Nostolepis scale remains (stem Chondrichthyes) from the Lower Devonian of Qujing, Yunnan, China (#55998)

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Nostolepis scale remains (stem Chondrichthyes) from the Lower Devonian of Qujing, Yunnan, China

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Based initially on microfossils, *Nostolepis* is one of the first known ‘acanthodians’, which constitute a paraphyletic assemblage of plesiomorphic members of the total group Chondrichthyes. Its wide distribution has potential implications for stratigraphic comparisons worldwide. Six species of *Nostolepis* have been reported in China, including one species from the Xitun Formation (Lochkovian, Lower Devonian) of Qujing, eastern Yunnan. Acid preparation of rock samples from the Xitun Formation has yielded abundant acanthodian remains. Based on both morphological and histological examinations, here we identify six species of *Nostolepis*, including two new species. *N. qujingensis* sp. nov. is characterized by thin scales devoid of the neck anteriorly and the dentine tubules rarely present on the anterior part of the crown. *N. digitus* sp. nov. is characterized by parallel ridges on anterior and lateral margins of the crown, and the neck constricted and ornamented with pore openings. We extend the duration of *N. striata* in China from the Pridoli of Silurian (Yulungssu Formation) to the Lower Devonian in Qujing and report the first occurrences of *N. amplifica*, *N. consueta* and *N. decor*a in this region. This study increases the diversity of the Lower Devonian Xitun Fauna and provides a better understanding of the paleogeographic distribution of *Nostolepis*.

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Abstract

Based initially on microfossils, *Nostolepis* is one of the first known 'acanthodians', which constitute a paraphyletic assemblage of plesiomorphic members of the total group Chondrichthyes. Its wide distribution has potential implications for stratigraphic comparisons worldwide. Six species of *Nostolepis* have been reported in China, including one species from the Xitun Formation (Lochkovian, Lower Devonian) of Qujing, eastern Yunnan. Acid preparation of rock samples from the Xitun Formation has yielded abundant acanthodian remains. Based on both morphological and histological examinations, here we identify six species of *Nostolepis*, including two new species. *N. qujingensis* sp. nov. is characterized by thin scales devoid of the neck anteriorly and the dentine tubules rarely present on the anterior part of the crown. *N. digitus* sp. nov. is characterized by parallel ridges on anterior and lateral margins of the crown, and the neck constricted and ornamented with pore openings. We extend the duration of *N. striata* in China from the Pridoli of Silurian (Yulungssu Formation) to the Lower Devonian in Qujing and report the first occurrences of *N. amplifica*, *N. consueta* and *N. decora* in this region. This study increases the diversity of the Lower Devonian Xitun Fauna and provides a better understanding of the paleogeographic distribution of *Nostolepis*.

Introduction

The Lower Devonian Xitun Formation exposed in Qujing, China has yielded a significant early vertebrate fauna, whose macrofossils are represented by jawless galeaspids and jawed members such as 'placoderms' and osteichthyans (*Chang, 1982*; *Chang & Yu, 1984*; *Zhu, 1996*; *Zhu, Yu & Janvier, 1999; Zhu, Yu & Ahlberg, 2001*; *Zhu & Yu, 2002*; *Zhu et al., 2006*). Probably due to the micromeric (small scales or tesserae on the head, instead of large dermal bones as of macromeric) skeletal nature of conventionally-defined chondrichthyans and 'acanthodians', no cranial remains of the two groups have been found in the Xitun Formation, although microfossils from the same bonebeds have been assigned to the two groups (*Wang, 1984*). Recent revisions on the early vertebrate phylogeny suggest that conventionally-defined chondrichthyans and 'acanthodians' form a clade, i.e. the total group Chondrichthyes, whose micromeric skeleton probably evolved from an ancestral macromeric condition possessed by 'placoderms' and osteichthyans (*Brazeau, 2009*; *Davis, Finarelli & Coates*, *2012*; *Zhu et al., 2013; Giles et al., 2015*; *Long et al., 2015; Burrow et al., 2016*). A better understanding of the chondrichthyan members from the Xitun Formation will provide a further glimpse of the diversity of jawed vertebrates in South China during the Early Devonian.

Based initially on microfossils, *Nostolepis* is one of the first known 'acanthodians', which constitute a paraphyletic assemblage of plesiomorphic members of the total group Chondrichthyes. Its wide distribution has potential implications for stratigraphic comparisons worldwide. Six species of *Nostolepis* have been reported in China, including one species from the Xitun Formation (Lochkovian, Lower Devonian) of Qujing, eastern Yunnan. Acid preparation of rock samples from the Xitun Formation has yielded abundant acanthodian remains. Based on both morphological and histological examinations, here we identify six species of *Nostolepis*, including two new species. *N. qujingensis* sp. nov. is characterized by thin scales devoid of the neck anteriorly and the dentine tubules rarely present ~~on~~ the anterior part of the crown. *N. digitus* sp. nov. is characterized by parallel ridges on anterior and lateral margins of the crown, and the neck constricted and ornamented with pore openings. We extend the duration of *N. striata* in China from the Pridoli of Silurian (Yulungssu Formation) to the Lower Devonian in Qujing and report the first occurrences of *N. amplifica*, *N. consueta* and *N. decora* in this region. This study increases the diversity of the Lower Devonian Xitun Fauna and provides a better understanding of the paleogeographic distribution of *Nostolepis*.

Nostolepis is a cosmopolitan acanthodian genus erected by *Pander* (*1856*) for scales. It was generally assigned to the family Climatiidae of the order Climatiiformes for the latter half of the twentieth century (*Berg, 1940*; *Gross, 1957*; *Gross, 1971*; *Denison, 1979*; *Tông-Dzuy & Janvier, 1994*; *Burrow, 1997*; *Miller & Marss*, *1999*; *Vergoossen, 2002a*; *Valiukevičius, 2003c*; *Wang, 2003*; *Vergoossen, 2004*; *Burrow, Lelièvre & Janjou*, *2006*). Considering that *Nostolepis* lacks circumorbital bones, dermal pectoral

girdle, and branchial plates, *Burrow & Turner* (*2010*) doubted its assignment to the Climatiidae. So far, the family for *Nostolepis* has been uncertain (*Burrow & Murphy, 2016)*.

Nostolepis was first reported in China as *Nostolepis* sp. indet. from the Xitun Formation (Lochkovian, Lower Devonian) in Qujing (*Wang, 1984*). The first nominal species of *Nostolepis* in China is *N. sinica* from the Yulungssu Formation (Pridoli, Silurian) in Qujing (*Gagnier, Jahnke & Yan, 1989*). Soon after, *N. striata* and *N.* sp. were described from the same horizon in Qujing (*Wang & Dong, 1989*). *N. striata* was also recorded from the Xiaputonggou Formation (Lochkovian) in West Qinling (*Wang et al., 1998*) and the Shanjiang Formation (Homerian, Wenlock) in Lijiang, Yunnan (*Wang, 2003*). *N. gracilis* was ~~known~~ from the Alengchu Formation and Shanjiang Formation (Wenlock, Silurian to Emsian, Lower Devonian) in Lijiang, Yunnan (*Wang, 2003*) and the Xiaputonggou Formation (Lochkovian) in West Qinling (*Wang et al., 1998*). From the latter site, *Wang et al.* (*1998*) also described *N. tewonensis* from Homerian (Wenlock, Silurian) to Lochkovian. *Nostolepis guangxi~~n~~ensis* was reassigned to *Nostovicina guangxi~~n~~ensis* because its crown lacks the Stranggewebe, e.g. fusiform cell spaces (*Valiukevičius & Burrow, 2005*).

Here, we describe six species of *Nostolepis*, including two new species, from the Xitun Formation in Qujing, Yunnan, China, thus increasing the diversity of the Early Devonian Xitun Fauna. We also summarize and discuss the paleogeographic distribution and chronological extensions of *Nostolepis* species.

Materials & Methods

This study is based on isolated scales of *Nostolepis* from the Xitun Formation (Lochkovian, Lower Devonian) in Xitun, Xishan subdistrict, Qujing, Yunnan, China (N:25°31.547′, E:103°31.547′). Studied scales were extracted by treatment with buffered 5% acetic acid from greenish-yellow muddy limestone of the Xitun Formation at the laboratory of Qujing Normal University.

~~Individual scales were embedded~~ in epoxy resin and ~~placed~~ in a vacuum desiccator oven for 4 hours. The cured resin blocks were cut with a low speed saw and 100–200 mm away from embedded specimens. Then the surface was ground with sand paper with grit sizes ranging from P600 to P4000 until the desired surface of the specimen was exposed. This surface was polished with a grinder/polisher and glued to a glass slide. Finally, the other surface was cut, ground and polished in the same way to produce doubly-polished thin sections. Scales of each species were sectioned in vertical longitudinally, vertical transversely and horizontally. Scanning electron microscope (Hitachi S-3700N) was used to take ~~photos~~. All specimens are housed in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), China.

Results

Systematic paleontology

‘Acanthodii’ Owen, 1846

Order and Family Incertae sedis

Genus *Nostolepis Pander, 1856*

Nostolepis striata Pander, 1856

1856 *Nostolepis striata*, Pander, pl.28, figs. 1, 7.

