

# Revision of the genus *Kujdanowiaspis* Stensiö, 1942 (Placodermi, Arthrodira, “Actinolepida”) from the Lower Devonian of Podolia (Ukraine)

Vincent DUPRET

Muséum national d’Histoire naturelle, Département Histoire de la Terre,  
USM 0203 - UMR 7207 du CNRS, CR2P,  
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)  
present address: University of Uppsala,  
Department of Physiology and Developmental Biology,  
Subdepartment of Animal Evolution and Development,  
Norbyvägen 18A SE-75236 Uppsala (Sweden)  
dupret@mnhn.fr

Dupret V. 2010. — Revision of the genus *Kujdanowiaspis* Stensiö, 1942 (Placodermi, Arthrodira, “Actinolepida”) from the Lower Devonian of Podolia (Ukraine). *Geodiversitas* 32 (1): 5-63.

## ABSTRACT

The genus *Kujdanowiaspis* Stensiö, 1942 has long been considered as the archetype of placoderms; hence, it has been often used as outgroup in phylogenetic analyses involving placoderms, or used as a representative of all the placoderms for all early vertebrate works. Nevertheless, there has been no real work on the taxonomy of this genus since Denison (1978). Here we propose a revision of the material of *Kujdanowiaspis* from the Old Red Sandstone of Podolia (including neurocrania, skull roofs and thoracic armours), together with the description of unpublished specimens of the genus *Heightingtoniaspis* White, 1969. Among the available Podolian material, three species are considered valid: *Kujdanowiaspis buczacziensis* (Brotzen, 1934), *K. podolica* (Brotzen, 1934) and *Erikaspis zychi* (Stensiö, 1945) (*K. podolica* and *K. buczacziensis* only differ in size and in the density and size of the tuberculated ornamentation; the dermal plate pattern of *E. zychi* differs from that of the genus *Kujdanowiaspis*). The axillar area of the scapulocoracoid of *K. podolica* is compared with those of an osteostracan “agnathan” and of a non-tetrapod sarcopterygian. In the three cases, the articulation of the pectoral fin is of the monobasal type. An analogy with the embryonic development of the pectoral fin of the actinopterygian *Danio rerio* (Hamilton, 1822) suggests that the monobasal articulation would correspond to the plesiomorphic condition compared with the multibasal one of the adult actinopterygians and some derived brachythoracid placoderms. The suprasynarcual is a newly identified, chondrified element of the vertebral column, supposed to respond to the height of the median dorsal plate in *Kujdanowiaspis podolica*.

## KEY WORDS

Placodermi,  
Arthrodira,  
“Actinolepida”,  
anatomy,  
pectoral fin articulation,  
vertebral column,  
evo-devo,  
Lower Devonian,  
Ukraine.

## RÉSUMÉ

Révision du genre *Kujdanowiaspis* Stensiö, 1942 (Placodermi, Arthrodira, «Actinolepida») du Dévonien inférieur de Podolie (Ukraine).

Le genre *Kujdanowiaspis* Stensiö, 1942 a été considéré pendant longtemps comme l'archétype des placodermes. En conséquence, il a souvent été utilisé comme extra-groupe dans les analyses phylogénétiques comprenant des placodermes, mais aussi comme représentatif de ce groupe dans des travaux portant sur un plus grand ensemble de vertébrés primitifs. Néanmoins, aucun réel travail de révision taxonomique ou nomenclaturale n'a été effectué sur ce taxon depuis Denison (1978). Ici, nous proposons une révision et une description de matériel en grande partie inédit de *Kujdanowiaspis* des Vieux Grès Rouges de Podolie (neurocrânes, toits crâniens, cuirasses thoraciques). Des spécimens inédits du genre *Heightingtonaspis* White, 1969, sont également décrits. Trois espèces sont identifiées comme valides dans le matériel podolien : *Kujdanowiaspis buczacziensis* (Brotzen, 1934), *K. podolica* (Brotzen, 1934) et *Erikaspis zychi* (Stensiö, 1945) (*K. podolica* et *K. buczacziensis* diffèrent en taille et dans la densité et la taille des tubercules; le patron des plaques dermiques d'*E. zychi* diffère de celui du genre *Kujdanowiaspis*). La région axillaire du scapulocoracoïde de *K. podolica* (Brotzen, 1934) est comparée à celles d'un «agnathe» ostéostracé et d'un sarcoptérygien non-tétrapode. Il s'avère que l'articulation de la nageoire pectorale est de type monobasal dans les trois cas. Une analogie avec le développement embryonnaire de l'actinoptérygien actuel *Danio rerio* (Hamilton, 1822) suggère un état plésiomorphe de la nageoire monobasale par rapport à la nageoire multirayonnée des actinoptérygiens adultes actuels et de certains placodermes brachythoracides dérivés. Le suprasynarcual est un nouvel élément cartilagineux de la colonne vertébrale permettant de répondre à la hauteur de la plaque médiane dorsale de *Kujdanowiaspis podolica*.

## MOTS CLÉS

Placodermi,  
Arthrodira,  
«Actinolepida»,  
anatomie,  
articulation de la nageoire  
pectorale,  
colonne vertébrale,  
évo-dévo,  
Dévonien inférieur,  
Ukraine.

## INTRODUCTION

The order Arthrodira Woodward, 1891, is by far the most successful group of Placodermi McCoy, 1848, both by its palaeobiodiversity and its time span. However the origin and the interrelationships of this group remain poorly known: the Actinolepida Miles, 1973, are commonly assessed as primitive arthrodires, but there has been no consensus on their phylogenetic status. Johnson *et al.* (2000), involved with the relationships within actinolepids, pointed out the necessity to revise the genus *Kujdanowiaspis* Stensiö, 1942. Indeed, Stensiö (1942, 1944, 1945, 1963, 1969) focused on the endocranial and encephalic structures mainly based on serial sections in order to reveal the anatomy of an "actinolepid type". The armour characters were poorly described,

especially on the thoracic armour. The revision of the genus *Kujdanowiaspis* from the Lower Devonian of Podolia (Ukraine) presented here leads to a reevaluation of the relationships of arthrodires (actinolepids, brachythoracids, phlyctaeniids, phyllolepid, antarctaspids and wuttagoonaspids).

A BRIEF REVIEW OF THE  
"KUJDANOWIASPIS" MATERIAL

Stensiö erected the genus *Kujdanowiaspis* in 1942 to gather the species created by Brotzen (1934) under the names *Phlyctaenaspis buczacziensis* Brotzen, 1934 (type species of *Kujdanowiaspis*), *P. podolica* Brotzen, 1934 and *P. rectiformis* Brotzen, 1934, from the Lower Devonian of Podolia (Ukraine). He also included with

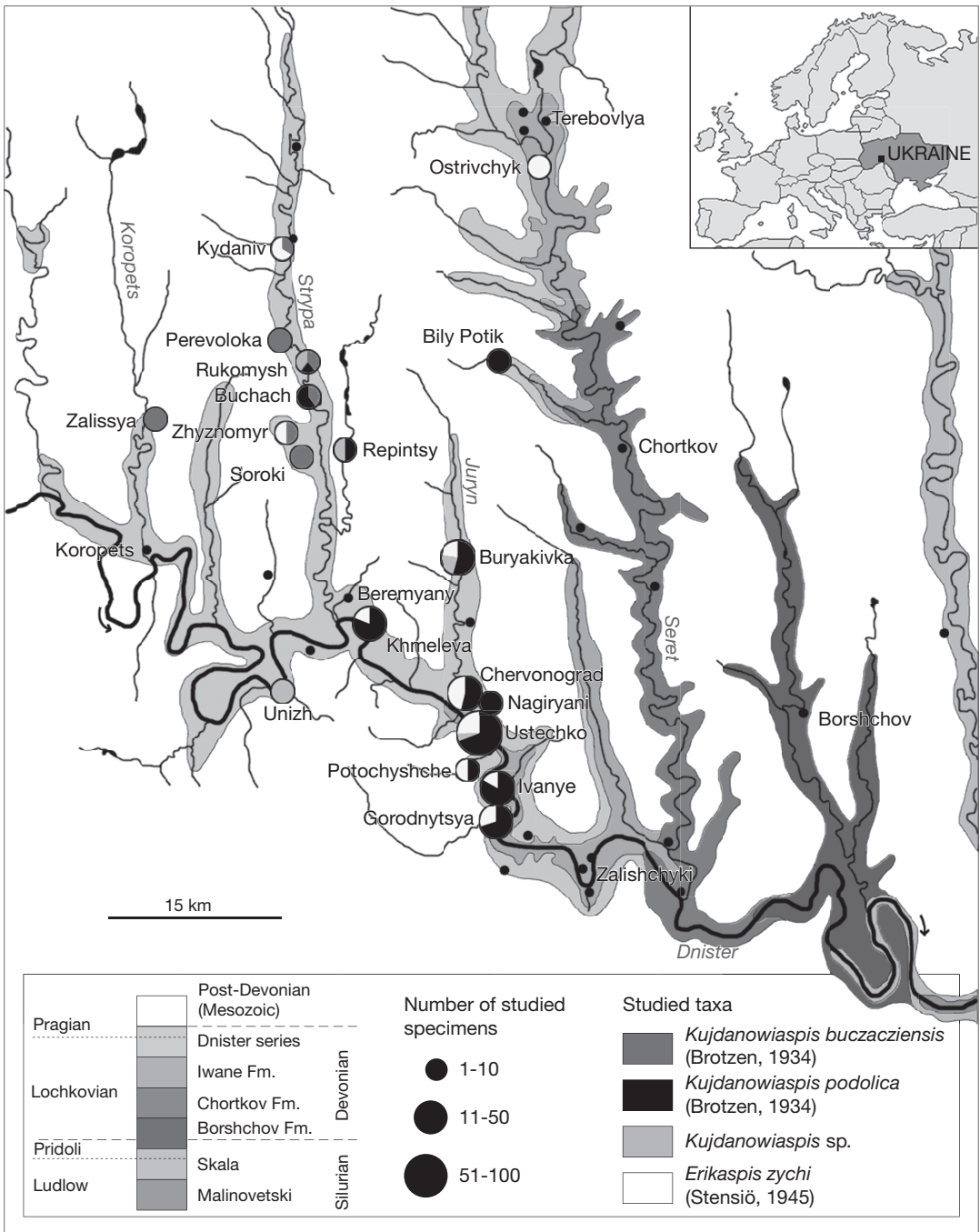


FIG. 1. — Lower Devonian deposits of Podolia (Ukraine), redrawn after Blicek (1984), with distribution of the placoderm material. The Dnister Series includes the Ustechko, Khmelewa, Strypa and Smerkliv Formations (Narbutas 1984). English transliteration for Ukrainian, Polish, and Russian names is given in Dupret & Blicek (2009: appendix).

doubt *Acanthaspis prominens* Brotzen, 1934 (Stensiö 1944). The other species erected by Brotzen (*P. extensa* Brotzen, 1934, *A. angusta* Brotzen, 1934 and *A. vomeriformis* Brotzen, 1934) were considered by Denison (1978) of uncertain affinities, but probably close to *Kujdanowiaspis*.

A reexamination of the “*Kujdanowiaspis*” material reveals that two genera can be considered as justified; they are *Kujdanowiaspis* including *K. buczacziensis* (Brotzen, 1934) and *K. podolica* (Brotzen, 1934), plus *Erikaspis* Dupret, Goujet & Mark-Kurik, 2007, for the species *Kujdanowiaspis zychi* Stensiö, 1945 (*K. podolica* and *K. buczacziensis* only differ in size and in the density and size of the tuberculated ornamentation; the dermal plate pattern of *E. zychi* differs from that of the genus *Kujdanowiaspis* (see below for *Kujdanowiaspis*; see Dupret *et al.* 2007 for *Erikaspis*). The other species (*P. rectiformis*, *P. extensa*, *A. angusta*, *A. prominens* and *A. vomeriformis*) are junior synonyms of *K. podolica* or belong to *Kujdanowiaspis* sp. indet. Indeed, Stensiö did not have any taxonomic consideration for the material he studied: that is why *K. podolica* refers mainly to the external side of the skull roof (Stensiö 1945: figs 8A, 9A; 1963: fig. 42B), whereas *K. rectiformis* refers to endocranial casts (dorsal, lateral, ventral and posterior views; Stensiö 1945: figs 1, 3-5, 9A, B, 10B, 11A, B; 1963: figs 13, 14, 16A, B, 41) and to internal side of the skull roof (Stensiö 1945: figs 8B, 9A, B, 10B, 11A, B; 1963: fig. 42C). Moreover, references to specimens are very rare in Stensiö’s work: only 11 specimens are referred to a taxon (unknown acanthaspid, Stensiö 1934: figs 26-28; NHMP 113, *Acanthaspis* sp., Stensiö 1934: figs 26-28; NHM P 114, *Acanthaspis?* sp., Stensiö 1934: pl. XII, fig. 3, pl. XIII, fig. 2; NHRM P 5000 *Kujdanowiaspis buczacziensis*, Stensiö 1942: figs 1-5; “Holotype in Berlin” [MB 288], *Kujdanowiaspis buczacziensis*, Stensiö 1942: fig. 6; NHRM P 5026, NHRM P 5027 and NHRM P 5028, *Kujdanowiaspis?* spp., Stensiö 1944: fig. 15A-C; “Holotype in Berlin”, *Kujdanowiaspis prominens*, Stensiö 1944: fig. 16; NHRM P 4001, *Kujdanowiaspis rectiformis*, Stensiö 1945: figs 1, 4; NHRM P 4002, *Kujdanowiaspis zychi*, Stensiö 1945: fig. 10A).

Some thoracic material of *Kujdanowiaspis* has been illustrated by Denison (1958: figs 105E, 107I, 108I, 109I, 110H, 112H, 114F) and he concluded that

“*Kujdanowiaspis* approaches most closely to [the] ideally primitive condition and both in its early appearance and [that] in its structure can be considered to be near the ancestry of other Arctolepida” (Denison 1958: 545).

White (1961) attributed some Welsh material to *Kujdanowiaspis* (*K. anglica* (Traquair, 1890b); *K. willsi* White, 1961; and *K. clarkei* Eastman, 1907), but later he erected the genus *Heightingtonaspis* White, 1969 for the species *Phlyctaenius anglicus* Traquair, 1890b (White 1969). The anterolateral plate of *Heightingtonaspis anglica* is higher than long, the spinal plate is shorter than that of *Kujdanowiaspis podolica* and does not extend beyond the anterior ventrolateral plate, the ornamentation is mostly relatively large tubercles with a linear arrangement; see Denison 1978).

Goujet & Blicek (1978) referred two anterolateral plates from the “Grès de Pernes” of Liévin (Pas-de-Calais, France) to *Kujdanowiaspis*. Based on the quadrate shape of these specimens also found in other “actinolepids” (*Aethaspis major* Denison, 1958, *Aleosteus eganensis* Johnson, Elliot & Wittke, 2000, *Baringaspis dineleyi* Miles, 1973, *Bryantolepis brachycephala* (Bryant, 1932), *Eskimaspis heintzi* Dineley & Liu, 1984, *Heightingtonaspis anglica* or *Simblaspis cachensis* Denison, 1958), and despite the different ornamentations displayed by those taxa, I consider this material as “Actinolepida” indet.

## GEOLOGICAL SETTING

All of the material of *Kujdanowiaspis* comes from Podolia (southwestern Ukraine) (Fig. 1). In Podolia, the Upper Silurian and Lower Devonian deposits consist of a slight westward monoclinic structure. The lower part of the Devonian sequence comprises the Dnister Series or “Babin Sandstones”. It contains the Lochkovian-Pragian boundary and has yielded the studied specimens (it is also noteworthy that some Middle Devonian deposits, poor in fossils, crop out on the Zoloto Lypa River to the West of the Koropets River; Narbutas 1984).

Valuable information on the early Devonian vertebrate dominated communities, prevailing in the Podolian Dnister Series, and dating of formations and a discussion of palaeogeography, is compiled in

Blicek & Janvier (1999: figs 9.4, 9.6). Podolia had direct connection with the marine basins in Lviv area in Ukraine and Radom and Lublin in Poland (Ziegler 1982). Elga Mark-Kurik (pers. comm.) discovered small lingulid fragments in reddish-brown thin-bedded siltstone from the Ivanye locality. It can be concluded that Podolian early Devonian placoderms and others lived in a shallow marine environment, *contra* Brovkov's opinion (1952, 1954), according to whom the Dnister Red Beds were deltaic.

As the Old Red Sandstones facies is not worthy for the preservation of the representatives of shelly faunas or conodonts, fossil vertebrates will be used as stratigraphic markers (Dupret 2003; Dupret & Blicek 2009). In this case, the first occurrence of the species *Kujdanowiaspis buczacziensis* marks the beginning of the Pragian. Hence, *Kujdanowiaspis podolica* occurs from the Upper Lochkovian to the Lower Pragian; *K. buczacziensis* occurs in the Lower Pragian.

An exhaustive vertebrate list is given by Voichyshyn (2001). Vertebrate remains are composed of thelodonts scales, heterostracans and osteostracans shields, placoderms plates (*K. buczacziensis*, *K. podolica* and a new genus), acanthodians and chondrichthyans fin spines. Vermiform reptation tracks have also been encountered.

Most of the vertebrates were detritivorous and microphageous. The predators were probably big arthropods, chondrichthyans or acanthodians. As for the three placoderm species, they were probably small opportunistic predators, feeding with small soft-bodied and thin-armoured invertebrates and maybe alevins. A microphageous feed is suggested as well, as acting during respiration; its role is maybe higher than an active predation.

## MATERIAL AND METHODS

Only four of the original specimens illustrated by Brotzen (1934: pl. 9) are still in collections (MB 87b, MB 88a, MB 282, and MB 290a); four others, though not illustrated, are labeled as belonging to Brotzen's collection (MB 87b, MB 88A, NHRM P 8418, NHRM P 8435). But since, an abundant material has been collected, and is

now dispatched in several institutions (list given in Appendix 1).

As the osseous tissues are very rarely well preserved, counterprints and silicone casts are studied. The most abundant material has been attributed to *Kujdanowiaspis podolica* (more than 150 specimens); *Kujdanowiaspis buczacziensis* is known by very few remains (eight specimens with certainty, three with doubts).

## ABBREVIATIONS

See appendix 2.

## SYSTEMATIC PALAEOLOGY

### Genus *Kujdanowiaspis* Stensiö, 1942

*Phlyctaenius* – Traquair 1890a: 55, pl. II figs 1, 2; 144.

*Acanthaspis* – Newberry 1889: 35, pl. XXX figs 1-4.

DIAGNOSIS. — Arthrodira “Actinolepidoidei” with long spinal plate extending beyond the posterior edge of the anterior ventrolateral plate, and mesial side of spinal plate bears anteriorly oriented denticles.

TYPE SPECIES. — *Phlyctaenaspis buczacziensis* Brotzen, 1934 (by monotypy).

SPECIES INCLUDED. — *K. buczacziensis* (Brotzen, 1934) and *K. podolica* (Brotzen, 1934).

## REMARKS

The genus diagnosis given by Denison (1978: 50) does not display derived states of characters, as most of the cited anatomical features can be encountered in most of the actinolepids (e.g., “The dermal plates covering the ethmoidal region are loosely attached and often broken of. The preorbital plates are shallowly notched anteriorly by the pineal, and are not greatly elongate. [...] The nuchal is rather long”), but rather consists in a determination key. The species diagnoses given by Denison (1978: 50) mainly refer to Brotzen's original work and Stensiö's anatomical (non systematic) studies. Last but not least, Denison (1978: 50) ends the genus diagnosis with this remark: “Although it is better known than most Actinolepidae, this genus has never been prop-

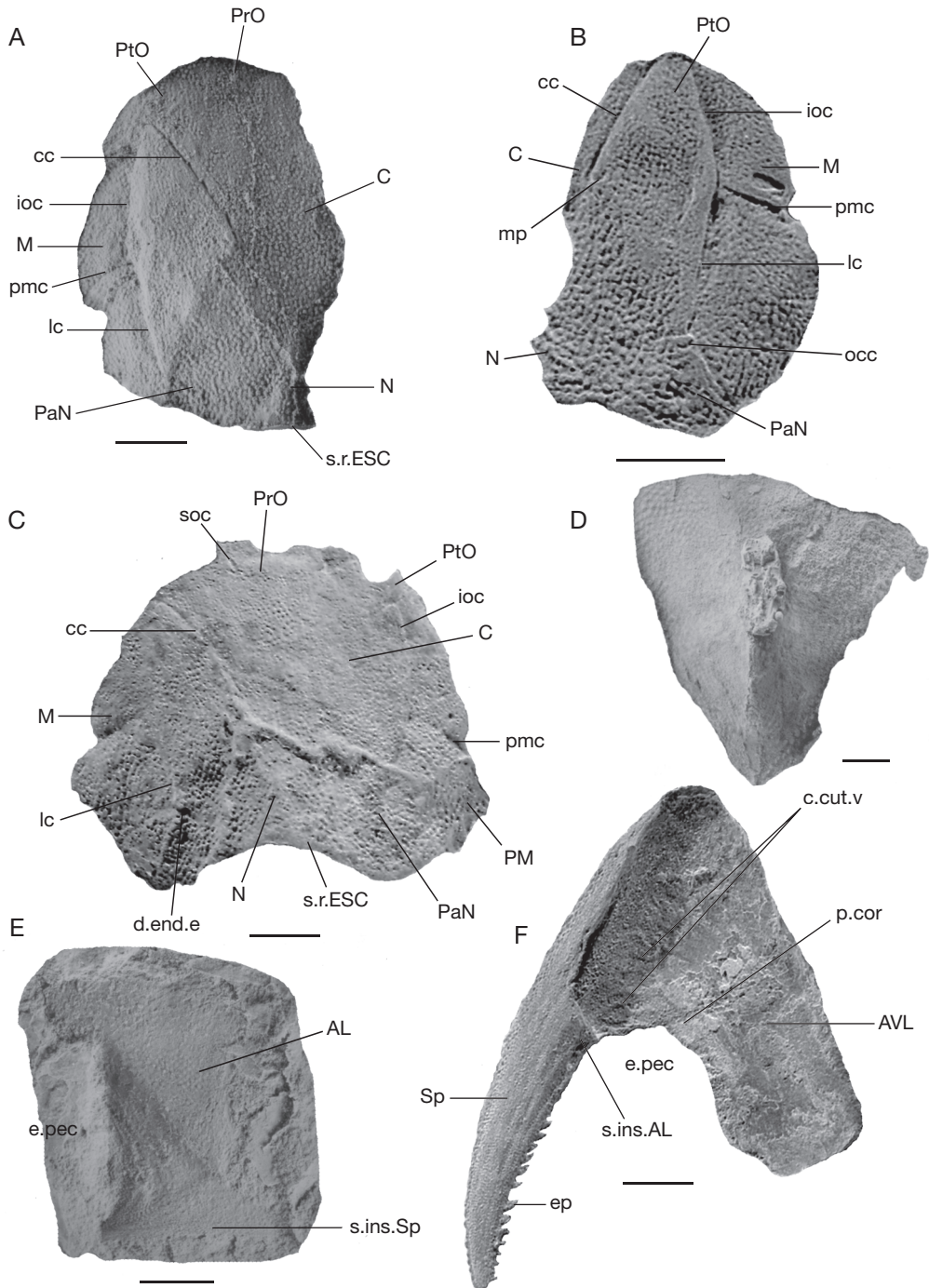


FIG. 2. — *Kujdanowiaspis buczacziensis* (Brotzen, 1934): **A-C**, silicone cast of a fragment of skull roof (external side); **A**, Pi 1204; **B**, GGI 15-631; **C**, NHRM P 8503; **D**, median dorsal plate (external side), MB 290a (lectotype); **E**, silicone cast of a right anterolateral plate (external side), Pi 1201; **F**, latex cast of a fragment of plastron and scapuloacoracoid print, GGI 15-664. Abbreviations: see Appendix 2. Scale bars: 1 cm.

erly defined nor distinguished from other genera. Moreover, none of the species referred here have been described or figured adequately from a systematic point of view, and must at present be considered indeterminate [...]”.

*Kujdanowiaspis buczacziensis* (Brotzen, 1934)  
(Figs 2-4)

*Phlyctaenaspis buczacziensis* Brotzen, 1934: 118, pl. 9 figs 1-3.

TYPE MATERIAL. — Lectotype MB 290A (median dorsal plate) (Brotzen 1934: pl. 9 fig. 2; this article, Fig. 2D) designated here; paralectotype MB 288 (mechanically prepared dorsal sides of the dermic nasal capsule and neurocranium, Fig. 3; Brotzen 1934: pl. 9 fig. 1), not found; unidentified paralectotype, fragment of ventral armour, not found (Brotzen 1934: pl. 9 fig. 3).

TYPE LOCALITY. — Buchach (Podolia, Ukraine) (Brotzen 1934: 119).

TYPE HORIZON. — Pragian (Early Devonian) (see Dupret & Blicek 2009).

MATERIAL EXAMINED. — List given in Appendix 1.

DIAGNOSIS. — Quite large *Kujdanowiaspis* species with very thin tubercles. High tubercle density. Anterolateral plate higher than long.

REMARKS

All specimens described by Brotzen (1934) are considered as syntypes. Stensiö (1942) designated as holotype specimen MB 288, without referring to the original type series. Hence, and as specimen MB 288 was not found, specimen MB 290a is designated as lectotype; the other specimens from the original type series are then paralectotypes, though not found; the type locality is that of the lectotype only (according to ICZN 1999: articles 72.1, 72.4.7, 73.1.3, 73.2, 74.1, 74.4, 74.5, 74.6, and 76.3).

*Kujdanowiaspis podolica* (Brotzen, 1934)  
(Figs 5; 6; 8; 9; 11-13; 15-25; 27; 28)

*Phlyctaenaspis podolica* Brotzen, 1934: 114, pl. 9 figs 8-11.

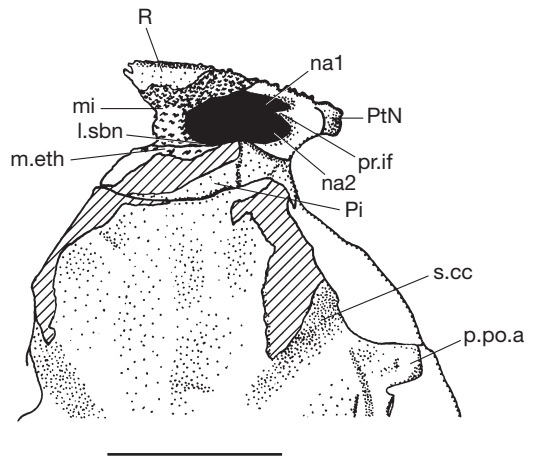


FIG. 3 — *Kujdanowiaspis buczacziensis* (Brotzen, 1934): neurocranium and dermal ethmoid capsule (dorsal view), MB 288 (paralectotype; N.B.: this specimen is lacking in the collections of the Museum für Naturkunde, Berlin, Germany; it would be curated in the Naturhistoriska Riskmuseet, Stockholm, Sweden, H.-P. Schultze, pers. comm.). The dorsal part of the nasal capsule has been removed by Stensiö in order to see the external nares. Redrawn after Stensiö (1942: fig. 6). Abbreviations: see Appendix 2. Scale bar: 1 cm.

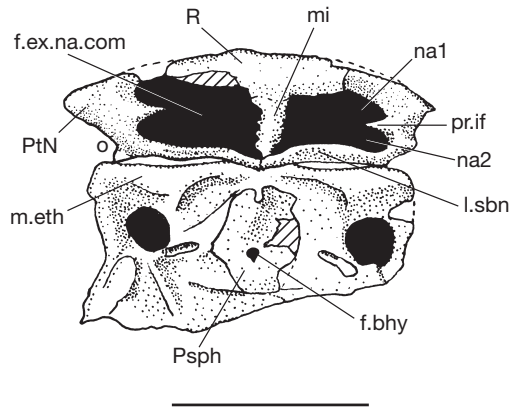


FIG. 4. — *Kujdanowiaspis buczacziensis* (Brotzen, 1934): neurocranium and dermal ethmoid capsule (ventral view), NHRM P 5000. Redrawn after Stensiö (1942: fig. 4A). Abbreviations: see Appendix 2. Scale bar: 1 cm.

*Phlyctaenaspis extensa* Brotzen, 1934: 116, pl. 9 figs 4, 5.

*Phlyctaenaspis rectiformis* Brotzen, 1934: 117, pl. 9 fig. 7.

*Acanthaspis prominens* Brotzen, 1934: 119, pl. 9 figs 12-14.

*Acanthaspis angusta* Brotzen, 1934: 121, pl. 9 fig. 16.

*Acanthaspis vomeriformis* Brotzen, 1934: 120, pl. 9 fig. 15.

TYPE MATERIAL. — Lectotype MB 282 (left anterolateral plate, external side, Fig. 20B; Brotzen 1934: pl. 9 fig. 9) designated here; other specimens (paralectotypes) referred to *Phlyctaenaspis podolica* were not found (Brotzen 1934: pl. 9 figs 8, 10, 11).

MATERIAL EXAMINED. — List given in Appendix 1.

TYPE LOCALITY. — Ivanye (Podolia, Ukraine; Brotzen 1934: 116).

TYPE HORIZON. — Lochkovian (Early Devonian) (see Dupret & Blicek 2009).

DIAGNOSIS. — Small *Kujdanowiaspis* species with relatively coarse tubercles. Median dorsal plate with posterior sagittal crest. A suprasynarcual element covers the internal side of the median dorsal plate. Four or five post-median dorsal plates with scar insertion for a little spine for some.

#### REMARKS

The type locality is that of the lectotype of *K. podolica* (ICZN 1999: article 76.3). Original syntypes MB 87b and MB 88a for *Acanthaspis vomeriformis* Brotzen, 1934 (fragment of thoracic armour, print and counterprint) are referred here to *Kujdanowiaspis? podolica*; Brotzen 1934: pl. 9 fig. 15; MB 88a was collected in Unizh (Brotzen 1934:120); other unidentified syntypes for *P. extensa* (Brotzen 1934: pl. 9 figs 4, 5), *P. rectiformis* (Brotzen 1934: pl. 9 fig. 7), *A. prominens* (Brotzen 1934: pl. 9 figs 12, 13), and *A. angusta* (Brotzen 1934: pl. 9 fig. 16) were not found; these specimens do not have type status for the species *Kujdanowiaspis podolica* (Brotzen, 1934).

#### DESCRIPTIONS

Unless indicated, comparisons are given with the very well known phlyctaeniid arthrodire *Dicksonosteus arcticus* Goujet, 1975.

#### *Kujdanowiaspis buczacziensis* (Brotzen, 1934)

The material of *K. buczacziensis* (Appendix 1) is rare and often badly preserved. From the specimens

described and figured by Brotzen (1934), just one remained (median dorsal plate MB 290a, Fig. 2D), the rest being probably lost. More material has since been collected: five fragments of skull roof described by Stensiö (1942) – redescrbed further –, an anterolateral plate (Pi 1201, Fig. 2E) and a portion of trunk armour (GGI 15-664, Fig. 2F). Consequently, the description of this species will be much more incomplete than that of *K. podolica*.

Stensiö (1942) thought that the skull roof of *Kujdanowiaspis buczacziensis* resembled that of *Phlyctaenius* Traquair, 1890a (Traquair 1890b: pl. 3; 1894: 369; Woodward 1892, pl. 1, fig. 7; Stensiö 1925: 167, fig. 21; Heintz 1933: 130-133, fig. 2), of *Arctaspis* Heintz, 1929b (“*Svalbardaspis*” Heintz 1929b: figs 6A, 23), of *Arctaspis* Heintz, 1929 (Heintz 1929a: fig. 2), of *Bryantolepis* Camp, Welles & Green, 1949, of “*Euryaspis*” Bryant, 1932 (Bryant 1932: fig. 1) and of *Anarthraspis* Bryant, 1934 (Bryant 1934: fig. 5), and differed from those of *Actinolepis* Agassiz, 1844 (see Gross 1940: 44-58, fig. 13) and of *Jaeckelaspis* Heintz, 1929b (1929a: fig. 1; 1929b: fig. 6B) – in fact, junior synonym of *Arctolepis* Eastman, 1908. Stensiö (1944) also remarked that as in all “acanthothoracids”, the plates are closely fused with each other, hence increasing the difficulty to identify the plate limits. The skull roof of *K. buczacziensis* would also be longer and thinner than the one of *Phlyctaenius acadicus*. As well, orbital notches are deeper in *Kujdanowiaspis* than in *P. acadicus*.

