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Occurrence of *Phoebodus gothicus* (Chondrichthyes: Elasmobranchii) in the middle Famennian of northwestern Iran (Province East Azerbaijan)

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ABSTRACT:

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Teeth of the stratigraphically relevant elasmobranch *Phoebodus gothicus* were recovered from samples collected from the Ilan-Ghareh Formation in the neighbourhood of Zonuz in East Azerbaijan province, Iran. The associated fauna confirms a middle Famennian age, *marginifera* and *trachytera* conodont Zone. Comparisons with European, North American, African and other Asian locations show a stratigraphically restricted distribution of *Phoebodus gothicus* in the Famennian, Early *marginifera* to Middle *praesulcata* Zone. The Zonuz sample furthermore contains conodonts, ostracods, gastropods, crinoids as well as tooth and bone fragments of other chondrichthyans, placoderms, and osteichthyans. The ostracods indicate a neritic, shallow water environment with a probable high nutrient flux.

Key words: Elasmobranch teeth, Ilan-Ghareh Fm, Azarbayjan-e Sharqi, Associated fauna, Biostratigraphy and Distribution.

INTRODUCTION

The elasmobranch genus *Phoebodus* is a common form in the Middle and Late Devonian and Early Carboniferous which unfortunately, to date, is only known by its teeth. No articulated remains are reported. The only articulated specimen related to *Phoebodus*, described by WILLIAMS (1985) as *"Ph". hesleronum* from the Mecca Quarry Shale/upper Westphalian C of Indiana, contains dislocated elements from the head (jaws, braincase) as well as the pectoral fins and dorsal fin spines. However, it is indeed not a phoebodontid, as investigation of the preserved teeth by GINTER (1998) revealed significant differences from the type specimen. Nevertheless, teeth of *Phoebodus* species are very valuable and helpful for stratigraphic analyses (GINTER 1990; GINTER & IVANOV 1992, 1995a, 1996; GINTER & TURNER 1999; IVANOV 1996; LONG 1990).

The material presented in this paper was recovered from a small sample collected in 1967 by a German-Iranian expedition of the Institute of Geosciences of the University of Mainz, Germany, which went to different isles in the Aegean Sea over Turkey to the Zagros Mountains in Iran. The main goal was to explore for fossil mammals (e.g. BERNOR & *al.* 1979). Participants, Jürgen A. BOY and Manutscher MEHRNUSCH, collected samples from a locality on a hill slope in the neighbourhood of Zonuz, a town situated about 60 km air distance NW of Tabriz in the border triangle of Armenia, Azerbaijan, and Turkey (Text-fig. 1). The place is located in a southern suburb of Zonuz near a mosque, on the eastern face of the hill in front of the Dehrgāh mountain. Small samples of a yellowish carbonate of nearly bonebed character were collected (BOY, pers. comm.). Over the years, the etched residue

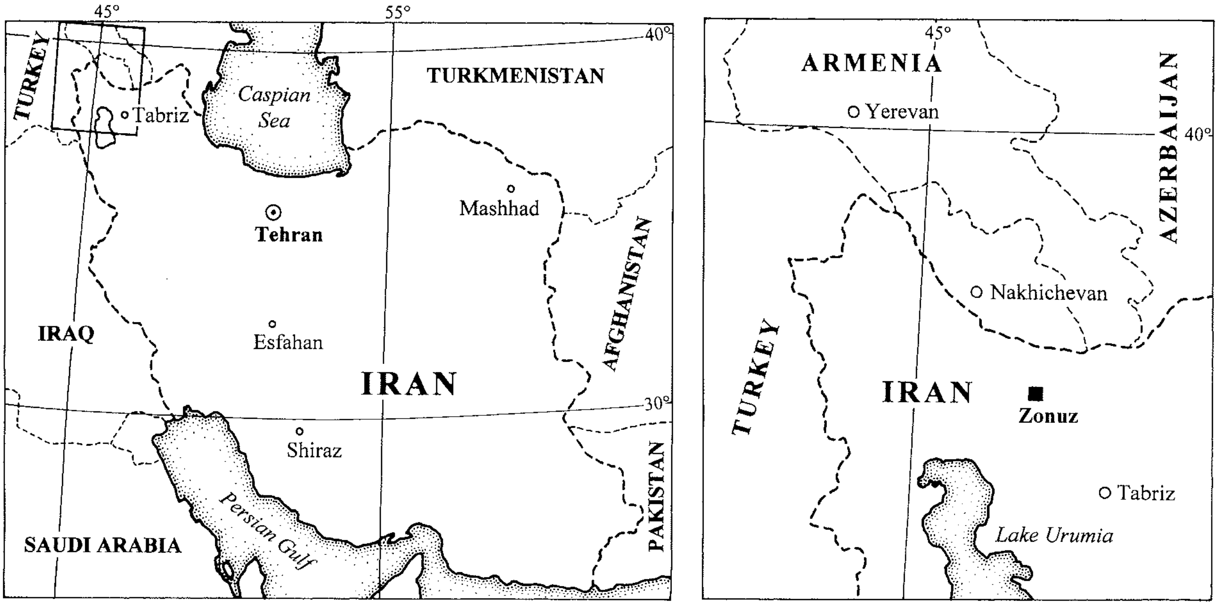

Fig. 1. Map of Iran including details of the northwestern region with the location of Zonuz.

of the samples was stored in a small glass tube in the collection of the Institute of Geosciences, Department of Palaeontolgy at Mainz.

Elasmobranch teeth including the biostratigraphically important *Phoebodus gothicus*, erected and diagnosed by GINTER (1990), were recently detected in the sample. The sample also contains remains of several different other fossil organisms. Vertebrate remains represent cladodont teeth and tooth fragments, acanthodian scales, bone fragments of placoderms, actinopterygian hard parts and lepidotrichia, and crossopterygian tooth fragments (Tab. 1).

Conodonts of the genera *Icriodus* and *Polygnathus* are present. The invertebrate fauna is represented by gastropods of the family Bellerophontidae, ostracods similar to forms of the Russian Platform (EGOROV 1950) and crinoid ossicles.

Research on fossil sharks is in the very beginning in Iran. First reports were given by JANVIER (1974) with scales of *Protacrodus* and ?*Holmesella*, GOLSHANI & JANVIER (1974) on a bradyodont tooth fragment, and JANVIER (1977, 1981) on teeth of cladodonts, *Phoebodus*, *Protacodus* as well as remains of dorsal fin spines, scales and teeth of *Ctenacanthus*. DASHTBAN (1996a) described *Phoebodus* sp. and *Ph.* cf. *australiensis* in his unpublished thesis on Late Devonian and Early Carboniferous fishes from Central Alborz.

A check of his collection at the Institute for Geology in Esfahan revealed teeth of *Denaea* sp., *Stethacanthus*, different undeterminable cladodonts, a polyacrodont, robust *Phoebodus* teeth, scales, and branchial denticles of late Frasnian/early Famennian age. However, all the material came from the central or eastern parts of Iran (Alborz mountains, Ābādeh, and Kerman region). Recently, a group of promising students started on further systematic investigations and biostratigraphic correlations. Here, HAIRAPETIAN & GHOLAMALIAN (1998) note *Stethacanthus*, *Protacrodus*, and *Thrinacodus* teeth from the Upper Devonian of the Chahriseh area NE of Esfahan.

Notwithstanding, this is the first report of elasmobranch remains from the NW Iranian province Azarbayjan-e Sharqi (East Azerbaijan). The analysis of the associated fauna confirms an early to middle Famennian age based on the discovered conodont assemblage of *Icriodus cornutus*, *I. costatus*, and *Polygnathus* cf. *nodocostatus*. The occurrence of *Phoebodus gothicus* supported a *marginifera* to *trachytera* conodont Zone interval for the sample of the investigated member.