1984 *Nostolepis* sp., Blieck et al., pl.1, figs. 3-4.

1989 *Nostolepis striata*, Wang & Dong, pl.II, figs. F-K.

1997 *Nostolepis striata,* Burrow, fig. 2A, B; pl. 1, figs. 13 a-c; pl.2, figs. 1-4.

1998 *Nostolepis striata*, Valiukevičius, pl.1, figs. 1-4; pl.2, figs. 4-7.

1998 *Nostolepis striata,* Wang et al., pl.1, figs. B-C.

1999 *Nostolepis striata,* Vergoossen, pl.2, fig. 15.

2002b *Nostolepis striata,* Vergoossen, pl.3, figs. 26-36.

2003a *Nostolepis striata,* Vergoossen, pl.6, figs. 71-76.

2003b *Nostolepis striata,* Vergoossen, pl.10, figs. 85-100.

2003 *Nostolepis striata,* Wang, fig.1.

2004 *Nostolepis striata,* Vergoossen, pl.5, figs. 54-61.

2005 *Nostolepis striata*, Valiukevičius, fig. 3, L and M.

2013 *Nostolepis striata*, Burrow et al., figs. 3, 4.1 and 4.2.

2018 *Nostolepis striata*, Turner and Burrow, fig. 6, A-D.

Other synonyms see *Valiukevičius* (*1998*).

Referred Material: 68 trunk scales (IVPP V26830.1-V26830.68).

Description:

Morphotype 1 (*Fig.1* A-D):

This type of scales has a broad triangular, flat, or slightly inclined crown. Crowns are about 0.207- 0.559 mm long and 0.282-0.514 mm wide. Three to four short, stout, longitudinal and converging ridges bend inward the anterior face of the crown and fade out at a quarter of the crown’s length. The distal pointed end of the crown overhangs the base slightly. Most of the scales have two smooth lateral slopes rising from the anterior crown-neck boundary and joining at the pointed posterior apex. The neck is smooth and indistinctive. The rhomboid base is strongly or moderately convex and fills up the entire crown except for the crown’s posterior end.

Morphotype 2 (*Fig.1* E-H):

One triangular scale has an inclined crown surface with an angle of nearly 30°. The crowns are slightly wider than long (0.5 mm wide and 0.3 mm long). Two strong ridges are running back from the anterior crown margin to one-third of the crown length with 1-3 subparallel ridges between them. The ridges slope down almost to the base rim anteriorly, thus distinctly lowering the scale’s anterior neck. The lateral slopes of the

crown are sharp and well developed. The neck is short, smooth anteriorly, deeper and more concave posteriorly. The base is rhomboid and moderately convex.

Histology (*Fig.4* A-B):

The scales of the first and second varieties have the same histology. The crown is composed of 3-4 odontodes, which are thick on top and sides. All the odontodes are filled with a network of dentine tubules. The canal system is visible on the crown's posterior part, but Stranggewebe only present in the primordial odontode. The base is pyramid-shaped and is composed of cellular bone. Long Sharpey's fibers penetrate radially the base.

Remarks:

Nostolepis striata has been frequently redefined since it was erected by *Pander* (*1856*) for scales from Estonia. *Gross* (*1947*) assigned some acanthodian species, erected by *Brotzen & Leham* (*1934*), into *Nostolepis striata*. *Vergoossen* (*2002b*) agreed with this assignment, but thought the morphological variations of *N. striata* were still too large. After careful observation, *Vergoossen* (*2002b*) defined seven different morphotypes according to the *Nostolepis* scales from Klinta, southern Sweden. We follow their classification and recent descriptions by *Burrow et al.* (*2013*) and *Turner & Burrow* (*2018*). We suggest two kinds of morphotypes here based on the new materials from the Xitun Formation. We combine types 1, 2 and 6, defined in *Vergoossen* (*2002b*), within one group, and types 3 and 7 within another group. The second kind of scales comprises pinnal scales or tesserae as in *Turner & Burrow* (*2018*). Both morphotypes have the typical *Nostolepis* structure with mesodentine and Stranggewebe.

Nostolepis amplifica Valiukevičius, *2003c*

1984 *Nostolepis* sp. indet., Wang, 1984, fig. 3, D-F.
1989 *Nostolepis sinica*, Gagnier et al., 1989, pl.1, figs.3-4.
1999 *Nostolepis striata*, Vergoossen, pl.2, figs. 16-17.
2003c *Nostolepis amplifica*, Valiukevičius, figs. 2, A-H and 3.

Referred Material: 41 trunk scales (IVPP V26832.1-V26832.41)

Description:

Morphotype 1 (*Fig.1* I-N):

The scale crown's length and width range from 0.317-0.658 mm and 0.309-0.647 mm, respectively. Morphotype 1 is elongated with rhombic to ellipsoidal in outline. The crown surface is concave and inclined, with one-fourth of the crown's length overhanging the base posteriorly. Two longest prominent ridges from an elevated median area of the crown, are sculptured by 2-6 rounded, short, subparallel anterior ridges. Most scales have an unsculptured lateral slope on each side of the median area, but some have several ridgelets (*Fig.1* M-N), which are finer and lower than those on the median area.

The neck is well defined and constricted. A row of 3-5 regularly spaced small openings are located on each side of the neck, and sometimes they are also visible anteriorly below the ridges (*Fig.1* I-L). The convex and rectangular base is equal or slightly larger than the crown.

Morphotype 2 (*Fig.1* O-P):

These scales have an inclined median crown surface with two strong main ridges and two inconspicuous lateral slopes on each side of the median area. Crown length varies from 0.6-0.75 mm and width from 0.5-0.65 mm. A shallow and wide longitudinal groove between the two central ridges is another characteristic, forming an incised anterior crown margin. The neck has a row of regularly spaced small openings locating on the side or below the ridge. The scale base of both morphotypes is shaped from isometric to asymmetric rhomboid, sometimes wider than long. The base protrudes anteriorly beyond the crown. It is moderately deep to deep, with the deepest point locating centrally or anteriorly.

Histology (*Fig.4* C-D):

The structures of tissues are similar in the two types. The crown is composed of dentine tubules and Stranggewebe. The winding and short dentine tubules orient upwards. Ascending and vaulted vascular canals can be seen in the posterior part of the crown. Stranggewebe is short, narrow, and medium dense, developing only in the first and second lamellae on the crown's posterior part. The base consists of cellular bone with osteocytes.

Remarks:

This species was erected by *Valiukevičius* (*2003c*) from Pridoli and Ludlow of Lithuania. *Valiukevičius* (*2003c*) indicated that *N. amplifica* was similar to the specimens of *N. striata* described by *Vergoossen* (*2002b*) (pl.14, figs. 85-87) obtained from Öved-Ramsåsa, the Sandstone Formation, Ludlow to Pridoli and *Vergoossen* (*2000*) (pl. 1, figs 4-5 and 7-8), obtained from Welsh Borderland, Silurian to Devonian. ~~But we~~ considered that the specimens described by *Vergoossen* (*2002b*) (pl.14, figs. 85-87) should be *N. striata* as originally suggested. Morphologically, *N. amplifica* is similar to *N. striata*, and the former usually has a shallow and longitudinal groove between the two central ridges. Another difference is that the neck has a row of regularly spaced small openings for *N. amplifica*, but it is rarely reported for *N. striata*. Only two exceptional specimens with neck opening were reported in *N. striata*, which differ from the trunk scales described by *Gross* (*1947*), pl. 7, fig. 13 and *Gross* (*1971*), pl. 5, fig. 3a. Histologically, *Valiukevičius* (*2003c*) also figured that both species have similar mesodentine, Stranggewebe, vascular canals, and large number of osteocytes, but the canal system is more advanced and Stranggewebe is shorter and denser in *N. amplifica*. *N. amplifica* was firstly found by *Wang* (*1984*) (fig. 3D-F) and described as *Nostolepis* sp. indet. from the Xitun Formation. In terms of morphology, some specimens described by *Gagnier et al.* (*1989*) (pl.1, figs. 3-4) from the Yulungssu

Formation, Hongmiao (Shiyanpo), Qujing, which differ from the holotype of *N. sinica* (pl.1, figs.1-2), probably belong to *N. amplifica*

Nostolepis consueta Valiukevičius, 2003c

1984 *Nostolepis* sp. indet., Wang, fig. 3A-C.
1997 *Gomphonchus sandlensis*? Märss, pl3, fig. 5.
1998 *Nostolepis minima*, Valiukevičius, pl1, fig.5.
1998 *Nostolepis* sp. or *Cheiracanthoides* sp., Valiukevičius, pl.1. figs. 10-15.
1998 *Nostolepis striata,* Wang et al., pl.1, fig. A.
2003c *Nostolepis consueta* Valiukevičius, figs 5A-I, 6 and 7.