According to the available material, the skull roof of *Kujdanowiaspis buczacziensis* is very similar to that of *K. podolica* (i.e. same relationships between plates and sensory lines grooves). The noticeable differences only concern the size (*K. buczacziensis* is almost twice the size of *K. podolica*) and the ornamentation (finer and more dense tubercles in *K. buczacziensis*; those of *K. podolica* are a bit larger and more widely spaced).

The two specimens of *K. buczacziensis* (Figs 3; 4) described by Stensiö (1942) provide important information on the internal structure of the rostrum that is unknown in *K. podolica*.

Stensiö (1942) noticed a contact between the postnasal and preorbital plates. The postnasal plates are wider than those of *Bryantolepis* (“*Euryaspis*”



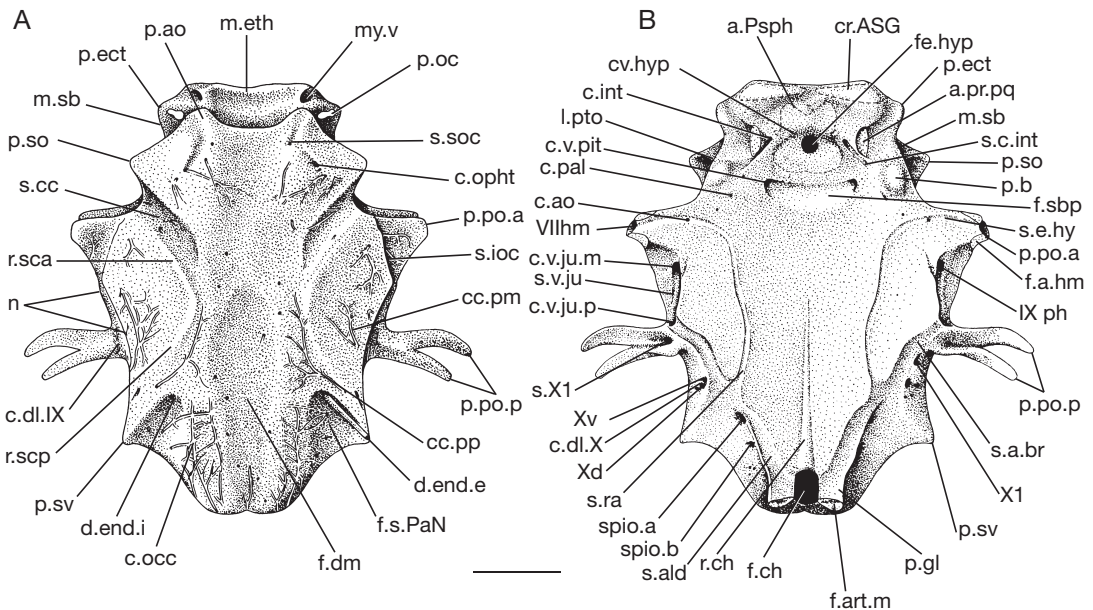


FIG. 5. — *Kujdanowiaspis* sp. aff. *K. podolica* (Brotzen, 1934): **A**, neurocranium, dorsal view. After Goujet (1984: fig. 9), modified from Stensiö (1945); **B**, neurocranium, ventral view, modified after Stensiö (1963a). The outline of the parasphenoid has been slightly modified. Abbreviations: see Appendix 2. Scale bar: 1 cm.

Bryant, 1932), and their radiation centre would be located laterally.

The rostral, pineal and postnasal plates forming the nasal capsule are located above the mouth. The dorsal side of this nasal capsule is classically composed by the median rostral and pineal plates and the lateral postnasal plates. The lateral sides ("orbital faces" of Stensiö 1942) are posteriorly and slightly laterally directed, and are composed by the postnasal plates alone, forming the anterior edge of the orbit. The anterior side is medially composed by the rostral plate and laterally by the postnasals. The anterior edge of the external inhalant naris (na1, Figs 3; 4) is formed by both the rostral and postnasal plates.

The internal structure shows the anteroventral part of the rostral plate and the postnasal plates anterolaterally. The postnasal plates produce a tiny interfenestral process mesially (pr.if, Figs 3; 4) separating laterally the external inhalant (na1, Figs 3; 4) and exhalant nares (na2, Figs 3; 4). The rostral plate produces a medial process posteriorly (the internasal wall, mi, Figs 3; 4; Ra of Stensiö

1942); Stensiö thought that this medial wall was an independent dermal bone. The ventral side is closed by a pair of subnasal laminae posteriorly (l.sbn, Figs 3; 4) produced by the postnasals, and in mesial contact.

#### Rostral plate

The rostral plate (R, Figs 3; 4) is trapezoidal dorsally, with a slightly bowed anterior edge. Its anterior side is quite high, flanked by the external inhalant nares laterally. On the ventral side, it protrudes the internasal wall (mi, Figs 3; 4), unless it is an independent ossification (see internasal plate of *Coccosteus cuspidatus* Miller, 1841). Both are tuberculated identically to the adjacent plates. The radiation centre is located on the anterodorsal edge, in the symmetry plane.

#### Pineal plate

The pineal plate (Pi, Figs 3; 4) is pentagonal. Its anterior edge (contacting the rostral plate) is straight, whereas the posterior one is slightly convex. Stensiö (1942: figs 1-3) suggested the presence of a pineal

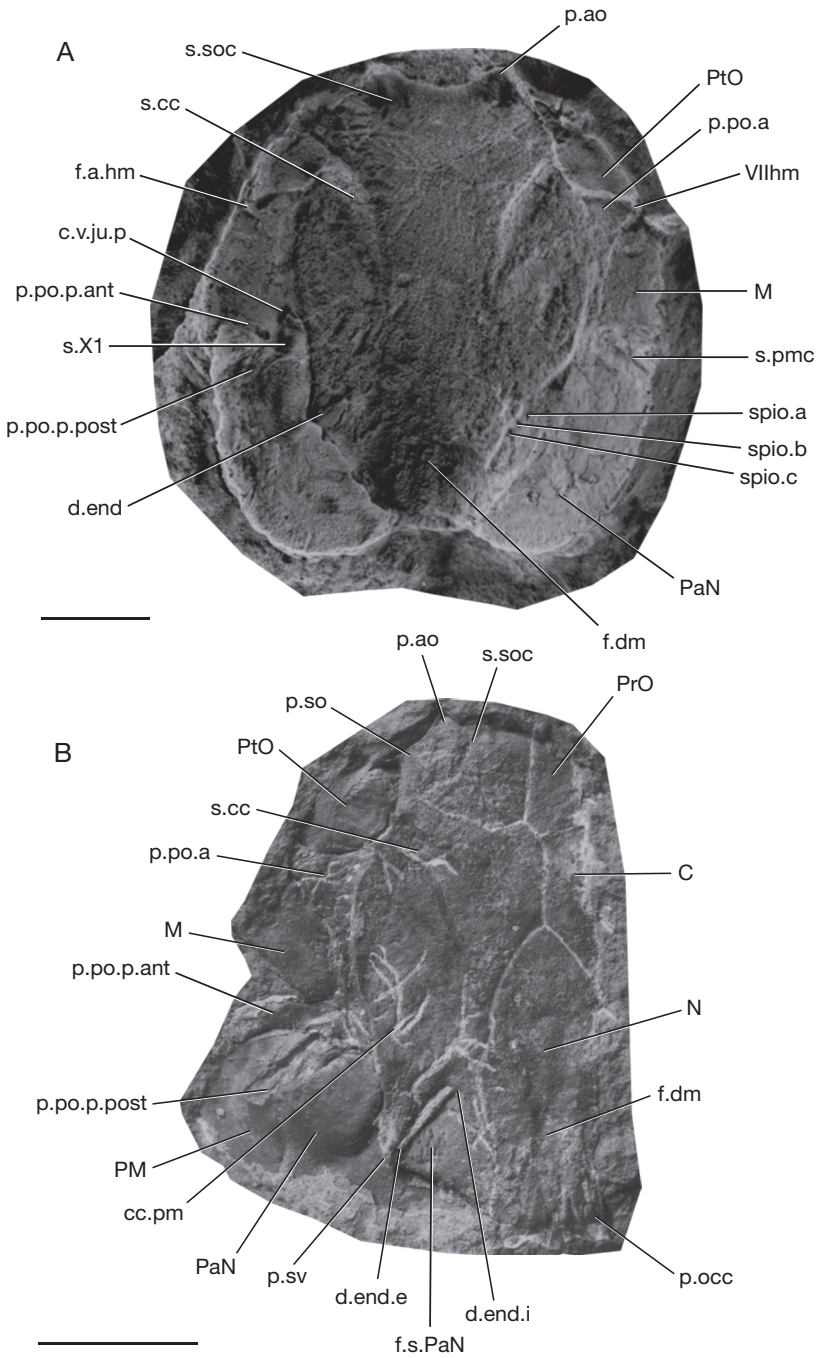


FIG. 6. — *Kujdanowiaspis podolica* (Brotzen, 1934): **A**, silicone cast of the dorsal side of a neurocranium and adjacent skull roof plates (visceral view), GGI 15-618; **B**, silicone cast of the dorsal side of an incomplete neurocranium, NHRM P 8458; **C**, dorsal side of a neurocranium and adjacent skull roof plates, NHRM P 2869; **D**, dorsal side of a neurocranium and adjacent skull roof, NHRM P 4001. Abbreviations: see Appendix 2. Scale bars: 1 cm.

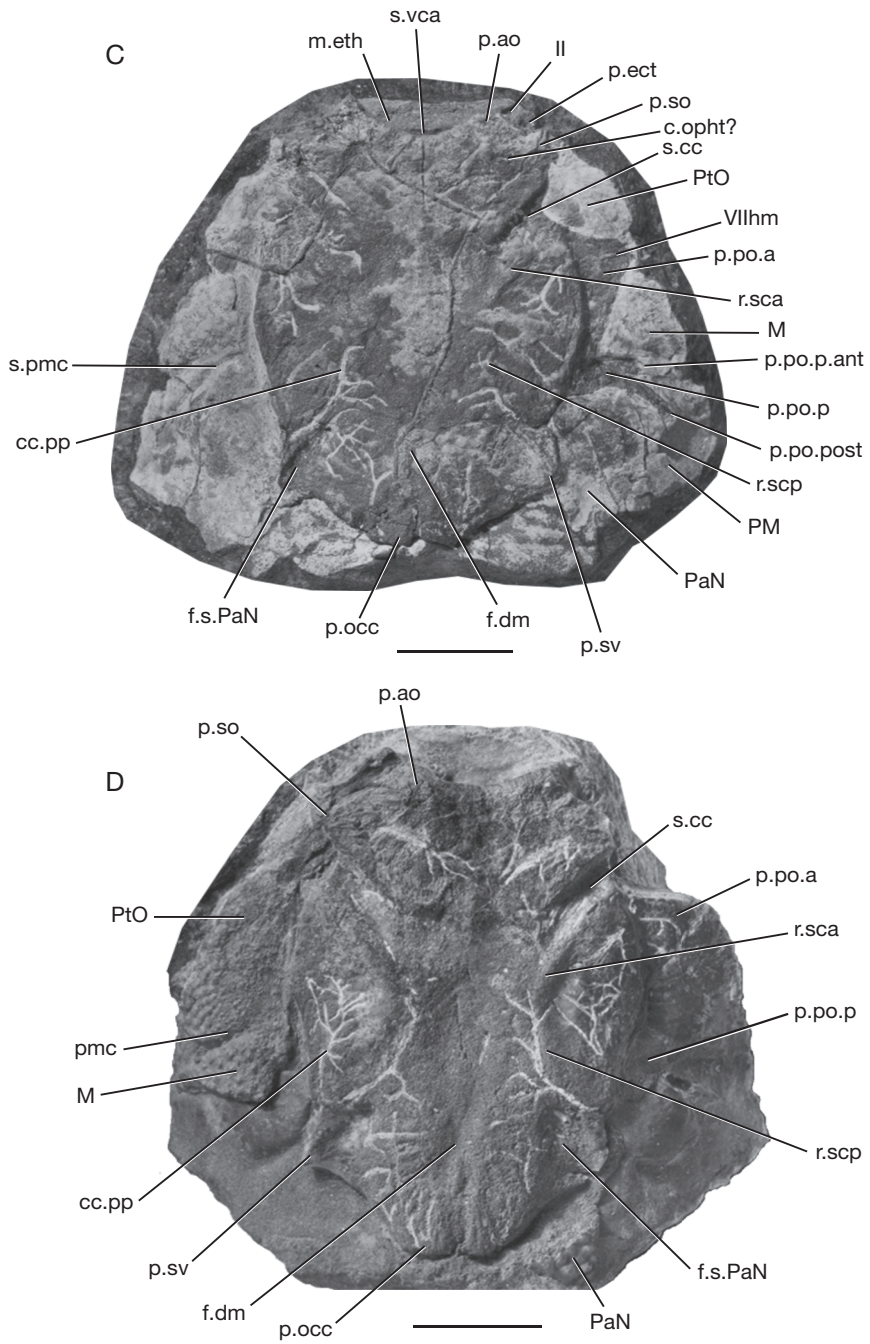


FIG. 6. — Continuation.

foramen; nevertheless, this part of specimen NHRM P 5000 was already damaged, and he could not conclude to a true foramen or a closed pit.

#### *Postnasal plate*

The postnasal plates (PtN, Figs 3; 4) compose the lateral part of the dermal nasal capsule. They can be divided into three parts ventrally:

- an anterior part constituting the lateral edge of the rostrum, and mesially to it is the external inhalant naris (na1, Figs 3; 4);
- a middle part showing the smooth short mesially directed interfenestral process (pr.if, Figs 3; 4);
- a posterior part posterolaterally composed by the smooth subnasal laminae (l.sbn, Figs 3; 4), which contact medially behind the internasal wall, contrary to Stensiö's (1942) interpretation that the internasal wall separated the two laminae. Laterally to the internasal wall are the external exhalant nares (na2, Figs 3; 4).

The external inhalant and exhalant nares form the *fenestra exonarina communis* (f.ex.na.com, Figs 3; 4). The inhalant naris is more laterally placed than the exhalant one.

#### *Parasphenoid*

The parasphenoid (Psph, Figs 3; 4) is more anteroposteriorly lengthened than that of *K. podolica*. Nevertheless, this element is too poorly represented (only one specimen) to consider it as a diagnostic character for a species (see also Dennis-Bryan 1995).

#### *Postethmoidal part of the skull roof*

The postethmoidal part of the skull roof (Fig. 2A-C) is covered by very fine tubercles. The plates show the same relationships as in *K. podolica*, notably the contact between the postorbital and paranuchal plates which separates the central and marginal plates. The nuchal plate is thickened posteromedially, and the posterior edge is smooth and unornamented and possibly for extrascapular elements, as is the case in *K. podolica*.

#### *Median dorsal plate*

The median dorsal plate (MD, Fig. 2D) is represented by a single specimen (MB 290a; Brotzen 1934: pl. 9

fig. 2). It is as wide and long as that of *K. podolica* but the tubercles are very much thinner and more densely distributed. Contrary to *K. podolica*, it does not show any posterosagittal crest.

The ventral armour (Fig. 2F) is known by left anterior ventrolateral and spinal plates only.

#### *Anterolateral plate*

The anterolateral plate (AL, Fig. 2E), represented by a single specimen, is higher than long (as is the case in *Actinolepis magna* Mark-Kurik, 1973) and is covered by very fine and dense tubercles.

#### *Anterior ventrolateral plate*

The anterior ventrolateral plate (AVL, Fig. 2F) is only visible internally. The outline of the cartilagineous scapulocoracoid (sc, Fig. 2F) shows the usual trifurcate shape. Vascular canalicles leading to the coracoid process are also visible (c.cut.v, p.cor, Fig. 2F).

#### *Spinal plate*

The spinal plate is visible in external view. Its distal end extends behind the posterior part of the anterior ventrolateral plate, as is the case in *K. podolica*. The tubercles are of two types. The first type is the same as that encountered elsewhere on the armour (round, fine and dense); it is located on the dorsal mesial and lateral sides; the lateral side shows slightly bigger tubercles, but still very dense. The second type is visible on the lateroproximal side of the plate, where the tubercles are lozenge in shape, the long axis being anteroposteriorly directed. The reason of this difference is unknown.

The dorsal side of the spinal plate shows the posterior part of the groove for the insertion of the anterolateral plate laterally to the pectoral notch (s.ins.AL, Fig. 2F).

### *Kujdanowiaspis podolica* (Brotzen, 1934)

#### *Neurocranium*

The ventral side of the neurocranium of *Kujdanowiaspis* is only known from Stensiö's work on seriated sections (Stensiö 1969); no specimen of *Kujdanowiaspis* exposes this side.

**General aspect of the postethmoid ossification (Fig. 5).** The neurocranium of *Kujdanowiaspis* is a perichondrally ossified structure, a “primitive” condition in arthrodires (i.e. actinolepids, phlyctaeniids, and primitive brachythoracids such as *Buchanosteus confertituberculatus* (Chapman, 1916)). It is composed of two separately ossified components: a rhinocapsular (or nasal capsule) and of a postethmoid ossification. Connection between these two elements may have been ligamentous and nasal capsules are rarely preserved, and consequently nicknaming them “losing-nose” fishes.

The dorsal side of the postethmoid ossification is lozengic and larger than the ventral side (specimen GGI 15-618, Fig. 6A). Radiation centres of the overlying dermal plates, as well as the plates limits, appear as shallow depressions on the dorsal side of the neurocranium (specimen NHRM P 8458, Fig. 6B). The neurovascular web, visible on the well-preserved specimens NHRM P 8458 and 2869a (Fig. 6B, C), is composed of different plexi surrounding the postorbital, otic and occipital regions, which are probably correlated with the overlying dermal bone development (Goujet 1984).

The nuchal depression (f.dm, Fig. 6), visible from the level of the posterior postorbital process to the posterior edge of the neurocranium, is longer than that of *Dicksonosteus*. It corresponds to a thickening of the nuchal plate as suggested by Goujet (Goujet 1984). The nuchal depression is anterolaterally surrounded by two angular ridges for the underlying anterior and posterior semicircular canals (r.sca, r.scp, Fig. 6).

A pair of subparanuchal fossae (f.s.PaN, Fig. 6), flanking the posterior half of the nuchal depression, corresponds to a thickening of the overlying paranuchal plates (PaN). These fossae, below the ossification centre of these plates, are located at the same level than the supravagal process (p.sv, Fig. 6). They are associated with the internal course of the endolymphatic duct (d.end, Fig. 6B), which is preserved as a long and thin oblique rod in specimen NHRM P 8458 (Fig. 6B). This duct opens internally within the neurocranium through the internal endolymphatic foramen (d.end.i, Fig. 6), and externally on the external

side of the paranuchal plate through the external endolymphatic foramen (d.end.e, Fig. 6). The subparanuchal fossae are more anteriorly located than those of *Dicksonosteus*.

The impression of the central sensory groove (s.cc, Figs 5; 6) is deep and wide in its proximal (lateral) extremity, is thinner distally and is not visible at the level of the radiation centre of the central plates. As well, the impression of the main cephalic lateral sensory line is visible as a longitudinal groove visible in the otico-occipital region.

Several processes are developed from the anterior lateral side of the postethmoid ossification of the neurocranium. They are the ectethmoid process (p.ect, Fig. 6C), the antorbital process (pao, Fig. 6C), the supraorbital process (pso, Fig. 6C), the anterior postorbital process (p.po.a, Fig. 6C), the bifid posterior postorbital process (p.po.p, Fig. 6C), the supravagal process (p.sv, Fig. 6C) and the dorsal occipital process (p.occ, Fig. 6C). The ethmoidal shelf (m.eth, Fig. 6C) is slightly concave anteriorly and contacted the posteroventral part of the nasal capsule. The subnasal laminae (l.sbn, Figs 3; 4), formed by the postnasal plates, faced the anterior side of the ethmoid shelf. A deep dorsal canal, posteromesially directed, appears in the anterolateral angle of the shelf, and bears the olfactory nerve tractus. The ectethmoid processes protrude laterally from the ethmoid shelf and are posteriorly overlid by the antorbital processes. The latter are anterolaterally directed and overlid the ethmoid shelf. The grooves for the optic nerve (II, Fig. 6C) and for the anterior cerebral vein (s.vca, Fig. 6C) are clearly visible, as these structures run under the antorbital processes. Goujet (1984) considered the antorbital process as absent in *Kujdanowiaspis* and in other actinolepids, although the present author thinks it is more visible in *Kujdanowiaspis* than in *Dicksonosteus*: this is a real process and not only a dorsal cover for the optical nerve and the anterior cerebral vein.

The supraorbital process is large and overlid the orbit posteriorly to the ocular stalk (p.oc, Fig. 9A). This process is absent in phlyctaeniids (Goujet 1984). Stensiö (1963) considered it as a primitive condition in placoderms, although persistent in

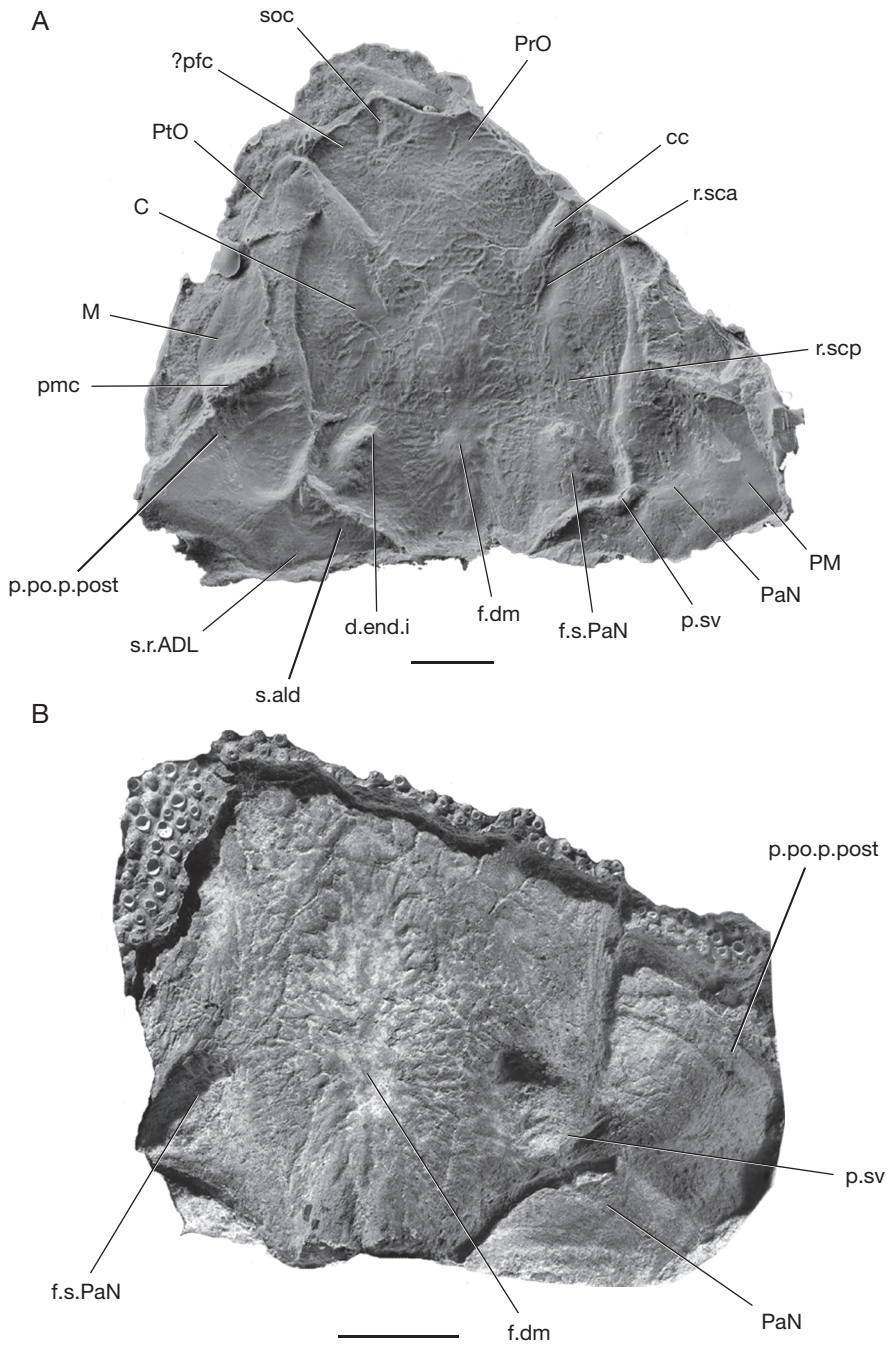


FIG. 7. — *Heightingtonaspis anglica* (Traquair, 1890b): **A**, silicone cast of the dorsal side of a neurocranium and of the visceral side of the associated skull roof, NHM P 21480; **B**, silicone cast of the dorsal side of an incomplete neurocranium and of the visceral side of the associated skull roof, NHM P 21454. Abbreviations: see Appendix 2. Scale bars: 1 cm.

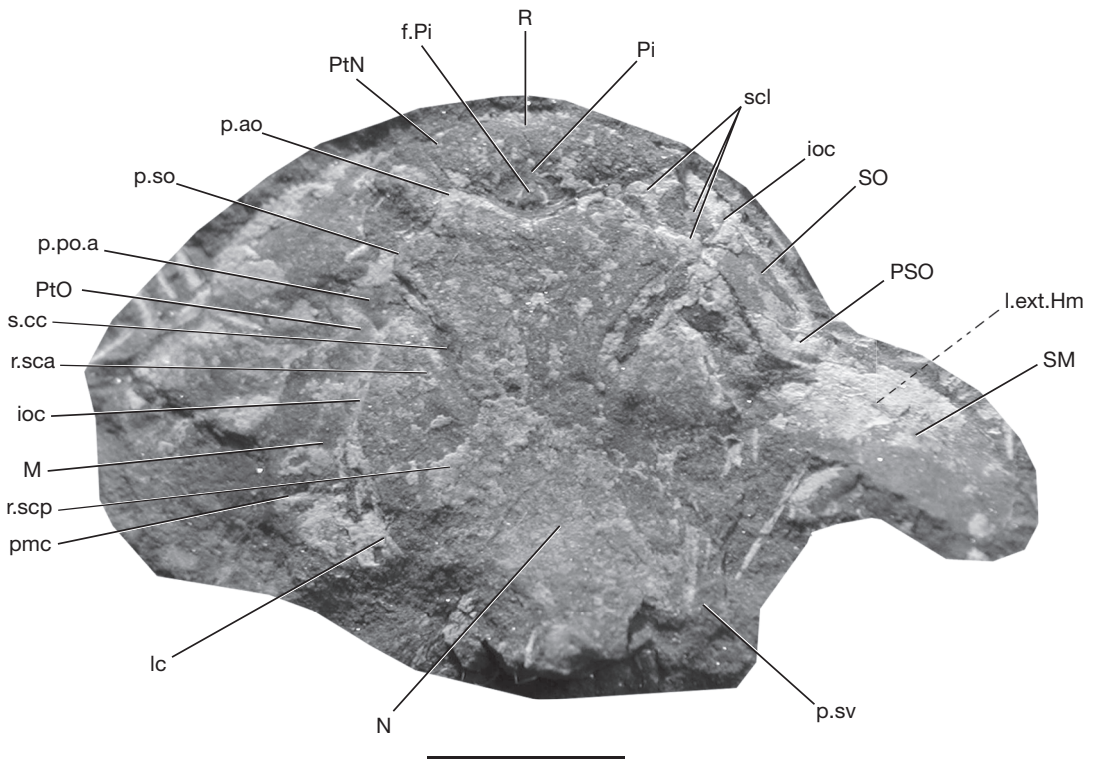


FIG. 8. — *Kujdanowiaspis podolica* (Brotzen, 1934), print of the external side of the skull roof and of the right cheek, NASU P 901/1 (Photo by V. Voichyshyn, NASU, Lviv). Abbreviations: see Appendix 2. Scale bar: 1 cm.

Pachyosteomorphi, Petalichthyida, Ptyctodontida, Rhenanida, Antiarchi and Coccoosteomorphi from the Upper Devonian. This process would have been lost in “Dolichothoracida”, Acanthothoraci and in Upper Devonian coccoosteomorphs (e.g., *Tapinosteus* Stensiö, 1963; *Pholidosteus* Jaekel, 1907). This process is found in “actinolepids” (Goujet 1984), and in buchanoosteids (Young 1979, 1981).

The anterior postorbital process is massive in dorsal view, but thin in ventral view, contrary to what can be observed in *Dicksonosteus*. As well as the different shape of this process between “actinolepids” and phlyctaeniids, the position of the foramen for the hyomandibular ramus of the facial nerve (VIIhm, Figs 5B; 6C) is also different. In actinolepids like *Kujdanowiaspis*, the foramen is placed on the distal end of the anterior postorbital process (in *Heightingtonaspis*, see NHM P 16030,

Fig. 7); in phlyctaeniids and brachythoracids it is positioned just posteriorly to it. The posterodistal face of the anterior postorbital process shows a scar in *Kujdanowiaspis* (f.a.hm, Figs 5B; 6A), probably for the attachment of hyomandibular (epihyal) element, distally associated with the internal side of the submarginal plate, as is observed in other well known arthrodires (e.g., *Dicksonosteus*, Goujet 1984; *Erikaspis*, Dupret *et al.* 2007).

The posterior postorbital process begins at the level of the posterior semi-circular canal ampula (a.post, Fig. 11). It is large at its base, and distally divided into two branches. This pattern is found in all “dolichothoracid” neurocrania. A foramen between the two branches for a ramus of the vagus nerve (X1) has the same position in *Dicksonosteus* (see Goujet 1984).

The supravagal process is posterolaterally directed, and its shape is similar with its homologues in

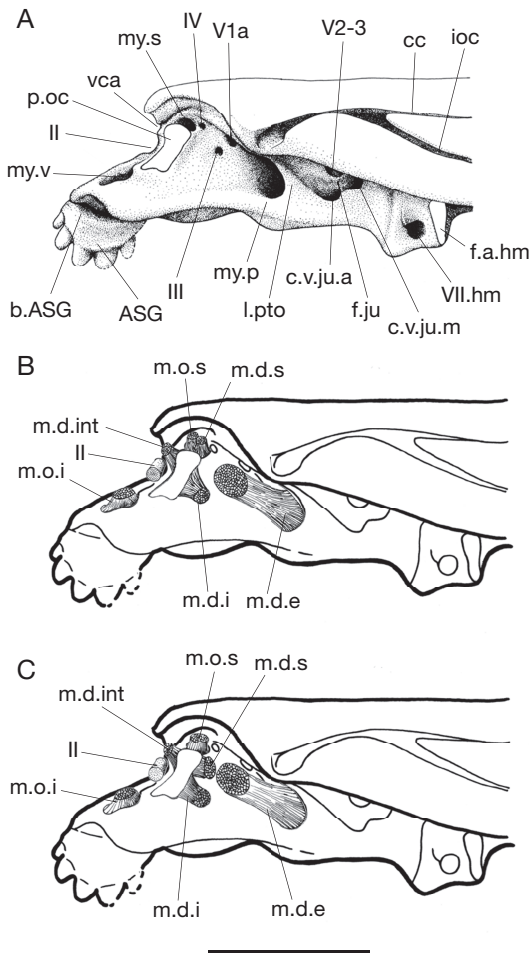


FIG. 9. — *Kujdanowiaspis podolica* (Brotzen, 1934), left lateral view of the orbital region of the neurocranium, and hypotheses about the proximal insertion of the oculomotor muscles; the muscular insertions are discussed in the text; the muscle direction is based on *Dicksonosteus arcticus* Goujet, 1975 reconstructions (Goujet 1984: fig. 17); **A**, left lateral view of the ocular part of the neurocranium (NHM P 18277) (after Goujet 1984: fig. 13); **B**, hypothesis of the *rectus superior* muscle attached in the upper myodome; **C**, hypothesis of the *rectus superior* muscle attached on the dorsal part of the dorsal side of the eye stalk. Abbreviations: see Appendix 2. Scale bar: 1 cm.

*Dicksonosteus* and *Lehmanosteus* Goujet, 1984 (see Goujet 1984), though it is thinner in *Kujdanowiaspis* and *Heightingtonaspis*.

The dorsal occipital process is posteriorly directed and its shape is similar to that of *Dicksonosteus* (see Goujet 1984).