SYSTEMATIC PALEONTOLOGY OF THE ELASMOBRANCH REMAINS

Class Chondrichthyes HUXLEY 1880
Subclass Elasmobranchii BONAPARTE 1838
Order incertae sedis
Familiy incertae sedis
Genus *Phoebodus* ST. JOHN & WORTHEN 1875

Table 1. List of fossil remains found in the sample from Zonuz of middle Famennian age housed in the Institute of Geosciences (Palaeontology) of the University of Mainz/Germany

Faunal content of the locality Zonuz, Azarbayjan-e Sharqi /Iran

Crossopterygians	Fam. Osteolepididae: tooth fragments Fam. Holoptychiidae: tooth fragments *Onychodus* sp.: teeth part of plate with tubercular ornamentation
Actinopterygians	palaeoniscoid teeth scale and bone fragments indet. lepidotrichia
Placoderms	bone fragments
Acanthodians	scales
Elasmobranchs	*Phoebodus gothicus* GINTER 1990: teeth *Stethacanthus thomasi* (TURNER 1982): one tooth additional cladodont and phoebodont tooth fragments
Conodonts	*Icriodus cornutus* SANNEMANN 1955 *Icriodus costatus* (THOMAS 1949) *Polygnathus* cf. *nodocostatus* BRANSON & MEHL 1934
Crinoids	ossicles
Ostracods	Fam. Nodellidae: *Schweyerina* cf. *zaspelovae* SHISHKINSKAJA 1968 Fam. Kloedenellidae: *Mennerella* sp., *Sulcella* sp., *Kloedenellitina* sp.
Gastropods	Fam. Bellerophontidae: *Tropidodiscus*, ?*Naticopsis*, ?*Loxonema*

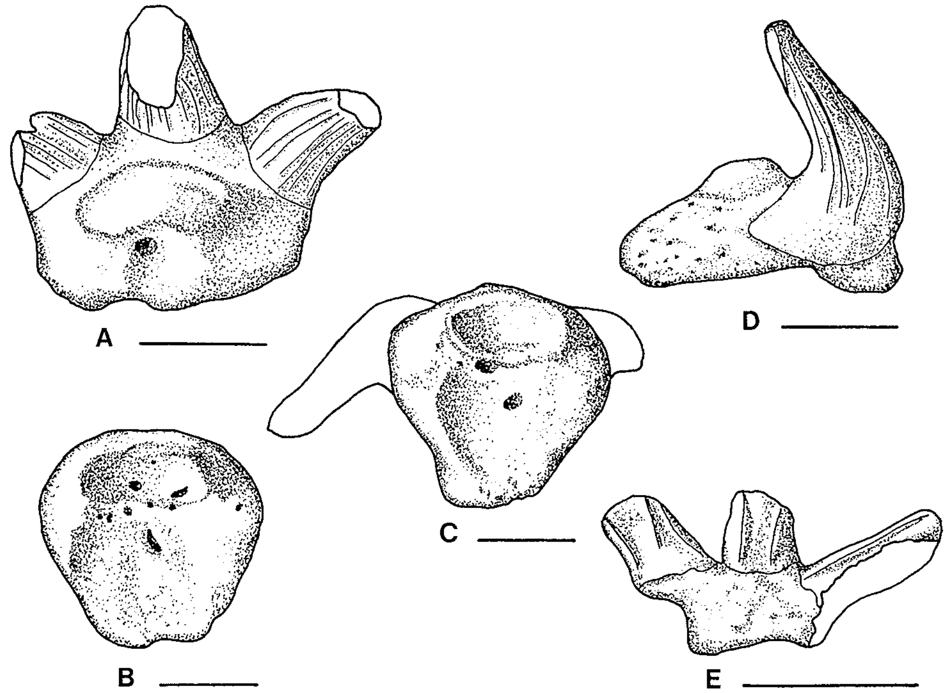

Fig. 2. *Phoebodus gothicus*, middle Famennian of Zonuz, Azarbayjan-e Sharqi/NW Iran. GPIM-M 3016: A- lingual view, B – basal view; GPIM-M 5831: C – basal view, D – lateral view; GPIM-M 5830: E – labal view. For general terminology of teeth, see HAMPE (1998, Fig.1) Scales = 1 mm

Phoebodus gothicus GINTER 1990
(Text-fig. 2, Pl. 1, Figs 1-9)

REMARKS: The diagnosis of the family Phoebodontidae WILLIAMS 1985 is preliminary based on the characterization of *Phoebodus heslerorum*, a partly articulated specimen, which is not a phoebodont (after GINTER 1998). The exact systematic position still remains unclear. The tooth morphology of many described species can vary severely. GINTER (1990) does not exclude the possibility that phoebodonts do not constitute a monophyletic group.

MATERIAL: Six complete teeth plus several fragments and isolated cusps at the Institute of Geosciences (Palaeontology) of the University of Mainz, Germany (collection abbreviation GPIM-M).

DESCRIPTION: The height of the teeth ranges from 1.5 to 3 mm. The crown consists of three equally sized, lingually turned cusps of which the lateral cusps diverge outwards (mesially and distally; Text-fig. 2A, E; Pl. 1, Figs 1, 2, 6, 8, 9). A sigmoidal curvature of a lateral cusp is observed in a complete specimen (Text-fig. 2D; Pl. 1, Fig. 5). All cusps wear a pattern of straight vertical cristae of different number (6 to16). The cristae often appear relatively strong, especially in smaller sized teeth, in contrast they can look more delicate in larger teeth (Text-fig. 2A, E). The cristae cover the entire cusps, bifurcations are possible (Pl. 1, Fig. 2).

The base is extended lingually (Text-fig. 2D; Pl. 1, Fig. 4) showing a rhombic to oviform outline, typically with a pointed lingual arch (Text-fig. 2B, C; Pl. 1, Fig. 5). The only slightly prominent coronal button is oval and mesio-distally extended; it has sometimes a rounded shape and is situated in the center of the base. It has an image of a little hump (e.g. Text-fig. 2D; Pl. 1, Figs 3, 5, 6). One big nutrient foramen is positioned lingually of the button (Text-fig. 2A; Pl. 1, Figs 1, 3, 5, 6, 8, 9). The canal runs through the base and opens in the center of the bottom side (= hemiaulacorhizide nutrition, Text-fig. 2C). The whole bottom side of the base is concavely depressed. Some additional, smaller foramina are placed between the main opening and the prominently developed labial margin of the bottom side. Sometimes, an oval or kidney shaped impression can be observed (Text-fig. 2B, C). There is no rounded basal tubercle like in xenacanthids (e.g. HAMPE 1988, 1989). A possible juvenile tooth was found with less vertical cristae, occurring mainly on the lateral sides of the cusps (Pl. 1, Fig. 9), and with a relatively broad lingual arch. A coronal button is only meagerly developed, documented earlier also in probable tooth embryos of xenacanthids (see HAMPE 1997).

DISCUSSION: The features of the Zonuz teeth are certainly diagnostic for *Phoebodus gothicus*. The species was originally defined by GINTER (1990) on specimens from the Famennian of Poland (Holy Cross Mountains). *Ph. gothicus* has been described shortly there after from localities of the southern Ural region in Russia (GINTER & IVANOV 1992, Fig. 8, I-K, Fig. 9). Another European find of *Ph. gothicus* is documented from a borehole in the German Bergisch Gladbach-Paffrath Syncline (HAMPE & SCHINDLER in press).