Emended diagnosis: The crowns are flat, never inclined, and sculptured with 6-12 short and parallel ridges. Low anterior ridges fade out at one-third of the crown's length. The posterior part of the crown is composed of ~~the~~ Stranggewebe and widened ascending vascular canals. The Stranggewebe is dense in each odontode.
Referred Material: around 23 trunk scales (IVPP V26834.1-V26834.23)
Description (*Fig.2* A-H):
The scale crown is flat, never inclined, and has a nearly triangular or ovoid shape. Crown length varies from 0.366-0.697 mm and width from 0.412-0.548 mm. Most of the scale crowns have 3-12 subparallel and short ridges extending one-third of the crown's length, converging towards the posterior end. Lateral slopes lobes are not well developed in most of the scales. The anterior edge of the crown is convex, curving down to the base. The neck is smooth and constricted for most of the scales. A rhombic base is slightly convex, anteriorly vaulted, so that the base protrudes the crown.
Histology (*Fig.4* E-F):
The crown has a relatively big primordial scale and a few growth lamellae thin on top but thick on anterior and posterior parts. The odontodes have dentine tubules, which are dense ~~on~~ anterior. The crown's posterior part is composed of Stranggewebe and widened ascending and vaulted vascular canals (over the base). Stranggewebe is short and densely presented in each odontode. The base is composed of compact, thin-lamellar bone, containing a large number of osteocytes.
Remarks:
For trunk scales, Valiukevičius identified two morphotypes of *N. consueta*. The first type has 8-12 ridges, and the second type has ~~less~~ than 6 ridges. In our collection, most of the referred scales have 6-10 ridges. *N. consueta* is so similar to *N. striata* that some *N. consueta* probably have been misassigned to the latter. *N. consueta* has a flat crown, never inclined, and the anterior ~~point~~ of the crown is ~~always protruding~~. More differences are present in the histological features. *N. consueta* has dense Stranggewebe in each odontode; *N. consueta* has a low number of osteocytes and no

obvious Sharpey's fibers in the base compared with *N. striata*. The scales assigned to *Nostolepis* sp. indet. (*Wang, 1984* fig. 3A-C) probably belong to *N. consueta*. And the specimen (V11528.1) described by *Wang et al.* (*1998*, pl.1, fig. A) from the lower Lochkovian Xiaputonggou Formation, West Qinling, China, should be *N. consueta*.

Nostolepis decora Valiukevičius, 2003a

1989c, *Nostolepis sinica*, Gagnier et al., pl.1, figs.6-7.
2003, *Nostolepis decora,* Valiukevičius, figs. 17 and 18.

Referred Material: 18 trunk scales (IVPP V26836.1-V26836.18).
Description (*Fig.2* I-P):
Small scales with crowns inclined downward at an angle of 30°-45°, ornamented with two ridges that form a medial area and meet together at the posterior end. Crown length varies from 0.227-0.459 mm and width from 0.191-0.337 mm. The distal pointed end overhangs the base posteriorly. Another noticeable characteristic is that the developed lateral crown margins are denticulated. Two distinct pores open laterally on the neck below the ridges. The base is rhomboid and slightly convex, protruding the front of the crown.
Histology (*Fig.5* A-B):
The scales have branching dentine tubules in each odontode. Radial and ascending vascular canals are present in the posterior part of the crown. The base contains abundant osteocyte spaces and Sharpey's fibers. Unfortunately, none of the Stranggewebe in the crown has been preserved due to the recrystallization.
Remarks:
A partially articulated *Nostolepis decora*, exposing lateral squamation, was described by *Valiukevičius* (*2003*) from lower Lochkovian of Severnaya Zemlya. *N. decora* is similar to *N. amplifica*, but the latter has a bigger size and more neck openings. *N. decora* has bigger osteocytes and more complicated system of ascending vascular canals, which is illustrated in a scale from the lateral line or the special tesserae-scale (*Valiukevičius, 200*). Morphologically, the specimens described by *Gagnier et al.* (*1989*) (pl.1, figs. 6-7) as *N. sinica* from the Yulungssu Formation, Hongmiao (Shiyanpo), Qujing, should be assigned to *N. decora*.

Nostolepis qujingensis sp. nov.

Deviation of name: After Qujing city, the fossil site.
Holotype: IVPP V26838.1.
Type locality and horizon: Xitun, Xishan subdistrict, Qujing, Yunnan, China; Xitun Formation, Lochkovian, Lower Devonian.

Referred Material: 16 trunk scales (IVPP V26838.1-V26838.16)
Diagnosis:
Trunk scales are of moderate size, ornamented with longitudinal ridges in the crown. The distal pointed end of the crown always overhangs the base at one-third of its length. The angle between crown and base can reach 45°maximally. The neck is absent anteriorly, but deeper and concave posteriorly. The base is rhomboid, thin, and concave. Dentine tubules rarely present ~~on~~ the anterior part of the crown. Scale base is composed of bone with few osteocytes.
Description (*Fig.3* A-H):
The scale crowns are triangular in shape or irregularly shaped (*Fig.3* E-H). They incline ~~anteriorly~~ at an angle of 30°-45°. Crown length varies from 0.332-0.495 mm and width from 0.357-0.514 mm. The crown is sculptured with longitudinal ridges extending the whole surface (*Fig.3* A-D) or ornamented with radial ridges and deep grooves (*Fig.3* E-H). The lateral slope usually develops in the former ~~ones~~ (*Fig.3* A-D). The crown length varies from 0.4-0.7 mm and width from 0.4-0.5 mm. The neck is absent anteriorly, but deeper and concave posteriorly. The base is rhomboid and thin, never protrudes the crown on all sides.
Histology (*Fig.5* C-D):
The crown's odontodes are very thin, and the dentine tubules are rarely present in each odontode. The Stranggewebe is present in the posterior part of the crown. Wide vascular canals rise from the neck and penetrate the posterior part of the crown. Scattered osteocytes form a low and flat base.
Remarks:
Nostolepis qujingensis is similar to *N. lineleyensis* in the crown sculptured with ridges and grooves at the anterior margin, sloping down at an angle of 30°-45. But *N. lineleyensis* has a much thicker crown and more ridges than *N. qujingensis.* More differences are found in histology. *N. qujingensis and N. lineleyensis* have a similar system of ~~the~~ vascular canal, but the latter ~~one~~ has a typical mesodentine ~~on~~ the crown and cellular bone with numerous large and elongate osteocytes (*Miller & Marss, 1999*).

Nostolepis digitus sp. nov.

Deviation of name: From the Latin *digitus*, referring to the appearance of the crown ornamentation.
Holotype: IVPP V26840.1
Type locality and horizon: Xitun, Xishan subdistrict, Qujing, Yunnan, China; Xitun Formation, Lochkovian, Lower Devonian.
Referred Material: 25 trunk scales (IVPP V26840.1-V26840.25).
Diagnosis:

Large-sized scale ~~bear~~ a sub-rhomboid crown with rounded and widened anterior edge and a slightly tapered posterior end. Short and parallel ridges ~~can be observed~~ on the crown's anterior and lateral margins, curving down to the base. The neck is constricted with small pores. Scale bases are strongly convex; their maximum depth slightly in front of the center. Dentine tubules are dense in each odontode of the crown, and the Stranggewebe is densely distributed in the posterior part of the odontodes. Ascending vascular canals are well developed. The base is filled with numerous osteocytes.

Description (*Fig.3* I-P):

Scale crowns are usually flat, or slightly inclined. Crown length varies from 0.451-0.768 mm and width from 0.413-0.702 mm. The rhombic crown has a round and wide anterior edge and a blunt posterior cusp. The posterior parts of some crowns tilt to one side (*Fig.3* I-J). The crown is ornamented with short and parallel ridges that do not extend to the middle of the crown posteriorly, but bend down anteriorly and laterally. The crown has a smooth lateral slope flanking the posterior part. The neck is short, low~~ered~~ anteriorly, but deeper and concave posteriorly. Only small pores are visible on the neck. The base is strongly convex, vaulted anteriorly and protruding the crown.

Histology (*Fig.5* E-F):

The crown is composed of 3-4 odontodes, and the young one envelops the older one completely. Dentine tubules are dense and discernable in each odontode. The growth lamella contains long ascending vascular canals placed posteriorly in the neck over the scale base. The Stranggewebe is densely present in the posterior part of the outermost odontode. The upper surface of the base forms a high pyramid, and the base is filled with many osteocyte cavities.

Remarks:

The referred specimens are similar to *Nostolepoides mingyinensis* in morphology and histology, which is described from another Devonian site in Yunnan Province (*Wang, 2003*) (p.8, ~~F~~ig 4). Morphologically, the crowns of both species are rhomboid, sculptured with short and parallel ridges, not extending half of the crown length, and the lateral slopes are less developed. But *N.digitus* has a constricted neck and a strong convex base. Histologically, their base tissues are similar in having dense osteocytes. The Stranggewebe is not visible in *Nostolepoides mingyinensis*, and the crown is composed of more odontodes. Morphologically, *N. digitus* is also similar to *Nostolepis* sp. aff. *N. multicostata* reported by *Burrow et al.* (*2006*) (fig.3, 11-12, 15-16) from the Lower Devonian Jawf Formation of northwestern Saudi Arabia. But the Arabian form is much larger than *N. digitus*, and its crown has more ridges.