The impression of the semicircular canals is shallow. The mesial edge of the anterior canal (r.sca, Figs 5A; 6C) is emphasized by the impression of the central sensory line groove (s.cc, Figs 5A; 6C).

The limits of the overlying dermal plates may be observed on the dorsal face of the neurocranium by the impression of their radiation of osseous fibers (e.g., NHRM P 4001, NHRM P 8458, Fig. 6C, D) or to slight and shallow grooves corresponding to thickenings at plate contacts (e.g., GGI 15-618, NHRM P 8458, Fig. 6A, C). Such observations may also be done in *Heightingtonaspis anglica* (Fig. 7): it is noteworthy that the shape of the nuchal plate of *Kujdanowiaspis* is similar to that of *Heightingtonaspis* and is therefore not as elongated as supposed by White (1969: pl. II, fig. D; Fig. 14) (i.e. the contact between the two central plates is not so short).

**Regional study of the neurocranium.** A unique specimen (NASU 901/1, Fig. 8) from Nagiryani shows the dorsal side of the connected ethmoid and postethmoid part of the neurocranium and the related skull roof, including cheek plates.

The orbitotemporal region is located between the antorbital process and the anterior edge of the anterior postorbital process, in the first third of the neurocranium.

*Dorsal side of the orbital region.* It shows a foramen for the ophthalmic canal (superficial ophthalmic ramus of trigeminal nerve; c.opht, Figs 5A; 6C), located at the level of the supraorbital processes (NHRM P 2869a, Fig. 6C). The homologous foramen in *Dicksonosteus* is located at the level of the anterior postorbital process (Goujet 1984), i.e. in the postorbital region. In lateral view, the orbital cavity is low and elongated, as is the case in *Dicksonosteus* (Goujet 1984; Fig. 9A). The supraorbital process defines part of the roof of this cavity. It is anteriorly limited by the anterior part of the postethmoid part of the neurocranium. A postocular lamina (l.pto, Fig. 9A), located in the posterior edge of the orbital area, links the base of the supraorbital process and the subocular shelf. The posterior myodome is located between the foramen for the pituitary vein anteriorly and the postocular lamina posteriorly. The



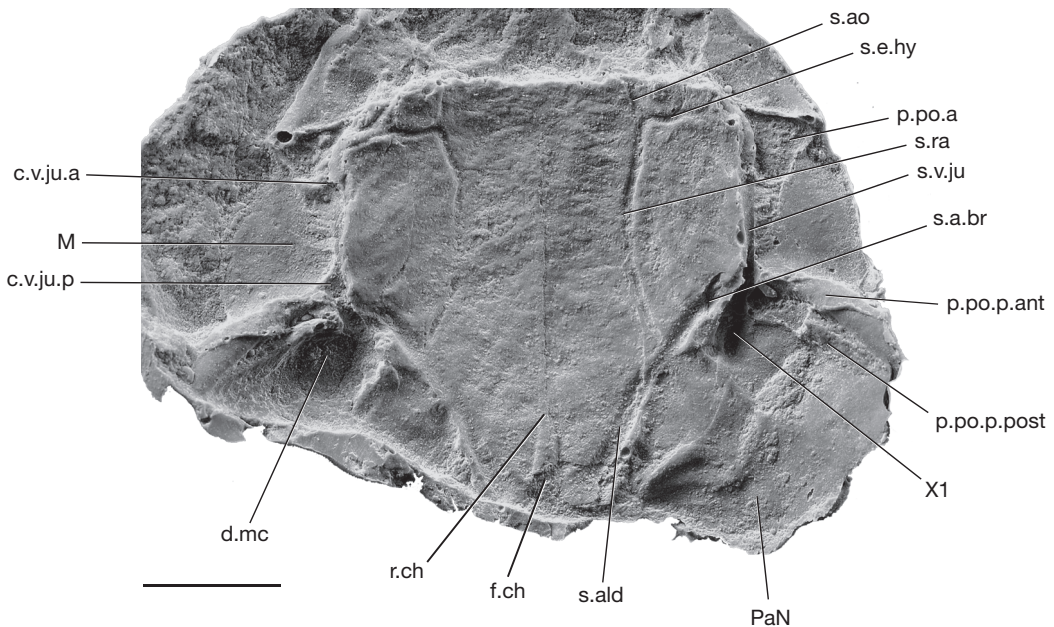


FIG. 10. — *Heightingtonaspis anglica* (Traquair, 1890b), silicone cast of the posterior part of the ventral side of a neurocranium and of the visceral side of the associated skull roof, NHM P 16030. Abbreviations: see Appendix 2. Scale bar: 1 cm.

eye stalk (p.oc, Fig. 9A) is located just posteriorly to the foramina for the anterior cerebral vein (vca, Fig. 9A) and the optic nerve (II, Fig. 9A). The ocular stalk is subquadrangular in shape and dorsoventrally elongated, as was pointed out for the first time by Goujet (1984). It is shorter than its homologue in *Dicksonosteus* and hence looks more like that of *Romundina* Örvig, 1975. The dorsal myodome (mys, Fig. 9A) is located dorsally to the eye stalk; the ventral myodome (my.v, Fig. 9A) is anteroventrally located. Behind the dorsal myodome, the foramen for the patheticus nerve (IV, Fig. 9A) is visible; the foramen for the communis oculomotoris nerve (III, Fig. 9A) is located posteriorly to it (two foramina for this nerve are displayed in the neurocranium of *Dicksonosteus*). A foramen for a ramus of the profundus nervus (V1a, Fig. 9A) is located posteriorly to the latter.

The orbital region and its processes, myodomes and eyestalk are all smaller in *Kujdanowiaspis* than in *Dicksonosteus*.

According to Goujet (1984), the posterior myodome of *Kujdanowiaspis* is sufficiently deep

to have contained both the obliquus superior and the rectus internus oculomotoris muscles. The large ventral myodome contained the obliquus inferior oculomotoris muscle. The posterior myodome contained the rectus externus oculomotoris muscle. Stensiö (1963; 1969) thought that the presence of the posterior myodome excluded the presence of an eye stalk, and that the rectus externus oculomotoris muscle was attached to its symmetric on the ventral side of the neurocranium via the pituitary canal. This latter hypothesis has been refuted by Goujet (1984), as the pituitary canal is too small to contain both a muscle and a vein, and because of a double torsion of the muscle between the eye-ball and the subpituitary fossa (Goujet 1984: 65, 66).

The rectus internus muscle was not located in the dorsal myodome in *Dicksonosteus* because of a pinch of the muscle (Goujet 1984). In *Kujdanowiaspis*, this muscle was probably not located in this myodome because the depression is too small to contain three muscles: the rectus internus muscle was therefore attached to the upper part



FIG. 11. — *Kujdanowiaspis podolica* (Brotzen, 1934), natural cast of the cerebral cavities with associated nervous system, NHRM P 8466b (material prepared and photographed by E. Stensiö, but never published). Abbreviations: see Appendix 2. Scale bar: 1 cm.

of the anterior side of the eye stalk (Fig. 9B, C). The rectus superior muscle was probably attached in the dorsal myodome (Fig. 9B) or to the dorsal side of the eye stalk (Fig. 9C).

The ventral side of the orbital region shows the scar insertions for the anterior superognathal plates (cr.ASG, Fig. 5B), the parasphenoid (Psph, Figs 5B; 15) covering the hypophyseal fenestra (fe.hyp) and the attachment areas for the palatoquadrate (a.pr.pq, Fig. 5B). A shallow anteromedially directed groove for the interna carotida arteria (s.c.int, Fig. 5B) leading to a foramen (c.int, Fig. 5B) runs between these two last structures courses.

*The postocular region.* It is located between the postorbital lamina and the anterior side of the anterior postorbital process, and is as long as the orbital region.

In lateral view, below the postorbital plate, the foramen for the profundus nerve (V2-3, Fig. 9A), the very small jugularis fossa (f.ju, Fig. 9A) and the two foramina for the anterior and medial jugular canals (c.v.ju.a and c.v.ju.m in front of and behind the anterior postorbital process, Fig. 9A) are visible.

On the ventral side, the medial subpituitary fossa (f.sbp, Fig. 5B) is laterally perforated by two foramina for the pituitary vein (c.v.pit, Fig. 5B). This fossa is much wider than that of *Lehmanosteus hyperboreus* Goujet, 1984.

The basal processes (p.b, Fig. 5B), supposed typical for actinolepids, are situated laterally to the subpituitary fossa, with the foramina for the palatine ramus of the facial nerve (c.pal, Fig. 5B) placed slightly posteriorly. These details are not shown in the studied material, but were demonstrated in Stensiö's (1963) serial sections of *Kujdanowiaspis* neurocrania.

*The otic region.* Between the anterior and the posterior postorbital processes, it is very well vascularized. It shows the impression for the central sensory groove and for the anterior and posterior semi-circular canals, and a weak cohesion between the overlying nuchal and central plates in the symmetry plane: the connection was made as a slight overlap, and not a simple apposition (Fig. 6B-D).

Unfortunately, the only specimen exposing the otic region in lateral view is very badly preserved (NHM P 20 588).

Short grooves and the long lateral groove for the jugular vein are observed between the two postorbital processes. This groove is more open than that of *Dicksonosteus*. It is connected anteriorly to the medium foramen for the jugular vein (c.v.ju.m, Fig. 5B), and posteriorly by the posterior foramen for the jugular vein (c.v.ju.p, Fig. 5B).

Specimen NHM P 16030 (referred to *Heightingtonaspis anglica*, Fig. 10) shows three foramina on the anterior branch of the posterior postorbital process: one mesial for the post-trematic ramus of the glossopharyngeal nerve (IX<sub>pt</sub>), and two laterally for the branchial vein (v.br) (as these two foramina are very close to each other, the vein was maybe bifid). Homologous structures were observed by Stensiö (1963) in *Kujdanowiaspis*, using the seriated sections method.

A foramen is observed slightly anteriorly to the posterior postorbital process in *Heightingtonaspis anglica* (on the ventrolateral edge of the neurocranium). This may correspond to the exit of the glossopharyngeal nerve (IX) or its pharyngeal ramus (IX<sub>ph</sub>). Because of its big size, the “glossopharyngeal hypothesis” is preferred.

*The occipital region.* It is located behind the posterior postorbital process.

Some foramina for the vagus nerve (X), firstly identified by Stensiö (1963), are visible on the lateral side of the occipital region, between the posterior postorbital and supravagal processes.

Foramina for the craniospinal nerves occur between supravagal and occipital processes (spioa,b,c, Figs 5B; 6A).

The ventral side of the occipital region in *Heightingtonaspis anglica* shows the chordal ridge (r.ch, Fig. 10), which becomes thinner anteriorly. The posterior side shows the chordal fissure (f.ch, Fig. 10), posterolaterally to which lay the – non preserved – occipital facets that were articulated to the synarcual. The groove for the laterodorsal aorta (s.ald, Fig. 10) is located ventrally to the occipital facets, is anteriorly directed and separated from the craniospinal foramina by a slight crest. This groove bifurcates at the level of the internal endolymphatic foramen. One ramus surrounds the semi circular canals and the saccula (groove for the anterior arterial root, s.ra, Fig. 10). The other ramus is straight and anterolaterally directed until the posterior postorbital process (groove for the branchial aorta, s.a.br, Fig. 10).

#### *Central nervous system*

The central nervous system was reconstructed by Stensiö (1963) using seriate sections, but photos of a mechanically prepared specimen (NHRM P 8466a, Fig. 11) were never published. Only the mesencephalic and the anterior rhombencephalic parts of the neurocranium are visible in dorsal view.

There is no constriction between the mesencephalon and the rhombencephalon. The pathetic nerve only (IV, Fig. 11) is visible; the communalis motor ocularis nerve (III) is located on the ventral side, and hence invisible here.

The anterior part of the rhombencephalon corresponds to the trigeminal nerve recessus (V). This subdivision corresponds to three quarters of the encephalon, as is the case in *Dicksonosteus*. The anterior region is located between the trigeminal nerve recessus and the facial (VII, Fig. 11) and acoustic (IX) nerves recessus. In *Dicksonosteus*, the facial and acoustic nerves branch independently from the metencephalon. The posterior part of the rhombencephalon is located posteriorly to the acoustic canal, and contains the medulla oblongata.

The proportions and the positions of the different encephalic structures reveal a primitive cerebral condition, because this pattern is presently found in extant gnathostomes embryos: a

very anterior position of the hypophysis (Moy-Thomas & Miles 1971), a nerves seriation, the same diameter between the encephalon and the spinal chord, and a very elongate myencephalic region (compared to the rest of the brain) are present in the first stages of the formation of the encephalon of extant vertebrates. Hence, the pattern of the placoderm brain could represent that of the ancestral gnathostome brain pattern.

#### *Dermal bones of the skull*

The plates of the skull roof are preferentially compared with those of two other actinolepids: *Heightingtonaspis* White, 1969 and *Eskimaspis* Dineley & Liu, 1984.

**General shape (Fig. 12).** The skull roof of *Kujdanowiaspis* is slightly wider than long. Its minimal width is located between the orbital notches, and its maximal width between the postmarginal plates, as is the case in all “actinolepids”. It is covered by tiny rounded tubercles (about 1 mm in diameter), with a roughly concentric distribution around the radiation centre of each plate.

On the internal side, the plates limits are indicated by very slight ridges, also impressed on the dorsal side of the neurocranium (see above). It is noteworthy that the plate sutures on the external surface do not strictly match with internal sutures, because of some slight overlappings.

The tuberculated layer of the specimen GGI 15-610 (Fig. 13A) was partly destroyed in order to reveal growth stages (s.Tn, Fig. 13A): some successive radiating osseous fibres, perpendicular to the plate limits, are also visible.

**The rostrum.** The rostrum is rarely preserved (only one specimen), as the two neurocranial components (ethmoid and postethmoid) were weakly attached. Nevertheless, the specimen discovered by V. Voichyshyn (NASU BP 901/1) provides some informations. It is also very similar to the one described (and attributed to *K. buczacziensis*) by Stensiö (1942).

Dorsally, the rostral capsule is convex, wide and short, which is a primitive arthrodire feature among arthrodires (Goujet 1984). In internal

view, the posterior half exposes a deep depression for the pineal pit (f.Pi, Fig. 8). Neither radiation centres nor plates limits are visible on this specimen. Nevertheless, it is possible to suppose that the limit between the rostral and pineal plates may correspond to the groove delimiting anteriorly the anterior edge of the pineal pit.

The connection between the ethmoid and postethmoid part of the skull roof is vertical and inflexes at the level of the ethmoid shelf (specimen NMH P 18277, Fig. 9).

**The rostral plate (R).** Its radiation centre is probably located on the anterior side. Dorsally, the plate is slightly trapezoidally shaped, and is surrounded laterally by the postnasal plates and posteriorly by the pineal plate.

**The pineal plate (Pi).** It shows slightly convex anterior and posterior edges. Its radiation centre is anterior to the “pineal pit”. This last structure does not correspond to a real foramen: the bone layer was very thin at this place and therefore easily breakable (see Stensiö 1942: 5, caption of fig. 1).

**The postnasal plates (PtN).** They are the lateral components of the dermal nasal capsule. The sutures with the rostral and the pineal plates are not visible, nor are the radiation centres (which would be at the level of their lateral extremity). Contrary to what Stensiö figured (1942: fig. 2), the supraorbital groove does not run behind the posterior edge of the postnasal plates, but in the most lateral part of the posterior edge of the pineal plate. Nevertheless, preorbital plates certainly contacted the postnasals.

The postnasal plates are small elements in *Kujdanowiaspis podolica*, compared with those of *Bryantolepis brachycephala*, where the anterior edge of the preorbital plates corresponds to the suture of the postnasals (see Denison 1958: fig. 105C), whereas in *Actinolepis magna* Mark-Kurik, 1973, the postnasals contact both preorbital and postorbital plates.

The eye opening with a sclerotic ring of the specimen from Nagiryani NASU 901/1 (scl, Figs 8; 12)

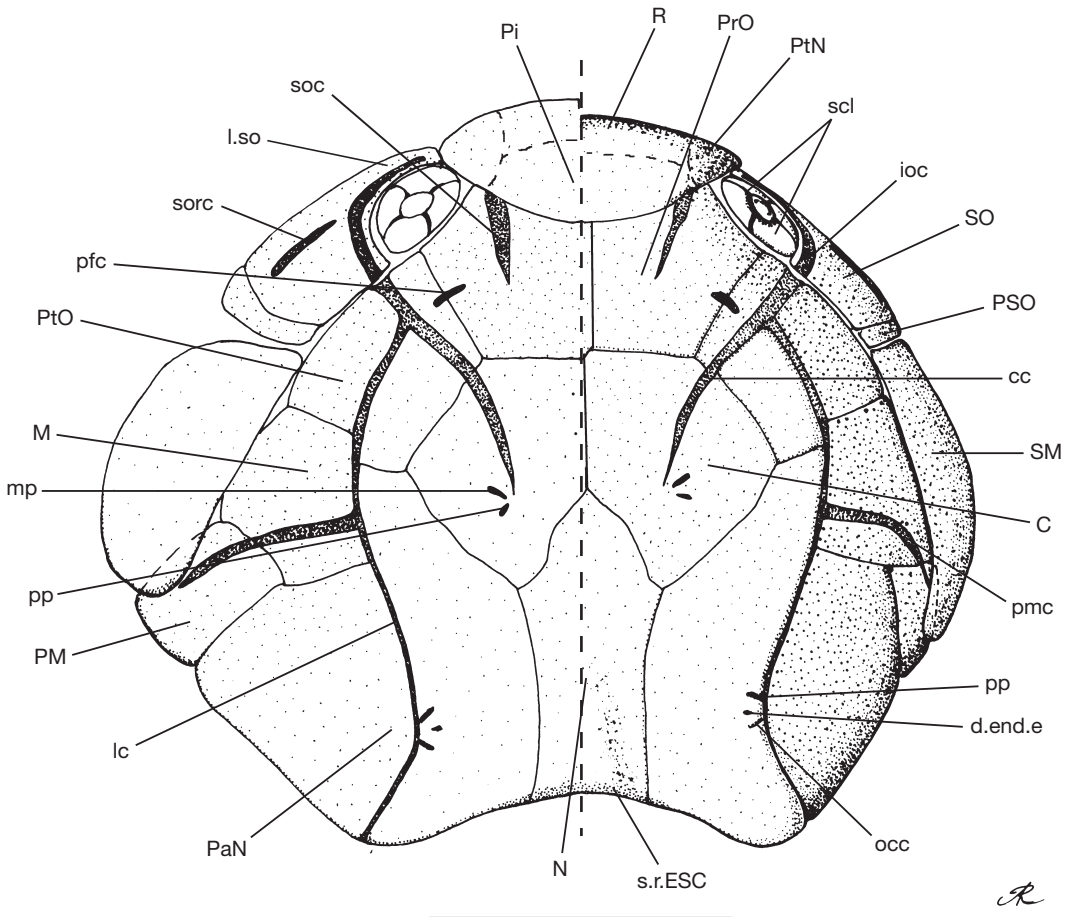


FIG. 12. — *Kujdanowiaspis podolica* (Brotzen, 1934): skull roof reconstruction (dorsal view); the right half takes the perspective into account (head down and lateral portion curved down). Drawing by Agathe Ravet (MNHN). Abbreviations: see Appendix 2. Scale bar: 1 cm.

is preserved and shows a clear (though short) contact between the postnasals and preorbital plates.

**The preorbital plates (PrO).** They are paired, small and pentagonal. Their anterior edge is slightly concave and receives the posterior part of the pineal plate. Their radiation centre corresponds to both the geometrical centre and the posterior end of the supraorbital groove. Their posterior edges are perpendicular to the symmetry plane but are never confluent with each other (i.e. the left preorbital contacts the two central plates). The limit between these plates is visible on specimen NHRM P 8420

(Fig. 13B). Each plate shows the anteroposteriorly and slightly mesially directed supraorbital groove (soc), which forms a ridge on the ventral side. A few specimens show a profundus sensory line (pfc, e.g., NHM P 20773, Fig. 13C). Laterally, the preorbital and postorbital plates show a shallow orbital notch.

**The postorbital plates (PtO).** They are slightly larger than the preorbitals, and smaller than the centrals. The radiation centre is situated at the level of the trifurcation between the central and the two rami of the infraorbital sensory lines. The posterior

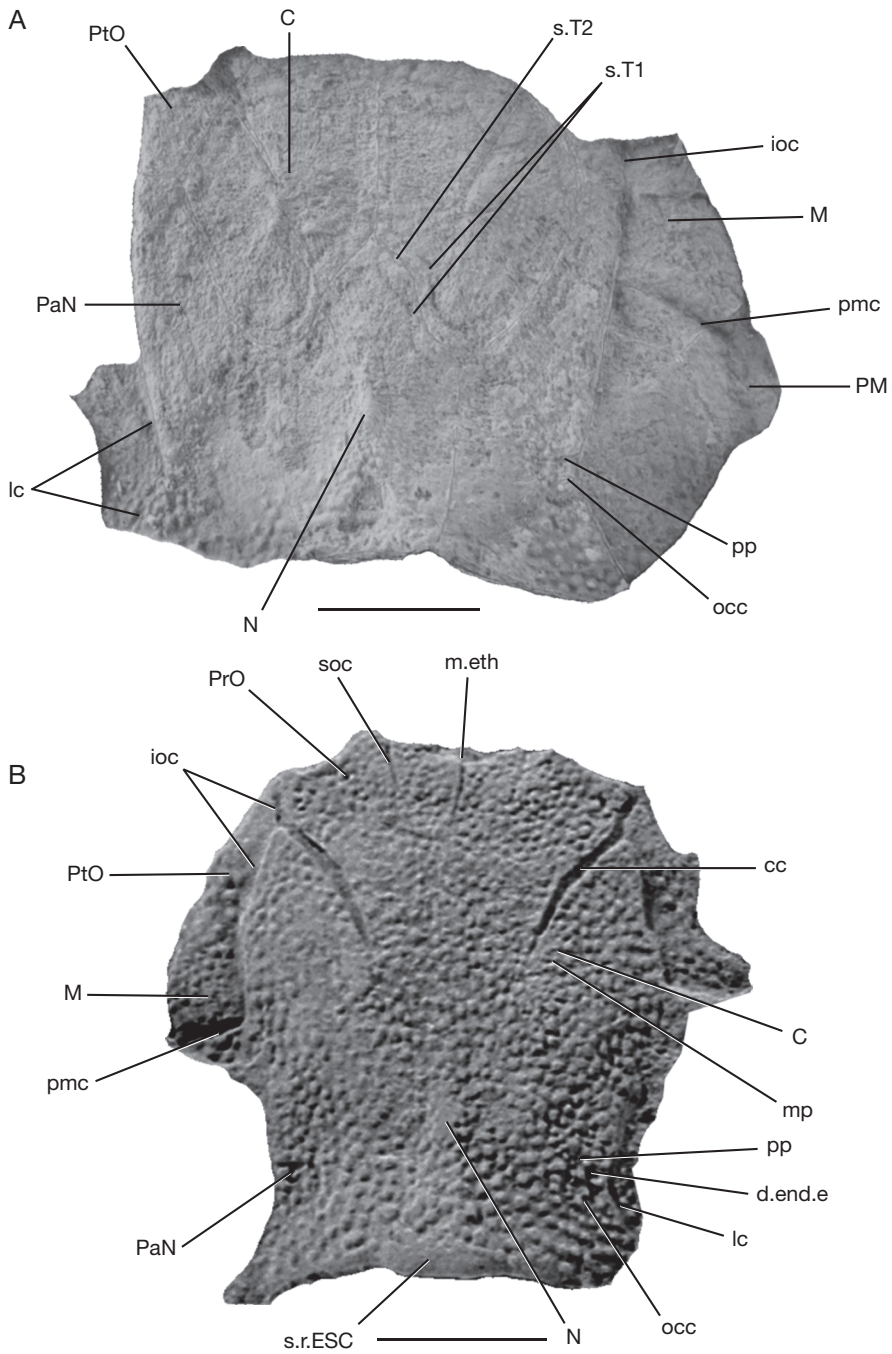


FIG. 13. — *Kujdanowiaspis podolica* (Brotzen, 1934): **A**, silicone cast of the external side of an incomplete skull roof, GGI 15-610; **B**, silicone cast of the external side of an incomplete skull roof, NHRM P 8420; **C**, silicone cast of the external side of a skull roof NHM P 20773 (plates limits drawn by D. Goujet); **D**, silicone cast of the external side of a skull roof, NHM P 20610 (plates limits drawn by D. Goujet); **E**, natural cast of an isoted nuchal plate, P 8426. Abbreviations: see Appendix 2. Scale bars: 1 cm.

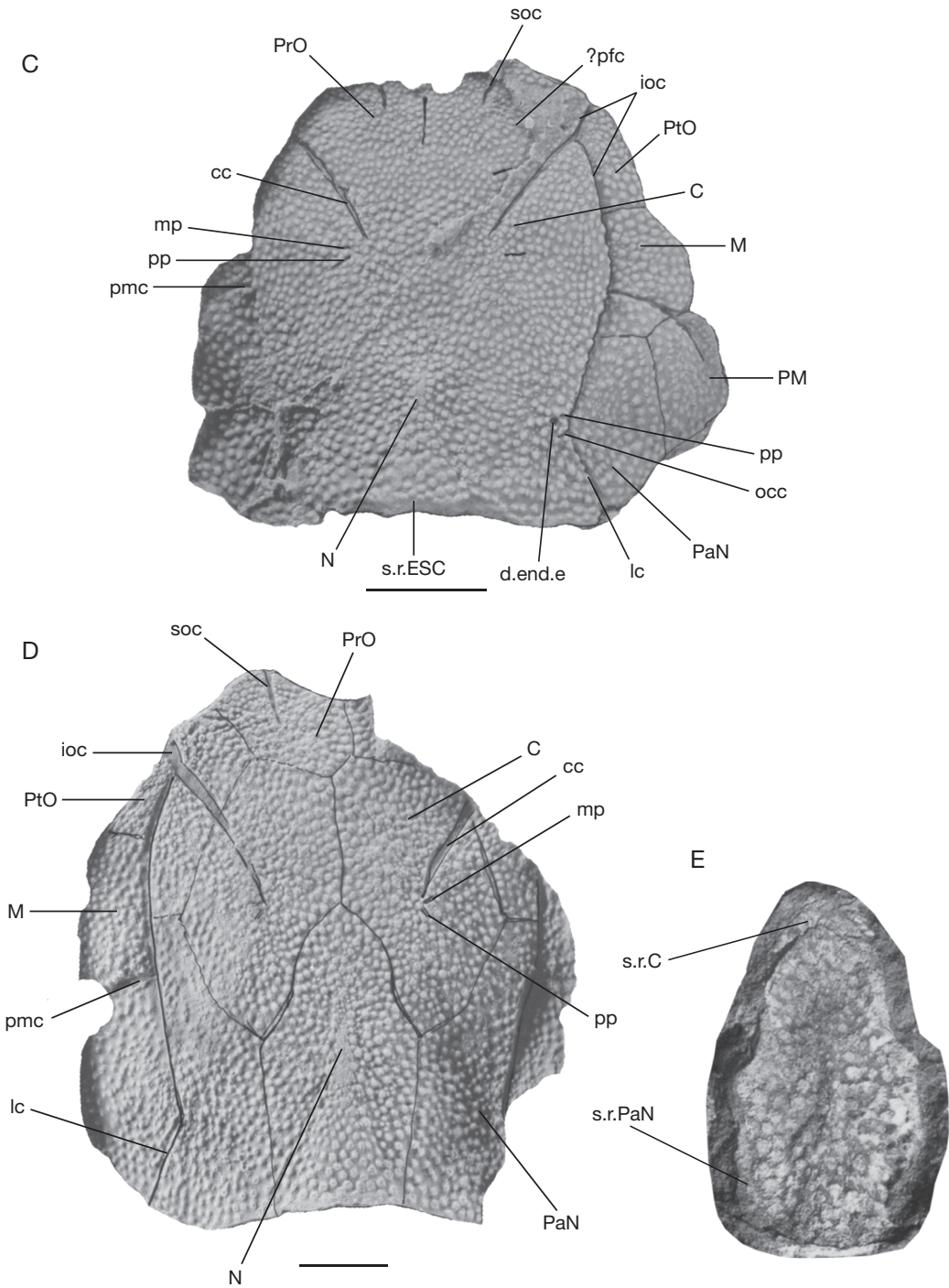


FIG. 13. — Continuation.

edge of the plates is displaced across the infraorbital groove which divides the plate into a dorsal (mesial) and a lateral laminae, which is very different from Denison's reconstruction (1958: fig. 105F). The most posterior edge, located on the dorsal lamina, contacts the anterior "process" of the paranuchal plate and laterally forms a small "canopy" over the infraorbital groove. The lateral lamina contacts the marginal plate. The ventral side of the plate bears ridges which correspond to the external infraorbital and central grooves.

**The central plates (C).** They cover the otic region of the neurocranium. They are slightly larger than the postorbitals. The radiation centre, at the geometric centre of the plate, is located around the extremities of the central groove and of the middle and posterior pit-lines.

**The marginal plates (M).** They are smaller than the preorbitals. The radiation centre does not correspond to the geometric centre but is located in the mesial edge of the plate, slightly anteriorly to the underlying posterior postorbital process. The plate does not extend mesially from the infraorbital and the main sensory grooves, contrary to what Stensiö assessed (e.g., Stensiö 1945: figs 8A, 9A, 11B; 1963; 1969, see also Denison 1958: fig. 105F; 1978: fig. 31B). The postmarginal groove runs all along the plate in *Kujdanowiaspis podolica*, but stops before the lateral edge in *Eskimaspis*.

**The postmarginal plates (PM).** They are slightly smaller than the marginals and are subquadrangular (Fig. 13C). They contact anteromesially the marginals, and posteromesially the paranuchals. The radiation centres correspond to the extremity of the postmarginal groove. A size gradient in the tuberculation indicates that these plates were probably somewhat covered by the "opercular" submarginal plate (SM), with the most lateral tubercles being much finer than the others (see specimen NHM P 20773, Fig. 13C).

**The nuchal plate (N).** It is long, as is the case in most actinolepids (except in *Actinolepis*, *Bryantolepis*, *Eskimaspis*, and *Simblaspis* where it is

relatively short). Its anterior part is lanceolate and separates the posterior half of the central plates (Fig. 13D). The radiation centre is located at the geometric centre. Its maximal width at the level of the contact with the central and paranuchal plates, then it slightly decreases posteriorly. The nuchal plate thickens from the radiation centre toward the posterior edge, and shows a shallow inverted "V"-shaped hump. The posterior edge is smooth; this may be related to the presence of some extrascapular element(s), not encountered anyway in the material. One specimen (NHRM P 8426, Fig. 13E) is an isolated nuchal plate in dorsal view, exposing the insertion surface for the centrals. The lateral edges of the nuchal cover the mesial border of the paranuchals.

**The paranuchal plates (PaN).** They are very wide and roughly heptagonal. The radiation centre corresponds roughly to the geometric centre. The groove for the main sensory line demarcates a dorsal and a lateral laminae. The dorsal lamina shows a slender anterior process which contacts the posterior edge of the postorbital plate, as is the case in, for example, *Heightingtonaspis* and *Eskimaspis*. The combination of these two processes entirely separates the central and marginal plates. The centre of the paranuchal plate is thickened. The external foramen for the endolymphatic duct (d.end.e, Figs 12; 13B, C), the posterior end of the posterior pit-line (pp, Fig. 13B, C) and the occipital cross-commissure (occ, Fig. 13B, C) are visible around a flexure of the main sensory groove. The dorsal lamina forms a little "roof" – continuing that of the postorbital plate – over the sensory groove. The tuberculation is uniform on the plate and does not show any overlapping by the submarginal plate.

