coil of specimen No 8-403/77 (× 6).
Both specimens from the Clansayesian, Pshekha River, NW Caucasus.

From all observations actually available on Cretaceous heteromorphs and descendants, one of us (J. W.) considers that this group presumably forms a monophyletic unit. Its origin still remains cryptogenic. It can be defined by its quadrilobate suture line starting either from the primary suture or from the primary constriction. Quinquelobate primary and early sutures are, however, more frequent as previously believed and are the proof of phyletic heritage (I. Michailova 1983) from quinquelobate neoammonoids. A further interesting pattern in heteromorph evolution is the widespread trend to recoil (Wiedmann 1969). Despite a final ammonitid coil in many heteromorph groups, the quadrilobate suture pattern remains almost unchanged. The only known exception are the Deshayesitaceae with the development of new umbilical lobes. While the descendance of deshayesitids from ancyloceratids (Wiedmann 1966) or heteroce-

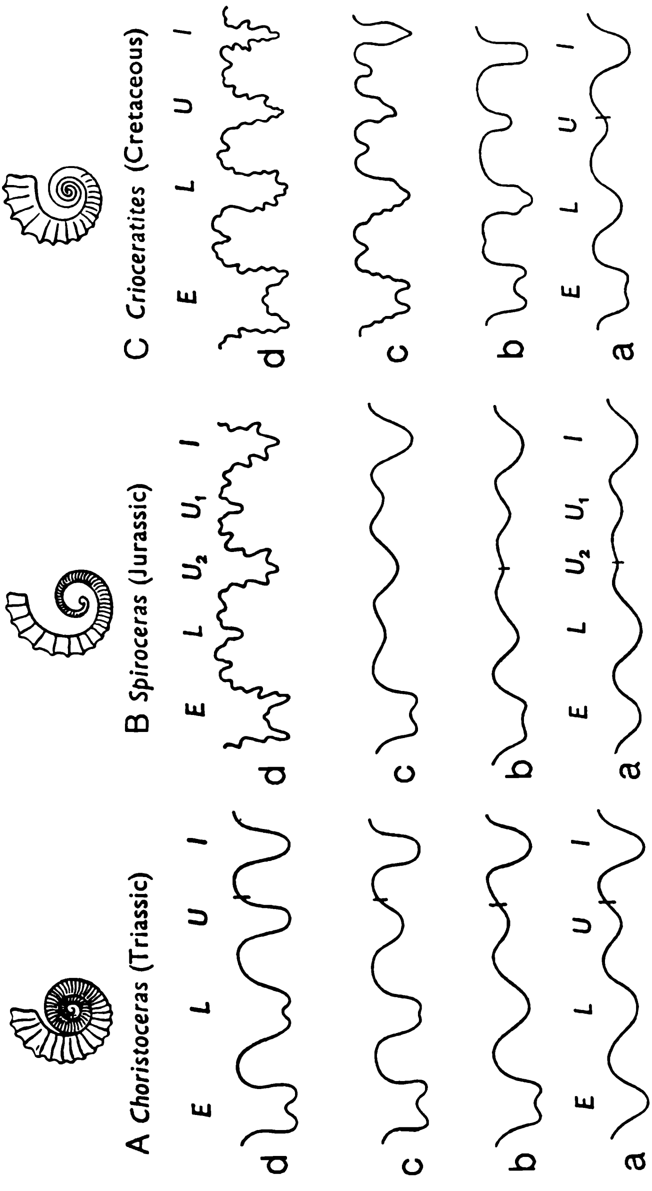

Fig. 11. Comparison of suture ontogeny (from Wiedmann 1969) in A: Triassic, B: Jurassic, and C: Cretaceous heteromorphs (a is not the primary suture).

ratids (TOVBINA 1963, 1965) previously was only assumed, BOGDANOVA (1971, 1979, text-fig. 1) gave a convincing proof of the descendance of deshayesitids from *Turkmeniceras* by passage forms in recoiling and suture ontogeny.

5. Conclusions

Investigating the ontogeny of ptychoceratids, interesting patterns in the development of shell and suture line and their eventual correlation were recognized. *Ptychoceras*, like all other heteromorphs, has an initial coil comprised of one whorl up to the primary constriction. In the species studied, the protoconch and the spiral portion are extremely reduced in size. Nevertheless, the primary suture is quinquelobate and consists of the elements ELU_2U_1I [VLUID]. These five lobes persist up to the end of the spiral portion which coincides with the primary constriction and the initiation of uncoiling. Thus, the quinquelobate stage clearly correlates with the presence of a concave dorsum and is to be considered a neoammonoid heritage. The ptychoceratid uncoiling in straight shafts is foreshadowed by dorsoventral compression of the protoconch. Uncoiling and the development of a rounded whorl section of the 1st shaft correlates with the loss of the lobe U_2 [U]. This permits the identification of the umbilical lobe in quadrilobate heteromorphs with the element U_1 [I] of neoammonoids. Even if a concave dorsum becomes reinstalled in the 2nd shaft, the quadrilobate suture pattern remains unchanged, as can also be observed in many other recoiled heteromorphs (e.g. douvilleiceratids). Only the saddle U_1/I becomes enlarged and asymmetric due to its position on the umbilical seam.

Of even greater interest is the recognition of two types of suture ontogenies in *Ptychoceras* species:

In *Pt. minimum* ROUCH., two different types of suture ontogeny were observed. In the first type (f. *typica*) the lobes L [L] and U_1 [I] develop with a bifid outline, while in the second type (f. *trifida*), both lobes have a trifid shape from the beginning. Comparison with the other existing species of *Ptychoceras* proves the instability of the lobe shape of L [L] and U_1 [U]. This means that the bifid/trifid outline of the lobes L [L] and U_1 [U] – as also of I [D] – has no greater systematic significance.

Since the modes of uncoiling and recoiling also greatly differ in different groups of Cretaceous heteromorphs, the existence of a quadrilobate suture line ELU_1I [VLID] might be a comparatively stable pattern in heteromorph evolution, either becoming installed with the primary suture or after formation of the primary constriction.

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