Discussion and Conclusion

Valiukevičius & Burrow (*2005*) classified the acanthodian scales with *Nostolepis*-like histology into five groups based on the presence or absence and extent of the Stranggewebe, and different types of dentine tubules in scale crowns, which we follow

here. Only the scales composing of typical Stranggewebe and simple odontocytic mesodentine in the crowns are referred to as *Nostolepis*, which is in accordance with the classical diagnosis of *Nostolepis* (*Pander*, *1856*; *Gross, 1971*).

The new *Nostolepis* microfossils in this study indicate a high diversity of 'acanthodian' taxa in the Xitun Formation. So far, 35 acanthodian species have been described from the Silurian and Devonian of China, including nine species of *Nostolepis* in total (*Fig. 6*). The other 31 *Nostolepis* species from the rest of the world are also listed here (*Fig. 6*). Here, we focus on the biostratigraphic and paleogeographic distribution of the *Nostolepis* species from China and discuss their potential biogeographic implications.

As shown in *Fig. 6*, most of *Nostolepis* species have been recorded from the Pridoli to Lochkovian, except for *N. infida* that was recorded in the Emsian. However, *N. musca* and *N. terraborea* were found in the beds from the Ludlow to Pridoli, and the earliest record of *N. consueta, N. tewonensis, N. gracilis* and *N. striata* back to Wenlock. (*Brotzen 1934*; *Babin et al., 1976*; *Denison, 1979*; *Gagnier et al., 1989*; *Wang & Dong, 1989*; *Valiukevičius, 1994*; *Valiukevičius, 1998*; *Wang et al., 1998*; *Miller & Marss, 1999*; *Wang, 2003*; *Valiukevičius, 2003a*; *Valiukevičius, 2003b*; *Valiukevičius, 2003c*; *Valiukevičius, 2004a*; *Valiukevičius, 2005*; *Burrow et al., 2006*; *Burrow & Sues, 2013*; *Pinakhina & Märss, 2018*; *Turner & Burrow, 2018*; *Wang, 2018*;). *N. kernavensis* and *N. gaujensis* are the only taxa from Middle Devonian and Upper Devonian (*Valiukevičius, 1985*; *Burrow, Janvier & Villarroel, 2003*; *Pinakhina & Märss, 2018*;). *N. striata* from many Silurian sites illustrates that it migrated at early time (*Denison, 1979*). *N.consueta* and *N. amplifica* might migrate from Baltic Block to South China (*Valiukevičius, 2003c*).

Some widely distributed 'acanthodians' such as *Gomphonchus*, *Ischnacanthidae*, *Cheiracanthoides*, *Poracanthodes*, *Acanthodes,* and *Machaeracanthus* have also been found in China, as shown in Fig. 6 (*Wang & Dong, 1989*; *Gagnier et al., 1989*; *Wang, 1992*; *Wang et al., 1998*; *Burrow et al., 2000*; *Wang, 2003*). But *Nostolepoides mingyinensis*, *Gansuichthys liui,* and *Lijiangichthys lembodes* were endemic to China (*Wang et al., 1998*; *Wang, 2003*). Most of these 'acanthodians' were described from the Devonian. But *Ischnacanthus* sp., *Hanilepis wangi*, *Gomphonchus sp*., *Poracanthodes qujingensis*, *Gomphonchus sandelensis* and Ischnacanthidae gen. indet. were reported from the Silurian (*Wang & Dong, 1989*; *Wang et al., 1998*) and *Acanthodes* cf. *A. dublinensis* extends to the Eifelian (*Burrow et al., 2000*).

Almost all the *Nostolepis* distribute around Paleo-Tethyes Ocean (*Fig.7*). *N.consueta*, *N. striata* and *N. amplifica* described here (Xitun Formation, Lochkovian) were all recorded from Baltica Block (*Valiukevičius, 2003c*; *Valiukevičius, 2005*). *N. sinica*, found from Qujing, is also morphologically and histologically similar to *N. musca* which is recorded from Baltica Block (*Gagnier et al., 1989*; *Valiukevičius, 2003*). Our new data of *Nostolepis* from Qujing suggest a correlation with East Baltica. Rare *Nostolepis* species was described from North China Block due to the Caledonian

orogeny (*Wang et al., 1998*). *N. striata* is a cosmopolitan ~~one~~, also described from Laurentia and Australia Blocks (*Denison, 1979*; *Valiukevičius, 2005*; *Burrow et al., 2013*; *Turner & Burrow, 2018*). Some other *Nostolepis* species, i.e., *N. alifera*, *N. alta*, *N. elegans*, *N. costata, N. obusta*, *N. robusta, N. magnicostata, N. minima, N. gaujensis, N. latvica, N. kozhymica*, *N. parathleta*, *N. taimyrica, N. tcherkesovae*, *N. terraborea* and *N. linleyensis* were also recorded in Baltica Block, but none of them has been reported in China (*Brotzen, 1934*; *Babin et al., 1976*; *Valiukevičius, 1994*; *Valiukevičius, 1998*; *Miller & Marss, 1999*; *Valiukevičius, 2003b*; *Valiukevičius, 2004b*; *Valiukevičius, 2005*; *Pinakhina & Märss, 2018*). *N. decora* described here had been described by *Valiukevičius* (*2003*) from the Siberia Block. *N. infida, N. arctica*, *N. matukhini*, *N. minima* and *N. taimyrica* were also found in Siberia Block (*Valiukevičius, 1994*). *N. costata* scales was recorded in Arabia Block and some *Nostolepis* spp. were recorded in Kazhakstan, Africa and Si Blocks (*Blieck et al., 1984*; *Tông-Dzuy & Janvier, 1994*; *Tông-Dzuy & Janvier,* 1990; *Burrow et al., 2006*; *Burrow et al., 2010*).

In summary, most of the *Nostolepis* species range from the Upper Silurian to Lower Devonian. *Nostolepis* distributes mainly in South China, Baltica, Siberia, Laurentia, and Australia blocks, ~~and scatters~~ in Arabia, Africa, Si and Kazhakstan Blocks. Biostratigraphic data of *Nostolepis* were very similar between South China and Baltica blocks.

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References

Babin C, Goujet D, Lardeux H, Lejal-Nicol A, Lethiers F, Morzadec P, Plusquellec Y, Weyant M. 1976. La formation des schistes de porsguen (Dévonien supérieur de la rade de Brest, Massif Armoricain) Lithologie, flore, faune. *Annales de la Société géologique du Nord* **96(4):**333-346.

Berg LS. 1940. Classification of fishes both recent and fossil. *Trudy Instituta Zoologicheskikh Akademiia Nauk* **5:**85-517.

Blieck A, Goujet D, Janvier P, Lelièvre H. 1984. Microrestes de vertébrés du Siluro-Dévonien d'Algérie, de Turquie et de Thaïlande. *Geobios* **17(6):**851-859 DOI 10.1016/S0016-6995(84)80125-4.

Brazeau MD. 2009. The braincase and jaws of a Devonian 'acanthodian' and modern gnathostome origins. *Nature* **457(7227):**305-308 DOI 10.1038/nature07436.

Brotzen F. 1934. Die Morphologie und Histologie der Proostea·(Acanthodiden) Schuppen. *Arkiv för Zoologi* **26:**1-27.

Burrow CJ. 1997. Microvertebrate Assemblages from the Lower Devonian (pesavis/sulcatus zones) of Central New South Wales, Australia. *Modern Geology* **21(1-2):**43-77.

Burrow CJ, den Blaauwen J, Newman M, Davidson R. 2016. The diplacanthid fishes (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland. *Palaeontologia Electronica* **19(1):**1-83.

Burrow CJ, Ivanov A, Rodina O. 2010. Emsian vertebrate microremains from the Zinzilban section, Uzbekistan. *Palaeoworld* **19(1-2):**75-86 DOI 10.1016/j.palwor.2009.11.004.

Burrow CJ, Janvier P, Villarroel C. 2003. Late Devonian acanthodians from Colombia. *Journal of South American Earth Sciences* **16(2):**155-161 DOI 10.1016/s0895-9811(03)00026-9.

Burrow CJ, Lelièvre H, Janjou D. 2006. Gnathostome microremains from the Lower Devonian Jawf Formation, Saudi Arabia. *Journal of Paleontology* **80(3):**537-560 DOI 10.1666/0022-3360(2006)80[537:GMFTLD]2.0.CO;2.

Burrow CJ, Murphy MA. 2016. Early Devonian (Pragian) vertebrates from the northern Roberts Mountains, Nevada. *Journal of Paleontology* **90(4):**734-740 DOI 10.1017/jpa.2016.58.

Burrow CJ, ~~Sues H. 2013.~~ Reassessment of Ischnacanthus? scheii Bjeldnaes (Acanthodii, Ischnacanthiformes) from the latest Silurian or earliest Devonian of Ellesmere Island, arctic Canada. *Canadian Journal of Earth Sciences* **50(9):**945-954 DOI 10.1139/cjes-2013-0068.

Burrow CJ, and Turner S. 2010. Reassessment of "Protodus" scoticus from the Early Devonian of Scotland. *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes* München: Verlag Dr. Friedrich Pfeil 123-144.