Some specimens show tubercles of different sizes. But there is no evidence to determine rather if the smallest or the largest are of second generation. Indeed, second generation tubercles used to cover the first generation which was then resorbed. Have the smallest tubercles, between the larger ones, not been covered, or did they appear during the second generation? It is nevertheless noteworthy that some Arthrodira show in cross sections of the exoskeletal plates a number of tubercle generations following



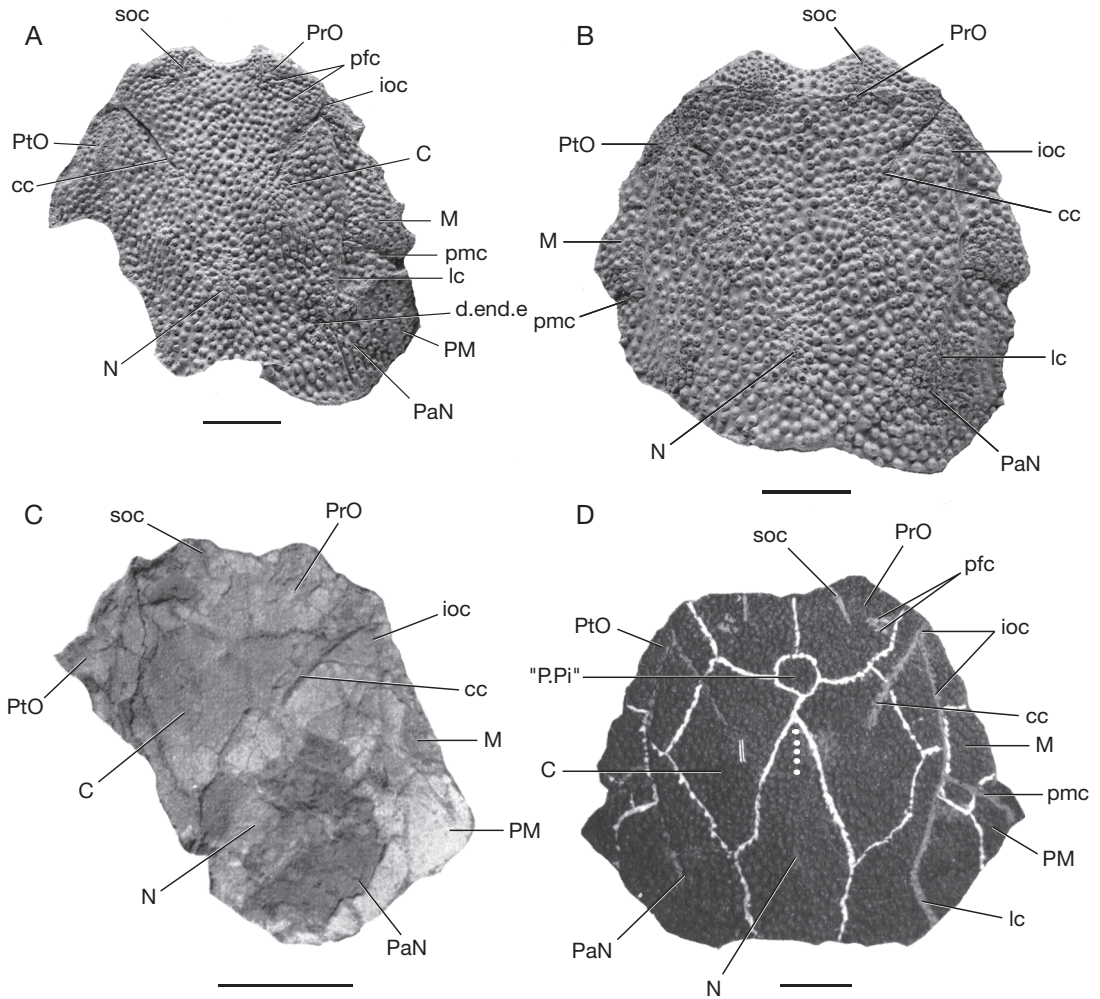


FIG. 14. — *Heightingtonaspis anglica* (Traquair, 1890b): **A, B**, silicone casts of the external side of a skull roof; **A**, NHM P 38032; **B**, NHM P 42147; **C**, incomplete skull roof (internal side), NHM P 27190 (White 1969: pl. II, fig. C); **D**, incomplete skull roof (external side), NHM P 4740 (White 1969: pl. II, fig. D) (plates limits painted by White); dashed line indicates the real contact between the two central plates. Abbreviations: see Appendix 2. Scale bars: 1 cm.

one another (e.g., *Homosteus* Asmuss, 1856, *Luetkeichthys* Bystrow, 1957). In other cases resorption of earlier generations took place.

The main sensory line groove shows two flexures on the paranuchal plate: an anterior one with a wide mesial concavity, and a posterior one with a sharper laterally directed concavity. Mesially to this last flexure are positioned the posterior pit-line extremity, the external foramen for the endo-

lymphatic duct and the lateral end of the occipital cross commissure. The groove for the main sensory line runs backwards until the posterolateral corner of the plate.

#### *Dermal elements of the ventral side*

The dermal elements of the ventral side of the neurocranium and of the palate are rarely and poorly preserved.

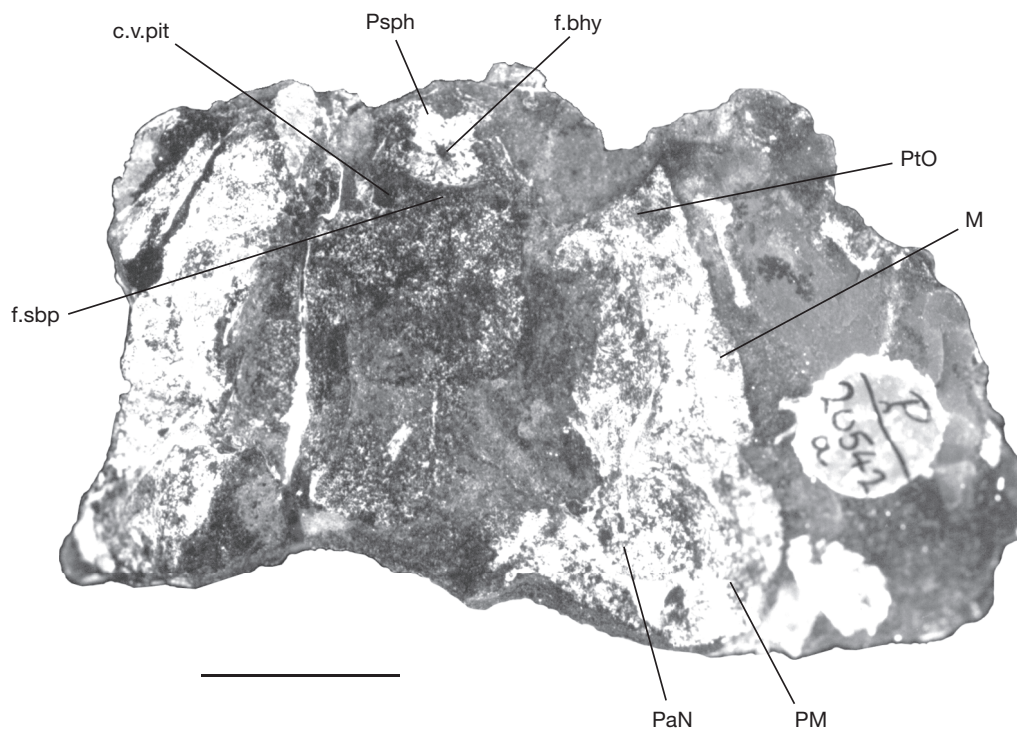


FIG. 15. — *Kujdanowiaspis podolica* (Brotzen, 1934): UV light photograph of the ventral side of a neurocranium pointing out the parasphenoid element, NHM P 20542a. Abbreviations: see Appendix 2. Scale bar: 1 cm.

**The anterior superognathal plates (ASG).** They are paired, and located on the lateral half of the ventral side of the ethmoid shelf. These plates are not entirely preserved, but their shape can be deduced from their scar insertion (wider than long) on the ventral side of the neurocranium (Fig. 5B). There is no evidence concerning the ossification centre of these plates in *Kujdanowiaspis*.

The specimen NHM P 18277 (Fig. 9A; Goujet 1984: pl. 29 fig. 1) shows the anterior and the left lateral sides of the anterior superognathals. Each plate may be divided in two parts: a flat osseous basal lamina (connecting the ethmoid shelf; b.ASG, Fig. 9A), and a tuberculated apical part. The anterior edge of the plate shows six tubercles, plus two others slightly posteriorly.

This kind of plate is primitive compared to the shearing ones of the ptyctodonts (e.g., *Ctenurella* Ørvig, 1960, see Long 1997) or the biting ones of

some derived brachythoracids (e.g., *Dunkleosteus* Lehman, 1956).

The posterior superognathals are not known. It is supposed that they were attached to the autopalatine (also unknown), presumably connected to the ventral side of the neurocranium, as it occurs in the phlyctaeniid *Dicksonosteus* (Goujet 1984) and other arthrodires.

**Parasphenoid (Psph).** Stensiö (1942: figs 4A, B, 5) first figured the parasphenoid (Psph) of *Kujdanowiaspis buczacziensis*, and considered it as a “tooth-bearing thickening on the lower side of the neurocranium presumably representing the fused anterior superognathals of both sides in Brachythoracid Euarthrodires”. He figured it as a very anteroposteriorly elongated hexagon. He only considered this element as a true parasphenoid in 1945 (addendum, p. 67), and reconstructed it a

bit wider than before, but with uncertain edges (Stensiö 1963).

Only one photo made under UV light of the ventral side of a neurocranium (specimen NHM P 20542a, Fig. 15; this photo is the only material the author accessed to) shows an almost complete parasphenoid (only the lateralmost flanges seem to be lacking), with the surrounding ventral side of the neurocranium which size is that of *K. podolica*. It is quite quadrangular in shape (33 mm wide) and is located anteriorly to the subpituitary fossa. The central part of the element is clearly visible owing to its thick spongiöse bone structure. The anterior and lateral edges are concave and the posterior edge convex. The left lateral edge shows a tiny notch. The thin layer of bone at the centre of the parasphenoid is broken, probably during preparation. Hence, as noticed by Stensiö (1942), the hypophyseal fenestra was probably ventrally closed.

It is impossible to determine whether *K. podolica* did really possess a parasphenoid of different shape than that of *K. buczacziensis*, because of the scarcity (one in each species) and the preservation of the material.

#### *Dermal elements of the cheek*

The dermal elements of the cheek are known by one specimen, exposing the external side only (NASU 901/1, Fig. 8), which size and ornamentation belong clearly to *K. podolica*. The author only studied a photo of the specimen, nicely communicated by V. Voichyshyn (NASU).

**Suborbital (SO) and the postsuborbital plates (PSO).** They show the typical tuberculated ornamentation. The anteriormost part of the suborbital plate corresponds to a ventral slender lamina that borders the ventral edge of the orbit (suborbital lamina, l.so, Fig. 12), and contacts sclerotic elements of the eye. The orbital notch is large and deep. The posterior part of the suborbital plate is higher. In its anterior part, the infraorbital groove (ioc) is vertical and surrounds the orbit in the suborbital lamina. The supraoral groove is parallel to the ventral edge of the suborbital plate, and seems to contact anteriorly the infraorbital groove (sorc) at the level of the radiation centre. This supraoral groove is larger

than that of *Dicksonosteus*, in which it does not contact the infraorbital groove, but Goujet (1984) proposed that the connection may have occurred in the most superficial layers of the dermis.

Though the internal side is unknown, the plate was probably connected to the palatoquadrate, itself linked to the neurocranium.

In its posteriormost part, the suborbital plate seems to overlap the postorbital plate (PSO, Figs 8; 12), which is much higher than long.

**Submarginal plate (SM).** It is the most posterior element of the cheek and assumed the opercular function in placoderms. The anterodorsal extremity shows a little spur which overhangs the dorsal edge of the suborbital and the postsuborbital plates. Because of the tuberculation zonation observed on the postmarginal plate (Fig. 13C), the submarginal plate certainly covered the most lateral part of the postmarginal.

**Epihyal element (l.ext.Hm, Fig. 8).** It was probably cartilaginous, and hence was not preserved. But both its shape and position can be determined owing to the print left on the external side of the submarginal plate (also occurs in *Erikapis zychi*; see Dupret *et al.* 2007). An oblique shallow and slender broken rod-like structure, with osseous fibers oriented along the great axis, is visible posteriorly to the anterodorsal spur of the submarginal plate. This rod would be the external expression of the epihyal element, fused to the internal side of the submarginal plate, as is the case in *Sigaspid lepidophora* Goujet, 1973 and *Dicksonosteus arcticus* Goujet, 1975. The disposition of this rod is similar to the ones assessed in the two previous cited species.

#### *The thoracic armour (Figs 16-25)*

**General features.** The dermal skeleton is relevant to discriminate the two species *Kujdanowiaspis podolica* and *K. buczacziensis*. The available material comprises various incomplete shields, showing connected plates and many isolated plates showing overlap areas, both in external or internal views.

The thoracic armour covers the body part comprised between the bottom of the branchial cavity and the anus. As in *Sigaspid lepidophora* Goujet,

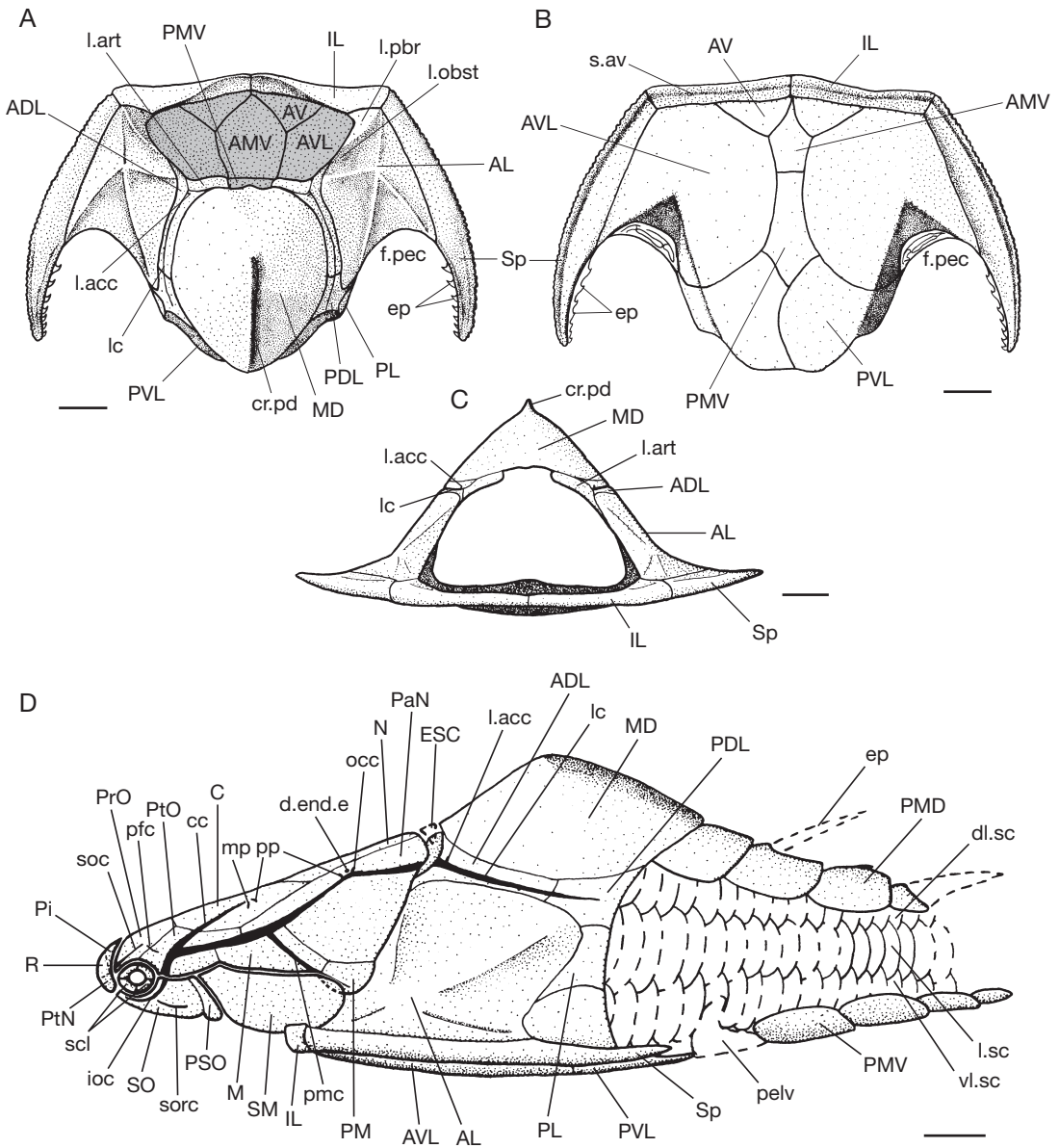


FIG. 16. — *Kujdanowiaspis podolica* (Brotzen, 1934), reconstruction of the thoracic armour: **A**, dorsal view; **B**, ventral view; **C**, anterior view; **D**, lateral view (with skull roof and cheek cover). Abbreviations: see Appendix 2. Scale bars: 1 cm.

1973, the anus was probably located just behind the posteroventral plates.

This armour is composed of all the classical plates previously described in arthrodires. No plate is regressed nor lacking as it occurs in some Brachy-

thoraci (e.g., Aspinothoraci, Pachyosteomorphi), Phyltaenioidi (lacking anteroventral plates) or Phyllolepida (lacking anterior and/or posterior median ventral plates). On the contrary, actinolepids were supposed unique among arthrodires

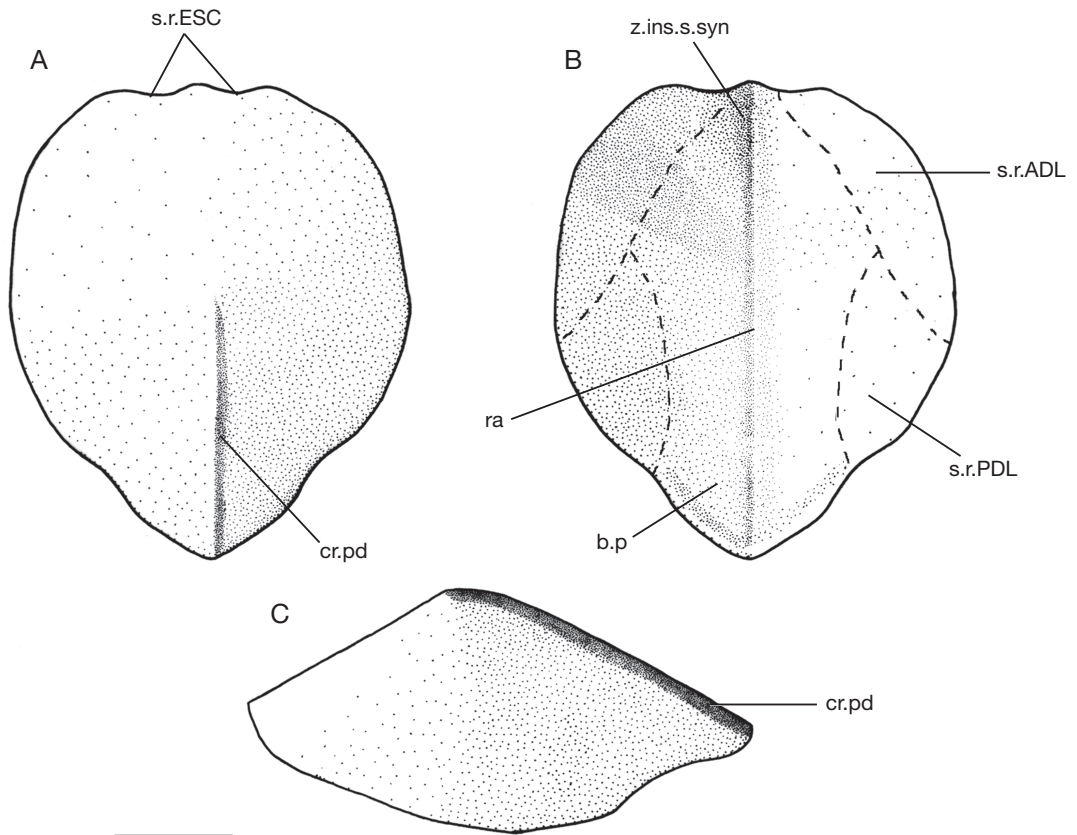


FIG. 17. — *Kujdanowiaspis podolica* (Brotzen, 1934), reconstruction of the median dorsal plate: **A**, dorsal (external) view; **B**, ventral (internal) view; **C**, left lateral external view. Abbreviations: see Appendix 2. Scale bar: 1 cm.

because of the possession of some anteroventral plates (see below).

The dorsal side of the armour is very high, convex and “roof-shaped”. The plastron is slightly convex posteriorly (at the level of the “box-shaped” posterior ventrolateral plates, flexing dorsally to meet the posterolaterals). No trace of annular thickening (“bourrelet annulaire” of Goujet 1984), as known in *Dicksonosteus* or *Arctolepis*, is visible.

**Extrascapular plates (ESC, Fig. 16D).** They are unknown, but the smooth areas on the posterior margin of the nuchal plate and on the anteromedial edge of the median dorsal plate indicate that these elements did exist, either as a pair of plates

or just a single element. No extrascapular plate was referred to *Eskimaspis* and *Heightingtonaspis* (White 1961, 1969; Dineley & Liu 1984).

**Median dorsal plate (MD).** It is almost as wide as long (previously considered as a characteristic of the actinolepids), whereas it is much longer than wide in phlyctaeniids like *Dicksonosteus* (Goujet 1984). The median dorsal plate of *Kujdanowiaspis* is roughly pentagonal, high and roof-shaped, with a rounded extremity pointing posteriorly. The tubercles are concentric around the radiation centre located one third of the length from the anterior margin. A posterior sagittal crest a few millimeters high extends posteriorly from the radiation centre (cr.pd, Figs 16A, C, D; 17; 18A-E).

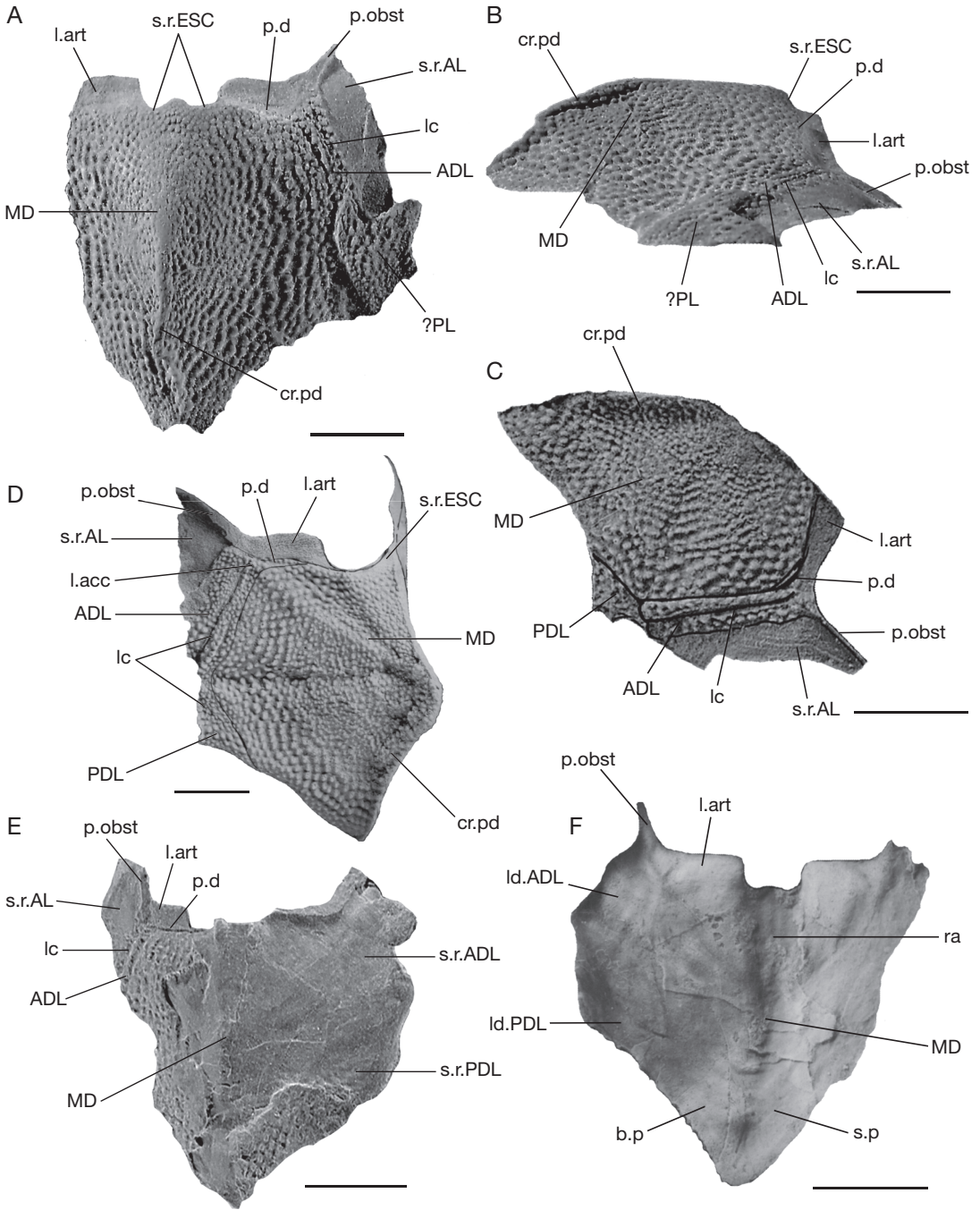


FIG. 18. — *Kujdanowiaspis podolica* (Brotzen, 1934): **A**, fragment of thoracic armour (dorsal part, dorsal view), GGI 15-617; **B**, fragment of thoracic armour (dorsal part, right lateral view), GGI 15-617; **C**, fragment of thoracic armour (dorsal part, right lateral view), GGI 15-612; **D**, fragment of thoracic armour (dorsal part), NHM P 20616; **E**, fragment of thoracic armour (dorsal part), NHRM P 8438; **F**, visceral side of the median dorsal plate, NHM P 18349. Abbreviations: see Appendix 2. Scale bars: 1 cm.

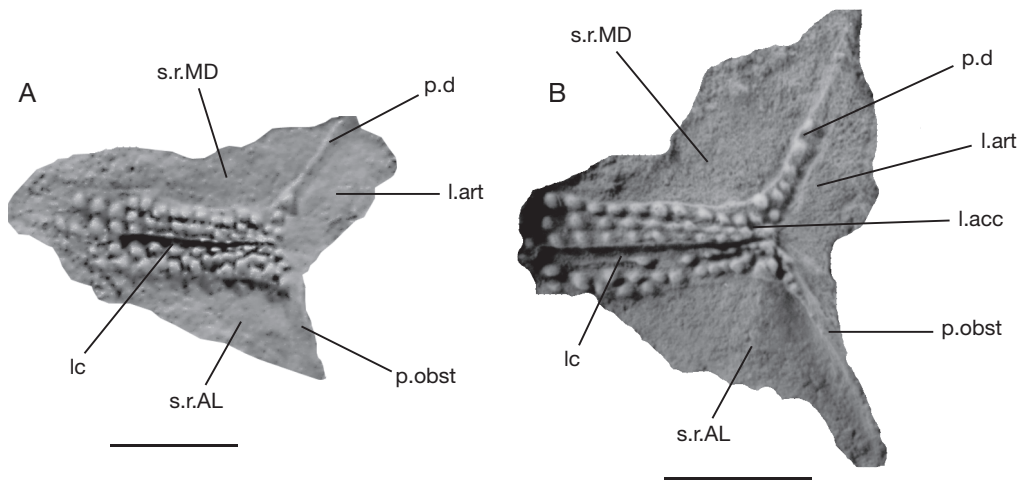


FIG. 19. — *Kujdanowiaspis podolica* (Brotzen, 1934), right anterior dorsolateral plate (external side): **A**, NHM P 53311; **B**, NHRM P 8432. Abbreviations: see Appendix 2. Scale bars: 1 cm.

Two small anteromesial notches probably housed the extrascapular element(s) (sr. ESC, Fig. 17A). These notches are more pronounced in *Eskimaspis heintzi* (Dineley & Liu 1984: figs 1A, 5A).

A few specimens (GGI 15-612 and NHM P 20616, Fig. 18C, D) show a strong tubercle differentiation in size, with bigger tubercles at the periphery, related to the age of individuals.

The internal view exposes well the overlap areas for the anterior and posterior dorsolateral plates (Figs 17B; 18E, F).

As in other “Dolicho thoraci”, there is no median keel, but just a small medial groove (ra, Figs 17B; 18F). This groove corresponds to a low and quite wide crest, that would be an attachment area for muscles connected to the synarcual and the vertebral column, as it occurred in *Dicksonosteus* (see Goujet 1984; and below).

The median dorsal plate of *Heightingtonaspis anglica* is unknown. That of *Eskimaspis* shows two unornamented areas on the anterior edge, probably for overlap by extrascapular elements (not found) (Dineley & Liu 1984: figs 1A, 5A).

**Anterior dorsolateral plate (ADL, Figs 16; 19).** It is a flat, anteroposteriorly lengthened plate. It is noteworthy that for phlyctaeniids like *Dicksonosteus*, *Arctaspis*, *Arctolepis* and *Heintzosteus*, the plate

shows a flexure dorsally to the main sensory line groove. The lack of this flexure in *Kujdanowiaspis* is compensated by the highly arched median dorsal plate.

The anterior part of the anterior dorsolateral shows a long and thin dorsal process (p.d) extending anterolaterally to the median dorsal. A thin ventrolateral process covers the anterior part of the obstaclic lamina of the anterolateral plate (p.obst).

A smooth articular lamina underlied the paranuchal plate on the anterior margin of the plate. This “sliding neck joint articulation” is typical for actinolepids (Miles 1973) and phyllolepids (Long 1984). The dorsomesial part of this articular lamina is larger than the ventrolateral one.

The anterior dorsolateral plate is broadly overlapped by the median dorsal plate anterodorsally and by the anterolateral plate ventrolaterally (cf. specimens NHRM P 8432, Fig. 19B), and overlaps the posterior dorsolateral plate posteriorly.

The posterior edge of the plate is approximately located at the level of the posterolateral flexure of the median dorsal plate.

The tubercles form rows parallel to the main sensory line groove.

Specimen NHRM P 8432 (Fig. 19B) shows a single row of tubercles within the main sensory line groove, suggesting a double line, as is known

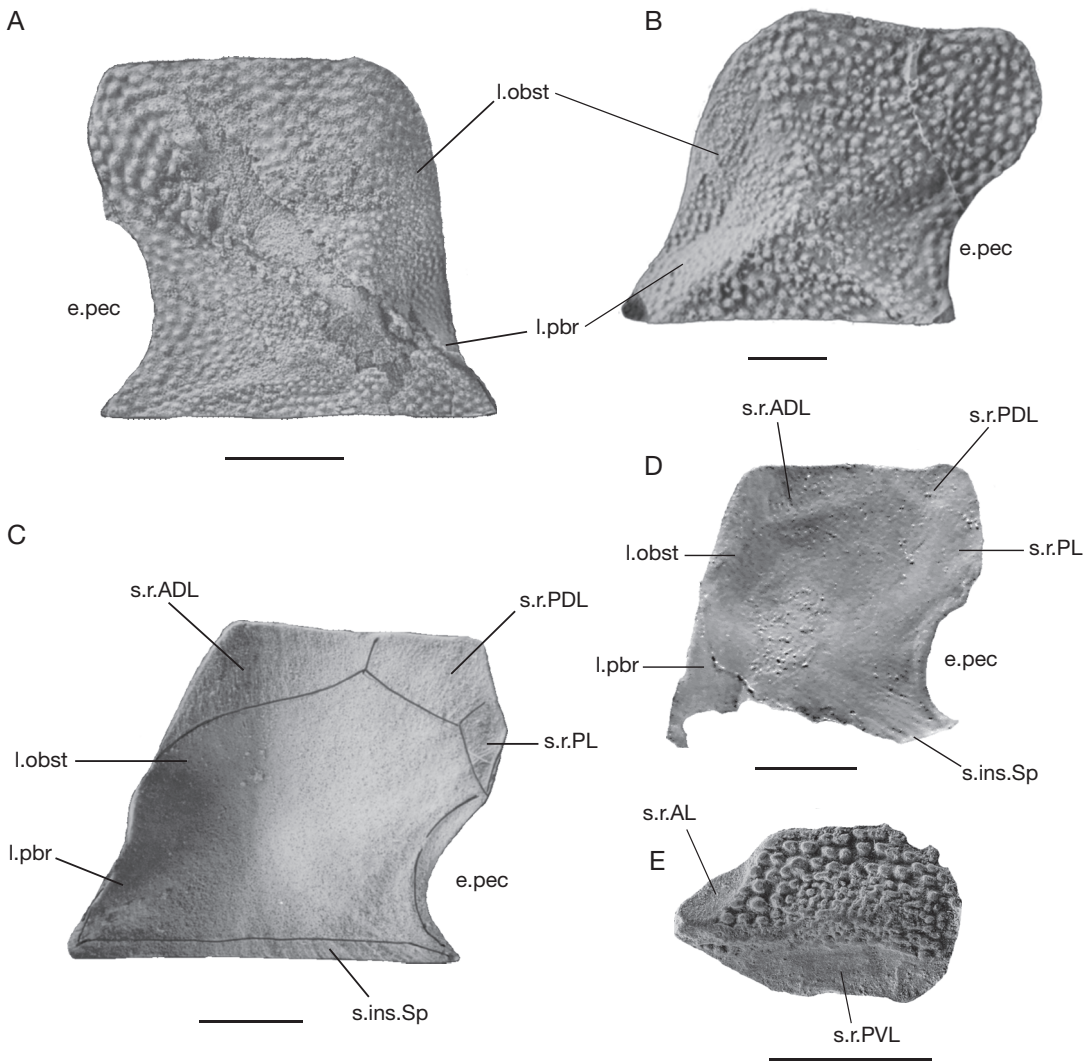


FIG. 20. — *Kujdanowiaspis podolica* (Brotzen, 1934): **A**, right anterolateral plate (external side), NHM P 20636; **B**, left anterolateral plate (external side), MB 282 (lectotype); **C**, **D**, right anterolateral plate (internal side); **C**, NHM P 18241; **D**, NHM P 20635; **E**, left posterolateral plate (external side), Pi 1202. Abbreviations: see Appendix 2. Scale bars: 1 cm.

in extant fishes, or in the brachythoracid *Holonema* Newberry, 1889 (see for example Lelièvre *et al.* 1990).