Remains are known from several additional places besides the newly recovered Iranian teeth. LONG (1993, Fig. 11.4.H) described a partial corroded tooth with broken median cusp as *Ph.* cf. *gothicus* from the upper Famennian Xom Nha Formation adjacent to a village of the same name in Vietnam. The fragment shows the characteristic labio-lingual elongation of the base which is in fact the most significant feature of *Ph. gothicus*. GINTER also includes specimens figured by GROSS (1973, Pl. 34, Figs 12-22) as *Ph. politus* from the Maple Mill Shale of Iowa. They are clearly identifiable because of the pointed lingual arch of the base (GROSS 1973, Pl. 34, Fig. 17). The typical place of the main foramina forming the hemiaulacorhizide nutrition is also documented in GROSS' figures. Some of the specimens carry two tiny additional cusplets between the median and the lateral cusps, a feature within the standard varability of the teeth of the species (GINTER 1990). The second North American place revealing *Ph. gothicus* is located in the Deadman Canyon of the Sacramento Mountains in South-Central New Mexico (KIETZKE & LUCAS 1992, Fig. 2A-C, as *Ph. politus*). GINTER & IVANOV (1992) designated this poor tooth to *Ph. gothicus*. The determination leaves a little doubt because the cusps are all broken and the base alone is not diagnostic enough, although the tendency of a lingual extension is clearly seen. It may represent a geographical variation which appears to be more robust. However, the Deadman Canyon tooth should be classified with a questionmark (see also BIOSTRATIGRAPHICAL COMMENTS). The New Mexican locality was situated on the eastern margin of the Protopacific Ocean, that means the only location of the Protopacific known so far with *Ph. gothicus* occurrence (Text-fig. 4). DERYCKE (1992, Pl. I, Fig. 6) reported a tooth from the locality Mfis in the Tafilalet Basin in Morocco as *Ph. politus*. However, nothing was stated about the stratigraphy of this occurence, whereas the age of the neighbouring locality Jbel Debouâa is clearly defined as Latest *marginifera* to Early *expansa* Zone (DERYCKE 1992, Figs 1 and 19) which corresponds explicitly with the occurence of *Phoebodus gothicus*.

Most of the other known Devonian *Phoebodus* species are distinctly different from *Ph. gothicus*. *Ph. limpidus* from Ostrówka (*expansa/praesulcata* Zone) exhibits five cusps on generally very fragile looking teeth with an almost mesio-distal extension (GINTER 1990, Pl. 4, Figs 2-6).

Ph. typicus from Ryauzyak/southern Ural and northern Queensland/Australia shows a mesio-distal extension of the base nearly without exception (GINTER & IVANOV 1995a, Pl. 1, Fig. 7; GINTER & IVANOV 1995b, Fig. 2; GINTER & TURNER 1999, Fig. 3A-D; Late *triangularis* to Early *marginifera* Zone). *Ph. rayi* from Melville Island in the Canadian Arctic (Early or Middle *crepida* Zone) has an obtuse lingual angle at the mesio-distally extended base (GINTER & TURNER 1999, Figs 4, 5). Sometimes the coronal button is doubled in this species.

Teeth of *Ph. latus* from southern Ural (*rhenana* Zone, Frasnian) shows e.g. up to seven cusps connected with a mesio-distally widened base (GINTER & IVANOV 1995a, Fig. 1). *Ph. bifurcatus* known from the Frasnian of Poland, Russia and Utah reveals two characteristic lingually extended lobes of the base and regularly a quincuspid crown (GINTER & IVANOV 1992, Fig. 4, 5D-H, TURNER & YOUNGQUIST 1995, Figs 1, 2). The Frasnian *Ph. fastigatus* from the Kuznetsk basin/Russia has three almost equally developed cusps and a trapezoid base which is narrow below the crown and has a wide lingual margin (GINTER & IVANOV 1992, Fig. 3A, B, G; GINTER 1995, Fig. 1C, D).

The mainly Givetian type species *Ph. sophiae* (e.g. GINTER 1995, Fig. 1A from Poland; TURNER 1997, Fig. 13 from New York State) has also a broad oval-shaped base.

Greater differences are displayed between *Ph. gothicus* and *Ph. australiensis*, occurring in Thailand, Poland, and Russia (from Middle *marginifera* Zone to the Tournaisian). *Ph. australiensis* has very robust teeth and strong cusps (LONG 1990, Fig. 2, 3F-O, 4; GINTER & IVANOV 1996, Fig. 3A-C) showing always bifurcating vertical cristae as inverted V's nested within one another. The latter feature occurs in teeth of the Carboniferous and Permian genus *Bransonella* which is considered also as a phoebodontid. IVANOV & GINTER (1996, Figs 1, 3-5) placed *Bransonella* with the xenacanthids. However, some characters disagree with this placement: the above mentioned pattern of the cristae, the occurrence of labial foramina, the kidney- or half-moon-shaped basal tubercle. These features occur never in xenacanthid teeth (see phylogeny in HAMPE & HEIDTKE 1997, HAMPE & LONG 1999). A similar design is reported also from teeth of *Adamantina* from the Upper Permian of East Greenland (BENDIX-ALMGREEN 1993, Fig. 3A-E, 9A-C) and the Tournaisian of Russia (IVANOV 1999, Fig. 4; Pl. 6, Fig. 11).

"Ph." marocensis (DERYCKE 1992, Pl. 1, Figs 4, 7, 8) from Hamar Laghdad in Morocco (*rhomboidea* or *marginifera* Zone) reveals relatively long lateral cusps so that the central cusp of the quincuspid crowns is as long as the lateral ones. The cross-section of the central cusp is wider than that in the lateral cusps. The striations on the cusps differ shorter cristae from *Ph. gothicus*. The cristae are arranged like inverted V's nested within one another. The coronal button is less developed than in *Ph. gothicus*. GINTER & IVANOV (1996) consider *"Ph." marocensis* as not *Phoebodus sensu stricto*.

The teeth of *"Phoebodus" heslerorum* (WILLIAMS 1985, Pl. 16, Figs 1-4, 8) from the upper Westphalian C Mecca Quarry Shale in Indiana differ considerably from those of other *Phoebodus* species. They reveal two buttons and a labial concave incision – *Phoebodus* has generally only one button and an even arcuate labial margin. Because of the ornamented fin spine, the relationship to ctenacanthoid sharks is more probable (see also discussion in GINTER 1998).

Ph. politus from the upper Famennian of Ohio is quite similar to *Ph. gothicus*. However, the teeth of *Ph. politus* are with 4 to 8 mm height almost larger than the Zonuz teeth (see NEWBERRY 1889: Pl. 27, Figs 27, 28). The North American teeth have three to five cusps, but show a lingual notch at the base which is not displayed in *Ph. gothicus*. Also the base is broadly elliptical in *Ph. politus*. The reported *Ph. politus* teeth in WANG & TURNER (1985, Pl. 2, Fig. 1; Pl. 3, Fig. 2) from the Devonian-Carboniferous boundary of the Guizhou province in China are too coroded to be identifiable to species level.

Most similarities exist between *Ph. gothicus* and *Ph. turnerae* (GINTER & IVANOV 1992, Fig. 8A-H). The fairly older species (*crepida* to *marginifera* Zone) is known from the southern Ural and Poland (Holy Cross Mountains). *Ph. turnerae* has a somewhat smaller median cusp, and all cusps are only slightly inclined lingually in comparison to *Ph. gothicus*. The sculpture of cristae is not as conspicuous as in *Ph. gothicus*. The bases of *Ph. turnerae* teeth have often a rhombic outline (GINTER & TURNER 1999, Fig. 3I).

The discussion shows that *Phoebodus gothicus* is closest to *Ph. turnerae* (*crepida* to *marginifera* Zone) which is possibly its direct ancestor (see GINTER & TURNER 1999, Fig. 9). The oldest *Phoebodus* species (*Ph. sophiae*; Givetian) is documented from central Europe (Poland) and North America (Iowa) which implies a possible origin for *Phoebodus* in the tropical coastal region of the Euramerican continent. The younger *Ph. politus* (Ohio, upper Famennian) which is also closely related to *Ph. gothicus* (see determinations in GROSS 1973, GINTER 1990, KIETZKE & LUCAS 1992, GINTER & IVANOV 1992) occurs south of the transcontinental arch of Euramerica (Text-fig. 4), a region in which *Ph. gothicus* is known from the Maple Mill Shale in Iowa (Early *marginifera* to Early *trachytera* Zone).

