

THE PHYLOGENY OF PHARCICERATIDS AND THEIR RELATIVES (AMMONOIDEA, ANARCESTIDA; LATE GIVETIAN TO MIDDLE FRASNIAN)

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The oldest pharciceratids (Middle Devonian III-A), *Ph. amplexum* and *Ph. tridens*, are still rather simple-lobed, widely umbilicate and have broad and depressed, slowly expanding, longidomic whorls. It seems that they were derived from tubby *Afromaenioceras* by heterochronic processes, resulting in an extension of evolute early ontogenetic maenioceratid stages whilst the second umbilical lobe shifted towards the flank, leaving space for additional lobes around the umbilicus. The subsequent main lineage of evolution (Pharciceratidae) is characterized by a gradual proliferation of umbilical lobes whilst conchs became more involute and compressed. *Stenopharciceras* (entering in MD III-B) includes open umbilicate species with more than four flank lobes, *Synpharciceras* (MD III-C) comprises involute taxa with seven to eight flank lobes, and in the basalmost Frasnian (UD I-A) *Neopharciceras* there are as many as 10-14 flank lobes. Within *Stenopharciceras* there are side-branches which may deserve taxonomic distinction. In *Steno. lunulicosta*, for example, the number of lobes increased whilst the shell became rather serpenticonic.

Another branch from *Stenopharciceras* led to the compressed Petteroceratidae with third ventral lobes. Two new species from the MD III-E of Morocco give evidence for morphological change within the suboxyconic *Petteroceras*. *Pett.* n.sp. I has less lobes than *Pett. errans*, *Pett.* n. sp. II is more advanced, rather involute and thin. *Pett. feisti* from UD I-A of the Montagne Noire shows that the group survived just into the basalmost Upper Devonian. It is unclear whether the extremely rare involute *Meropharciceras* with rounded venter belongs to the same lineage or whether it branched off independently from early neopharciceratids.

Contemporaneously with youngest maenioceratids (MD II-D), the first species of a second multilobed group, the Eobeloceratidae, appeared in North Afrika. Members are characterized by faster expanding, mesodomic and compressed shells. Early stages are typically ribbed and there is a wide mid-flank saddle as in homoemorphic Frasnian Koenenitidae. *Mzerrebites* with rounded venter resembles *Koenenites* but lacks the pointed first ventral lobe. In *Mz. erraticus* (MD III-B), the outer flank lobe is unusually enlarged. The open umbilicate Gen. nov. I ("*Timanites meridionalis* Gp.", MD III-C) increased the number of lobes and developed oxyconic venters. This trend continued in the involute Gen. nov. II ("*Ph. taouzensis* Gp.", MD III-D) and there was a significant size increase. *Eobeloceras* represents a poorly known gigantic convolute side-branch. A third new genus ("*Ph. kayseri* Gp.") has flattened rather than acute venters.

Since the most primitive member of the strongly ribbed mostly Frasnian Triainoceratidae, the serpenticonic *Tamarites*, has a much simpler suture than *Maenioceras*, the ancestry of the family remains enigmatic. Ribbing was also found in evolute early stages of early Pharciceratidae. Multilobed Frasnian genera such as *Komioceras* and *Devonopronorites* have phylogenetic affinities with the Koenenitidae whilst *Nordiceras* evolved in parallel with beloceratids from Acanthoclymeniidae.