A tiny dorsal branch of the main sensory line groove at the anteriormost part of the plate is visible: “accessory groove” (l.acc) (see specimens NHRM P 8419, NHRM P 8432, GGI 15-615, NHM P 20616, NASU 28555, Figs 16A, C,

D; 19B). This groove can also be observed in phlyctaeniids like *Dicksonosteus arcticus*, *Arc-tolepis decipiens* Woodward, 1891, or *Heintzosteus brevis* (Heintz 1929b; Goujet 1984), and is much longer in some (e.g., *Holonema westolli* Miles, 1971; dlc, in Denison 1978). This character is too much frequent to be considered as a simple teratologic feature.



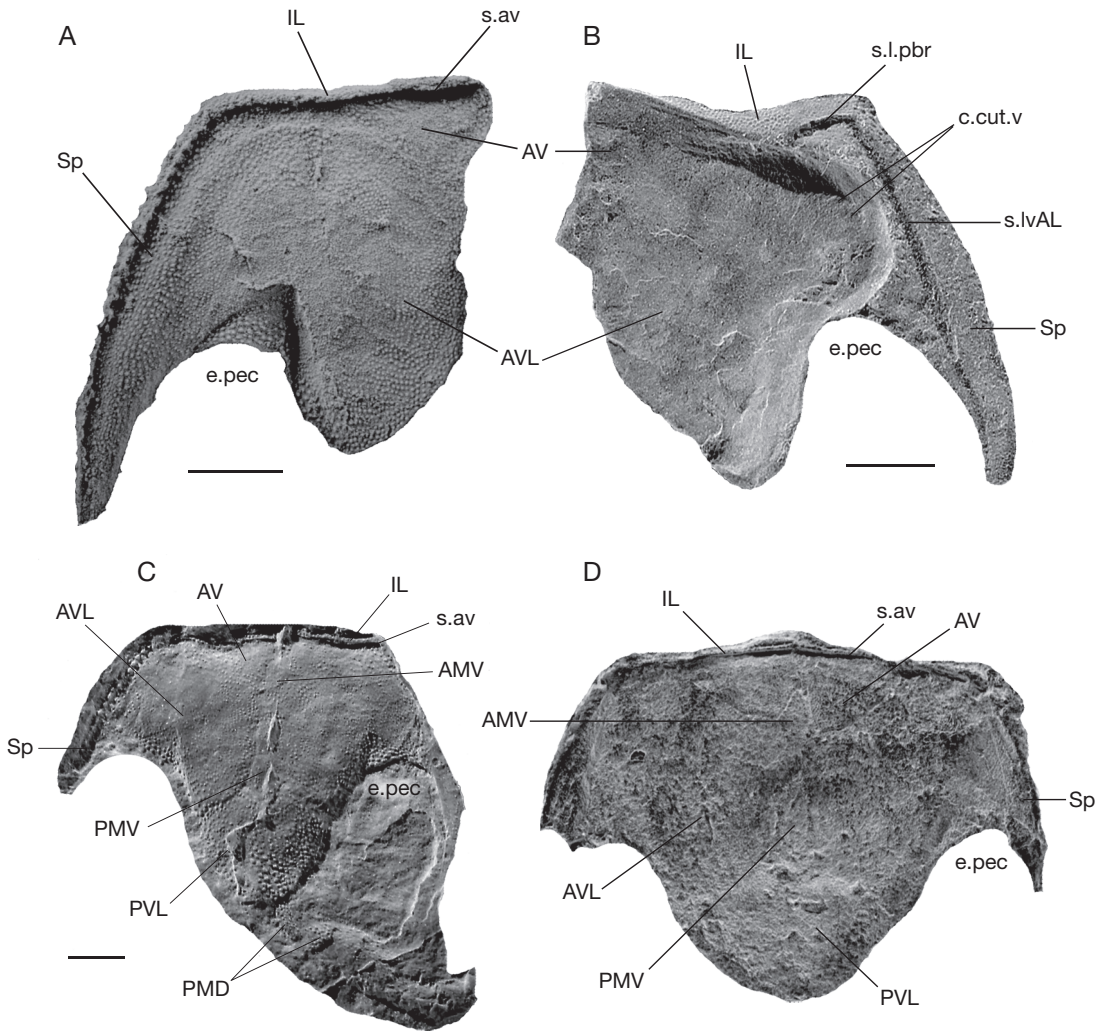


FIG. 21. — *Kujdanowiaspis podolica* (Brotzen, 1934): **A, B**, fragment of plastron (external side); **A**, NHM P 34852; **B**, NHRM P 8512; **C**, plastron and postmedian dorsal plates of the tail (external side), NHM P 18140; **D**, fragment of plastron (external side), NHRM P 8490. Abbreviations: see Appendix 2. Scale bars: 1 cm.

**Posterior dorsolateral plate (PDL, Figs 16; 18C).** It is quadrangular and twice shorter than the anterior dorsolateral. The groove for the main sensory line runs until the geometric centre that corresponds to the radiation centre. Tubercles are arranged as parallel rows along the groove.

The posterior dorsolateral plate is overlapped by the anterior dorsolateral plate anteriorly and by the median dorsal plate dorsally; it overlaps the

anterolateral plate ventrolaterally, and at a lesser degree the posterolateral plate.

The posterior dorsolateral plate of *Kujdanowiaspis podolica* is higher than that of *Eskimaspis* in which the groove for the lateral line is visible all along the plate.

**Anterolateral plate (AL, Fig. 20A-D).** It is trapezoidal. The radiation centre is located slightly ventrally to the

geometric centre (e.g., specimen MB 282; Brotzen 1934: fig. 9; Fig. 20B). From this radiation centre, four crests reach the angles of the plate, hence defining four triangles: the anterior (bearing the postbranchial and obstatic laminae, l.pbr and l.obst, Fig. 20A, B), dorsal, posterior and ventral. The tubercles are concentrically arranged around the radiation centre. The tubercles of the postbranchial lamina are finer than elsewhere on the plate. This was covered by the back of the skull roof and the submarginal plate. The postbranchial lamina is oriented at almost 90° from the rest of the anterolateral plate.

The pectoral notch (e.pec, Fig. 20A-D) is a two dimensioned structure emerging the posterior edge of the anterolateral plate (compared to the pectoral fenestra which is a three dimensioned structure), and is shallower than that of *Dicksonosteus* (Goujet 1984). The suprapectoral lamina is high (almost one half of the height of the plate; e.g., specimen NHM P 18241; Fig. 20C).

The contact faces for adjacent plates are visible on the internal side of specimen NHM P 18241, owing to the radiating striae (Fig. 20C): that for the posterolateral plate being smallest (s.r.ADL, s.r.PDL, s.r.PL, Fig. 20C, D). The area for the spinal plate is very low (s.ins.Sp, Fig. 20C, D) and inserted in a groove of the interolateral and spinal plates (s.ins.AL, Fig. 21B).

In *Heightingtonaspis anglica* and *Eskimaspis heintzi*, the pectoral notch is shallower than in *K. podolica*. Nevertheless, the anterolateral plate of *Heightingtonaspis anglica* is of higher proportions than those of *K. podolica* and *Eskimaspis heintzi*.

**Posterolateral plate (PL).** It is illustrated by one isolated plate (specimen Pi 1202, Fig. 20E). The shorter (anterior) overlap area connected the anterolateral plate, as the larger (ventral) one was overlapped by the posterior ventrolateral plate. A longitudinal ridge, or lateral crest, separates the posterolateral plate in two laminae, in the middle of which is located the radiation centre. As is the case in *Dicksonosteus*, the ventral part is the smallest, and shows one single row of tubercles decreasing in size posteriorly. The dorsal part shows two sizes of tubercles: some very fine around the radiation centre, and some larger at the peripheries beyond. The internal side is not exposed.

**Interolateral plate (IL, Figs 16; 21; 22).** It is transverse, elongated, articulating with its antimeric in the midline, but its sutures are rarely visible (Fig. 21), and no isolated plate is known. As in all arthrodires (Denison 1958; Stensiö 1959), the interolateral plate consists in two laminae: a ventral one (external) forming the anterior edge of the ventral armour, and an ascending one (internal) which is laterally associated with the postbranchial lamina of the anterolateral plate in order to close posteriorly the branchial cavity.

The ascending lamina widens laterally and its tuberculation is always very fine. The interolateral plates of *Eskimaspis* and *Heightingtonaspis* are straighter than that of *K. podolica*. Moreover, the dorsal lamina of *Eskimaspis heintzi* is a little bit higher and unornamented (Dineley & Liu 1984).

The tubercles form parallel rows on the ventral lamina, the biggest being on its anterior side.

A shallow groove (s.av, anteroventral sulcus) is visible on the ventral external side, and is oriented in the plate direction before turning (at almost 90°) on the spinal plate where it is shallower (cf. NHM P 34 852 and NHM P 18 140, Fig. 21A, C). Miles (1965) considered this sulcus functioned as a probable locus for neuromasts, or for Lorenzini ampullae, or both. As this sulcus is tuberculated, Goujet (1984) does not allow any peculiar function to it.

**Paired anteroventral plates (AV).** They are triangular and probably anamestic ("filling in" plates). They articulate with the interolateral and anterior ventrolateral plates (specimen GGI 15-634, Fig. 22A). The tuberculation is very fine. The radiation centre corresponds to the geometric centre.

Concerning the "evolution" of these anteroventral plates among placoderms, some authors (e.g., Stensiö 1971; Ørvig 1975) considered that they were lost by fusion with an adjacent plate in phlyctaenioids (i.e. phlyctaeniids and brachythoracids). The anteroventral plate is found only in actinolepids, some petalichthyids (e.g., *Eurycaraspis incilis* Liu, 1991), and acanthothoracids (e.g., *Romundina* Ørvig, 1975) and has been recently described in the groenlandaspidid *Mulgaspis* Ritchie, 2004. But as noticed by Goujet (1984), if fusion occurred, one would have found some teratologic specimens. But it is noteworthy that this

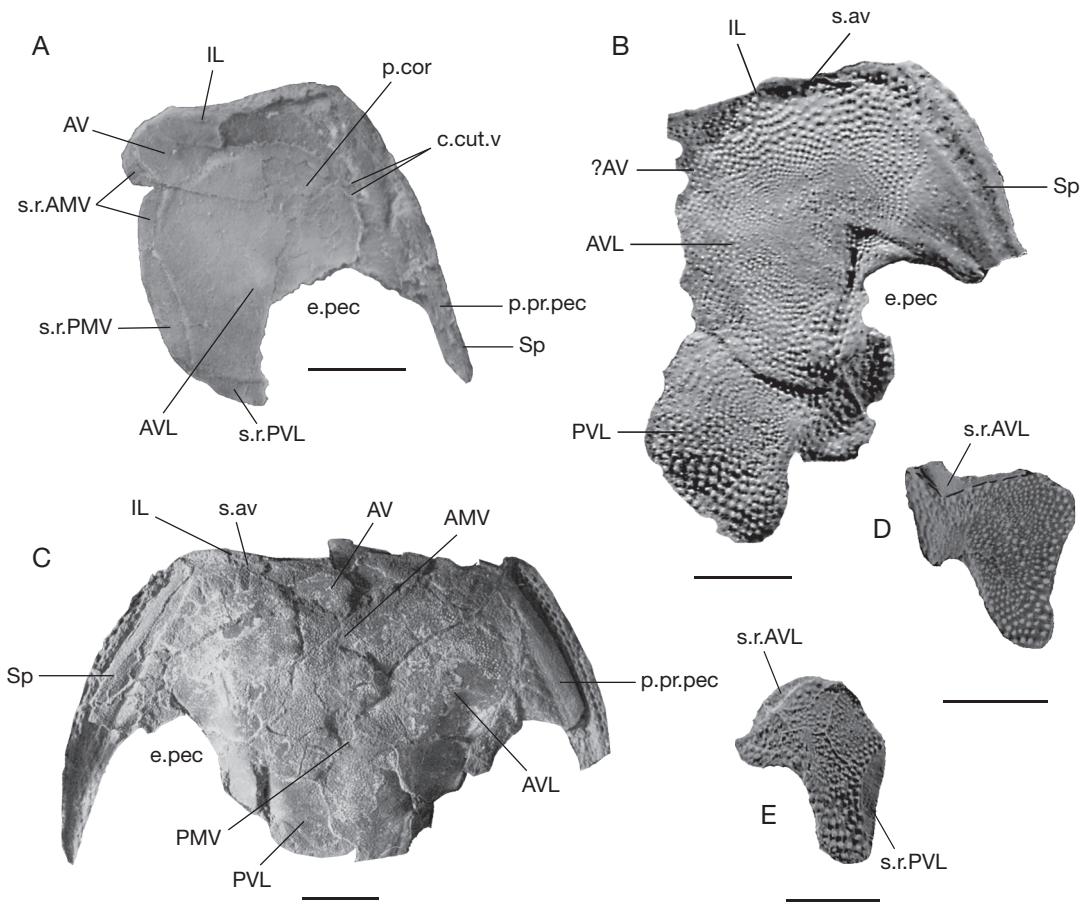


FIG. 22. — *Kujdanowiaspis podolica* (Brotzen, 1934): **A**, fragment of plastron (internal side) and impression of the scapuloacoroid, GGI 15-634; **B**, fragment of plastron (external side), NHM P 20574; **C**, fragment of plastron (external side), RAS 2172/2; **D**, **E**, right posterior ventrolateral plate (external side); **D**, GGI 15-624; **E**, GGI 15-625. Abbreviations: see Appendix 2. Scale bars: 1 cm.

last argument is far from receivable, because of the many biases occurring during fossilization. A better knowledge of the transition between actinolepids and phlyctaenioids is required.

Anyway, as these anteroventral plates are no more unique in actinolepids, they cannot be diagnostic of the group. Otherwise, alone they cannot provide a monophyletic status to actinolepids.

**Anterior ventrolateral plates (AVL).** Their radiation centre corresponds to the geometric centre (if abstraction of the pectoral sinus, i.e. the pectoral notch). As is the case in most “dolichothoracids”, this plate is not flat (see specimens RAS 2172-2,

Fig. 22C, and NHRM P 8512, Fig. 21B). A mesioventral and a lateral laminae are separated by a ventrolateral crest which is more marked posteriorly. The lateral lamina is divided in two parts: a long infraspinal lamina (limited by the suture with the spinal plate anterolaterally, and by a posterolateral tip posteriorly), and a lateral lamina (edging the pectoral fenestra ventrally), and developing a post-pectoral lamina. This latter lamina, associated with that of the posterior ventrolateral plate, connects with the anterolateral plate.

The anterior and lateral edges of the anterior ventrolateral plate are straight, but the mesial and posterior edges are rounded and overlap the adjacent

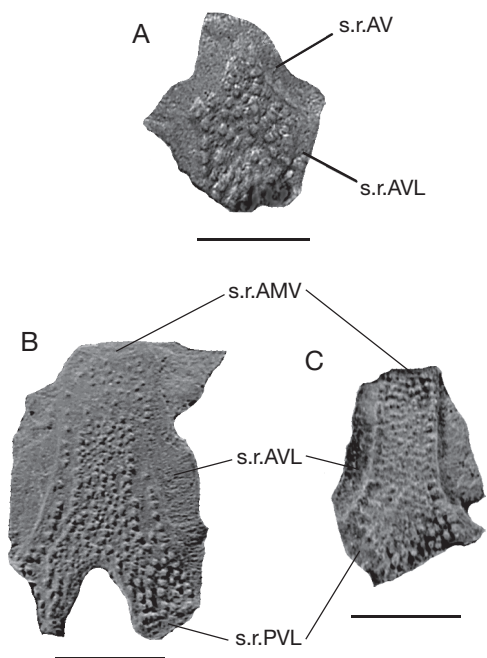


FIG. 23. — *Kujdanowiaspis podolica* (Brotzen, 1934): **A**, anterior median ventral plate (external side), NHRM P 8511; **B**, **C**, posterior median ventral plate (external side); **B**, NHRM P 8440; **C**, NHRM P 8484. Abbreviations: see Appendix 2. Scale bars: 1 cm.

plates (anterior and posterior median ventral and posterior ventrolateral plate).

The tuberculation shows a slight regional differentiation with finest tubercles on the ventral surface, and some slightly coarser tubercles on the lateral laminae.

The margins of the scapulocoracoid attachment are visible internally. It is associated with tiny foramina, and sometimes traces for neurovascularization of this area (c.cut.v, Fig. 22A).

In *Kujdanowiaspis podolica* and *Eskimaspis*, the lateral edges of the anterior ventrolateral plate are less angular than in *Heightingtonaspis*.

**The posterior ventrolateral plate (PVL).** It is as long as the anterior ventrolateral plate (but shorter than that of *Eskimaspis*). Contrary to other paired plates of the armour, it is not strictly symmetric with its antimeric, with the left plate slightly overlapping ventrally (externally) the right one. The suture between these paired elements is therefore rather simple, as in other

actinolepids (e.g., *Sigaspis lepidophora* Goujet, 1973). In phlyctaeniids like *Arctolepis*, *Dicksonosteus* or *Heintzosteus*, this suture shows a sinusoidal pattern (Goujet 1984). The posterior ventrolateral plate is overlapped anteriorly by the anterior ventrolateral plate, and medially the posterior median ventral plate.

The plates of the plastron are partly disassembled on NASU 25567a (Fig. 24A), to reveal the smooth overlap areas and the two laminae of the posterior ventrolateral plates, the lateral lamina connecting the anterolateral plate.

The posterior ventrolateral plate is composed by two laminae: a folded ventromesial and a lateral, visible on specimen NASU 25567a (Fig. 24A), the latter connecting the anterior posterolateral plate.

A regional differentiation in the ornamentation is visible on the specimens GGI 15-624 and GGI 15-625 (Fig. 22D, E). As for the anterior ventrolateral plate, the lateral lamina shows bigger tubercles than the ventral. The radiation centre is slightly anteriorly displaced from the geometric centre. The lateral lamina is much shorter than the ventral one.

There is no “annular thickening” on the internal side as it occurs in *Dicksonosteus* (Goujet 1984).

**Anterior median ventral plate (AMV).** It is short and wide, pentagonal and probably anamestic (Fig. 23A). It is slightly pointing anteriorly. The radiation centre corresponds to the geometric centre. It is overlapped anterolaterally by the anterior ventrolaterals. It overlaps posteriorly the posterior median ventral plate. Tubercles are fine.

**Posterior median ventral plate (PMV, Fig. 23B, C).** It is almost twice longer than wide, and also probably anamestic. The radiation centre is slightly posteriorly located compared to the geometric centre. The ornamentation is slightly coarser posteriorly. The plate is overlapped by the anterior median ventral plate anteriorly, by the anterior ventrolateral plates laterally, and by the posterior ventrolateral plates posterolaterally.

The specimen NHRM P 8440 (Fig. 23B) shows in its posterior part a large notch which could be interpreted as 1) a simple corrosion gap (but it is curiously symmetric), 2) a non-ossification during

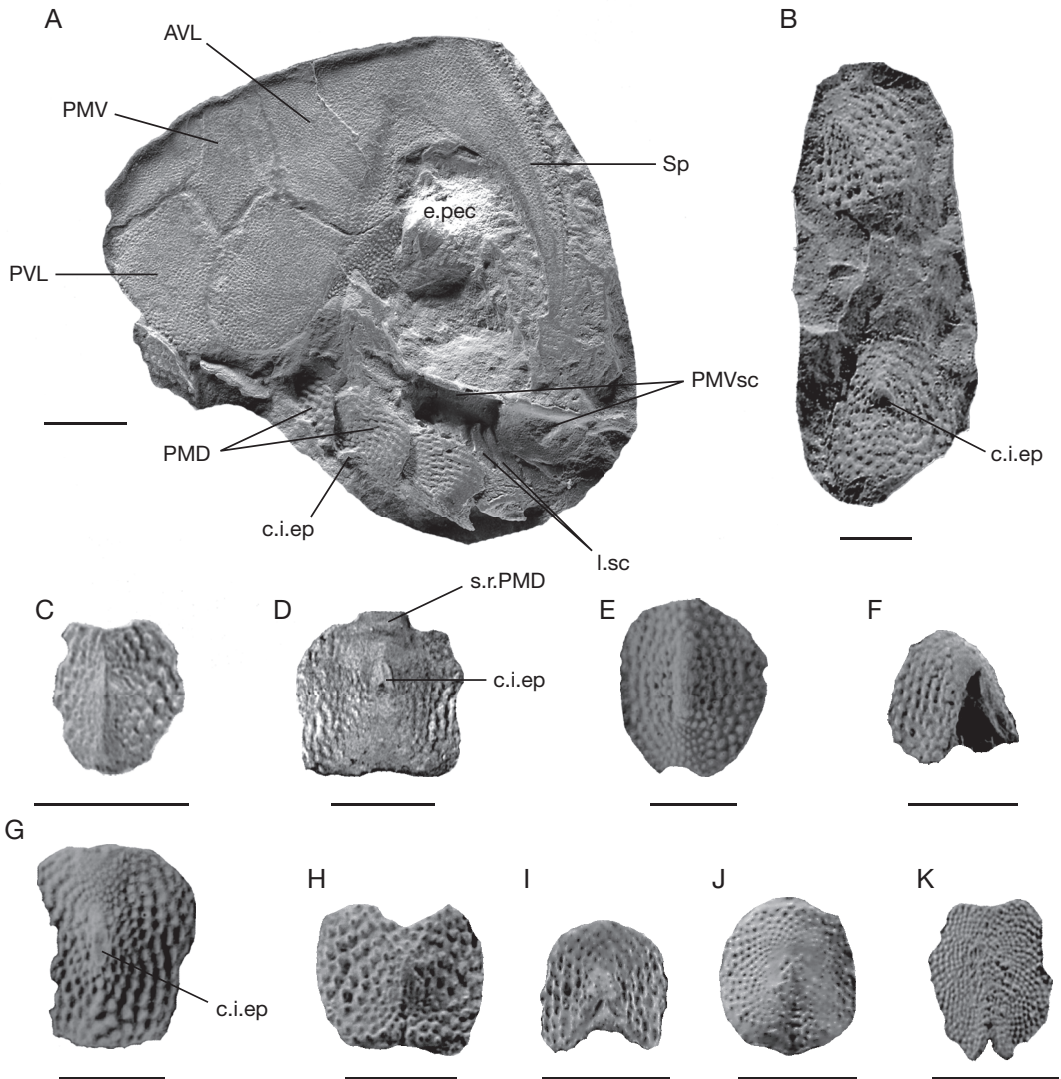


FIG. 24. — *Kujdanowiaspis podolica* (Brotzen, 1934): **A**, fragment of plastron and dermic elements of the tail (external side), NASU 25567c; **B-H**, posterior median dorsal plates (external side); **B**, NHM P 18161; **C**, NHRM P 8430; **D**, NHRM P 8476; **E**, Pi 1200; **F**, GGI 15-626; **G**, GGI 15-627; **H**, GGI 15-628; **I**, posterior median ventral plate of the tail (external side), GGI 15-649; **J**, posterior median dorsal plate (external side), NHRM P 8504; **K**, posterior median ventral plate of the tail (external side), GGI 15-632. Abbreviations: see Appendix 2. Scale bars: 1 cm.

life of the animal, or 3) an insertion area for a sur-numeral plate (but no overlapping area is visible, at least on this side).

**Spinal plate (Sp).** It is long (see NHM P 34852, Fig. 21A) and terminates as a smooth tip, slightly

anteriorly to the level of the posterior edge of the posterior ventrolateral plates (see specimens NHRM P 8512, NASU 25567a, Figs 21B; 24A). The radiation centre corresponds to the tip apex. The plate is situated in a slightly upper plane than the ventral armour surface (Fig. 16D). As in all arthrodiras,

it was filled in with cartilage (prolongation of the scapulocoracoid, see below).

The lateral sides are ornamented with rough tubercles longitudinally disposed (about two rows). The dorsal and ventral sides are covered with thin tubercles. The trench in which the anterolateral plate articulated is visible on the specimen NHRM P 8512 (Fig. 21B). When well preserved, the free mesial side of the spinal plate shows slightly anteriorly pointed spur-like denticles (5 on NASU 25567a, Fig. 24A). Because of the preservation of the material, no variation in the number of denticles can be provided.

The anteroventral sulcus continues on the ventral side of the spinal plate, its height decreasing distally. Another groove runs along the mesial edge of the ventral side, and a third one on the mesial side of the plate.

The spinal plate articulates with the anterolateral plate dorsally, with the interolateral plate anteromesially, and with the anterior ventrolateral plate mesially (along the infraspinal lamina of the latter).

#### *Dermal elements of the tail*

The plates covering the tail are found in association (subarticulated and slightly displaced) with the body armour in two specimens (NHM P 18140 and NASU 25567c; Figs 21C; 24A); they are more numerous as isolated specimens (see Appendix 1; Fig. 24B-H). Scales are only preserved on specimen NASU 25567c. Two isolated postmedian ventral plates have been identified.

#### **Postmedian dorsal plates (PMD, Figs 21C; 24A-I).**

They are small finely tuberculated elements covering the dorsal side of the tail. The first element was probably weakly inserted under the median dorsal plate (as no overlap area or scar is visible on the internal side of the median dorsal plate). Contrary to Dupret (2004: fig. 5), the first postmedian dorsal plate does not contact the posterior dorsolateral plate, because 1) tubercles are all of the same size on the tail dermal elements, 2) the insertion surface is always medial and does not extend very much laterally, and 3) the plates are not high enough (even if diagenesis plays some role in it).

Hence, there are four or five successive plates, each one covering posteriorly the very anterior part of the next one (specimen NASU 25567a, Fig. 24A): a small overlap area is seen at the very anterior edge of the isolated elements (Fig. 24C, D). The last dorsal plate of the tail, being higher and strongly arched indicates most likely a slender thickness of the tail, hence a distal position for this element (Fig. 24F, I).

The second and fourth postmedian dorsal plates show on their dorsal side a little scar, that is probably an attachment area for a – separately ossified – little dorsal spine (bigger for the last plate), however not found in the material.

#### **Post-median ventral “scutes” (PMV.sc, Fig. 24A,**

**J, K).** They covered the ventral side of the tail. Tubercles are finer than on the postmedian dorsal plates. The ventral series begins more posteriorly than the dorsal one, in order to let the cloacal pore (or at least the anus) free. The specimen NASU 25567a (Fig. 24A) shows a series of four plates, very low and slightly transversally curved. The posterior edge of each plate covers (externally) the anterior edge of the next one. The last plate is the smallest.

#### **Four lateral scales of the tail (l.sc, Fig. 24A).**

They, being bean-shaped, can be seen on the specimen (Fig. 24A) (8 mm high × 3 mm long). The concavity is forwardly directed. The reconstruction of the dorso- and ventrolateral scales in *Kujdanowiaspis podolica* (dl.lc, vl.lc, Fig. 16D) is based on what Goujet observed in *Sigaspis lepidophora* (Goujet 1973: fig. 3A).

#### *Endoskeletal pectoral girdle*

The endoskeletal pectoral girdle consists in an undivided and trifurcate scapulocoracoid, surrounded by the anterolateral, anterior ventrolateral, interolateral and spinal plates. The girdle can be divided into three parts: a coracoid and a prepectoral processes and an axillar area.

#### **Coracoid process (p.cor, Fig. 22A).**

It is visible as an impression on specimen GGI 15-634 (Fig. 22A), as well as the neurovascularization

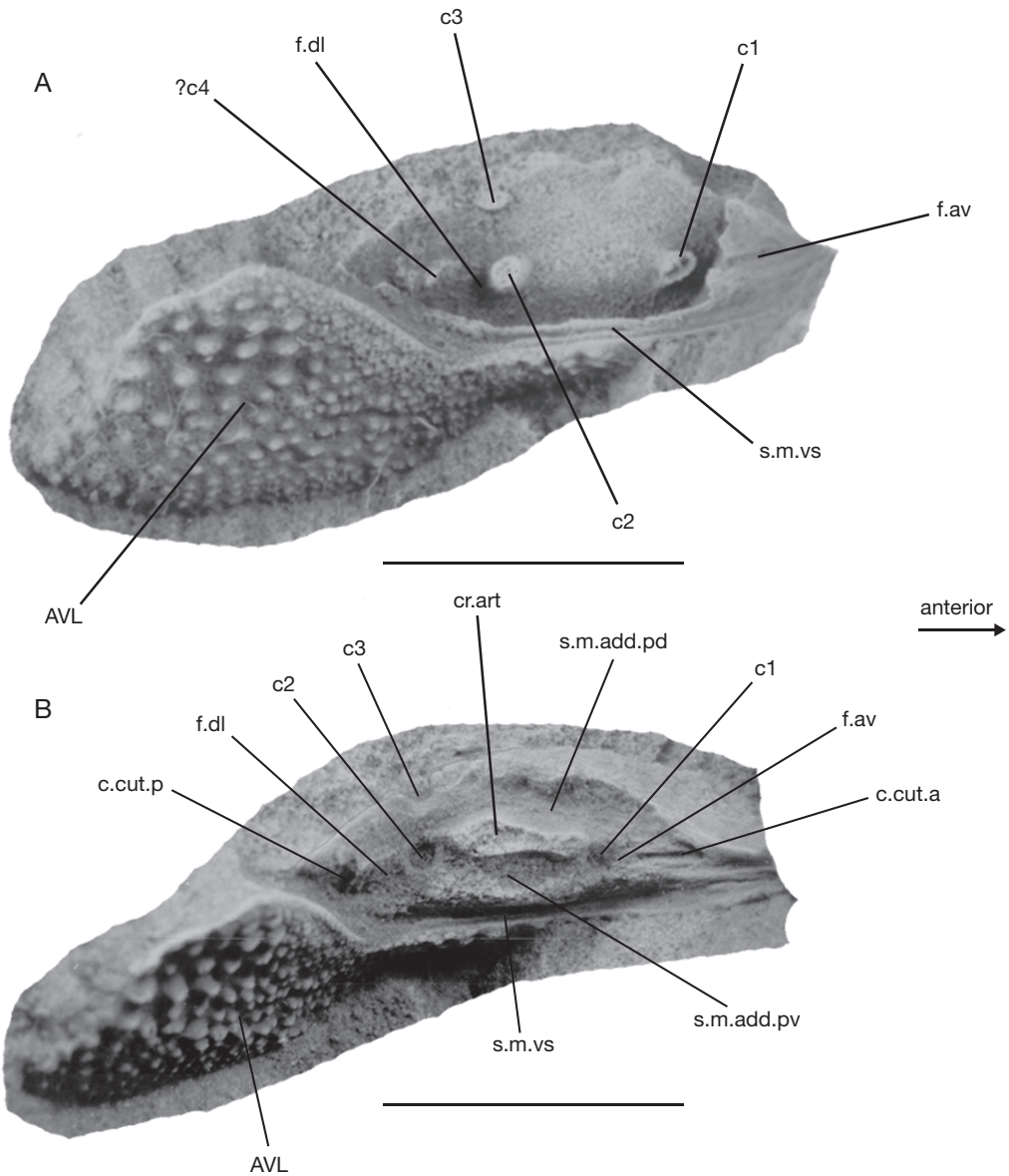


FIG. 25. — *Kujdanowiaspis podolica* (Brotzen, 1934), axillar area of the scapulocoracoid, NHM P 18226: **A**, internal view; **B**, external view. Abbreviations: see Appendix 2. Scale bars: 1 cm.