It seems, that evolution in the genus *Phoebodus* consisted of separate developments, interrupted by the Kellwasser Event. Morphologically distinctive Frasnian species disappeared after the Kellwasser Event (*Ph. fastigatus*, *Ph. latus*, *Ph. bifurcatus*) with the single exception of the *Ph. sophiae* lineage (Lazarus species, see GINTER & TURNER 1999). *Ph. gothicus* is distinct from *Ph. australiensis* and *"Ph". marocensis*. They represent an isolated lineage, perhaps ancestral to the younger Paleozoic genus *Bransonella*.

OCCURRENCE: Upper Devonian, middle Famennian, Ilan-Ghareh Formation (*marginifera* and *trachytera* conodont Zone) of Zonuz, Azarbayjan-e Sharqi/NW Iran.

FURTHER DISTRIBUTION: Bergisch Gladbach-Paffrath Syncline, Germany (Middle and Late *expansa* Zone); Holy Cross Mountains, Poland (Early *marginifera* to Middle *praesulcata* Zone); South Ural, Russia (*postera* and *expansa* Zone); Tafilalet Basin, Morocco (?Latest *marginifera* to ?Early *expansa* Zone); Xom Nha Region, Vietnam (*marginifera* Zone); Maple Mill Shale, Iowa (Early *marginifera* to Early *trachytera* Zone); ?Sacramento Mountains, New Mexico (most probably Famennian).

Order Symmoriida ZANGERL 1981
Family Stethacanthidae LUND 1974
Genus *Stethacanthus* NEWBERRY 1889

Stethacanthus thomasi (TURNER 1982)
(Pl. 2, Figs 1-4)

MATERIAL: One tooth at the Institute of Geosciences (Palaeontology) of the University of Mainz, Germany.

DESCRIPTION: The nearly unworn tooth is 1.5 mm high from the bottom to the tip of the longest cusp in the middle (e.g. Pl. 2, Fig. 1). The robust central cusp is flanked by two smaller cusps on each mesial and distal shoulder (Pl. 2, Figs 1, 2). All cusps have a low number of strong vertical cristae covering the entire cusps (about 12 on the central cusp; 5-8 on the smaller cusps). The cusps curve slightly lingually (Pl. 2, Fig. 4). The base is elongated in mesio-distal direction by oval or diamond-shaped outline (Pl. 2, Fig. 3). An also mesio-distally stretched button is placed in front of the main cusp and shows a pair of larger foramina on its lingual margin (Pl. 2, Figs 1, 3). Several smaller nutrient foramina perforate the surface of the base. Four foramina, arranged in a row, are located in the median field on the labial side of the base (Pl. 2, Fig. 2). The labial margin projects basally beneath the central cusp and the adjacent inner cusps.

DISCUSSION: TURNER (1982, Fig. 8J) introduced the new species, "*Cladodus*" *thomasi*, from the Lower Carboniferous (Upper Bundock Creek Formation) of the Broken River embayment in Queensland/ Australia. LONG (1991, p. 347) was the first to attribute this species to *Stethacanthus*. Generally, it is quite difficult to determine cladodont teeth. Cladodont teeth are a heterogenous mixture from monocuspids to tri- or multicuspids. ZIDEK (1993) found gnathal teeth of four morphological types in different jaw remains of *Stethacanthus* cf. *altonensis* (symphysial whorl, quincuspid and tricuspid teeth as well as tricuspid pseudocladodont teeth with equal sized cusps). The main feature of cladodont teeth is a long, prominent central cusp accompanied by a changing number of shorter, accessory lateral cusps which are positioned labially in a row on a mainly plane, lingually extended base.

LUND (1974) described the teeth of *St. altonensis* from the Mississippian of Montana only unsufficiently. Tiny cusplets next to the central cusp are a significant feature (LUND 1974, Fig. 11a). The following lateral cusps are higher but normal in comparison to other "cladodont" teeth. ZIDEK (1993, Fig. 2A) figured a five-cusped tooth of *St.* cf. *altonensis* from the Mississippian of Oklahoma which is very similar to the tooth from Zonuz. The figured tooth is completely preserved. The pattern of the cristae is similar as well as the design of the base (coronal button, labial foramina in a row). The cusps appear to be strong but longer. However, the tips of the cusps are eroded in the Iranian species. Teeth of *Stethacanthus* sp. from the upper Mississippian (Namurian E2b) of Montana (LUND 1985, Fig. 8, A-D) have two coronal buttons on the upperside as well as a pair of basal tubercles on the bottom side of the base and shares herewith features with *Symmorium* (s. below).

LEBEDEV (1996, Fig. 4) reported teeth of *St. obtusus* from the lower Tournaisian of the Tula region in Russia and considered *St. thomasi* a junior synonym of the Russian species. LEBEDEV errored because there are some striking differences between them: *St. obtusus* has up to nine cusps (one central and up to four on each lateral side). The coronal button is not so well developed as in *St. thomasi* and keeps two to six big nutrient foramina on the lingual face of the button.

Whereas GROSS' Late Devonian cladodont teeth from the Maple Mill Shale of Iowa (GROSS 1973, Pl. 34, Figs 6-10) seem to be also a stethacanthid, the specimen from Hessen and Harz in Central Germany (GROSS 1973, Pl. 33, Figs 24-26; Pl. 34, Figs 1-5) look more like that of *Symmorium*. *Stethacanthus* teeth, if they are nearly completely preserved, can be distinguished from *Symmorium* species. *Symmorium* teeth have a pair of distinct prominent tubercles on the lower labial margin (see a.o. ZIDEK 1973, Fig. 2 for *Sy. occidentalis*; LONG 1990, Fig. 7F-L, 8A-D; IVANOV 1996, Fig. 5, both *Symmorium* sp.). This very characteristic type of tooth occur in Upper Devonian and particularly Carboniferous strata in many places of the world. LEIDY (1860) introduced this morphological type for *Cladodus occidentalis*. However, teeth of the holotype of *Symmorium reniforme* to which these characteristic teeth were assigned, do not have the two buttons nor a pair of basal tubercles (GINTER 1998). There exists still confusion about the exact generic classification. Indeed, the name "*Cladodus*" which was erected by AGASSIZ (1843) and used to describe isolated teeth, needs seriously a revision (DUFFIN, in prep.). WOODWARD (1889), for example, assigned alone 52 species to this taxon.

Teeth of the genus *Denaea* (e.g. *Denaea meccaensis* in WILLIAMS 1985, Text-fig. 7) have in comparison to *Stethacanthus* long and extremely slender cusps (up to seven in number) which are sigmoidally curved in lateral view. They lack coronal and basal buttons/tubercles on the more or less irregular hexagonal outlined base (watch also MADER & SCHULTZE 1987, Fig. 6d, e, GINTER 1990, Pl. 4, Fig. 7, IVANOV 1996, Fig. 5H, I each for *Denaea* sp.; IVANOV 1999, Pl. 8 for "*Denaea*" *decora*).

It appears that *Stethacanthus thomasi* was not effected by the Kellwasser and Hangenberg events. Its first appearance is in the upper Frasnian (*rhenana* Zone) of central Europe (Poland). All other discoveries of *St. thomasi* document a dispersion from west to east (Iran – middle Famennian, Queensland – Lower Carboniferous).

OCCURRENCE: As for *Phoebodus gothicus* in East Azerbaijan province.

FURTHER DISTRIBUTION: Frasnian to Famennian of Holy Cross Mts., Poland (?Early *rhenana* to ?Late *rhomboidea* Zone); ?Hamar Laghdad, Morocco (*rhomboidea* or *marginifera* Zone); Broken River embayment, Queensland/Australia (Lower Carboniferous).

OTHER VERTEBRATE REMAINS

Besides the invertebrates (details, see Pl. 2, Figs 5-9; Pl. 3, and Tab. 1), tooth fragments of holoptychiid and osteolepid crossopterygians were discovered. The characteristic long and sigmoidal curved, hook-like symphyseal teeth of *Onychodus*, which describes one of the most common remains in Upper Devonian aquatic deposits, are found in the residue of the Zonuz sample. *Onychodus firouzi* from the middle Frasnian of Hutk (Kerman area) is the only described species of this genus in Iran so far (JANVIER & MARTIN 1979, 1981).