Burrow CJ, Turner S, Nowlan GS, Denison RH. 2013. Vertebrate Microremains from the Late Silurian of Arisaig, Nova Scotia, Canada. *Journal of Paleontology* **87:**1041-1059 DOI 10.1666/12-154.

Burrow CJ, Turner S, Wang ST. 2000. Devonian microvertebrates from Longmenshan, Sichuan, China: Taxonomic assessment. *Courier Forschungsinstitut Senckenberg* **223(223):**391-451.

Chang MM. 1982. The braincase of *Youngolepis,* a Lower Devonian crossopterygian from Yunnan, south-western China. Stockholm: University of Stockholm, Department of Geology.

Chang MM, Yu XB. 1984. Structure and phylogenetic significance of *Diabolichthys speratus* gen. et sp. nov., a new dipnoan-like form from the Lower Devonian of eastern Yunnan, China. *Proceedings of the Linnean Society of New South Wales* **107:**171-184.

Davis SP, Finarelli JA, Coates MI. 2012. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature* **486:**247-250 DOI 10.1038/nature11080.

Denison RH. 1979. *Acanthodii*. Stuttgart: Gustav Fischer Verlag.

Gagnier PY, Jahnke H, Shi Y. 1989. A fish fauna of the Lower Yulongsi Formation (Upper Silurian) of Qujing (E. Yunan, S.W.China) and its depositional environment. *Courier Forschungsinstitut Senckenberg* **110:**123-135.

Giles S, Friedman M, Brazeau MD. 2015. Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome. *Nature* **520:**82-85 DOI 10.1038/nature14065.

Gross W. 1947. Die Agnathen und Acanthodier des Obersilurischen Beyrichienkalks. *Palaeontographica Abteilung A* **96:**91-158.

529 **Gross W. 1957.** Mundzähne und Hautzähne der Acanthodier und Arthrodiren.
530 *Palaeontographica Abteilung A* **109:**1-40.
531 **Gross W. 1971.** Downtonische und dittonische Acanthodier-Reste des Ostseegebietes.
532 *Palaeontographica Abteilung A* **136(1-6):**1-82.
533 **Huang BC, Yan YG, Piper JDA, Zhang DH, Yi ZY, Yu S, Zhou TG. 2018.**
534 Paleomagnetic constraints on the paleogeography of the East Asian blocks
535 during Late Paleozoic and Early Mesozoic times. *Earth-science reviews* **186:** 8-
536 36 DOI 10.1016/j.earscirev.2018.02.004.
537 **Long JA, Mark-Kurik E, Johanson Z, Lee MS, Young GC, Zhu M, Ahlberg PE,**
538 **Newman M, Jones R, Blaauwen JD, Choo B, Trinajstic K. 2015.** Copulation in
539 antiarch placoderms and the origin of gnathostome internal fertilization. *Nature*
540 **517:**196-199 DOI 10.1038/nature13825.
541 **Märss T. 1997.** Vertebrates of the Pridoli and Silurian-Devonian Boundary beds in
542 Europe. *Modern Geology* **21(1):**17-41.
543 **Miller CG, Märss T. 1999.** A conodont, thelodont and acanthodian fauna from the
544 Lower Pridoli (Silurian) of the Much Wenlock area, Shropshire. *Palaeontology*
545 **42(4):**691-714.
546 **Owen R. 1846.** Lectures on the Comparative Anatomy and Phvslology of the Vertebrate
547 Animals, Part I. London: Longman, Brown, Green and Longman.
548 **Pander CH. 1856.** Monographie der fossilen Fische des silurischen Systems der
549 russischbaltischen Gouvernements. St Petersburg: Akademie der
550 Wissenschaften.
551 **Pinakhina DV, Märss T. 2018.** The Middle Devonian acanthodian assemblage of the
552 Karksi outcrop in Estonia. *Estonian Journal of Earth Sciences* **67:**96 DOI
553 10.3176/earth.2018.07.
554 **Tông-Dzuy T, Janvier P. 1990.** Les Vertébrés du Dévonien inférieur du Bac Bo oriental
555 (provinces de Bac Thaï et Lang Son, Viêt Nam). *Bulletin du Muséum national*
556 *d'Histoire naturelle, Paris 4e sér, Section C* **12(2):**143-223.
557 **Tông-Dzuy T, Janvier P. 1994.** Early Devonian fishes from Trang Xa (Bac Thai,
558 Vietnam), with remarks on the distribution of the vertebrates in the Song Cau
559 Group. *Journal of Southeast Asian Earth Sciences* **10:**235-243.
560 **Turner S, Burrow CJ. 2018.** Microvertebrates from the Silurian–Devonian boundary
561 beds of the Eastport Formation, Maine, eastern USA. *Atlantic Geology* **54:**171-
562 187 DOI 10.4138/atlgeol.2018.006.
563 **Valiukevičius J. 1985.** Acanthodians from the Narva Regional Stage of the Main
564 Devonian Field. *Mokslas, Vilnius* **1:**144.
565 **Valiukevičius J. 1994.** Acanthodians and their stratigraphical significance. *Stratigraphy*
566 *and Fauna of the Lower Devonian of the Tareya Key Section (Taimyr), Leningrad,*
567 *Nedra*:131-197.
568 **Valiukevičius J. 1998.** Acanthodians and zonal stratigraphy of Lower and Middle
569 Devonian in East Baltic and Byelorussia. *Palaeontographica Abteilung A* **248:**1-
570 53.
571 **Valiukevičius J. 2003a.** Devonian acanthodians from Severnaya Zemlya Archipelago
572 (Russia). *Geodiversitas* **25(1):**131-204.
573 **Valiukevičius J. 2003b.** New Late Silurian to Middle Devonian acanthodians of the
574 Timan-Pechora region. *Acta Geologica Polonica* **53(3):**209-245.

Valiukevičius J. 2003c. New silurian nostolepids (acanthodii, Pisces) of Lithuania. *Geologija* **42:**51-68.
Valiukevičius J. 2004a. New Wenlock-Pridoli (Silurian) acanthodian fishes from Lithuania. *Acta Palaeontologica Polonica* **49(1):**147-160.
Valiukevičius J. 2004b. Silurian acanthodian succession of the Luzni-4 borehole (Latvia). *Acta Universitatis Latviensis* **679:**120-147.
Valiukevičius J. 2005. Silurian acanthodian biostratigraphy of Lithuania. *Geodiversitas* **27(3):**349-380.
Valiukevičius J, Burrow CJ. 2005. Diversity of tissues in acanthodians with Nostolepis−type histological structure. *Acta Palaeontologica Polonica* **50(3):**635-649.
Vergoossen JMJ. 1999. Late Silurian fish microfossils from an East Baltic-derived erratic from Oosterhaule, with a description of new acanthodian taxa. *Geologie en Mijnbouw* **78(2):**231-251.
Vergoossen JMJ. 2000. Acanthodian and chondrichthyan microremains in the Siluro-Devonian of the Welsh Borderland, Great Britain, and their biostratigraphical potential. *Courier Forschungsinstitut Senckenberg* **223:** 175-200.
Vergoossen JMJ. 2002a. Late Silurian fish microfossils from Ramsåsa, locality H, Scania, South Sweden, with some remarks on the body zonation scheme used in thelodont studies. *Scripta Geologica* **123:**41-69.
Vergoossen JMJ. 2002b. Late Silurian fish microfossils from Klinta and Rinnebäcks Bro (Scania, South Sweden), with remarks on the morphology of Nostolepis striata trunk scales. *Scripta Geologica* **123:**71-92.
Vergoossen JMJ. 2003a. First record of fish microfossils from Ramsåsa, site C, Skåne, southern Sweden. *Scripta Geologica* **126:**1-78.
Vergoossen JMJ. 2003b. Fish microfossils from the Upper Silurian Oved Sandstone Formation, Skane, southern Sweden. Ph.D. Rijksuniversiteit Groningen.
Vergoossen JMJ, Pickerill RK. 2004. Fish microfossils from Ramsasa, site E, Scania, southern Sweden (mid Palaeozoic). National Natuurhistorisch Museum.
Wang HH, Ma XP, Ladislav S, Wei F, Zhang MQ, Lv D. 2018. Lower devonian conodont biostratigraphy of the Alengchu Section in Western Yunnan Province, South China. *Journal of Stratigraphy* **(42)3:**288-300.
Wang NZ. 1984. Thelodont, acanthodian, and chondrichthyan fossils from the Lower Devonian of southwestern China. *Proceedings of the Linnean Society of New South Wales* **107:**419-441.
Wang NZ. 1992. Microremains of agnathans and fishes from Lower Devonian of Central Guangxi with correlation of Lower Devonian between central Guangxi and eastern Yunnan, South China. *Acta Palaeontologica Sinica* **31(3):**280-303.
Wang NZ, Dong ZZ. 1989. Discovery of Late Silurian microfossils of Agnatha and fishes from Yunnan, China. *Acta Palaeontologica Sinica* **28(2):**192-206.
Wang NZ, Wang JQ, Zhang GR, Wang ST. 1998. The first discovery of Silurian and Early Devonian acanthodians from Zoige and Tewo counties, west Qinling Mountains. *Vertebrata PalAsiatica* **36(4):**268-281.
Wang W. 2003. First occurrence of acanthodian microfossils from the Early Devonian of Lijiang, Yunnan, China. *Vertebrata PalAsiatica* **41(1):**1-16.
Zhao WJ, Zhu M. 2015. A review of Silurian fishes from Yunnan, China and related

biostratigraphy. *Palaeoworld* **24(1-2):** 243-250 DOI 10.1016/j.palwor.2015.02.004.