(both small foramina and short grooves) that occurred between the anterior ventrolateral and spinal plates. The process was located against the ventrolateral and ventral parts of the anterior ventrolateral plate.

**Prepectoral process (p.pr.pec, Fig. 22A, C).** It consisted in a cartilaginous filling of the hollow spinal plate (see GGI 15 634, RAS 2172/2). As the cartilage did not extend to the apex of the plate, the apex appears always rounder than the compacted rest of the plate.

**Axillary area (Fig. 25A, B).** It is visible on specimen NHM P 18226, already figured by Goujet (1984: fig. 71C, D, pl. 13, fig. 1). Two natural casts show respectively the internal side of the plastron (with the scapulocoracoid impression surrounded by the right interolateral plate), and both the internal and external structures of the axillary area (surrounded by the right anterior ventrolateral, anterolateral and spinal plates).

The relief is quite complex. The articular crest (cr.art, Fig. 25B) is not located on any larger base, as occurs in *Dicksonosteus arcticus* (Goujet 1984). It is 5 mm long. A shallow longitudinal depression indicates that the articular surface of this crest was not ossified perichondrally. This articular crest is slightly bilobate (the anterior part is larger than the posterior), like in *Dicksonosteus*. Hence Goujet (1984) believed that two basalia could attach this crest, as is the case in *Pseudopetalichthys* Moy-Thomas, 1939 (Gross 1962: figs 7, 8A; Stensiö 1969: fig. 246, p. 609), or maybe three as in selachians (Bendix-Almgreen 1975). In the latter case, the median basalia (mesopterygium) would have been reduced compared with anterior (anterior propterygial) and posterior (posterior mesopterygial) elements. On the contrary, a large cartilaginous disc attached on the biggest lobe of the crest and maybe a smallest element on its shortest part would be a better interpretation of this pattern (see Goujet 2001 and further).

Dorsally and ventrally to the crest, two longitudinal depressions can be seen, on which are attached the levator (s.m.add.pd, Fig. 25B) and depressor muscles of the pectoral fin (s.m.add.pv, Fig. 25B). It is noteworthy that in *Dicksonosteus*, these depressions are situated on the base of the articular crest. The pectoral fins unlikely had any important role in the locomotion of the fish; it is more likely that they had a stabilizing function, some supplementar “flying surface”, and/or were used as plane ailerons and flats in order to swim up and down in the water.

Four foramina are visible both on the external and internal sides.

The anterior foramen (c1) is located just posteriorly to the lengthened anterior pit (f.av), whereas in *Dicksonosteus* this pit is shorter and deeper, and

the c1 foramen is located in its middle. From this foramen runs a short anterolaterally directed canal (external view, Fig. 25B).

The medial foramen (c2) is located just behind the articular crest, and has the same size as c1. A short posteriorly and slightly dorsally directed canal runs from this foramen. This aperture (c2) is positioned below the opening of the c3 foramen. As is the case in *Dicksonosteus*, the medial foramen is located anteromedially in the posterior pit. This pit is divided into a dorsal and a ventral parts, demilited by a slight longitudinal crest (visible on the internal side).

The posterior foramen (c3) is situated above and behind the articular crest, in the dorsalmost part of the posterior pit. It is slightly smaller than the other two foramina (in the internal side of the axillary area of *Dicksonosteus*, c3 is the biggest foramen, on the external side it is about the same size as c1; Goujet 1984: figs 69, 70).

The excellent preservation of this specimen shows that, as assessed by Goujet (1984) observing *Dicksonosteus*, the first two foramina are endoskeletal, and the third one is rather a notch in the postero-dorsal edge of the endoskeleton than a real pore.

Anteriorly to the anterior foramen c1 is located the anterior pit, which is hollowed out by a shallow groove (probably a muscle insertion, c.cut.a, Fig. 25B).

The complex formed by the articular crest, the foramina and the anterior and posterior pits is surrounded by a very thin and shallow groove (dorsally s.m.ds, and ventrally s.m.vs, Fig. 25B). This groove corresponds to the junction between the dermal exoskeletal bone and the perichondral bone. Goujet (1984) thought that it may also have an attachment area for the superficial muscular undercutaneous muscles, disposed as a dorsal sheet.

The fourth foramen (?c4, Fig. 25A), without any identified homologous structure in *Dicksonosteus*, opens posteriorly to (and in the same plane as) the medial foramen (c2). The corresponding canal is posterodorsally directed. The foramen is not visible on the internal side; it would be located at the level of the posterior pit, according to Goujet (1984) (f.dl, Fig. 25).



A minor foramen opens in the distal angle of the anterior fossa (c.cut.a) on the internal side. Another opens in the distal angle of the posterior fossa, but its shape is blurred (c.cut.p, Fig. 25B). These structures can be seen at the same place in *Dicksonosteus*, and were interpreted by Goujet (1984); they would consist in canalicles of the anterior and posterior cutaneous nerves of the scapulocoracoid. The anterior canal should come from the same group as the vessels and nerves from foramen c1. A similar condition occurs in *Dicksonosteus*. The posterior canal, as in *Dicksonosteus*, should have been linked to the internal side of the armour via an oblique canal, and probably let the passage for some vessels and/or nerves coming from the abdominal area and going to the natatory lobe of the tegument (Goujet 1984).

As assessed by Goujet (1984), one can propose an analogy rather than a homology between these three main canals and the encountered disposition in extant fishes (selachians: *Squatina* Linnaeus, 1758, Marples 1936; actinopterygians: see Jessen 1972) and other placoderms illustrated by Stensiö (1944, 1959, 1969).

#### *Suprasynarcual: a new element of the vertebral column*

The elements of the vertebral column were cartilaginous and hence are very rare in the fossil record. One isolated specimen was found in the material. It is a new element called "suprasynarcual" (NHRM P 8479, Fig. 27). Indeed, it does not look like the synarcual of *Dicksonosteus arcticus* (Goujet 1984: fig. 73, p. 150) or of any other placoderm.

The suprasynarcual described herein is an unpaired medial chondrified element that was stuck against the internal side of the median dorsal plate of *Kujdanowiaspis* (the latter being very easy to recognize because of its curvature). So, the suprasynarcual is visible in its ventral side only. The dorsal side of the suprasynarcual likely moulded the visceral side of the median dorsal plate.

The suprasynarcual looks like a concave reversed water-drop. It shows an eroded medial crest (cr, Figs 27; 28), apart of which three pairs of foramina can be seen (the left most posterior one is slightly laterally displaced compared to the others). These were probably vascular foramina, rather than neural ones.

A reconstruction of the suprasynarcual in the armour is attempted as a hypothetical transversal cut in the anterior part of the thoracic armour (Fig. 28). This shows that the suprasynarcual is placed higher than the occipital condyles of the neurocranium. Possibly its ventral crest contacted the neural arch of the synarcual (an.syn, Fig. 28). So the foramina of the suprasynarcual were probably not neural structures, but rather nutritive foramina for the cartilage.

As the overlapping areas of the anterior dorsolateral plates are quite important, it is likely to consider that the lateral edges of the suprasynarcual contacted the mesiodorsal borders of these overlapping areas. This assemblage probably assessed a better cohesion of the thoracic armour, as it reinforced the anterior part of the vertebral column rigidity.

Goujet (1984) thinks that the synarcual of *Dicksonosteus arcticus* was attached to the anterior crest of the visceral side of the median dorsal plate (ra, Goujet 1984: fig. 59B, p. 130). These two elements were not fused, but more probably attached by ligaments and/or muscles. An anterior crest is also visible on the median dorsal plate of *Arctolepis decipiens* (Goujet 1984: pl. 19, fig. 6). It is unlikely that these two phlyctaeniids genera also possessed a suprasynarcual element. The presence of such an element in *Kujdanowiaspis podolica* would more likely be an answer to the height of the median dorsal plate.

The presence of this suprasynarcual element and its function in maintaining the vertebral column reminds the ventral keel of the brachythoracids. But the suprasynarcual of *Kujdanowiaspis* is chondrified, whereas the brachythoracid ventral keel is clearly ossified and consists in a true process of the median dorsal plate, not as an annex ossification. But if these two structures are homologous, it is possible that during evolution the suprasynarcual fused with the median dorsal plate in brachythoracids. Nevertheless, this hypothesis is still impossible to test.

#### *Ornamentation of Kujdanowiaspis podolica (Brotzen, 1934)*

Tubercles are generally coarser on the dorsal and lateral sides rather than the ventral side of the armour. This differentiation is maybe linked to a sub-benthic life of the fish. Nevertheless, no worn surface is visible.

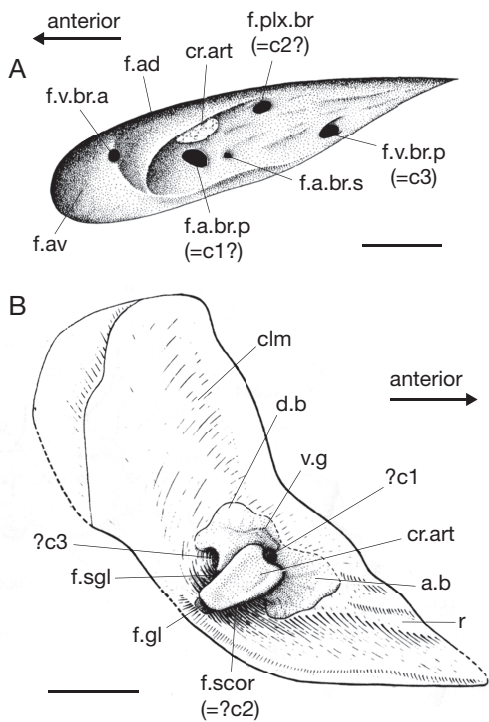


FIG. 26. — Scapular girdles of an osteostracan (A) and of a sarcopterygian (B) compared with the one of *Kujdanowiaspis podolica* (Brotzen, 1934): A, right scapular girdle of the osteostracan *Norselelaspis glacialis* Janvier, 1981 (slightly modified after Janvier 1985a: fig. 46); B, left scapular girdle of an osteolepid sarcopterygian (genus and species unknown, slightly modified after Janvier 1980: fig. 5A). Abbreviations: see Appendix 2. Scale bars: 1 cm.

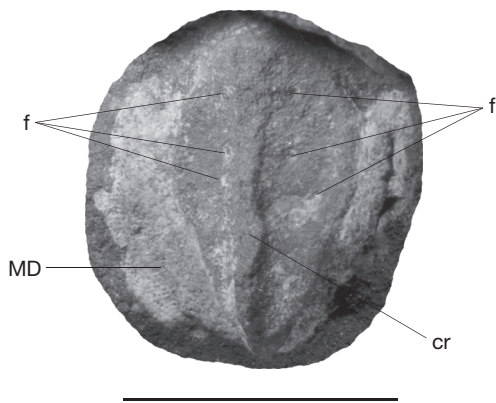


FIG. 27. — *Kujdanowiaspis podolica* (Brotzen, 1934), suprasynarcual element (internal side), NHRM P 8479. Abbreviations: see Appendix 2. Scale bar: 1 cm.

Tubercles are also finer beneath areas loosely covered by another (e.g., the submarginal over the postmarginal plate).

Another function of the ornamentation consists in a passive defence. The plates of the armour are generally robust. Moreover, the long spinal plates may play a dissuasive role, virtually increasing the volume of the animal (cf. Janvier 1985a: 225, discussion about the boreaspidid osteostracans). As well, the mesial denticles of the spinal and post median dorsal plates are as numerous spines.

The whole armour could also consist in a phosphat reserve for the muscular activity of the fish. This would imply that tubercles did not emerge from the superficial layers of the dermis.

## DISCUSSION

### COMPARISON WITH TWO OTHER EARLY VERTEBRATES: OSTEOSTRACI AND SARCOPTERYGII *Osteostraci*

Janvier (1985a: fig. 46) described the pectoral fin articulation of the osteostracan *Norselelaspis glacialis* Janvier, 1981. Using thin serial sections, he discovered on one specimen the presence of an articular crest, around which were three foramina that the present author considers as homologous to those of *Kujdanowiaspis podolica* and *Dicksonosteus arcticus*, and *a fortiori* of all “dolicho thoracid” arthrodires with a short pectoral girdle (Figs 25; 26A).

The foramen located beneath the anterior part of the articular crest in *Norselelaspis* (c1, Fig. 26A) was interpreted as the main brachial artera foramen (Janvier 1985a). It is here considered homologous of the anterior foramen (c1) of *Kujdanowiaspis podolica*.

The median foramen homologous (c2, Fig. 26A), corresponding to the brachial plexus foramen, is located in the longitudinal axis of the articular crest and very posteriorly to it.

The posterior foramen homologous (c3, Fig. 26A), corresponding to the main brachial vein foramen, is located posteroventrally to the latter.

Goujet (1984) based his interpretations on what can be observed on extant fishes and on Stensiö's

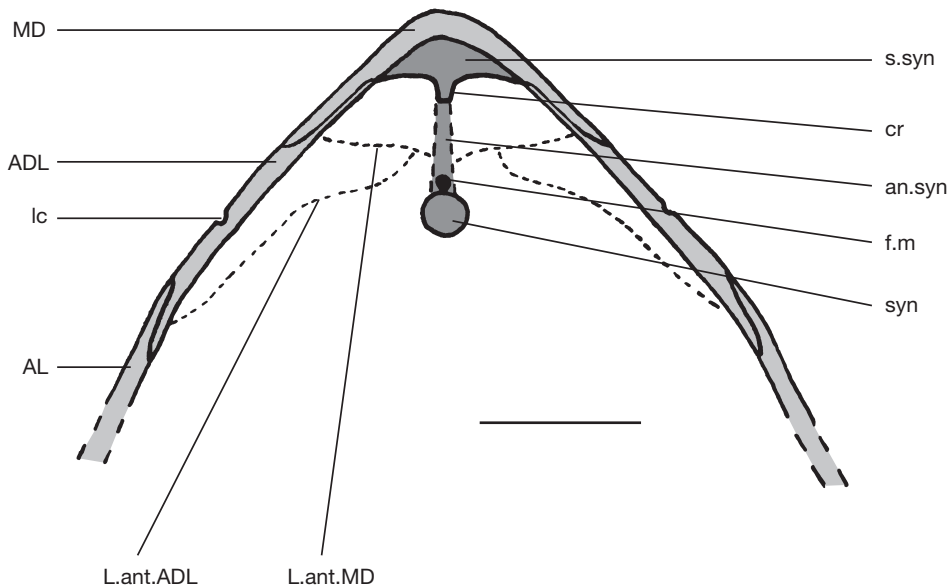


FIG. 28. — *Kujdanowiaspis podolica* (Brotzen, 1934), schematical section through the anterior part of the median dorsal plate; the dermal bones are in light grey; vertebral column elements in dark grey; projection in the figure plane of the anterior part of the armour in dashed lines. Abbreviations: see Appendix 2. Scale bar: 1 cm.

work (mainly concerning the acanthothoracid *Palaeacanthaspis vasta* Brotzen, 1934, see Stensiö 1944, 1959, 1969). Hence he determined the neurovascular canals in the pectoral girdle in *Kujdanowiaspis*: the anterior foramen (c1) for the main brachial artery and vein, the medium foramen (c2) for the metapterygial canal only, and the posterior foramen (c3) without any precise equivalent structure amongst other placoderms. Its position would indicate it led to the metapterygium, and then would lead a passage for the metapterygial vein, whose course would have been dissociated from the linked artery, as occurs in *Squatina* (Bertin 1958).

The posterior edge of the pectoral fenestra in *Dicksonosteus* would have obliged all the posterior pterygial nerves to follow the posterior canal (ends in c3). On the contrary, in *Kujdanowiaspis podolica*, the presence of a fourth foramen (c4, four times smaller than c2) would indicate a possible other course for the posterior pterygial nerves.

#### *Osteolepidida*

As for osteolepidid sarcopterygians, the same structures are identified: an “articular” crest,

surrounded by the main foramina (cf. Janvier 1980: fig. 5A, p. 237); nevertheless the proximal limb element inserted in a glenoid fossa (f.gl, Fig. 26B) and not against the crest. As above, a homology is proposed for these structures and those encountered in *Kujdanowiaspis* and *Dicksonosteus* (Fig. 26B).

#### THE EMBRYONIC DEVELOPMENT OF THE PECTORAL FIN IN THE EXTANT ACTINOPTERYGIAN *DANIO RERIO*

Goujet (2001) reviewed his hypothesis concerning the number of pterygial elements attached to the axillary area in “dolichotheoracids”, and suggested that one single flat element was attached to the articular crest. This turnover is notably due to the recent discoveries of the embryonic development on some teleost actinopterygians, mainly the zebra-fish *Danio rerio* (Hamilton, 1822) (Sordino *et al.* 1995; Duboule & Sordino 1996; Grandel & Schulte-Merker 1998).

The endoskeletal elements of the pectoral fin are derived from the same cells concentration as that that produces the scapulocoracoid. A chondri-

fied disc appears, articulating only on one point of the pectoral girdle in the first part of the ontogenic development of the fish fin (Grandel & Schulte-Merker 1998: fig. 7C). The adult radial elements of the pectoral girdle appear later during the development, by two apoptosis steps (corresponding to three apoptic zones) of some of the disc cells. It is nevertheless noteworthy that for the pelvic girdle, the radials appear as soon as the development of the fin begins.

Besides, in the actinopterygian *Clupea pilchardus* Walbaum, 1792 (see Goodrich 1958: fig. 178, p. 170), a chondrified disc is visible with three radial trenches, linked anteriorly to a small radial element.

These data challenge the polarity of the character “number of radials in the limb”: the monobasal fin has been considered as the derived condition according to Goodrich’s “fin-fold theory” (Goodrich 1909). Indeed, within placoderms, only brachythoracids were multibasal-finned. All of the other groups show a monobasal type (see Goujet 2001).

In a high number of chondrichthyans, the monobasal pattern is the most frequently encountered (Zangerl 1981: figs 33, 35): one single element (most often the metapterygial) articulates on the pectoral girdle. If more elements are present, they ride over the scapulocoracoid without connecting it directly.

Hence, within major gnathostomes groups, a “true” multibasal fin is encountered only in actinopterygians and brachythoracid placoderms. One would conclude that, contrary to what is implied by the “fin-fold” theory, the monobasal fin would be primitive and, the multibasal fin derived. This would have appeared independently in brachythoracid placoderms and actinopterygians.

This challenges the monophyly using sarcopterygian monobasal fin (Janvier 1996). Better definition of the character is highly desirable, since this monobasal articulation is also encountered in primitive gnathostomes and some “agnathans” (cf. *Norselaspis*). A difference noted above is that in the monobasal sarcopterygian fin, the humerus does not articulate on a crest but in a glenoid fossa.

#### GENERAL SHAPE AND HYDRODYNAMICS

The proposed reconstruction reveals the fish general profile is hydrodynamic (Fig. 16D).

The first body structure to penetrate the aqueous environment is the rostrum that would direct the water in four directions (dorsally, ventrally and laterally). Dorsally, the median dorsal crest could help to stabilize, acting as a small dorsal fin in sharks. Laterally, the spinal plates and the pectoral fins would have reinforced the stability.

The dorsal side of the spinal plate is longer anteroposteriorly (because rounder) than the ventral one. Hence, water would travel further dorsally than ventrally, but at the same speed, inducing an upward lift of the fish in the water. This hydrodynamic principle is the same than aerodynamic lift in the wings of birds and planes. This would have reduced the amount of energy required for swimming.

Nevertheless, despite its hydrodynamic shape, the enclosing armour meant reduced mobility. The pectoral fins muscles were probably too weak for propulsion. The fish used more likely its fins to stabilize and slightly direct in the water. The main locomotion motor remained the tail, quite large at its base, and hence probably muscular. But still, we can have no idea of the tail shape (i.e. simple whip, heterocercal or else). Other actinolepids and phyllolepid show a whip-tail, terminated by a ventral and a dorsal net (e.g., *Bollandaspis woschmidti* Schmidt, 1976; or, at a lesser degree, *Cowralepis mclachlani* Ritchie, 2005). Hence, the distal part of the tail propelled the fish.

#### CONCLUSION

The redescription of the arthrodiran material from the Lower Devonian of Podolia leads to conclusion of the occurrence of two genera: *Kujdanowiaspis* Stensiö, 1942 with the species *K. podolica* (Brotzen, 1934) and *K. buczacziensis* (Brotzen, 1934), and another genus (referred to “*Kujdanowiaspis*” *zychi* Stensiö, 1945). The abundance of the material of *K. podolica* allows an accurate description of the endocranium and the dermal armour. The characters pointed out by the light of this description

will be relevant as for a phylogenetic analysis of the actinolepids.

The pectoral fin was probably monobasal in *Kujdanowiaspis*. As this disposition is also encountered in other early vertebrates (osteostracan agnathans and non-tetrapod sarcopterygians), the exclusivity of the monobasal pectoral articulation for the sarcopterygians is challenged. Better than the deletion of this character from the sarcopterygian diagnosis, it is suggested a reevaluation or reformulation of this character.

### Acknowledgements

The author is grateful to Daniel Goujet (Ph.D. supervisor, MNHN), Philippe Janvier and Hervé Lelièvre (MNHN), Elga Mark-Kurik (Institute of Geology, Tallinn University of Technology, Estonia), Valentina Karatajūte-Talimaa (GGI), Gaël Clément (MNHN), Alain Blicek (Université des Sciences et Technologies de Lille 1, Villeneuve d'Ascq, France) and Hans-Peter Schultze (Natural History Museum, University of Kansas, USA) for their numerous advices and comments. Gavin Young (Australian National University, Canberra), Elga Mark-Kurik and Annemarie Ohler (MNHN) provided helpful reviews. Special thanks to Victor Voichyshyn and Daniel Drygant (National Academy of Sciences, Lviv, Ukraine) for their help in the field in Podolia and their welcome in Ukraine. V. Voichyshyn discovered, prepared and took photographs of specimen NASU 901/1. Other photographs are by Denis Serrette and Philippe Loubry (MNHN). Agathe Ravet (MNHN) drew the Figure 12.

### REFERENCES

- AFANASSIEVA O. B. 1989. — Novie tsephalaspidi (Agnatha) iz nizhnego devona Podolii [New Cephalaspids (Agnatha) from Lower Devonian of Podolia]. *Paleontologicheskij Journal* 3: 51-59 (in Russian).
- AFANASSIEVA O. B. 1990. — *Benneviaspis* (Agnatha) iz nizhnedevoevskikh otlozhenij Podolii [A new *Benneviaspis* (Agnatha) from the Lower Devonian of Podolia]. *Paleontologicheskij Journal* 4: 128-131 (in Russian).
- AFANASSIEVA O. B. 1991. — *Tsefalaspidy Sovetskogo Soyuza* (Agnatha) [*Cephalaspids of USSR*]. Nauka, Moskva, 144 p. (in Russian).
- ALTH A. 1874. — Über die paläozoischen Gebilde Podoliens und deren Vesteinerungen. *Abhandlungen der K. K. geologischen Reichsanstalt Österreich* 7, 80 p.
- ANONYMOUS 1900. — *Atlas geologiczny Galicyi. Tekst do zeszytu osmego* [Geological atlas of Galicia. Text of book eight]. Widaw, Komisji fizyograficznej Akademii Umiejetnosci, Krakow, 330 p. (in Polish).
- BALABAĬ P. P. 1957. — K voprosu o vertikal'nom rasprostraneniĭ pteraspid podolskogo oldreda [On the question of vertical distribution of the pteraspids in the Old Red deposits of the Podolia]. *Geologicheskij sbornik* 4: 305-309 (in Russian).
- BALABAĬ P. P. 1959. — Do vivchennya pteraspid nizhnogo devonu Podillya. Povidomlenya 1 [On the known pteraspids of the Lower Devonian of Podolia. Part 1]. *Naukovi Zapisky Naukovo Prirodoznavchogo muzeyu AN URSSR* 7: 3-21 (in Ukrainian).
- BALABAĬ P. P. 1960. — Do vivchennya pteraspid nizhnogo devonu Podillya. Povidomlenya 2 [On the known pteraspids of the Lower Devonian of Podolia. Part 2]. *Naukovi Zapisky Naukovo Prirodoznavchogo muzeyu AN URSSR* 8: 124-133 (in Ukrainian).
- BALABAĬ P. P. 1961a. — Geterostraki verkhнього siluru Podillya [Heterostracans of the Upper Silurian of Podolia]. *Naukovi Zapisky Naukovo Prirodoznavchogo muzeyu AN URSSR*: 3-11 (in Ukrainian).
- BALABAĬ P. P. 1961b. — Do pitaniya pro mezhu mizh silurom i devonom na Podilli [About the nutrition distinction between the Silurian and Devonian in Podolia]. *Dopovidi Akademii nauk Ukrainkoi RSR*: 1212-1214 (in Ukrainian).
- BALABAĬ P. P. 1962. — Do fauni tsefalaspid Podilskoi pliti [On the fauna of Cephalaspids of the Podolian slab]. *Naukovi Zapisky Naukovo Prirodoznavchogo muzeyu AN URSSR* 10: 3-8 (in Ukrainian).
- BALABAĬ P. P. & OPALATENKO L. K. 1957. — Pro faunu verhiv old-redu Podilskoi pliti [On the fauna of the top of the slab of Podolia]. *Doklady Akademii Nauk Ukraine RSR* 4: 406-409 (in Ukrainian).
- BELLES-ISLES M. & JANVIER P. 1984. — Nouveaux Ostéostracés du Dévonien Inférieur de Podolie (RSS d'Ukraine). *Acta Palaeontologica Polonica* 29: 195-208.
- BENDIX-ALMGREEN S. E. 1975. — The paired fins and shoulder girdle in *Cladoselache*, their morphology and phyletic significance, in LEHMAN J.-P. (ed.), *Problèmes actuels de Paléontologie – Évolution des Vertébrés. Colloques internationaux du Centre national de la Recherche scientifique*, Paris: 113-123.
- BERTIN L. 1958. — Appareil circulatoire, in GRASSÉ P. P. (ed.), *Traité de Zoologie*. Masson, Paris: 1399-1458.
- BLIECK A. 1984. — Les Hétérostracés Pteraspidoformes (système phylogénique-biostratigraphie-biogéographie). *Cahiers de Paléontologie (section vertébrés)*, Paris, 199 p.
- BLIECK A. & JANVIER P. 1999. — Silurian-Devonian vertebrate dominated communities, with particular

- reference to agnathans, in BOUCOT A. J. & LAWSON J. D. (eds), *Paleocommunities: a Case Study from the Silurian and Lower Devonian*. Cambridge University Press, Cambridge: 79-105.
- BROTZEN F. 1933a. — Die silurischen und devonischen Fischvorkommen in Westpodolien I. *Palaeobiologica* 5: 423-466.
- BROTZEN F. 1933b. — *Weigeltaspis* nov. gen. und die Phylogenie der panzertragenden Heterostraci. *Zentralblatt für Mineralogie, Geologie und Paleontologie* B: 648-656.
- BROTZEN F. 1934. — Die silurischen und devonischen Fischvorkommen in Westpodolien II. *Paleobiologica* 6: 111-131.
- BROTZEN F. 1936. — Beiträge zur Vertebratenfauna des Westpodolischen Silurs und Devons. I. *Protaspis arnelli* n. sp., und *Brachipteraspis* n. gen. *latissima* Zych. *K. Svenska Vetenskapsakad. Arkiv för zoologi* 28A: 1-52.
- BROVKOV G. N. 1952. — *Litologiya i paleogeografiya nijnedevonskikh otlojenii Pridnestrovya (Kand. Dissertatsiya) [Lithology and palaeogeography of Cis-Dnister Lower Devonian sediments]*. Kharkovskii GU thesis/dissertation (in Russian).
- BROVKOV G. N. 1954. — Ob usloviyakh nakopleniya krasnotsvetnoj tolshchi nijnego devona Pmridnestrovya [Conditions of formation of the Red Layers]. *Doklady A. N. SSSR, nov. ser.* XCIV: 121-124 (in Russian).
- BRYANT W. L. 1934. — The fish fauna of Beartooth Butte, Wyoming. Parts II and III. *Proceedings of the American Philosophical Society* 73: 127-162.
- DENISON R. H. 1958. — Early Devonian Fishes from Utah – Part. III. Arthrodira. *Fieldiana: Geology* 11: 461-551.
- DENISON R. H. 1978. — Placodermi, in SCHULTZE H.-P. (ed.), *Handbook of Paleichthyology* 2. Gustav Fischer Verlag, Stuttgart; New York, 128 p.
- DENNIS-BRYAN K. 1995. — Some comments on the placoderm parasphenoid. *Bulletin du Muséum national d'Histoire naturelle de Paris*, 4<sup>e</sup> série, sect. C 17 (1-4): 127-142.
- DINELEY D. L. & LIU Y.-H. 1984. — A new actinolepid arthrodire from the Lower Devonian of Arctic Canada. *Palaeontology* 27: 875-888.
- DUBOULE D. & SORDINO P. 1996. — Des nageoires aux membres: l'apport de la génétique moléculaire du développement dans l'étude de l'évolution des morphologies chez les vertébrés. *Médecine/Science* 12: 147-154.
- DUPRET V. 2003. — *Étude anatomique des genres Kujdanowiaspis Stensiö 1942 et Erikaspis nov. gen. (Placodermi Arthrodira « Actinolepida ») du Dévonien inférieur de Podolie (Ukraine)*. Nouvelle proposition de la phylogénie des Arthrodira. Ph.D. thesis. Département Histoire de la Terre, Muséum national d'Histoire naturelle, Paris, France, 403 p.
- DUPRET V. 2004. — The phylogenetic relationships between actinolepids (Placodermi: Arthrodira) and other arthrodirés (phlyctaeniids and brachythoracids). *Fossils and Strata* 50: 40-55.
- DUPRET V. & BLIECK A. 2009. — The Lochkovian-Pragian boundary in Podolia (Lower Devonian, Ukraine) based upon placoderm vertebrates. *Comptes Rendus Geoscience (Paris)* 341: 63-70.
- DUPRET V., GOUJET D. & MARK-KURIK E. 2007. — A new genus of placoderm (Arthrodira: "Actinolepida") from the Lower Devonian of Podolia (Ukraine). *Journal of Vertebrate Paleontology* 27: 266-284.
- GOODRICH E. S. 1909. — Vertebrata Craniata I – Cyclostomes and Fishes, in LANKESTER E. R. (ed.), *Treatise on Zoology*, Volume 9. Black, London, 518 p.
- GOODRICH E. S. 1958. — *Studies on the Structure and Development of Vertebrates*. Chapter 4. *Limb Girdles*, Volume 1. Dover Publication, New York: 163-212.
- GOUJET D. 1973. — *Sigaspis*, un nouvel arthrodire du Dévonien inférieur du Spitzberg – *Sigaspis*, a new arthrodire from the lower Devonian of Spitzbergen. *Palaeontographica* 143: 73-88.
- GOUJET D. 1984. — Les poissons placodermes du Spitzberg – Arthrodirés Dolichothoraci de la formation de Wood Bay (Dévonien inférieur), *Cahiers de Paléontologie (section vertébrés)*, CNRS, Paris, 284 p.
- GOUJET D. 2001. — Placodermes and basal gnathostome apomorphies, in AHLBERG P. E. (ed.), *Major Events in Early Vertebrate Evolution – Palaeontology, Phylogeny, Genetics and Development*. Taylor & Francis, London: 209-222.
- GOUJET D. & BLIECK A. 1978. — Les Vertébrés de l'Assise des Schistes et Grès de Pernes (Dévonien du Nord de la France). *Annales de la Société géologique du Nord* 98: 263-278.
- GRANDEL H. & SCHULTE-MERKER S. 1998. — The development of paired fins in the Zebrafish (*Danio rerio*). *Mechanisms of Development* 79: 99-120.
- GROSS W. 1940. — Acanthodier und Placodermen aus den *Heterostius*-Schichten Estlands und Lettlands. *Annales Societatis Rebus Naturae Investigandis in Universitate Tartuensi constitutae* 46: 12-99.
- GROSS W. 1962. — Neuuntersuchung des Stensioellida (Arthrodira, Unterdevon). *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden* 90: 48-97.
- HEINTZ A. 1929a. — Die downntonischen und devonischen Vertebraten von Spitzbergen III. Acanthaspida (Nachtrag). *Skrifeter om Svalbard og Ishavet* 23: 1-12.
- HEINTZ A. 1929b. — Die downntonischen und devonischen Vertebraten von Spitzbergen II. Acanthaspida. *Skrifeter om Svalbard og Ishavet* 22: 1-81.
- HEINTZ A. 1933. — Some remarks about the structure of *Phlyctaenaspis acadica* Whiteaves. *Norsk Geologisk Tidsskrift* 14: 127-144.
- JANVIER P. 1980. — Osteolepids remains from the De-