Undeterminable is a part of a plate with tubercular ornamentation. Dipnoan remains could not be recognized in the residue. Lungfishes are reported so far from the lower to middle Frasnian of central Iran with ?*Dipterus*, ?*Chirodipterus*, *Rhinodipterus*, *Iranorhynchus* (JANVIER 1974, 1981, JANVIER & MARTIN 1978) and the upper Famennian of central Alborz with *Dipterus* and *Rhinodipterus* (DASHTBAN 1996b, c).

Palaeoniscoid teeth, scales, bone fragments and lepidotrichia are recognized as well as placoderm bone fragments and acanthodian scales. Unfortunately, the fragmentary preservation and the low number of additional specimens of the mean sample allows no further determinations.

BIOSTRATIGRAPHICAL COMMENTS

Upper Devonian deposits are distributed widely throughout Iran. This country represents the northern margin of Gondwana during the whole Devonian period and is a focus for current bioevent and biogeography studies (MAWSON & *al.* 1998). Palaeontological research was concentrated in the past to north (Alborz range) and central Iran (e.g. Tabas and Kerman region; see short review in DASTANPOUR 1996). Only a few investigations in NW Iran deal with the invertebrate fauna (nautiloids, gastropods, bivalves, brachiopods, corals and crinoids) from the Permian of the Dzhulfa area (FRECH & ARTHABER 1900, GRÄF 1964), Foraminifera from the Permian south of Tabriz (KAHLER & KAHLER 1979), and give reference to different fossil remains from the Devonian up to the Tertiary (RIEBEN 1935, see below) of the Zonuz and Harzand regions.

As mentioned in the introduction, the fauna presented here originated from an etched residue of yellowish carbonate collected near Zonuz on the eastern face of a hill situated in front of the Dehrgāh mountain. The sample was classified as a condensation horizon with high organic content and bonebed-like character.

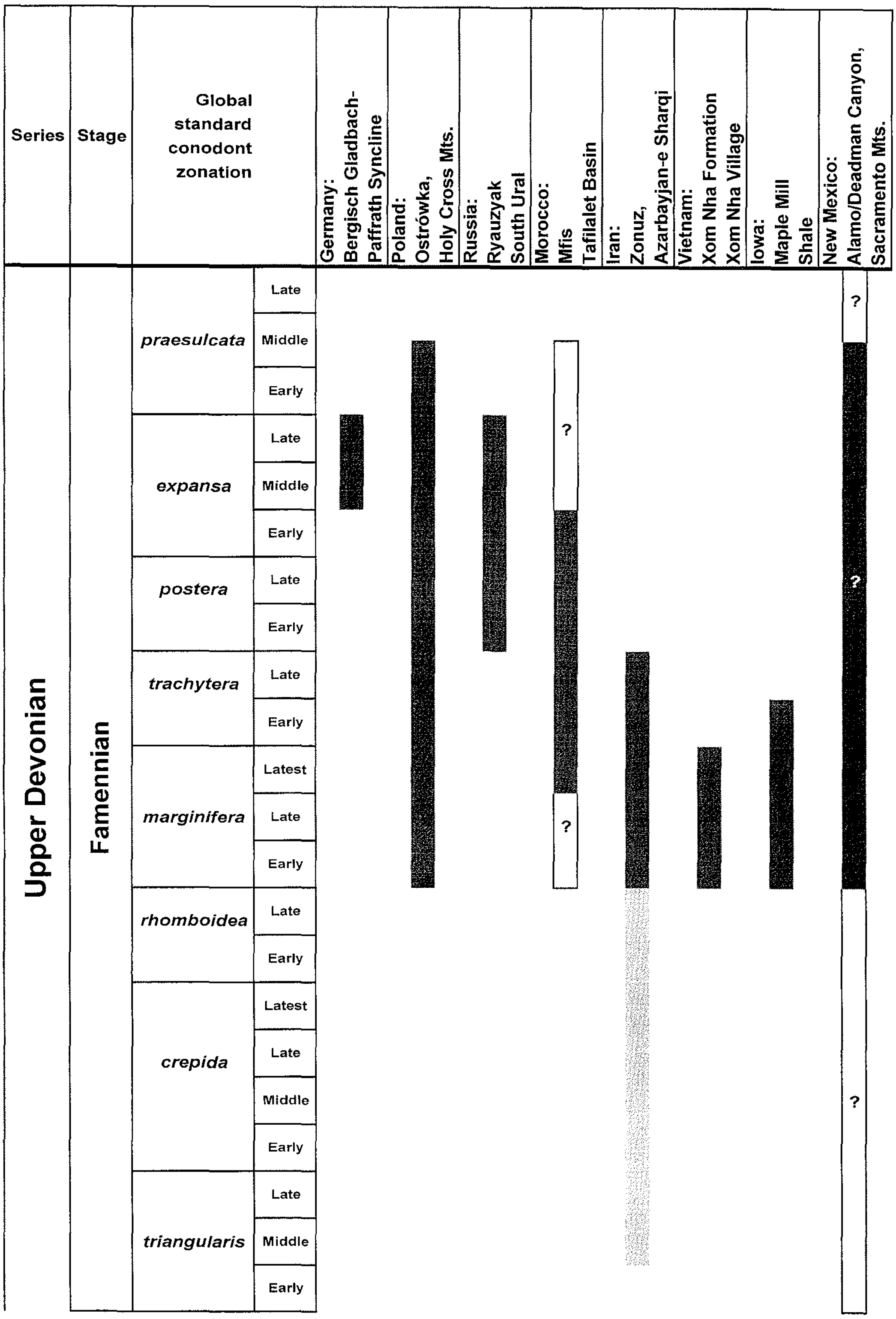

Fig. 3. Stratigraphic distribution of *Phoebodus gothicus* in the famennian (dark grey) in comparison to the global standard conodont zones; the light grey field on the Iranian locality marks the additional known distribution of the conodonts found in the sample (*Icriodus cornutus, I. costatus, Polygnathus* cf. *nodocostatus*); the exact position of the New Mexican finds can not be stated because the conodonts have not yet been investigated; detailed information about the age of the Mfis locality in Morocco is lacking (see map and table in DERYCKE 1992)

The sediment probably came from below a quartzite horizon which is characterized by imprints of many placoderm bones. No articulated material could be observed. The quartzite is interpreted as the result of a high energy shallow water environment (BOY, pers. comm.).

Only RIEBEN (1935, p. 82f) described a few details of the Upper Devonian deposits of the Zonuz area which are represented by fossiliferous psammites, conglomerates, marbles, and oolithic carbonates. Brachiopods, especially spiriferids and rhynchonellids are common. All deposits are rich in hematite. The complete succession is not demonstrated. RIEBEN illustrated only the succession for the ridges NW and NE of Dehrgāh. The following members are described from the top to the base: a) an oolithic red ironstone member containing brown carbonate nodules, b) a bed of dark red carbonate with "*Spirifer* cf. *verneuili*", and c) a sandy and mica rich brownish carbonate unit showing imprints of bivalves and brachiopods.

Fish remains are only recorded from a red sandstone at the northern face of the Dehrgāh: plates and bone fragments which are attributed to the porolepiform *Holoptychius* cf. *flemingi*, and to the placoderms *Bothriolepis* and "*Dinichthys*" (RIEBEN 1935). No elasmobranch remains were reported so far. The listed invertebrate fauna (brachiopods and molluscs) does not indicate any exact stratigraphic age. RIEBEN believed a Famennian to Tournaisian age. However, the particular unit from which the German group collected the sample, could not be related to the observations given by RIEBEN (1935). The complete Famennian succession in NW Iran belongs today to the so called Ilan-Ghareh Formation (SABOURI 1998). The interval illustrated here represents only a part of the successions.