Zhu M. 1996. The phylogeny of the Antiarcha (Placodermi, Pisces), with the description of Early Devonian antiarchs from Qujing, Yunnan, China. *Bulletin du Muséum national d'Histoire naturelle* **18:**233-347.

Zhu M, Yu XB. 2002. A primitive fish close to the common ancestor of tetrapods and lungfish. *Nature* **418(6899):**767-770.

Zhu M, Yu XB, Ahlberg PE. 2001. A primitive sarcopterygian fish with an eyestalk. *Nature* **410(6824):**81-84.

Zhu M, Yu XB, Janvier P. 1999. A primitive fossil fish sheds light on the origin of bony fishes. *Nature* **397:**607-610.

Zhu M, Yu XB, Wang W, Zhao WJ, Jia LT. 2006. A primitive fish provides key characters bearing on deep osteichthyan phylogeny. *Nature* **441(7089):**77-80. DOI 10.1038/nature04563

Zhu M, Yu XB, Ahlberg PE, Choo B, Lu J, Qiao T, Qu QM, Zhao WJ, Jia LT, Blom H, Zhu YA. 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* **502(7470):**188-193 DOI 10.1038/nature12617.

Figure 1

Figure 1: SEM photos of *Nostolepis striata* and *Nostolepis amplifica* scales.

(A)-(H) *Nostolepis striata*. (A) Crown view, IVPP V26830.1. (B) Crown view, IVPP V26830.2. (C) Crown view, IVPP V26830.3. (D) Crown view, IVPP V26830.4. (E) Crown view and (F) Base view, IVPP V26830.5. (G) Crown view, IVPP V26830.6. (H) Crown view, IVPP V26830.7. (I)-(P) *Nostolepis amplifica*. (I) Crown view and (J) Antero-lateral view, IVPP V26832.1. (K) Crown view and (L) Antero-lateral view, IVPP V26832.2. (M) Crown view and (N) Lateral view, IVPP V26832.3. (O) Crown view and (P) Base view, IVPP V26832.4. Scale bars 0.1 mm. Lochkovian, Early Devonian, Xitun Formation, Qujing.

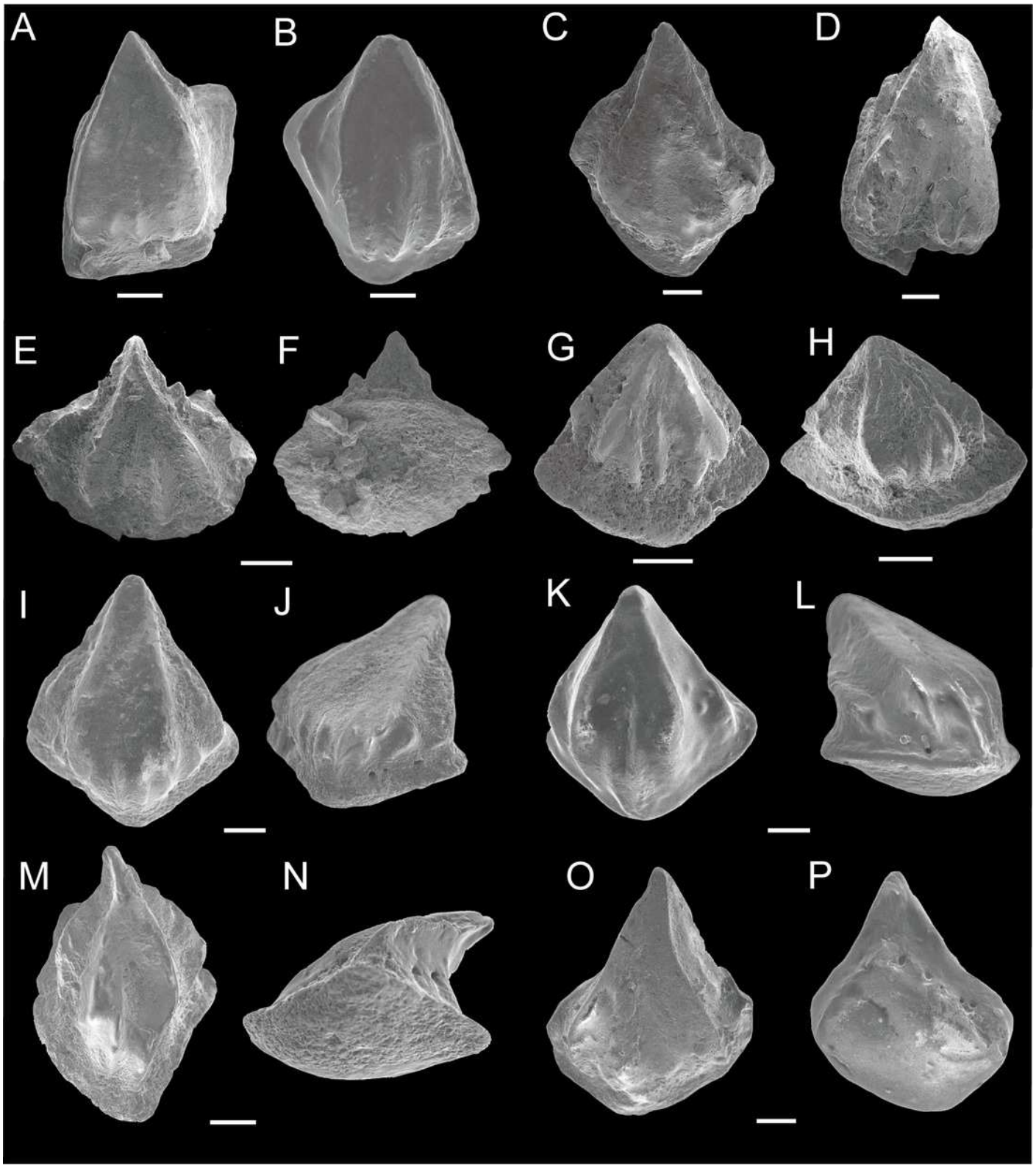
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Figure 2

Figure 2: SEM photos of *Nostolepis consueta* and *Nostolepis decora* scales.

(A)-(H) *Nostolepis consueta*. (A) Crown view and (B) Postero-lateral view, IVPP V26834.1. (C) Crown view and (D) Base view, IVPP V26834.2. (E) Crown view and (F) Antero-lateral view, IVPP V26834.3. (G) Crown view, IVPP V26834.4. (H) Antero-lateral view, IVPP V26834.5. (I)-(P) *Nostolepis decora*. (I) Crown view and (J) Base view, IVPP V26836.1. (K) Crown view, IVPP V26836.2. (L) Crown view, IVPP V26836.3. (M) Crown view, IVPP V26836.4. (N) Crown view, IVPP V26836.5. (O) Crown view, IVPP V26836.6. (P) Antero-lateral view, IVPP V26836.7. Scale bars 0.1 mm. Lochkovian, Early Devonian, Xitun Formation, Qujing.