- vonian of the Middle East, with particular reference to the endoskeletal shoulder girdle, in PANCHEN A. L. (ed.), *The Terrestrial Environment and the Origin of Land Vertebrates*. Academic Press, London, New York: 223-254.
- JANVIER P. 1985a. — Les Céphalaspides du Spitzberg. *Cahiers de Paléontologie (section vertébrés)*, CNRS, Paris, 244 p.
- JANVIER P. 1985b. — Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian S.S.R.). *Bulletin of the British Museum (Natural History)* 38: 309-334.
- JANVIER P. 1988. — Un nouveau céphalaspide (Osteostraci) du Dévonien inférieur de Podolie (R.S.S. d'Ukraine). *Acta Palaeontologica Polonica* 33: 353-358 (in French with Polish summary).
- JANVIER P. 1996. — *Early Vertebrates*. Oxford Monographs on Geology and Geophysics 33. Clarendon Press, Oxford, xiii + 393 p.
- JESSEN H. 1972. — Schültörgürtel und Pectoralflosse bei Actinopterygien. *Fossils and Strata* 1: 1-101.
- JOHNSON H. G., ELLIOT D. K. & WITTKE J. H. 2000. — A new actinolepid arthrodire (Class Placodermi) from the Lower Devonian Sevy Dolomite, East-Central Nevada. *Zoological Journal of the Linnean Society* 129: 241-266.
- KARATAJŪTE-TALIMAA V. N. 1968. — Novie telodonty, geterostraki i artrodირი iz chortkovskogo gorizonta Podolii. *Ocherki po filogenii i sistematike iskopaemykh ryb i beschelyustnykh*. [New telodonts, heterostracans and arthrodires in the Chortkov Horizon of Podolia]. *Nauka* 1: 33-42 (in Russian).
- KARATAJŪTE-TALIMAA V. N. 1978. — *Telodonty silura i devona SSSR i Shpitsbergena* [Silurian and Devonian telodonts of USSR and Spitsbergen]. Mokslas, Vilnius: 334 p. (in Russian).
- LELIÈVRE H., GOUJET D. & HENN A. 1990. — Un nouveau spécimen d'*Holonema radiatum* (Placodermi, Arthrodira) du Dévonien moyen de la région d'Oviedo, Espagne. *Bulletin du Muséum national d'Histoire naturelle de Paris*, 4<sup>e</sup> série, sect. C 12: 53-83.
- LONG J. A. 1984. — New phyllolepid from the Victoria and the relationships of the group. *Proceedings of the Linnean Society of New South Wales* 107: 263-308.
- LONG J. A. 1997. — Ptyctodontid fishes (Vertebrata, Placodermi) from the late Devonian Gogo Formation, Western Australia, with a revision of the European genus *Ctenurella* Ørvig, 1960. *Geodiversitas* 19 (3): 515-555.
- MARPLES M. J. 1936. — The blood vascular system of the Elasmobranch fish *Squatina squatina*. *Transactions of the Royal Society of Edinburgh* 58: 817-840.
- MILES R. S. 1965. — Ventral thoracic neuromast lines of placoderm fishes. *Nature* 206: 524-525.
- MILES R. S. 1973. — An actinolepid arthrodire from the Lower Devonian Peel Sound Formation, Prince of Wales Island. *Palaeontographica A* 143: 109-118.
- MOY-THOMAS J. A. & MILES R. S. 1971. — *Paleozoic Fishes*. Second ed. Chapman & Hall, London, 259 p.
- NARBUTAS V. V. 1984. — *Krasnotsvietnaya formatsiya nijnego devona Pribaltiki i Podolii* [Lower Devonian redbeds of the Baltic area and Podolia], Mokslas, Vilnius, 136 p. (in Russian).
- NEWBERRY J. S. 1889. — The Paleozoic fishes of North America. *U.S. Geological Survey Monograph* 16: 1-340.
- NOVITSKAYA L. I. 1986. — Drevneishie beschelyustnye SSSR. Geterostraki: tsiataspidy, amphiaspidy, pteraspidy [The most ancient agnathans of USSR. Heterostraci: cyathaspids amphiaspids, pteraspids]. *Akademya Nauk SSSR, Trudy Paleontologicheskogo Instituta* 219, 160 p.
- ØRVIG T. 1975. — Description, with special reference to the dermal skeleton, of a new radotinid arthrodire from the Gedinnian of Arctic Canada. *Extrait des Colloques internationaux du Centre national de la Recherche scientifique – Problèmes actuels de Paléontologie – évolution des Vertébrés* 218: 41-71.
- PAUCA M. 1941. — Poissons paléozoïques de la rive bucovinienne du Dniestr. *Comptes rendus de l'Institut de Géologie de Roumanie* 26: 14-31.
- SIEMIRADZKI J. 1906. — Die paläozoischen Gebilde Podoliens II. *Beiträge Paläont. Geol. Österreich-Ungarns und des Orients* 19: 213-286.
- SORDINO P., HOEVEN P. V. D. & DUBOULE D. 1995. — Hox gene expression in teleost fins and origin of vertebrate digits. *Nature* 375: 678-681.
- STENSIÖ E. 1925. — On the head of the macropetalichthyids with certain remarks on the head of the other Arthrodires. *Field Museum of Natural History Publications (geological series)* 4: 87-197.
- STENSIÖ E. 1934. — On the heads of certain Arthrodires. *Kungliga Svenska Vetenskapsakademiens Handlingar*, ser. 3, 13: 1-79.
- STENSIÖ E. 1942. — On the snout of Arthrodires. *Kungliga Svenska VetenskapsAkademiens Handlingar* 20: 1-32.
- STENSIÖ E. 1944. — Contributions to the knowledge of the vertebrate fauna of the Silurian and Devonian of Podolia II – Note on two Arthrodires from the Downtonian of Podolia. *Arkiv för Zoologi* 35: 1-83.
- STENSIÖ E. 1945. — On the heads of certain arthrodires. II. On the cranium and cervical joint of the Dolichothoracids (Acanthaspida). *Kungliga Svenska VetenskapsAkademiens Handlingar* 22: 1-70.
- STENSIÖ E. 1959. — On the pectoral fin and shoulder girdle of the Arthrodires. *Kungliga Svenska VetenskapsAkademiens Handlingar*, ser. 4, 8: 1-229.
- STENSIÖ E. 1963. — Anatomical studies on the arthrodiran head. Part 1. Preface, geological and geographical distribution, the organisation of the arthrodires, the

- anatomy of the head in the Dolichothoraci, Cocco-steomorphi and Pachyosteomorphi. Taxonomic appendix. *Kungliga Svenska VetenskapsAkademiens Handlingar*, ser. 4, 9: 1-419.
- STENSIÖ E. 1969. — Arthrodires, in PIVETEAU J. (ed.), *Traité de Paléontologie*. Masson, Paris: 71-693.
- STENSIÖ E. 1971. — Anatomie des arthrodires dans leur cadre systématique. *Annales de Paléontologie (Vertébrés)* 57: 1-39.
- TARLO L. B. 1965. — Psammosteiformes (*Agnatha*). A review with description of new material from the Lower Devonian of Poland. II. Systematic part. *Palaeontologica Polonica* 15,168 p.
- TRAQUAIR R. H. 1890a. — Notes on the Devonian fishes of Scaumenac Bay and Campbelltown in Canada. *The Geological Magazine*, New Series, decade III 7: 15-22.
- TRAQUAIR R. H. 1890b. — On *Phlyctaenius*, a new genus of Coccosteidae. *The Geological Magazine*, New Series, decade III 7: 55-60.
- TRAQUAIR R. H. 1894. — Notes on Palaeozoic Fishes. I. *Annales and Magazine of Natural History*, série 6 14: 368-374.
- VOICHYSHYN V. K. 1994. — Novij predstavnik rodu *Mimetaspis* (*Agnatha*) z nizhnogo devonu Podillya [New species of the genus *Mimetaspis* (*Agnatha*) from the Lower Devonian of Podolia]. *Paleontologichnii Zbirnik* 30: 19-24 (in Ukrainian).
- VOICHYSHYN V. K. 1998. — Novij predstavnik rodu *Zychaspis* (*Agnatha*) z Dnistrovskoi Serii (rannij devon) Podillya [A new specimen of the genus *Zychaspis* (*Agnatha*) from the Dnister Series (Lower Devonian)]. *Paleontologichnii Zbirnik* 32: 25-29 (in Ukrainian).
- VOICHYSHYN V. K. 1999. — The new forms of pteraspids (*Agnatha*, Heterostraci) from Podolian Early Devonian. *Vestnik zoologii* 33: 47-56.
- VOICHYSHYN V. K. 2001. — Mistseznakhodjennya ikhtiofauni rannogo devonu na Podilli [Ichthyofaunas localities of the Early Devonian of Podolia]. *Paleontologichnii Zbirnik* 33: 134-143 (in Ukrainian).
- WALBAUM J. J. 1792. — Petri Artedi sueci genera in quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Redactis speciebus 242 ad genera 52. *Ichthyologiae, pars iii. Ant. Ferdin. Rose, Grypeswaldiae. Artedi Piscium*: 1-723.
- WHITE E. I. 1961. — The Old Red Sandstone of Brown Cleve Hill and the adjacent area. *Bulletin of the British Museum (Natural History)* 5: 243-310.
- WHITE E. I. 1969. — The deepest vertebrate fossil and other arctolepid fishes. *Biological Journal of the Linnean Society* 1: 293-310.
- Whiteaves J. F. 1881. — On some fossil fishes, crustacea, and mollusca from the Devonian rocks at Campbellton, N. B., with description of five new species. *Canadian Naturalist* 2: 93-101.
- WOODWARD A. S. 1892. — On the Lower Devonian Fish-Fauna of Campbellton, New Brunswick. *Geological Magazine* 9: 233-235.
- YOUNG G. C. 1979. — New information on the structure and relationships of *Buchanosteus* (Placodermi: Euarthrodira) from the Early Devonian of New South Wales. *Zoological Journal of the Linnean Society* 66: 309-352.
- YOUNG G. C. 1981. — New Early Devonian Brachythoracids (placoderm fishes) from the Taemas-Wee Jasper region of New South Wales. *Alcheringa* 5: 245-271.
- ZANGERL R. 1981. — Chondrichthyes 1 - Paleozoic Elasmobranchii, in SCHULTZE H.-P. (ed.), *Handbook of Palaeoichthyology*. Gustav Fischer Verlag, Stuttgart; New-York: 1-115.
- ZIEGLER P. A. 1982. — *Geological Atlas of Western and Central Europe*. Shell Internationale Petroleum Maatschappij B. V., 130 p.
- ZYCH W. 1927. — Old-Red Podolski. *Prace Polskiego Instytutu. Geologicznego* 2: 1-65.
- ZYCH W. 1931. — *Fauna ryb dewonu i downtonu Podola. Pteraspidomorphi: Heterostraci* [Faunas of the Devonian and Downtonian of Podolia], Volume 1. Czesc, Lviv, 92 p (in Polish).
- ZYCH W. 1937. — *Cephalaspis kozlowskii* n. sp. from the Downtonian of Podole (Poland). *Archiwum Towarzystwa Naukowego we Lwowie* 9: 46-96.

Submitted on 15 September 2005;  
accepted on 28 November 2008.



APPENDIX 1: list of the material examined of *Kujdanowiaspis* Stensiö, 1942. Abbreviations: see Appendix 2.

Number	Collection	Material location	Species	Identification	Locality
GIG 15-559	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull, endocranium	Ustechko
GIG 15-610	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	uncomplete skull roof	Gorodnytsya
GIG 15-611	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	uncomplete skull roof	Gorodnytsya
GIG 15-612	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right MD, ADL, PDL	Gorodnytsya
GIG 15-614	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right AVL, IL, AV, Sp	Chervonograd
GIG 15-615	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right MD, ADL	Gorodnytsya
GIG 15-616	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	left MD, ADL	Chervonograd
GIG 15-617	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right MD, ADL, PDL, AL	Ustechko
GIG 15-618	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull roof (internal side)	Gorodnytsya
GIG 15-619	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	left AVL, AV, IL, Sp	Gorodnytsya
GIG 15-620	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	MD and ADL	Khmeleva
GIG 15-621	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull roof	Chervonograd
GIG 15-622	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right MD, PDL ADL	Ivanye
GIG 15-623	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right MD, ADL	Ivanye
GIG 15-624	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right PVL	Ustechko
GIG 15-625	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right PVL	Ustechko
GIG 15-626	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	PMD	Ustechko
GIG 15-627	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	PMD	Ivanye
GIG 15-628	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	PMD	Ustechko
GIG 15-629	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull roof	Ivanye
GIG 15-630	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	MD, ADL, PDL (internal side)	Ustechko
GIG 15-631	Talimaa	Vilnius, Lithuania	<i>K. bucza- ziensis?</i>	uncomplete skull roof	Buchach
GIG 15-632	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	PMD	Ustechko
GIG 15-633	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right MD, ADL	Ivanye
GIG 15-634	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right AVL, AV, IL, Sp (internal side)	Chervonograd
GIG 15-635	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	MD	Ivanye
GIG 15-637	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	left AVL	Ustechko
GIG 15-638	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right Sp	Ustechko
GIG 15-639	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right AL (internal side)	Gorodnytsya
GIG 15-640	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	left AVL, IL, Sp	Ivanye
GIG 15-641	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	MD	Ustechko
GIG 15-644	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull roof (internal side)	Ivanye
GIG 15-645	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull roof and endocranium	Ivanye
GIG 15-646	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull roof	Ustechko
GIG 15-647	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	left MD, ADL, PDL	Ivanye
GIG 15-649	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	PMD	Ustechko
GIG 15-650	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	PMD	Chervonograd
GIG 15-651	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	AVL, Sp, AV, IL	Khmeleva
GIG 15-652	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	endocranium	Ustechko
GIG 15-653	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	uncomplete skull roof	Ustechko
GIG 15-654	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right AL (internal side)	Ivanye
GIG 15-655	Talimaa	Vilnius, Lithuania	<i>K. sp.</i>	skull roof	Buryakivka
GIG 15-656	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right AVL, AV, IL, Sp	Ustechko
GIG 15-657	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	left AVL, AV, IL, Sp (internal side)	Ustechko
GIG 15-658	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull endocranium	Ustechko
GIG 15-661	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull roof, endocranium	Ustechko
GIG 15-662	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	skull roof	Buryakivka
GIG 15-663	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	left ADL	Ustechko
GIG 15-664	Talimaa	Vilnius, Lithuania	<i>K. bucza- ziensis</i>	AVL, Sp	Perevoloka
GIG 15-665	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right PaN	Ivanye
GIG 15-666	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	PMD	Ivanye

Number	Collection	Material location	Species	Identification	Locality
GIG 15-667	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	MD	Ivanye
GIG 4 514	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	MD, ADL, PDL	Ivanye
GIG 5 550	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	sull roof and endocranium	Ivanye
GIG 550	Talimaa	Vilnius, Lithuania	<i>K. podolica</i>	right MD, ADL	Ivanye
MB 282	Brotzen	Berlin, Germany	<i>K. podolica</i>	left AL (Lectotype)	Ivanye
MB 283	Brotzen	Berlin, Germany	cf. <i>K. podolica</i>	AVL, SP	Ustechko
MB 284		Berlin, Germany	<i>K. podolica</i>	skull roof	Ivanye
MB 290 a-b	Brotzen	Berlin, Germany	<i>K. buczaczensis</i>	MD (Lectotype)	Buchach
MB 295	Brotzen	Berlin, Germany	<i>K. podolica</i>	AVL, Sp	Ustechko
MB 296		Berlin, Germany	<i>K. podolica</i>	left AVL, Sp	Ustechko
MB 311	Brotzen	Berlin, Germany	<i>K. podolica</i>	AVL, PVL, IL right	Ustechko
MB 87 a	Brotzen	Berlin, Germany	<i>K. sp.</i>	AVL, IL, AV, Sp	Rabrovec
MB 88 a	Brotzen	Berlin, Germany	<i>K. sp.</i>	left AVL, Sp, AV, IL	Unizh
NASU 25567a		Lviv, Ukraine	<i>K. podolica</i>	Sp, PMV, AVL, PVL, PMD, PMV	Ustechko
NASU 25567b		Lviv, Ukraine	<i>K. podolica</i>	skull roof	Ustechko
NASU 25567c		Lviv, Ukraine	<i>K. podolica</i>	MD, PMD	Ustechko
NASU 28555		Lviv, Ukraine	<i>K. podolica</i>	left MD, ADL	Ivanye
NASU 28568		Lviv, Ukraine	<i>K. podolica</i>	MD, 2 ADL, 2PDL	Gorodnytsya
NASU 28570	Balabai	Lviv, Ukraine	<i>K. podolica</i>	skull roof	Buchach
NASU BP 901/1		Lviv, Ukraine	<i>K. podolica</i>	complete skull roof (+ rostrum Pi, Ro, PtN, + cheek : SO, PSO, SM)	Nagiryani
NHM P 18140		London, UK	<i>K. podolica</i>	AVL, Sp, IL, AMV, PMV, PVL, scales	Khmeleva
NHM P 18226	Zych	London, UK	<i>K. sp.</i>	AVL, axillar area	Potochyshe
NHM P 18228		London, UK	<i>K. podolica</i>	skull roof	Potochyshe
NHM P 18241		London, UK	<i>K. podolica</i>	right AL	Bily Potik
NHM P 18277	Zych	London, UK	<i>K. podolica</i>	skull roof	Ustechko
NHM P 18349	Zych	London, UK	<i>K. podolica</i>	MD, ADL, PDL	Ustechko
NHM P 20542a		London, UK	<i>K. sp.</i>	endocranium (ventral side) and Psp	Ustechko?
NHM P 20542b	Zych	London, UK	<i>K. podolica</i>	AVL, Sp, axillar area	Ustechko
NHM P 20574		London, UK	<i>K. podolica</i>	left AVL and Sp, right PVL	Gorodnytsya
NHM P 20591		London, UK	<i>K. podolica</i>	left AL	Gorodnytsya
NHM P 20610		London, UK	<i>K. podolica</i>	skull roof	Ustechko
NHM P 20616		London, UK	<i>K. podolica</i>	MD, ADL	Gorodnytsya
NHM P 20624		London, UK	<i>K. podolica</i>	skull roof	Gorodnytsya
NHM P 20627		London, UK	<i>K. podolica</i>	right MD, PDL	Gorodnytsya
NHM P 20635		London, UK	<i>K. podolica</i>	left AL	Gorodnytsya
NHM P 20636		London, UK	<i>K. podolica</i>	right AL	Gorodnytsya
NHM P 20637		London, UK	<i>K. podolica</i>	MD	Gorodnytsya
NHM P 20773		London, UK	<i>K. podolica</i>	skull roof	Ustechko
NHM P 29222		London, UK	<i>K. podolica</i>	PMD	Khmeleva
NHM P 29253		London, UK	<i>K. podolica</i>	skull roof	Khmeleva
NHM P 29339		London, UK	<i>K. sp.</i>	AVL	Ostrivchik
NHM P 34852		London, UK	<i>K. podolica</i>	right AVL, Sp, IL, AV	Gorodnytsya
NHM P 53311		London, UK	<i>K. podolica</i>	left ADL	Khmeleva
NHRM P 8416		Stockholm, Sweden	<i>K. podolica</i>	MD	Repintsy
NHRM P 8417	Zych	Stockholm, Sweden	<i>K. podolica</i>	MD	Bily Potik
NHRM P 8418	Brotzen	Stockholm, Sweden	<i>K. podolica</i>	MD ?	Gorodnytsya
NHRM P 8419		Stockholm, Sweden	<i>K. podolica</i>	right MD, ADL, PDL	Buryakivka
NHRM P 8420		Stockholm, Sweden	<i>K. podolica</i>	skull roof	Ustechko
NHRM P 8421		Stockholm, Sweden	<i>K. podolica</i>	skull roof	Ustechko
NHRM P 8422	Zych	Stockholm, Sweden	<i>K. podolica</i>	AL	Khmeleva
NHRM P 8424	Zych	Stockholm, Sweden	<i>K. podolica?</i>	AL	Ustechko

Number	Collection	Material location	Species	Identification	Locality
NHRM P 8425	Zych	Stockholm, Sweden	<i>K. podolica</i>	MD	Buryakivka
NHRM P 8426		Stockholm, Sweden	<i>K. podolica</i>	Nu	Ustechko
NHRM P 8430		Stockholm, Sweden	<i>K. podolica</i>	PMD	Buchach
NHRM P 8431		Stockholm, Sweden	<i>K. podolica</i>	uncomplete skull roof	Ustechko
NHRM P 8432	Zych	Stockholm, Sweden	<i>K. podolica</i>	ADL	Khmeleva
NHRM P 8433	Zych	Stockholm, Sweden	<i>K. podolica</i>	MD	Ustechko
NHRM P 8434		Stockholm, Sweden	<i>K. podolica</i>	left AVL, AV, IL, Sp	Ivanye
NHRM P 8435	Brotzen	Stockholm, Sweden	<i>K. podolica</i>	MD, ADL	Ustechko
NHRM P 8436	Zych	Stockholm, Sweden	<i>K. podolica</i>	skull roof	Gorodnytsya
NHRM P 8437	Zych	Stockholm, Sweden	<i>K. podolica</i>	uncomplete skull roof	Gorodnytsya
NHRM P 8438	Zych	Stockholm, Sweden	<i>K. podolica</i>	MD, ADL, PDL	Ustechko
NHRM P 8439		Stockholm, Sweden	<i>K. sp.</i>	AVL, AV, Sp, IL	Buryakivka
NHRM P 8440		Stockholm, Sweden	<i>K. podolica</i>	PMV	Ustechko- Leichenfeld
NHRM P 8441	Zych	Stockholm, Sweden	<i>K. podolica</i>	uncomplete skull roof	Gorodnytsya
NHRM P 8442	Zych	Stockholm, Sweden	<i>K. podolica</i>	axillar area	Gorodnytsya
NHRM P 8443	Zych	Stockholm, Sweden	<i>K. podolica?</i>	skull roof	Gorodnytsya
NHRM P 8444	Zych	Stockholm, Sweden	<i>K. podolica</i>	skull roof	Khmeleva
NHRM P 8445	Zych	Stockholm, Sweden	<i>K. podolica</i>	AL	Khmeleva
NHRM P 8446	Zych	Stockholm, Sweden	<i>K. podolica?</i>	SM	Ustechko
NHRM P 8449	Zych	Stockholm, Sweden	<i>K. podolica</i>	skull roof	Ustechko
NHRM P 8450a		Stockholm, Sweden	<i>K. podolica</i>	AVL, AV, IL, Sp	Khmeleva
NHRM P 8450b		Stockholm, Sweden	<i>K. podolica</i>	Sp	Khmeleva
NHRM P 8452		Stockholm, Sweden	<i>K. podolica</i>	skull roof	Gorodnytsya
NHRM P 8453		Stockholm, Sweden	<i>K. podolica</i>	skull roof	Ustechko
NHRM P 8454	Zych	Stockholm, Sweden	aff. <i>K. podolica</i>	skull roof	Khmeleva
NHRM P 8456	Zych	Stockholm, Sweden	<i>K. podolica</i>	skull roof	Buryakivka
NHRM P 8457		Stockholm, Sweden	<i>K. sp.</i>	skull roof	Repintsy
NHRM P 8458		Stockholm, Sweden	<i>K. sp.</i>	endocranium	Ustechko
NHRM P 8459	Zych	Stockholm, Sweden	aff. <i>K. podolica</i>	skull roof and endocranium	Ustechko
NHRM P 8463		Stockholm, Sweden	<i>K. sp.</i>	skull roof	Buryakivka
NHRM P 8465a-b		Stockholm, Sweden	aff. <i>K. podolica?</i>	skull roof	Gorodnytsya
NHRM P 8466		Stockholm, Sweden	<i>K. sp.</i>	skull roof	
NHRM P 8469		Stockholm, Sweden	aff. <i>K. podolica</i>	endocranium	Buryakivka
NHRM P 8474		Stockholm, Sweden	aff. <i>K. podolica</i>	AVL, AV, IL, Sp, PVL (internal side)	Gorodnytsya
NHRM P 8476	Zych	Stockholm, Sweden	<i>K. podolica</i>	PMD	Ustechko
NHRM P 8477	Zych	Stockholm, Sweden		AVL, Sp, axillar area	Kydaniv
NHRM P 8478		Stockholm, Sweden		skull roof	Ustechko - Leichenfeld
NHRM P 8479	Zych	Stockholm, Sweden	<i>K. sp. aff. K. podolica</i>	“supra-synarcual”	Khmeleva
NHRM P 8481		Stockholm, Sweden	<i>K. podolica</i>	AVL, IL, Sp	Buryakivka
NHRM P 8482		Stockholm, Sweden	<i>K. sp.</i>	skull roof	Buryakivka
NHRM P 8483		Stockholm, Sweden	<i>K. podolica</i>	AL	Ustechko
NHRM P 8484		Stockholm, Sweden	<i>K. podolica</i>	PMV	Ustechko
NHRM P 8485		Stockholm, Sweden	<i>K. podolica</i>	PMD	Ustechko
NHRM P 8486		Stockholm, Sweden	<i>K. sp.</i>	skull roof	Buryakivka
NHRM P 8487		Stockholm, Sweden	<i>K. podolica</i>	MD	Buryakivka
NHRM P 8488	Zych	Stockholm, Sweden	<i>K. podolica</i>	skull roof	Ustechko
NHRM P 8489		Stockholm, Sweden	<i>K. podolica</i>	MD uncomplete	Ustechko
NHRM P 8490		Stockholm, Sweden	<i>K. podolica</i>	plastron	Buryakivka
NHRM P 8491		Stockholm, Sweden	<i>K. podolica</i>	AVL, AV, IL, Sp	Chervonograd

Number	Collection	Material location	Species	Identification	Locality
NHRM P 8492		Stockholm, Sweden	<i>K. podolica</i>	MD	Buryakivka
NHRM P 8493		Stockholm, Sweden	<i>K. podolica</i>	skull roof	Buryakivka
NHRM P 8496a-b		Stockholm, Sweden	<i>K. podolica?</i>	skull roof	Khmeleva
NHRM P 8497		Stockholm, Sweden	<i>K. podolica</i>	MD	Khmeleva
NHRM P 8501		Stockholm, Sweden	<i>K. sp.</i>	AVL, IL, Sp	Ustechko
NHRM P 8502		Stockholm, Sweden	<i>K. podolica</i>	skull roof	Chervonograd
NHRM P 8503		Stockholm, Sweden	<i>K. bucza-</i> <i>czensis ?</i>	skull roof	Soroky
NHRM P 8504		Stockholm, Sweden	<i>K. podolica</i>	PMD	Ustechko
NHRM P 8505		Stockholm, Sweden	<i>K. podolica</i>	AL	Ustechko
NHRM P 8506	Zych	Stockholm, Sweden	<i>K. podolica</i>	AVL, Sp	Ustechko
NHRM P 8508		Stockholm, Sweden	<i>K. podolica?</i>	MD, ADL, PDL	Ivanye
NHRM P 8510		Stockholm, Sweden	<i>K. podolica</i>	MD	Buryakivka
NHRM P 8511		Stockholm, Sweden	<i>K. podolica</i>	AMV	Buryakivka
NHRM P 8512		Stockholm, Sweden	<i>K. podolica</i>	AVL, AV, IL, Sp	Buryakivka
NHRM P 8513		Stockholm, Sweden	<i>K. sp.</i>	MD	Buryakivka
NHRM P 8514		Stockholm, Sweden	<i>K. sp. aff. K.</i> <i>podolica</i>	MD, ADL, PDL	Buryakivka
P 8427		Upsala, Sweden	<i>K. podolica</i>	skull roof	Buchach
Pi 1200	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	PMD	Khmeleva
Pi 1201	Mark-Kurik	Tallinn, Estonia	<i>K. bucza-</i> <i>czensis</i>	right AL	Kydaniv
Pi 1202	Mark-Kurik	Tallinn, Estonia	<i>K. podolica?</i>	left PL	Rukomysh
Pi 1203	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	endocranium	Ustechko
Pi 1204	Mark-Kurik	Tallinn, Estonia	<i>K. bucza-</i> <i>czensis</i>	uncomplete skull roof	Perevoloka
Pi 1205	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	right PVL	Khmeleva
Pi 1206	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	left MD + ADL + PDL (internal side)	Ivanye
Pi 1207	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	right ADL	Ivanye
Pi 1208	Mark-Kurik	Tallinn, Estonia	<i>K. bucza-</i> <i>czensis</i>	uncomplete endocranium	Rukomysh
Pi 1209	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	MD	Ustechko
Pi 1210	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	MD (internal side)	Ustechko
Pi 1211	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	left AL young	Ivanye
Pi 1212 b	Mark-Kurik	Tallinn, Estonia	<i>K. podolica</i>	left PaN, M	Rukomysh
Pi 1213	Mark-Kurik	Tallinn, Estonia	<i>K. bucza-</i> <i>czensis</i>	skull roof + rostrum	Rukomysh
Pi 1215	Mark-Kurik	Tallinn, Estonia	<i>K. sp.</i>	Sp, AVL uncomplete	Rukomysh
Pi 1216	Mark-Kurik	Tallinn, Estonia	<i>K. bucza-</i> <i>czensis</i>	MD, AVL	Zalissy
Pi 1218	Mark-Kurik	Tallinn, Estonia	<i>K. bucza-</i> <i>czensis?</i>	MD uncomplete	Zalissy
Pi 1219	Mark-Kurik	Tallinn, Estonia	<i>K. bucza-</i> <i>czensis</i>	left PNu	Zhyznomyr
RAS 2172 / 2		Moscow, Russia	<i>K. sp.</i>	plastron	Ustechko

## APPENDIX 2 : abbreviations

## INSTITUTIONAL ABBREVIATIONS

AM	Australian Museum, Sydney, New South Wales;
CNHM	The Field Museum of Natural History, Chicago;
GGI	Institute of Geology and Geography, Vilnius, Lithuania;
GM	National Geological Museum of the University of Ivano-Frankivsk, Ukraine;
MB	Institut für Paläontologie Museum für Naturkunde der Humboldt-Universität, Berlin;
MNHN	Muséum national d'Histoire naturelle, Paris;
MZ	Museum Ziemi, Warsaw;
NASU	State Natural History Museum, Lviv, Ukraine;
NHM	Natural History Museum, London;
NHRM	Naturhistoriska Riskmuseet (Royal Swedish State Museum in Woodward 1891);
NMC	National Museum of Canada, Ottawa;
NMP	Museum of Victoria, Melbourne;
Pi	Institute of Geology at Tallinn University of Technology, Estonia;
RAS	Russian Academy of Sciences, Palaeontological Institute, Moscow;
SVD	Dévonien du Svalbard, Laboratoire de Paléontologie, Département histoire de la Terre, Muséum national d'Histoire naturelle, Paris.