The age of the sample can be determined relative accurately. The teeth of the elasmobranch *Phoebodus* can be used for stratigraphic correlations. Michał GINTER developed a stratigraphic table in correlation to the conodont zonation for Eastern Europe in a first step (GINTER & IVANOV 1992; compare WEDDIGE 1998). An analysis of the associated faunal elements confirms an early to middle Famennian age (about Middle *triangularis* to Late *trachytera* Zone) based on the discovered conodont assemblage of *Icriodus cornutus* (Pl. 2, Figs 5, 6), *I. costatus*, and *Polygnathus* cf. *nodocostatus* (Pl. 2, Figs 7-9). The appearence of *Ph. gothicus* limits the base of the time span to the beginning of the *marginifera* Zone, because comparisons with *Ph. gothicus* occurrence of central and eastern Europe show a stratigraphically restricted distribution from the *marginifera* up to the Middle *praesulcata* Zone (Text-fig. 3). Using the overlap and considering the corresponding vertical distribution of *Phoebodus gothicus* from other places in the world, an interval from *marginifera* to *trachytera* conodont zones is most likely.

Ph. gothicus was first described from the Early *marginifera* to Middle *praesulcata* Zone of the Holy Cross Mountains, Poland (GINTER 1990, 1995). In addition, this significant species was found so far in the *postera* and *expansa* zones of Ryauzyak in the southern Urals, Russia (GINTER & IVANOV 1992), in the *marginifera* Zone of Xom Nha Region in Vietnam (LONG 1993), and in the Middle and Late *expansa* Zone of the Bergisch Gladbach-Paffrath Syncline (drilling core section), Germany (HAMPE & SCHINDLER in press). The teeth from the Tafilalet Basin, Morocco (most probably Latest *marginifera* to Early *expansa* Zone, DERYCKE 1992) belong also to *Ph. gothicus* as well as the figured specimens in GROSS (1973, Pl. 34, Figs 12-22) which GINTER & IVANOV (1992) attributed correctly to *Ph. gothicus*. The latter teeth appear in the Early *marginifera* to Early *trachytera* zones in the Maple Mill Shale of Iowa (compare stratigraphic location on conodonts in ANDERSON 1965, Tab. 2; 1966, Text-fig. 3, Tab. 2). The occurrence of *Ph. gothicus* at Deadman Canyon of Alamo in the Sacramento mountains of New Mexico (KIETZKE & LUCAS 1992) is questionable. On one hand, little doubt remains on morphological aspects (see discussion above), on the other hand, the stratigraphic position is not clear. There exists an unconformity at the Devonian-Carboniferous boundary in New Mexico. The Frasnian is overlain by Mississippian units. The hiatus between the beds is filled by a black shale of which top and bottom is marked by bone beds. The shale is regarded as Mississippian or Upper Devonian (Famennian; KIETZKE & LUCAS 1992, p. 17f). Considering the maximum range of *Ph. gothicus* and the possibility of future verification of this species in that location, the New Mexican member could then only be placed between *marginifera* and *praesulcata* Zone. Unfortunately, the conodont fauna has not yet been investigated. After all, *Phoebodus gothicus* disappeared definitely during the Hangenberg Event (see GINTER 1995, Tab. 1).

The first occurrence of *Ph. gothicus* is later than that of *Stethacanthus thomasi*. A slow dispersal eastwards through Prototethys is documented for *St. thomasi*, but *Ph. gothicus* appears contemperanously at several places (Text-fig. 3) suggesting relatively rapid dispersal.

The ostracods reveal some further informations. Specimens of the family Nodellidae have been detected with *Schweyerina* cf. *zaspelovae* (Pl. 3, Figs 7-9), a taxon which disappeared with *Sch. reichsteini* in the Late *crepida* Zone (BECKER & BLUMENSTENGEL 1995, BECKER 1998). *Schweyerina zaspelovae* was described

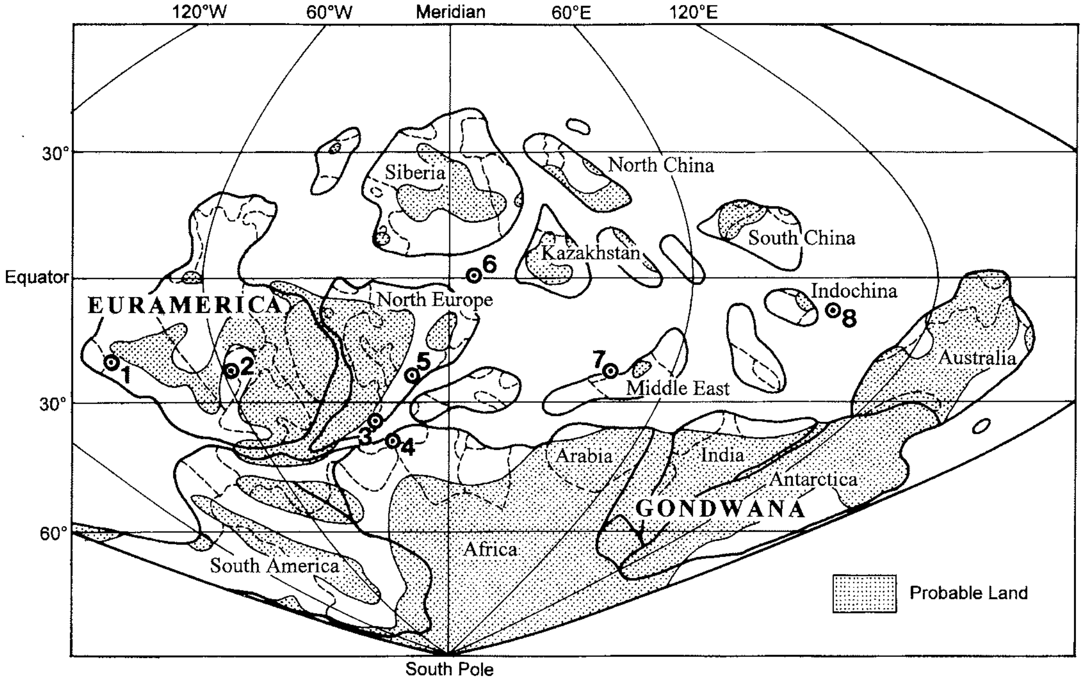

Fig. 4. Paleogeographical map of the Late Devonian based on reconstructions of KLAPPER (1995) and BECKER (in press); the occurence of *Phoebodus gothicus* is concentrated in the shelf areas of the inner tropical zone; to date this species is known from New Mexico (1, very probable), Iowa (2), Germany (3), Morocco (4), Poland (5), Urals (6), Iran (7), Vietnam (8), see also Text-fig. 3

by SHISHKINSKAJA (1968) from the Frasnian of the Wolgograd area in Russia. Examples of the family Kloedenellidae (see Tab. 1) are found in steinkern preservation. These specimens show similarities to those known from the Frasnian and Famennian of the Russian Platform (EGOROV 1950). Their occurrence suggests a neritic, shallow water environment, flooded with sunlight which is characterized by high nutrient content. Further investigations of the ostracod fauna are expected (G. BECKER in prep.).

RESULTS AND CONCLUSIONS

1) Teeth of the elasmobranch *Phoebodus gothicus* with very characteristic morphological features are documented for the first time from the yet less investigated area of Zonuz in East Azerbaijan (NW Iran).

2) An interval containing the *marginifera* and *trachytera* Zone is most probable for the Zonuz sample according to the conodont assemblage with *Icriodus cornutus*, *I. costatus*, and *Polygnathus* cf. *nodocostatus*. The sample is a part of the Ilan-Gareh Formation which covers the entire Famennian.

3) Biostratigraphical distribution of *Phoebodus gothicus* at different places worldwide (Text-fig. 3) confirms that this species can function as an index fossil from the Early *marginifera* to Middle *praesulcata* Zone (Hangenberg Event).

4) The sediment collected from the Ilan-Gareh Formation represents a condensation horizon and had a bonebed-like character. The sample shows a high diversity of faunal elements (conodonts, crinoids, ostracods, gastropods, crossopterygian, actinopterygian, placoderm, acanthodian, and elasmobranch remains).

