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.