## ANATOMICAL ABBREVIATIONS

a.b	anterior buttress;
a.pr.pq	articular area for reception of the palatoquadrate;
a.Psph	parasphenoid outline;
ADL	anterior dorsolateral plate;
AL	anterolateral plate;
AMV	anterior median ventral plate;
an.syn	neural arch of the synarcual;
ASG	anterior superognathal plate;
AV	anteroventral plate;
AVL	anterior ventrolateral plate;
b.ASG	basal layer of the anterior superognathal plate;
b.p	posterior thickening;
C	central plate;
c.ao	canal for the orbital artera;
c.cut.a	canaliculi for the anterior cutaneous nerves of the scapulocoracoid;
c.cut.p	canaliculi for the posterior cutaneous nerves of the scapulocoracoid;
c.cut.v	canaliculi for the ventral cutaneous nerves of the scapulocoracoid;

c.dl.IX	canaliculi for the dorsal branches of the glossopharyngeal nerve;
c.dl.X	canals for the sensory branches of the vagus nerve;
c.e	endocranial cavity;
c.i.ep	scar insertion for a dorsal spine;
c.int	foramen for the internal carotid artera;
c.occ	occipital neurovascular plexus;
c.opht	foramen of the canal for the lateral ophtalmic nerve;
c.pal	foramen for the ramus palatinus of the facialis nerve;
c.v.ju.a	anterior foramen for the jugularis vein;
c.v.ju.m	median foramen for the jugularis vein;
c.v.ju.p	posterior foramen for the jugularis vein;
c.v.pit	foramen for the pituitary vein;
c1	anterior foramen or canal of the axillar area;
c2	medium foramen or canal of the axillar area;
c3	posterior foramen or canal of the axillar area;
c4	foramen or canal for the posterior metapterygial nerves;
cc	groove for the central sensory line;
cc.pm	canalicles leading to the median pit line;
cc.pp	canalicles leading to the posterior pit line;
clm	cleithrum;
cr	median crest of the suprasynarcual element;
cr.art	articular crest for the pectoral fin;
cr.ASG	articular crest for the anterior superognathal plate;
cr.pd	posterodorsal crest of the median dorsal plate;
cr.vl	ventrolateral ridge;
cv.hyp	canal for the hypophyseal veins;
d.b	dorsal buttress;
d.end	endolymphatic duct;
d.end.e	exoskeletal part of the endolymphatic duct;
d.end.i	endocranial part of the endolymphatic duct;
d.mc	cucullaris fossa;
dl.sc	dorsolateral scute;
dlc	groove for the dorsal lateral sensory line;
e.pec	pectoral notch;
ep	median spinelet of the spinal plate;
ESC	extrascapular plate;
f	foramen;
f.a.br.p	foramen for the main brachial artery;
f.a.br.s	foramen for the secondary brachial artery;
f.a.hm	articular area for the hyomandibular element;
f.ad	anterior fossa of the attach area of the pectoral girdle;
f.art.m	articular occipital neurocranial facette;
f.av	anterior fossa of the axillar area;
f.bhy	buccohypophyseal foramen;

f.ch	chordal fissure;	n	lateral bourrelete of the otic region;
f.dl	posterior fossa of the axillar area;	na1	incurrent nostril;
f.dm	sub-nuchal depression;	na2	excurrent nostril;
f.ex.na.com	fenestra exonarina communis;	occ	groove for the occipital cross commissure;
f.gl	glenoid fossa;	p.ao	antorbital process;
f.ju	jugularis fossa;	p.b	basal process;
f.m	foramen magnum;	p.cor	coracoid process of the scapulocoracoid;
f.pec	pectoral fenestra;	p.d	dorsal process (on ADL);
f.Pi	pineal fontanelle;	p.ect	ectethmoid process;
f.plx.br	foramen for the brachial plexus;	p.gl	occipital glenoid process;
f.s.PaN	sub-paranuchal depression;	p.obst	obstantic process (on ADL);
f.sbp	subpituitary fossa;	p.oc	eye stalk;
f.scor	supracoracoid foramen;	p.occ	dorsal occipital process;
f.sgl	supraglenoid foramen;	Pi	post-pineal plate;
f.v.br.p	foramen for the posterior brachial vein;	p.po.a	anterior postorbital process;
f.v.br.a	foramen for the brachial vein;	p.po.p	posterior postorbital process;
fe.hyp	hypophyseal fenestra;	p.po.p.ant	anterior branch of the posterior postorbital process;
IL	interolateral plate;	p.po.p.post	posterior branch of the posterior postorbital process;
ioc	groove for the infraorbital sensory line;	p.pr.pec	prepectoral process of the scapulocoracoid;
l.acc	groove for the accessory sensory line (on ADL);	p.so	supraorbital process;
L.ant.ADL	projection in the plane of the schematic cut of the anterior boundary of the anterior dorsolateral plate;	p.sv	supravagal process;
L.ant.MD	projection in the plane of the schematic cut of the anterior boundary of the median dorsal plate;	PaN	paranuchal plate;
l.art	articular lamina of the anterior dorsolateral plate;	PDL	posterior dorsolateral plate;
l.ext.Hm	external limit of the epihyal element;	pelv	pelvic girdle;
l.obst	obstantic lamina (on AL);	pf	groove for the profundus sensory line;
l.pbr	postbrachial lamina (on AL);	Pi	pineal plate;
l.pto	postocular lamina of the endocranium;	PL	posterolateral plate;
l.sbn	subnasal lamina;	PM	postmarginal plate;
l.sc	lateral scute;	pm	groove for the medium pit-line;
l.so	suborbital lamina;	pmc	groove for the postmarginal sensory line;
lc	groove for the main lateral sensory line;	PMD	post median dorsal plate;
ld.ADL	surface of the MD overlapping the ADL;	PMV	posterior median ventral plate;
ld.PDL	surface of the MD overlapping the PDL;	PMVsc	osseous post median ventral scute;
M	marginal plate;	a.post	posterior ampullae cavity;
m.d.s	superior right oculomotor muscle;	pp	groove for the posterior pitline;
m.d.e	external right oculomotor muscle;	pr	internarinal process of the postnasal plate;
m.d.i	inferior right oculomotor muscle;	pr.if	interfestral process;
m.d.int	internal right oculomotor muscle;	PrO	preorbital plate;
m.eth	ethmoid shelf;	PSO	postsuborbital plate;
m.o.i	inferior oblique oculomotor muscle;	Psph	parasphenoid;
m.o.s	superior oblique oculomotor muscle;	PtN	postnasal plate;
m.sb	subocular shelf;	PtO	postorbital plate;
MD	median dorsal plate;	PVL	posterior ventrolateral plate;
mi	internasal wall;	R	rostral plate;
mp	median pit line;	r	ridge;
Ms	mesencephalon;	r.ch	chordal ridge;
my.p	posterior myodome;	r.sca	external ridge of the anterior semi-circular canal;
my.s	dorsal myodome;	r.scp	external ridge of the posterior semi-circular canal;
my.v	ventral myodome;	Ra	ventral internasal process of the rostral plate or independent element;
N	nuchal plate;	ra	anterior crest;
		re.VII-VIII	recessus for facial and acoustic nerves;

Rh	rhombencephalon;	sac	saccula;
s.a.br	groove for the branchial aort;	sca	anterior semicircular canal;
s.ald	groove for the laterodorsal aort;	sce	external semicircular canal;
s.ao	groove for the orbital aort;	scl	sclerotic ring;
s.av	anteroventral transverse groove of the interolateral plate;	scp	posterior semicircular canal;
s.c.int	groove for the internal carotid artera;	SM	submarginal plate;
s.cc	dorsal expression of the central sensory line groove on the dorsal side of the neurocranium;	SO	suborbital plate;
s.e.hy	groove for the hyoidian efferent artera;	so.p	supraorbital process;
s.ins.Sp	attach area for the spinal plate (on AL);	sorc	groove for the supraorbital sensory line;
s.ins.AL	groove for the insertion of the anterolateral plate;	Sp	groove for the supraoral sensory line;
s.ioc	dorsal expression of the infraorbital sensory line groove on the dorsal side of the neurocranium;	spio.a,b,c	spinal plate;
s.l.pbr	groove for the insertion of the postbranchial blade of the AL on the IL;	syn	foramina for the craniospinal nerves;
s.lvAL	groove for the insertion of the ventral blade of the AL on the Sp;	v.br	synarcual;
s.m.add.pd	groove for the dorsal deep muscles of the pectoral fin;	v.g	foramen for the branchial vein;
s.m.add.pv	groove for the ventral deep muscles of the pectoral fin;	vca	vascular groove;
s.m.ds	groove for the dorsal superficial muscles of the pectoral fin;	vl.sc	foramen/groove for the anterior cerebral vein;
s.m.vs	groove for the ventral superficial muscles of the pectoral fin;	z.ins.s.syn	ventrolateral scute;
s.pmc	dorsal expression of the postmarginal sensory line groove on the dorsal side of the neurocranium;	II	zone of insertion of the suprasynarcual element;
s.r.X	overlap area for the X plate;	III	foramen for the optic nerve;
s.ra	groove for the anterior arterial root;	IV	foramen for the communalis motor ocularis nerve;
s.soc	dorsal expression of the supraorbital sensory line groove on the dorsal side of the neurocranium;	V1	foramen for the patheticus nerve;
s.syn	suprasynarcual element;	V1a	profundus nerve;
s.T1	suture between two plates at time T1;	V2-3	foramen for the profundus nerve;
s.T2	suture between two plates at time T2 (T2>T1);	VII	foramen for the maxillar and mandibular branches of the profundus nerve;
s.v.ju	groove for the jugularis vein;	VII.hm	facial nerve;
s.vca	groove for the anterior cerebral vein;	VIII	foramen for the hyomandibularis branch of the facial nerve;
		IX	foramen for the acousticus nerve;
		IXph	foramen for the glossopharyngus nerve;
		IXpt	foramen for the pharyngial ramus for the glossopharyngus nerve;
		X	post-trematic branch of the glossopharyngus nerve;
		X1	foramen for the vagus nerve;
		s.X1	first branch of the vagus nerve;
		Xd	groove for the first branche of the vagus nerve;
		Xv	dorsal foramen (of the vagus nerve);
			ventral foramen (of the vagus nerve).

### APPENDIX 3: Faunal list of vertebrates of podolia (translated from Voichyshyn 2001, without modification).

Abbreviations for collections: **B**, Balabai; **V**, Voichyshyn, NASU; **NASU**, State Natural History Museum, Lviv, Ukraine; **GM**, Geological Museum of the Ivan Franko National University of Lviv, Ukraine; **MZ**, Museum Ziemi, Warsaw (Poland).

Remark: the *Kujdanowiaspis* material displayed in this appendix is the same as that given in the original publication by Voichyshyn (2001); for an update concerning the localities, one can refer to Figure 1 (geological map) and Appendix 1 (list of material and localities) of the present article for the genus *Kujdanowiaspis*, and to Dupret *et al.* 2007 for the genus *Erikaspis*.

Agnatha Cope, 1889	Localities and references
Class Diplorhina Hawle & Corda, 1847 (Pteraspidomorphi Goodrich, 1909)	
Subclass Thelodonti Kiaer, 1932	
<i>Apalolepis brotzeni</i>	Dobrivlyani & Zalishchyki (Karatajüte-Talimaa 1978, V), Ivanye-Zolote & Ustechko (V)
Karatajüte-Talimaa, 1978	
<i>Apalolepis obruchevi</i>	Doroshivtsi, Zalishchyki, Ivanye-Zolote, Pechirna & Cemakivtsi
Karatajüte-Talimaa, 1978	(Karatajüte-Talimaa 1968), Vinogradiv, Gorodok, Dobrivlyani, & Zozilintsi (Karatajüte-Talimaa 1968, Karatajüte-Talimaa 1978), ?Yagilnitsya (V)
<i>Gampsolepis insueta</i>	Vinogradiv, Gorodok, Dobrivlyani, Ivanye-Zolote (Karatajüte-Talimaa 1978)
Karatajüte-Talimaa, 1978	
<i>Nikolivia balabayi</i>	?Bila, Gorodok, Kapustintsi, Lisivtsi & Semakivtsi (Karatajüte-Talimaa 1978), Vinogradiv (Karatajüte-Talimaa 1978, V)
Karatajüte-Talimaa, 1978	
<i>Nikolivia elongata</i>	Gorodok & Dobrivlyani (Karatajüte-Talimaa 1978), Zalishchyki (Karatajüte-Talimaa 1978, V), Ivanye-Zolote, Semakivtsi & Ustechko (V)
Karatajüte-Talimaa, 1978	
<i>Nikolivia oervigi</i>	Gorodok (Karatajüte-Talimaa 1968), Dobrivlyani & Zalishchyki (Karatajüte-Talimaa 1978, V), Ivanye-Zolote, Semakivtsi & Ustechko (V)
Karatajüte-Talimaa, 1978	
<i>Turinia pagei</i> (Powrie, 1870)	Gorodok & Dobrivlyani (Karatajüte-Talimaa 1978), Zalishchyki (Karatajüte-Talimaa 1978, V)
<i>Turinia polita</i>	Gorodok & Dobrivlyani (Karatajüte-Talimaa 1978), Zalishchyki, Ivanye-Zolote & Ustechko (Karatajüte-Talimaa 1978, V)
Karatajüte-Talimaa, 1978	
Thelodonti indet Kiaer, 1932	Karatajüte-Talimaa 1978
Subclass Heterostraci Lankester, 1868	
<i>Alaeckaspis ?depressa</i> (Stensiö, 1958)	Kasperivtsi (Belles-Isles & Janvier 1984, Blicek 1984)
<i>Alaeckaspis magnipinealis</i> (Brotzen, 1933)	Ivanye-Zolote (Blicek 1984, Brotzen 1933a, Voichyshyn 1999)
<i>Alaeckaspis ustetchkiensis</i> Voichyshyn, 1999	Ustechko (Voichyshyn 1999)
<i>Alaeckaspis verbivtsiensis</i> Voichyshyn, 1999	Verbivtsi (Voichyshyn 1999)
<i>Althaspis elongata</i> (Zych, 1927)	Zhiznomir (Zych 1927, GM), Zvenigorod (Novitskaya 1986, Zych 1927), Perevoloka & Rykomish (Novitskaya 1986), Kydaniv (Novitskaya 1986, Blicek 1984, Brotzen 1936), Ripintsi (Zych 1927), Ryblin (B), Sapova (Novitskaya 1986, NASU)
<i>Althaspis longirostra</i> (Zych, 1927)	Kydaniv & Perevoloka (Novitskaya 1986), Kopachintsi (Zych 1927), Koropets (Blicek 1984, B), Unizh (Brotzen 1933a)
<i>Althaspis sapovensis</i> Novitskaya, 1986	Zarivintsi (V), Kydaniv, Perevoloka & Rykomish (Novitskaya 1986), Sapova (Novitskaya 1986, B)
<i>Althaspis</i> sp.	Kydaniv (Novitskaya 1986), Zhiznomir, Zalissyia, Koropets, Rykomish, Sapova & Stinka (B), Zarivintsi (V), ? Potochishche (NASU), Zolotniki (DPM)
<i>Althaspis ?spathulirostris</i> (Stensiö, 1958)	Soroki (Blicek 1984)
<i>Pteraspis (Belgicaspis) crouchi</i> (Lankester, 1868)	Pechirna (Novitskaya 1986)
<i>Brachipteraspis latissima</i> (Zych, 1938)	Buchach (Balabai 1959, Brotzen 1933a, Brotzen 1936), Zavadisvka (Balabai 1960), Kydaniv (Novitskaya 1986, Brotzen 1936), Kovalivka & Chekhiv (Balabai & Opalatenko 1957), Perevoloka (Balabai 1960, Zych 1927), Sapova (Balabai 1959, Zych 1927)
<i>Corvaspis kingi</i> Woodward, 1934	Dobrivlyani (V)
<i>Ctenaspis kiaeri</i> Zych, 1931	Yagilnitsya Stara (Zych 1931, NASU)
<i>Djurinaspis prima</i> Novitskaya, 1983	Verbivtsi (B), Ustechko (Novitskaya 1986)
<i>Dnestraspis firma</i> Novitskaya, 1983	Ustechko (Novitskaya 1986, V)



<i>Europrotaspis arnelli</i> (Brotzen, 1936)	Kydaniv (Novitskaya 1986, Brotzen 1936), Perevoloka (Blieck 1984), Sapova (Novitskaya 1986, B)
<i>Irregulariaspis seretensis</i> Novitskaya, 1986	Zvinyach (Novitskaya 1986)
<i>Irregulariaspis skalskiensis</i> Novitskaya, 1986	Dnistrove (Novitskaya 1986)
<i>Irregulariaspis stensioi</i> Zych, 1931	Dobrivlyani (Novitskaya 1986), Yagilnitsya Stara (Zych 1931, NASU)
<i>Larnovaspis iwaniensis</i> (Brotzen, 1933)	? Zalishchyki (Balabaï 1961a), Ivanye-Zolote (Novitskaya 1986, Brotzen 1933a)
<i>Larnovaspis kneri</i> (Lankester, 1868)	Dobrivlyani (B), Zalishchyki (Novitskaya 1986, V), Zastinoche (Novitskaya 1986)
<i>Larnovaspis major</i> (Zych, 1927)	Gorodnitsya (V), Gorodok (Blieck 1984), Zalishchyki & Mogilnitsya (Novitskaya 1986, Zych 1927), Nirkiv (B), Ustechko (Brotzen 1933a, B, V)
<i>Larnovaspis mogielensis</i> Blieck, 1984	Buryakivka (B), Gorodnitsya (B, V), Mogilnitsya & Potochishche (Blieck 1984), Chervonograd (B)
<i>Larnovaspis</i> cf. <i>goujeti</i> (Blieck, 1982)	Chervonograd (Blieck 1984)
<i>Larnovaspis</i> ? <i>brotzeni</i> (Stensiö, 1958)	Dobrivlyani & Kasperivtsi (Blieck 1984)
<i>Larnovaspis</i> sp.	Buryakivka, Verbivtsi, Zalishchyki, Sapova & ? Ustechko (B), Mogilnitsya (Zych 1927), ?Potochishche (NASU)
<i>Loricopteraspis althi</i> (Stensiö, 1958)	The author did not show localities (Novitskaya 1986); ?Potochishche & ?Yagilnitsya (Blieck 1984)
<i>Mylopteraspidella gracilis</i> Blieck, 1984	Verbivtsi (B), Zastinoche & Khmeleva (Blieck 1984), Potochishche (NASU), Ustechko (Novitskaya 1986, Blieck 1984, B, NASU)
<i>Mylopteraspis robusta</i> Stensiö, 1958	?Ustechko (Novitskaya 1986)
<i>Parapteraspis lata</i> (Stensiö, 1958)	Zalishchyki (Novitskaya 1986), Ivanye-Zolote (B), Yagilnitsya Stara (Novitskaya 1986, Blieck 1984)
<i>Parapteraspis plana</i> Stensiö, 1958	Ustechko (Novitskaya 1986, Blieck 1984, V)
<i>Pavloaspis pasternaki</i> Voichyshyn, 1999	Ustechko (Voichyshyn 1999)
<i>Podolaspis lerichei</i> (Zych, 1927)	Verbivtsi (B), Gorodnitsya (NASU), Zalishchyki (Novitskaya 1986, B), Zastinoche (Novitskaya 1986), Ivanye-Zolote (Brotzen 1933a), Mogilnitsya (Balabaï 1959, Zych 1927), Pechirna (Novitskaya 1986), Ustechko (Novitskaya 1986, B, MZ, V, NASU)
<i>Podolaspis podolica</i> (Alth, 1874)	Zalishchyki (B), Zastinoche (Novitskaya 1986), Ustechko (Novitskaya 1986, ?Zych 1931, B, V), Khreshchatik (Zych 1927)
<i>Podolaspis zychi</i> (Brotzen, 1933)	Dobrivlyani (Novitskaya 1986), Zhezhava (Brotzen 1933a), Zalishchyki (Balabaï 1961a, Novitskaya 1986), Ustechko (Novitskaya 1986, B)
<i>Podolaspis</i> sp.	Bedrikivtsi, ?Buryakivka, ?Gorodnitsya, Zastinoche & Mogilnitsya (B), Vorulintsi (Zych 1931), Dobrivlyani (Blieck 1984), Gorodok, Khmeleva & Yagilnitsya Stara (Zych 1931), Zalishchyki (Zych 1931, B), Ivanye-Zolote (B, ?NASU), Maliv, Khreshchatik & Yagilnitsya (Zych 1927), Potochishche & Ustechko (NASU)
<i>Poraspis pompeckii</i> (Brotzen, 1933)	Zalishchyki (Novitskaya 1986, Brotzen 1933a), Ivanye-Zolote & Ustechko (Brotzen 1933a)
<i>Poraspis siemiradzki</i> (Zych, 1931)	Yagilnitsya Stara (Zych 1931, GM, NASU)
<i>Poraspis simplex</i> (Brotzen, 1933)	Dobrivlyani (Novitskaya 1986), Zalishchyki (Brotzen 1933a)
<i>Poraspis sturi</i> (Alth, 1874)	Dobrivlyani, Doroshchivtsi & Zozulintsi (Novitskaya 1986), Zalave (B), Zalishchyki (Balabaï 1961a), Ivanye-Zolote (Zych 1927), Ustechko (Novitskaya 1986, V), Yagilnitsya Stara (Balabaï 1961a)
<i>Poraspis</i> sp.	Voyske (Zych 1927), ?Gorodnitsya (Zych 1927), Dobrivlyani (Novitskaya 1986, B), Zalishchyki (Novitskaya 1986, Zych 1931, B), Kapturi (NASU), Pidgaychiki (V), Ustechko (Novitskaya 1986, Zych 1931, B, V), Yagilnitsya (Novitskaya 1986), Yagilnitsya Stara (Zych 1931, NASU)
" <i>Pteraspis</i> " <i>angustata</i> Alth, 1874	Ustechko (V), Khreshchatik (Zych 1927)
<i>Seretaspis zychi</i> Stensiö, 1958	The author did not show localities (Novitskaya 1986)
<i>Weigeltaspis alta</i> Brotzen, 1933	Buryakivka (Tarlo 1965), Gorodnitsya (V), Ustechko (Brotzen 1933b, Tarlo 1965, V)
<i>Weigeltaspis brotzeni</i> Tarlo, 1965	Ustechko (Tarlo 1965, V)
<i>Zascinaspis bryanti</i> (Brotzen, 1936)	Dobrivlyani (Blieck 1984, Brotzen 1936), ?Zalishchyki (Balabaï 1961a), ?Ivanye-Zolote (Novitskaya 1986), ?Yagilnitsya Stara (NASU)

<i>Zascinaspis heintzi</i> (Brotzen, 1936)	Verbivtsi (B), Zastinoche (Novitskaya 1986, Blicck 1984, Brotzen 1936), Ivanye-Zolote (Balabaï 1959, Brotzen 1936, NASU), Koshilivtsi (Brotzen 1936), Mogilnitsya (Novitskaya 1986), Rizdvanyi (Blicck 1984, Brotzen 1936), Terebovlya (Balabaï 1959, Novitskaya 1986, Brotzen 1936), Ustechko (Novitskaya 1986, Blicck 1984, Brotzen 1936, B, GM, V)
Heterostraci indet.	Babin & Rigotin (Pauca 1941), Bazar (Balabaï 1959, Balabaï 1960, Zych 1927, B), Beremyani (Brotzen 1933a, Zych 1927), Bila, Zastinka, Zvinyach, Zozulintsi, Slobidka Strusivska, Krivki & Mariv (Zych 1927), Budaniv & Krobinka (Balabaï 1961a), Buryakivka, Verbivtsi, Zalissy, Zastinoche, Krinitsya, Lishchintsi, Nirkiv, Rykomish, Rysiliv & Stefaneshiti (B), Vasiliv, Doroshivtsi, Kapustintsi (Alth 1874), Buchach & Fedorivka (Alth 1874, Siemiradzki 1906), Voyske (Alth 1874, Siemiradzki 1906, Zych 1927), Gorodnitsya (Balabaï 1959, Zych 1927, B, GM, NASU), Gorodok (V), Dobrivlyani (Balabaï 1961a, Alth 1874, Siemiradzki 1906, B, GM, MZ), Zhyznomir (B, NASU), Zalishchyki (Balabaï 1959, Balabaï 1961a, Balabaï 1961b, Alth 1874, Siemiradzki 1906, Zych 1927, B, GM, NASU), Zolotniki (Siemiradzki 1906), Ivanye-Zolote (Balabaï 1959, Balabaï 1961b, Alth 1874, Siemiradzki 1906, Zych 1927, B, GM, NASU), Kapturi & Strilche (NASU), Kovalivka (Balabaï 1961a), Koropets (Balabaï 1959, Balabaï & Opalatenko 1957, B), Lyka (Balabaï 1961a, Alth 1874, Siemiradzki 1906), Novosilka Koropetska (Balabaï 1959, Balabaï 1960, Balabaï & Opalatenko 1957, B), Papirnya (Balabaï 1961a, B, NASU), Pechirna (Balabaï 1959, Balabaï 1961a, b, Siemiradzki 1906, B, MZ, NASU), Pidgaychiki (B, V), Potochishche (Balabaï 1959, NASU), Rublin (Balabaï & Opalatenko 1957, B), Rizdvyania & Slovidka (Balabaï 1960, NASU), Sapova (B, GM), Smikivtsi (Balabaï 1961a, NASU), Stinka (Balabaï & Opalatenko 1957, B), Torske, Tsvitova, Yablunivka & Mikhalche (Balabaï 1960), Unizh (Balabaï 1959), Ustechko (Balabaï 1957, Balabaï 1959, Balabaï 1961b, Alth 1874, Siemiradzki 1906, Zych 1927, B, GM, MZ, V, NASU), Khmeleva (MZ), Khreshchatik (Balabaï 1961a, Alth 1874, Siemiradzki 1906, Zych 1927, GM), Chervonograd (Balabaï 1959, B, MZ, V, NASU), Chekhiv (Balabaï 1959, Balabaï & Opalatenko 1957, B), Yagilnitsya Stara (Balabaï 1961a, Zych 1931, NASU)
Class Monorhina Kiaer, 1924 (Cephalaspidomorphi Stensiö, 1927)	
Subclass Osteostraci Lankester, 1868	
<i>Benneviaspis talimaae</i>	Gorodnitsya (Afanassieva 1990)
Afanassieva, 1990	
<i>Benneviaspis whitei</i>	Ustechko (Belles-Isles & Janvier 1984, V)
Belles-Isles & Janvier, 1985	
<i>Benneviaspis zychi</i> Afanassieva, 1989	Kydaniv & Sapova (Afanassieva 1989)
" <i>Cephalaspis</i> " cf. <i>acutirostris</i>	Gorodnitsya (Janvier 1985b), Ustechko (V)
Stensiö, 1932	
" <i>Cephalaspis</i> " <i>mikrolepidota</i>	Gorodnitsya (Balabaï 1962, B)
(Balabaï, 1962)	
<i>Citharaspis junia</i> Afanassieva, 1989	Kydaniv & Sapova (Afanassieva 1989)
<i>Citharaspis polonica</i>	Buchach (Afanassieva 1989, Belles-Isles & Janvier 1984)
(Belles-Isles & Janvier, 1985)	
<i>Diademaspis stenioei</i> Afanassieva, 1989	Ustechko (Afanassieva 1989, NASU)
<i>Diademaspis</i> sp.	Bily Potik (NASU), Gorodnitsya (GM, V), Chervonograd (Janvier 1985b), Ustechko (Janvier 1985b, V)
<i>Heraspis kozlowskii</i> (Zych, 1937)	Vorvulintsi & Zalishchyki (Afanassieva 1991, Zych 1937), Gorodnitsya (V), Ustechko (Afanassieva 1991, ?GM, V)
<i>Machairaspis</i> sp.	Gorodnitsya (Janvier 1985b)
<i>Mimetaspis concordis</i> Voichyshyn, 1944	Gorodnitsya (V), Ustechko (Voichyshyn 1994)
<i>Mimetaspis glazewskii</i> Janvier, 1985	Buryakivka (Afanassieva 1991), Gorodnitsya (V), Ustechko (Janvier 1985b, V)
<i>Mimetaspis</i> sp.	?Gorodnitsya (Janvier 1985b)

<i>Parameteoraspis dobrovlensis</i> Afanassieva, 1991	Dobrivlyani (Afanassieva 1991)
<i>Pattenaspis rogalai</i> (Balabaï, 1962)	Gorodnitsya (Balabaï 1962, NASU), Nagiryani & Ustechko (V), Os-trivech & Rizdviani (Balabaï 1962, B), Khmeleva (Janvier 1988)
<i>Stensiopelta pustulata</i> Janvier, 1985	Bily Potik & Byrakivka (Janvier 1985b), Ustechko (Afanassieva 1991, Janvier 1985b), V, NASU, Gorodnitsya (Janvier 1985b, B, V), Nagiryani (V), Chervonograd (Janvier 1985b)
<i>Stensiopelta</i> sp.	Gorodnitsya, Khmeleva & Nagiryani (V), Zastinoche & Ripintsi (Janvier 1985b)
<i>Tegaspis waengsjoei</i> Belles-Isles & Janvier, 1985	Zastinoche (Belles-Isles & Janvier 1984)
<i>Zenaspis ?podolica</i> (Balabaï, 1962)	Gorodnitsya (Balabaï 1962, B, V), Ustechko (V)
<i>Zenaspis cf. salweyi</i> (Egerton, 1857)	Gorodnitsya (Janvier 1985b, V), Ustechko (Janvier 1985b)
<i>Zychaspis granulata</i> Voichyshyn, 1998	Ustechko (Voichyshyn 1998)
<i>Zychaspis siemiradzki</i> Janvier, 1985	Buryakivka (NASU), Gorodnitsya (Afanassieva 1991, Janvier 1985b, V), Ustechko (Afanassieva 1991, V), ?Khomakivka & Chervonograd (Janvier 1985b)
Osteostraci indet.	Bily Potik (Balabaï 1962, Janvier 1985b), Birki Veliki, Butsniv, Varvarintsi & Strusiv (Anonymous 1900), Buryakivka (Balabaï 1962, NASU), Budaniv (V), Voyske (Alth 1874, Siemiradzki 1906), Gorodnitsya (Balabaï 1962, Janvier 1985b, B, GM, V, NASU), Ivanye-Zolote (Balabaï 1962, Alth 1874, Siemiradzki 1906, Zych 1927, GM, NASU), Kapturi, Kydaniv, Pidverbti, Strilche & Khomyakivka (NASU), Nirkiv, Sadove & Stefaneshi (B), Pechirna (B, NASU), Potochishche (Janvier 1985b), Ostrovets & Pizdviani (Balabaï 1962, NASU), Ripintsi & Sapova (Zych 1927), Ustechko (Balabaï 1962, Janvier 1985b, B, GM, MZ, V, NASU), Xhmeleva (Balabaï 1962, B, V), Chervonograd (GM, NASU)
Agnatha indet.	Beremyani (NASU), Budanov, Mikhalthom & Pidgaychiki (B), Nagiryantsi, Pechirni, Ustechko & Chervonogradi (MZ)
<b>Gnathostomata</b> Zittel, 1879	<b>Localities and references</b>
Class Placodermi M'Coy, 1848	
<i>Kujdanowiaspis podolica</i> (Brotzen, 1934)	Buchach (B), Gorodnitsya & Potochishche (NASU), Ustechko (B, MZ, NASU)
<i>Erikaspis zychi</i> (Stensiö, 1945)	Buryakivka (NASU), Ivanye-Zolote (B, NASU), ?Pidgaychiki (B), Ustechko (B, V, NASU), Khmeleva (V, NASU)
<i>Tyriolepis radiata</i> Karatajüte-Talimaa, 1968	Gorodok, Dobrivlyani, Zalishchiki & Ivanye-Zolote (Karatajüte-Talimaa 1968)
Placodermi indet.	Voyske (Alth 1874, Siemiradzki 1906, Zych 1927), Zhiznomir, Kydanov (Siemiradzki 1906), Zalishchyki (Brotzen 1934), Ivanye-Zolote & Khreshchatik (Alth 1874), Mogilnitsya (GM), Sapova & Chervonograd (Zych 1927)
Class Acanthodii Ozen, 1846	
<i>Gomphodus</i> sp.	Mishkivtsi & Yagilnitsya (V)
<i>Nostolepis</i> sp.	Ivanye-Zolote, Mazurivka, Mishkivtsi, Ustechko & Yagilnitsya (V)
<i>Seretolepis elegans</i> Karatajüte-Talimaa, 1968	Dobrivlyani (Karatajüte-Talimaa 1968, V), Zalishchiki (Karatajüte-Talimaa 1968)
Acanthodii indet.	Tselievi (V)
Class Chondrichthyes Huxley, 1880	
Subclass Holocephali Bonaparte, 1832-41	
<i>Polymerolepis whitei</i> Kar. Tal.	Vinogradiv, Gorodok & Dobrivlyani (Karatajüte-Talimaa 1968), Zalishchiki (V)
Chondrichthyes indet.	Bilche-Zolotoe & Tovstoluga (GM), Vinogradiv & Semakivtsi (V)