5) The associated ostracod fauna indicates a warm, neritic shallow water environment with high nutrient content.

6) Generally, *Phoebodus gothicus* seems to live preferably in near-shore areas (see Text-fig. 4 “palaeogeographical map”) within the tropical zone. A dispersal eastwards through Prototethys is documented for *Stethacanthus thomasi* (Poland – late Frasnian to early Famennian, ?Morocco – early Famennian, Iran – middle Famennian, Queensland – Lower Carboniferous).

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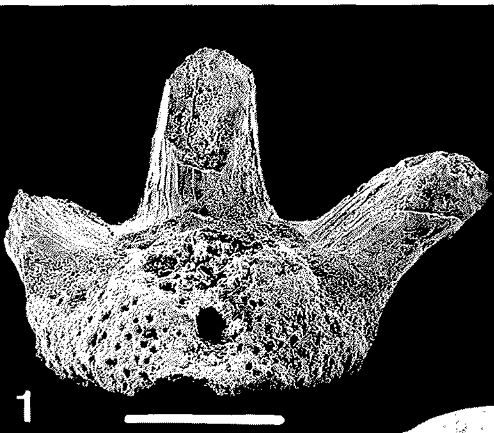
PLATE 1

Phoebodus gothicus from the middle Famennian of Zonuz,
East Azerbaijan province / NW Iran

1 – GPIM-M 3016: lingual aspect
2 – GPIM-M 3016: labial aspect
3 – GPIM-M 3016: coronal aspect
4 – GPIM-M 3016: lateral aspect
5 – GPIM-M 5831: coronal aspect
6 – GPIM-M 5831: lingual aspect
7 – GPIM-M 5831: labial aspect
8 – GPIM-M 5830: lingual aspect
9 – GPIM-M 5833: lingual aspect of a possible juvenile specimen

Scale bars = 1 mm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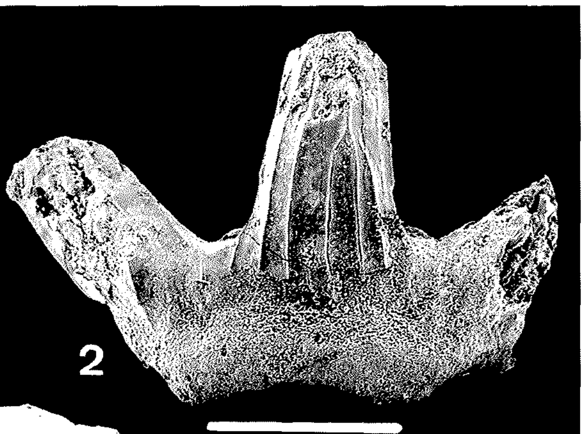
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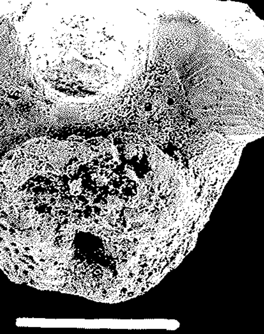
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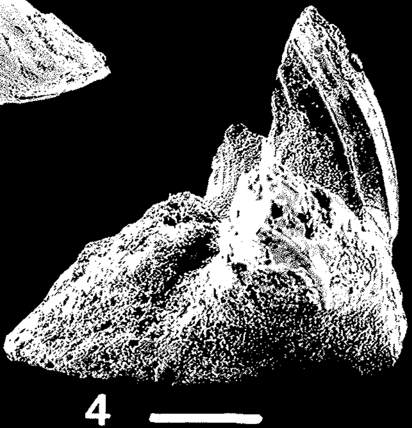
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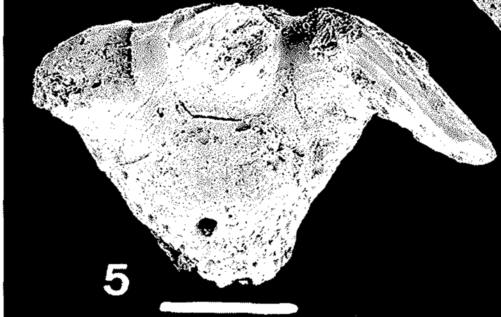
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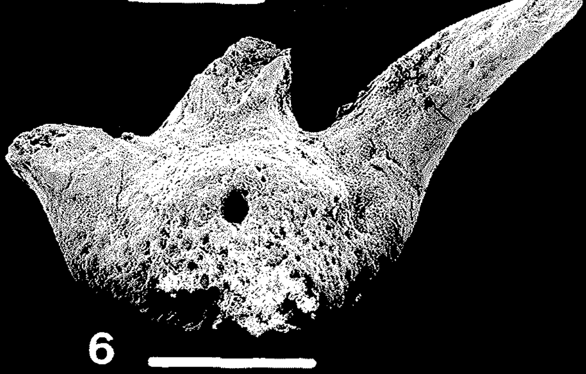
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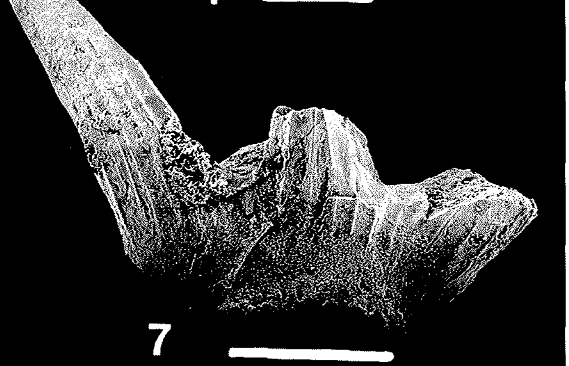
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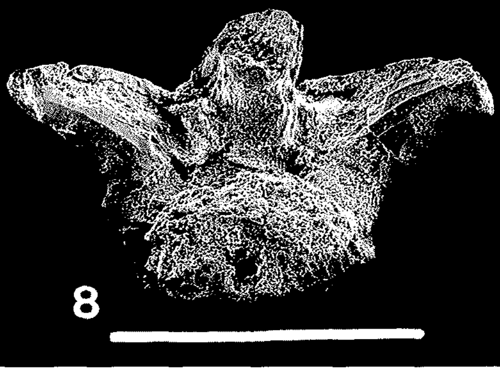
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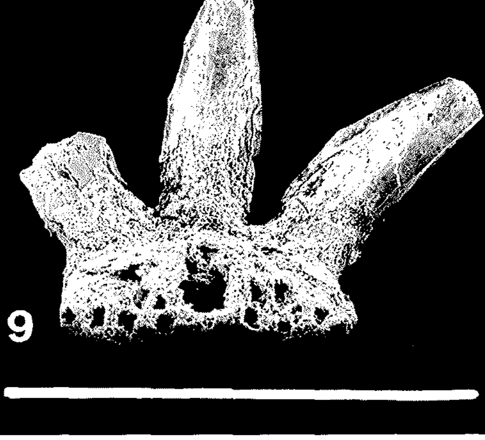
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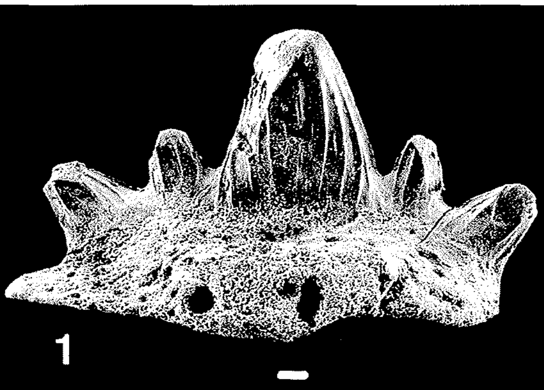
PLATE 2

Elasmobranch teeth (Figs 1-4) and conodonts (Figs 5-9), middle Famennian of Zonuz, East Azerbaijan province / NW Iran