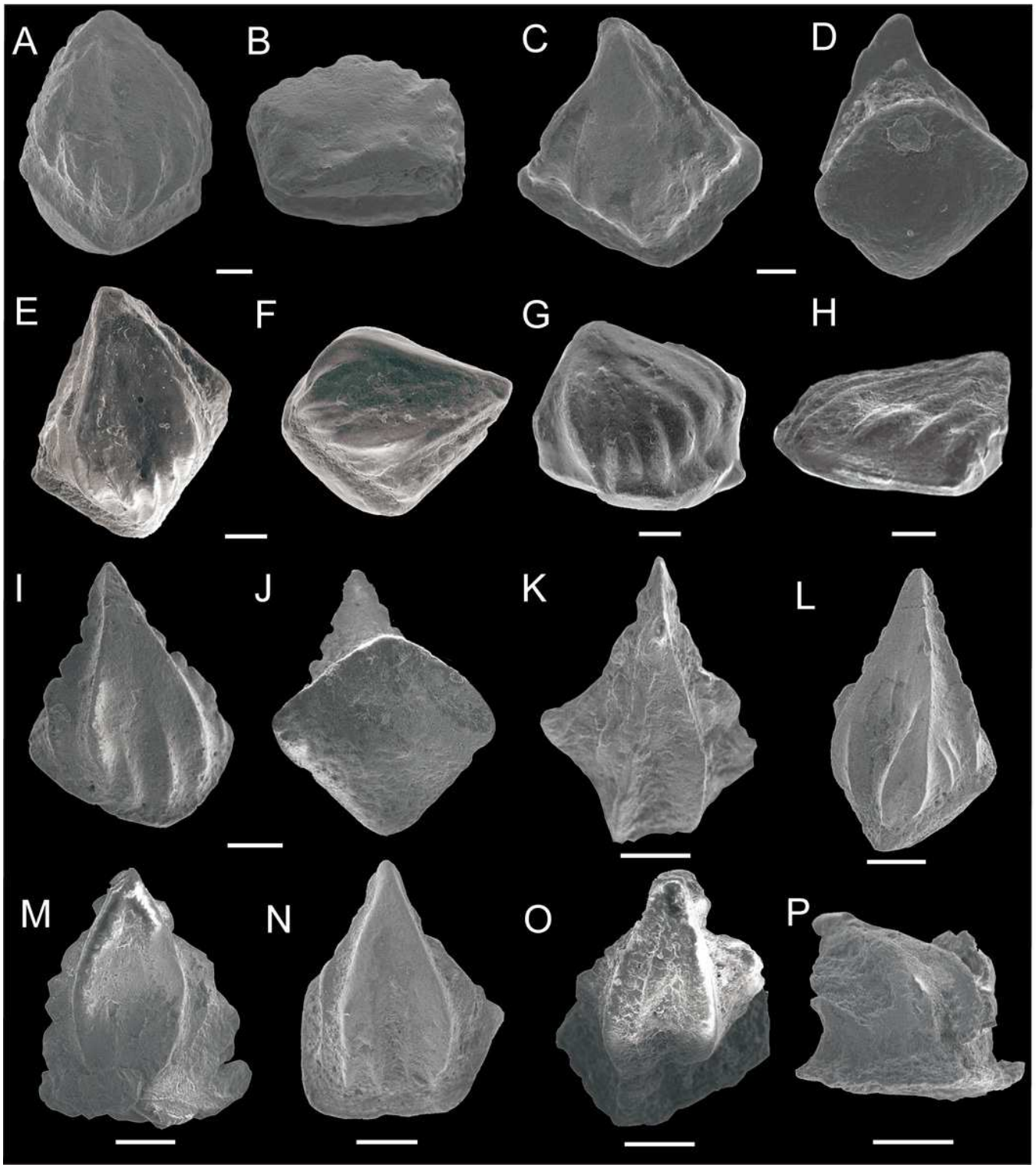
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Figure 3

Figure 3: SEM photos of *Nostolepis qujingensis* sp. nov and *Nostolepis digitus* sp. nov. scales.

(A)-(H) *Nostolepis qujingensis* sp. nov. (A) Crown view and (B) Base view, IVPP V26838.1, holotype. (C) Crown view and (D) Lateral view , IVPP V26838.2 . (E) Antero-lateral view and (F) Crown view, IVPP V26838.3. (G) Crown view and (H) Base view, IVPP V26838.4. (I)-(P) *Nostolepis digitus* sp. nov. (I) Crown view, IVPP V26840.1, holotype. (J) Crown view, IVPP V26840.2. (K) Lateral view, IVPP V26840.3. (L) Lateral view, IVPP V26840.4. (M) Crown view and (N) Lateral view, IVPP V26840.5. (O) Crown view and (P) Base view, IVPP V26840.6. Scale bars 0.1 mm. Lochkovian, Early Devonian, Xitun Formation, Qujing.

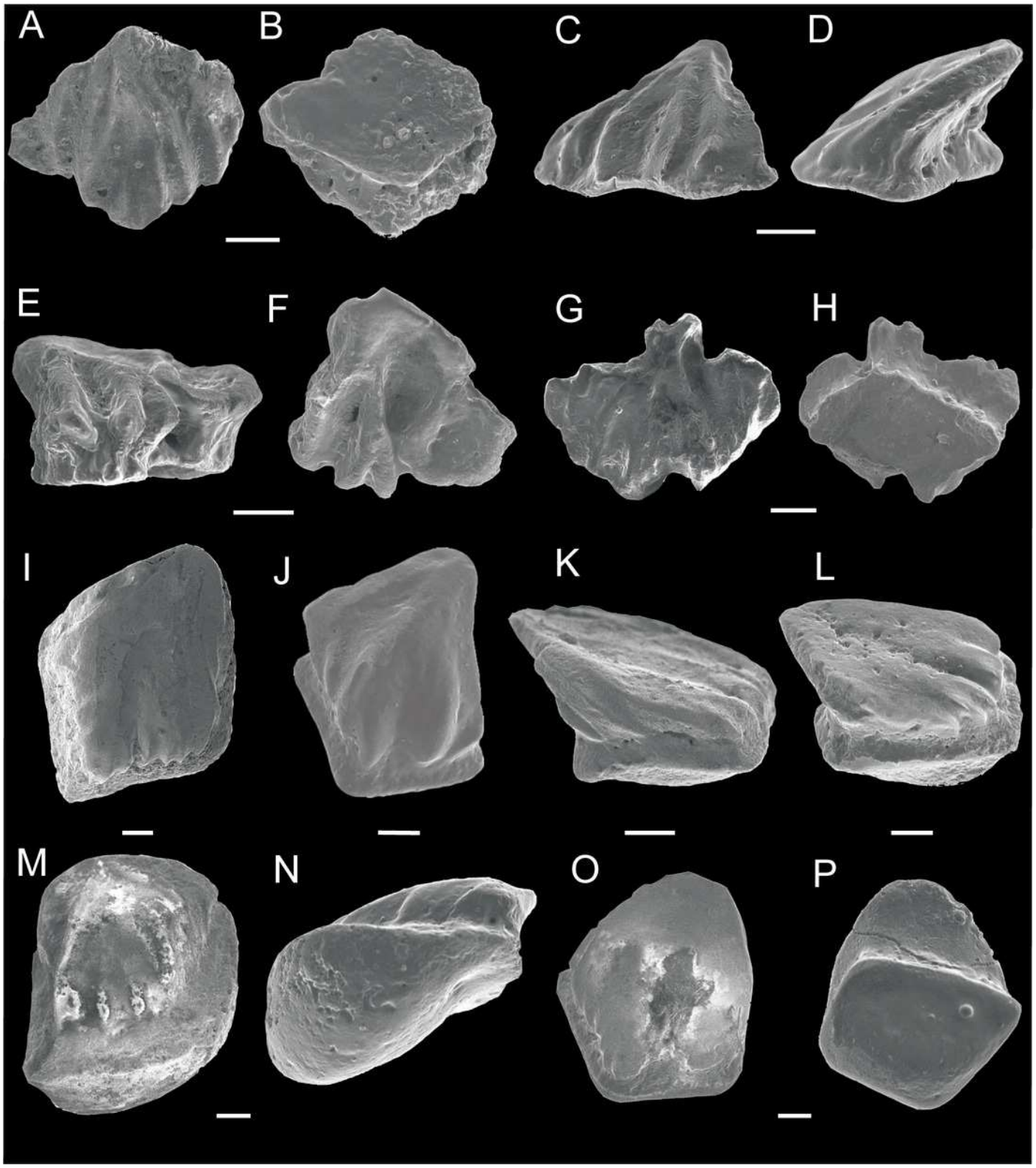
A
B
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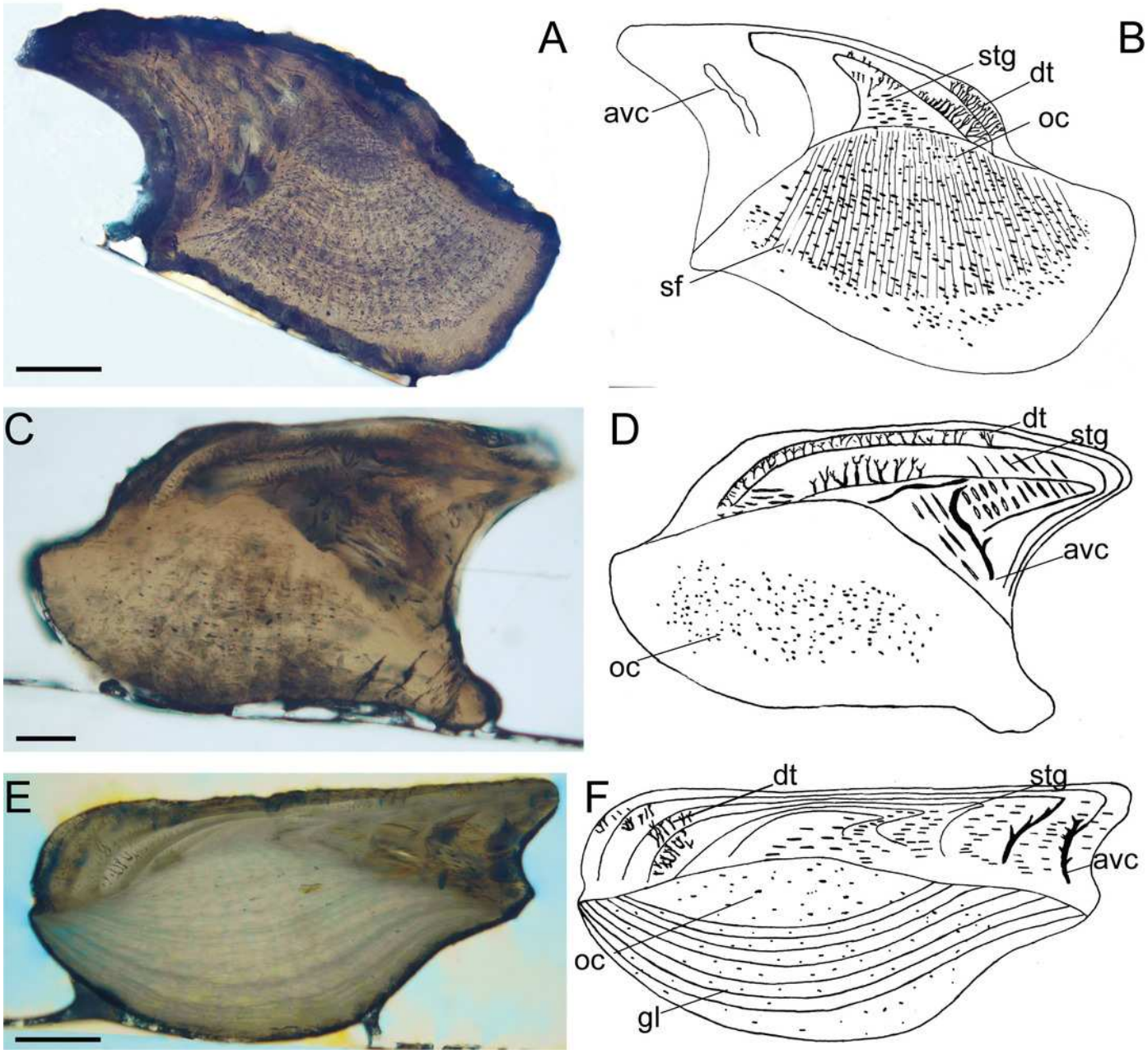
Figure 4