1 – *Stethacanthus thomasi*, GPIM-M 5832: lingual aspect
2 – *Stethacanthus thomasi* , GPIM-M 5832: labial aspect
3– *Stethacanthus thomasi* , GPIM-M 5832: occlusal aspect
4 – *Stethacanthus thomasi*, GPIM-M 5832: lateral aspect
5 – *Icriodus cornutus*, GPIM-M 5835: lateral surface with characteristic straight posterior denticle
6 – *Icriodus cornutus*, GPIM-M 5835: oral surface
7 – *Polygnathus* cf. *nodocostatus*, GPIM-M 5834: oral surface of this platform conodont
8 – *Polygnathus* cf. *nodocostatus*, GPIM-M 5834: lateral surface
9 – *Polygnathus* cf. *nodocostatus*, GPIM-M 5834: posterior view

Scale bars = 100 μm



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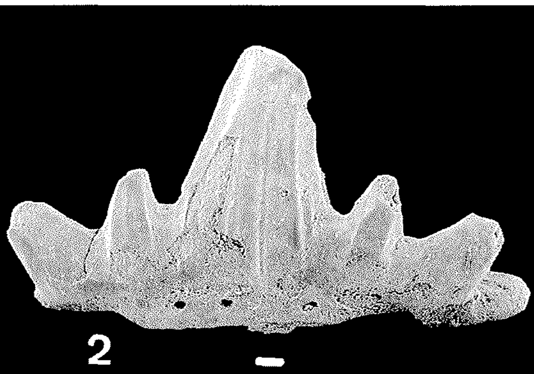

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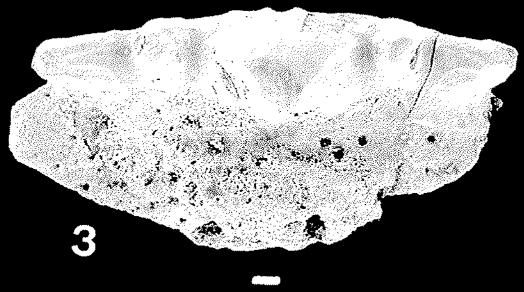

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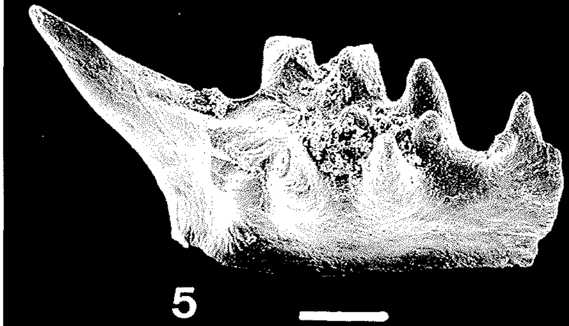

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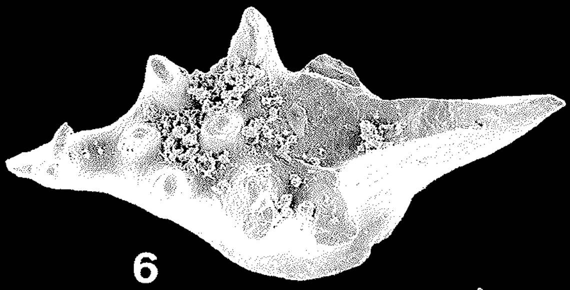

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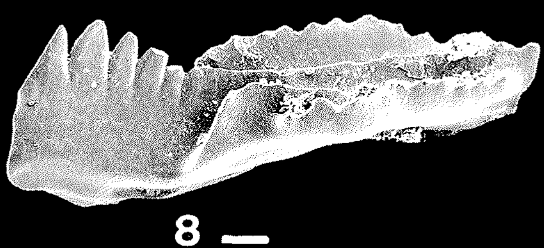

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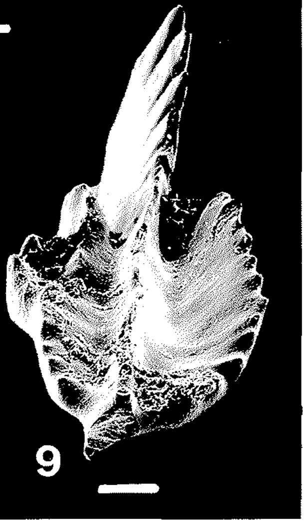

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PLATE 3

Gastropods (Figs 1-6) and ostracods (Figs 7-9), middle Famennian of Zonuz, East Azerbaijan province / NW Iran

1 – *Tropidodiscus* sp., GPIM-F 8655: lateral view
2 – *Tropidodiscus* sp., GPIM-F 8656: adoral view
3 – ?*Naticopsis* sp., GPIM-F 8658: lateral view
4 – ?*Naticopsis* sp., GPIM-F 8658: apical view
5 – ?*Loxonema* sp., GPIM-F 8657: lateral view
6 – ?*Loxonema* sp., GPIM-F 8657: apical view
7 – *Schweyerina* cf. *zaspelovae*, GPIM-G 1082: left side of steinkern
8 – *Schweyerina* cf. *zaspelovae*, GPIM-G 1080: silicified left valve, inner view
9 – *Schweyerina* cf. *zaspelovae*, GPIM-G 1083: ventral view

Scale bars = 100 μm

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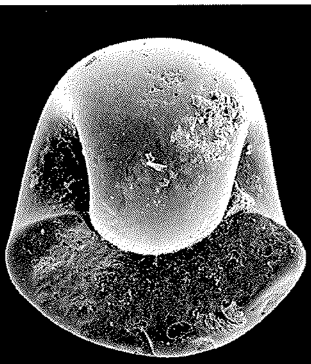

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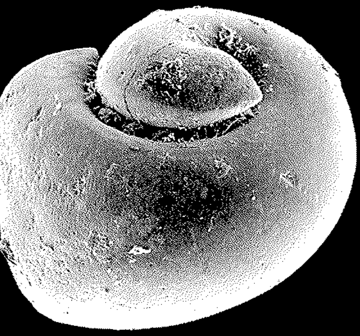

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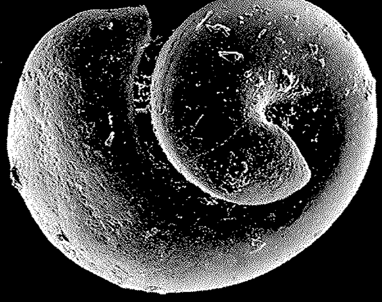

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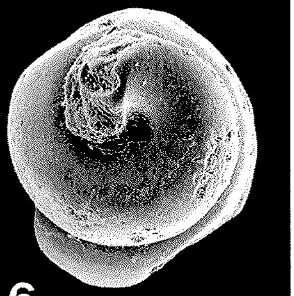

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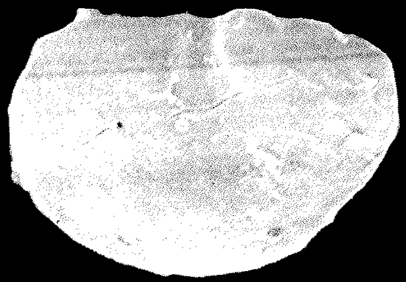

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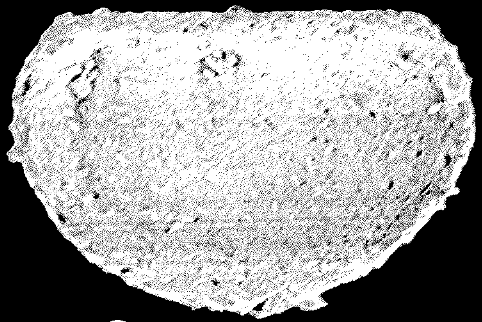

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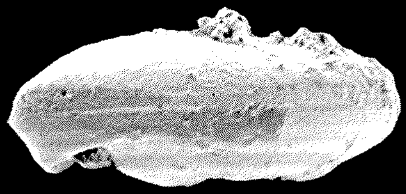

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