Figure 4: Histological microstructure and illustrative drawings of *Nostolepis striata, Nostolepis amplifica*, and *Nostolepis consueta* scales in vertical longitudinal sections.

(A)-(B) *Nostolepis striata,* IVPP V26831. (C)-(D) *Nostolepis amplifica*, IVPP V26833. (E)-(F) *Nostolepis consueta*, IVPP V26835. *dt*-dentine tubule; *oc*-osteocyte cavity; *stg-Stranggewebe*; *gl*-growth lamella; *avc*-ascending vascular canal; *sf*-Sharpey's fibers. Scale bars 0.1 mm.


A
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gl

Figure 5

Figure 5: Histological microstructure and illustrative drawings of *Nostolepis decora, Nostolepis qujingensis* sp. nov.and *Nostolepis digitus* sp. nov. scales in vertical longitudinal sections.

(A)-(B) *Nostolepis decora*, IVPP V26837. (C)-(D) *Nostolepis qujingensis* sp. nov., IVPP V26839. (E)-(F) *Nostolepis digitus* sp. nov., IVPP V26841. *dt*-dentine tubule; *oc*-osteocyte cavity; *stg*-*Stranggewebe*; *gl*-growth lamella; *avc*-ascending vascular canal; *sf*-Sharpey's fibers. Scale bars 0.1 mm.

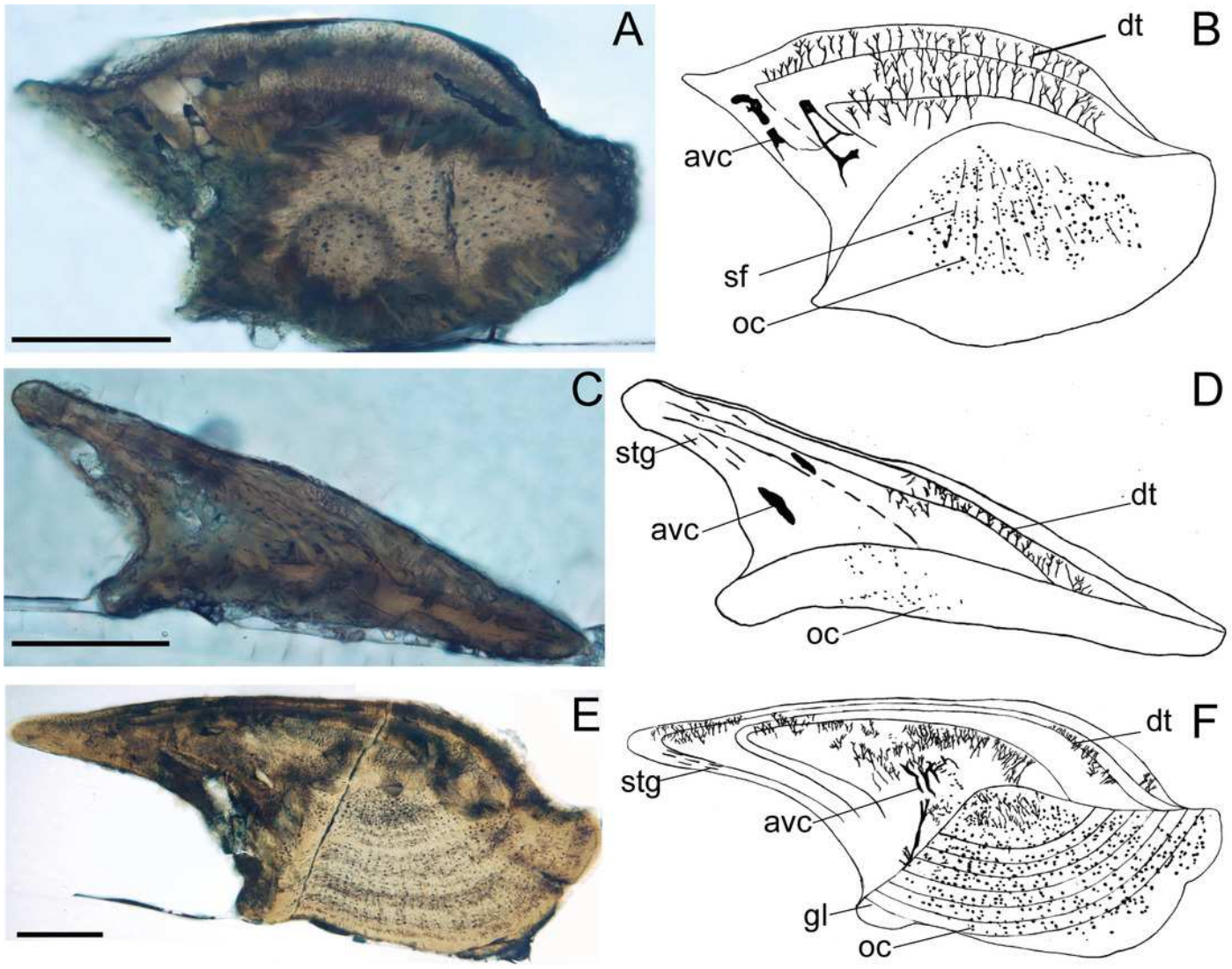

Figure 6

Figure 6: Stratigraphical ranges of *Nostolepis* in the world and acanthodians in China from Silurian to Middle Devonian.

Modified from *Wang, 2003*; *Valiukevičius, 2003b*; *Valiukevičius, 2005* and *Zhao & Zhu, 2015*.


Wen-lock
Ludlow
Pridoli
Lower Devonian
Middle Devonian
species
Home-rian
Gors-tian
Ludfo-rdian
Lochkovian
Prag-ian
Emsian
Eifelian
Givetian
N. consueta
N. tewonensis
N. gracilis
N. striata
N. musca
N. terraborea
N. sinica
N. amplifica
N. latvica
N. magnicostata
N. linleyensis
N. alifera
N. alta
N. elegans
N. robusta
N. decora
N. kozhymica
N. parathleta
N. taimyrica
N. costata
N. scotica
N. obusta
N. matukhini
N. tcherkesovae
N. minima
N. digitus
N. qujingensis
N. arctica
N. infida
N. kernavensis
N. gaujensis
Ischnacanthys sp.
Hanilepis wangi
Gomphonchus sp.
Poracanthodes qujingensis
Gomphonchus sandelensis
Ischnacanthidae gen. indet.
Cheiracanthoides sp.
Cheiracanthoides cf. C. wangi
Nostolepoides mingyinensis
Gansuichthys liui
Poracanthodes zoigenensis
Poracanthodes cf. P. porosus
Nostovicina guangxiensis
Gomphonchus liujingensis
Machaeracanthus? bohemicus
Lijiangichthys lembodes
Tareyacanthus aff. T. magnificus
cf.Trundlelepis sp.
Cheiracanthoides cf. C. comptus
Cheiracanthoides comptus
Cheiracanthoides dolosus
Acanthodes cf. A. dublinensis
Machaeracanthus? sp.
Cheiracanthoides wangi
Youngacanthus gracilis
Rhadinacanthus? sp.

Figure 7

Figure 7: *Nostolepis* distribution in Lower Palaeozoic terranes around 400 Ma (Early Devonian).

Modified from *Huang et al., 2018*.