Chondrichthyan remains from the Lower Carboniferous of Muhua, southern China

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The shallow water assemblage of chondrichthyan microremains, teeth, tooth plates and scales, from the middle Tournaisian (Mississippian) of the vicinity of Muhua village, Guizhou province, southern China, is thus far the richest and most diverse association of this age collected from a single locality and horizon, and represents a chondrichthyan community very restricted in time and space. It was recovered from a small bioclastic limestone lens, MH-1, occurring among basinal marls near the base of the Muhua Formation, and dated as to the *Siphonodella crenulata* conodont Zone. The majority of the fauna presented here consists of teeth with euselachian-type bases and crushing crowns belonging to bottom-dwelling durophagous chondrichthyans, most probably feeding on shelly invertebrates such as the abundant brachiopods. We assigned most of these teeth to Euselachii (six species, among them *Cassisodus margaritae* gen. et sp. nov.), Petalodontiformes (two species), Holocephali (five species), and Euchondrocephali incertae sedis (*Cristatodens sigmoidalis* gen. et sp. nov.). We also identified primitive polycuspid, clutching teeth representing Phoebodontiformes (*Thrinacodus bicuspidatus* sp. nov.), Symmoriiformes, and Ctenacanthiformes. The scales are typical growing, compound forms of the protacrodont, ctenacanth, and hybodont types. Two problematic denticulated plates were found, one of which resembles mandibular or palatal plates of *Sibyrhynchus* (Iniopterygii). Several of the identified chondrichthyan taxa have hitherto been known only from Laurussia, especially from the British Isles and central USA. In particular we found the first record of *Chondrenchelys* sp. and *Diclitodus denshumani* outside their type locality. *Th. bicuspidatus* sp. nov., also known from Nevada, Iran, and NW Australia, appears to be a cosmopolitan, middle Tournaisian index fossil.

Key words: Chondrichthyes, Elasmobranchii, Euchondrocephali, teeth, tooth plates, Carboniferous, Tournaisian, China.

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Introduction

Despite the large number of publications describing assemblages of isolated chondrichthyan remains from the Mid- to Late Palaeozoic rocks, relatively few papers deal with the middle Tournaisian. Most works concentrated on the Middle (Long and Young 1995) and Late Devonian (particularly Famennian, e.g., Gross 1973; Ginter et al. 2002), the Devonian–Carboniferous boundary (e.g., Ivanov 1996; Wang and Turner 1985; Wang 1989), and the late Mississippian (Agassiz 1833–44 and many others). Newberry and Worthen (1866) and St. John and Worthen (1875, 1883) did describe chondrichthyan teeth and tooth plates from the Kinderhookian (lower part of the Tournaisian) of central USA, but their works are based on superficial collecting of specimens as macrofossils, so probably a lot of smaller teeth, available only by acid leaching, escaped their attention. There are several interesting collections of chondrichthyan microremains from the higher zones of the Tournaisian around the world, such as the assemblages from Kilbride in Ireland (Duncan 1999), from the Canning Basin in NW Australia (John Talent's collection, Macquarie University, Sydney), and from Nevada and adjacent states (Charles A. Sandberg's collection, Denver). These collections are precisely dated by conodonts, but thus far they were only preliminarily studied or selected taxa were published (Duncan 2003, 2004).

The rich and diverse assemblage that we present herein, consisting of more than 100 chondrichthyan teeth and tooth-plates, plus numerous shark and actinopterygian scales (Fig. 13), is unique, because it comes from a single sample, or rather a few pieces of rock from a small limestone lens. The samples, numbered collectively as MH-1, were collected near the base of the Muhua Formation (middle Tournaisian, *Siphonodella crenulata* conodont Zone) in the vicinity of the Muhua III Section of Hou et al. (1985: 11), Changshun, Guizhou, southern China (Fig. 1B). The GPS coordinates of the sampling site is N 25°47'59'' and E 106°24'11''.

The natural outcrop MH is located northwest of the small village of Muhua (Fig. 1A) and belongs to a series of outcrops of Late Devonian and Mississippian beds. The lens which yielded the studied material is built of detrital, bioclastic limestone and surrounded by marls (Fig. 1C). It is 10 cm thick and

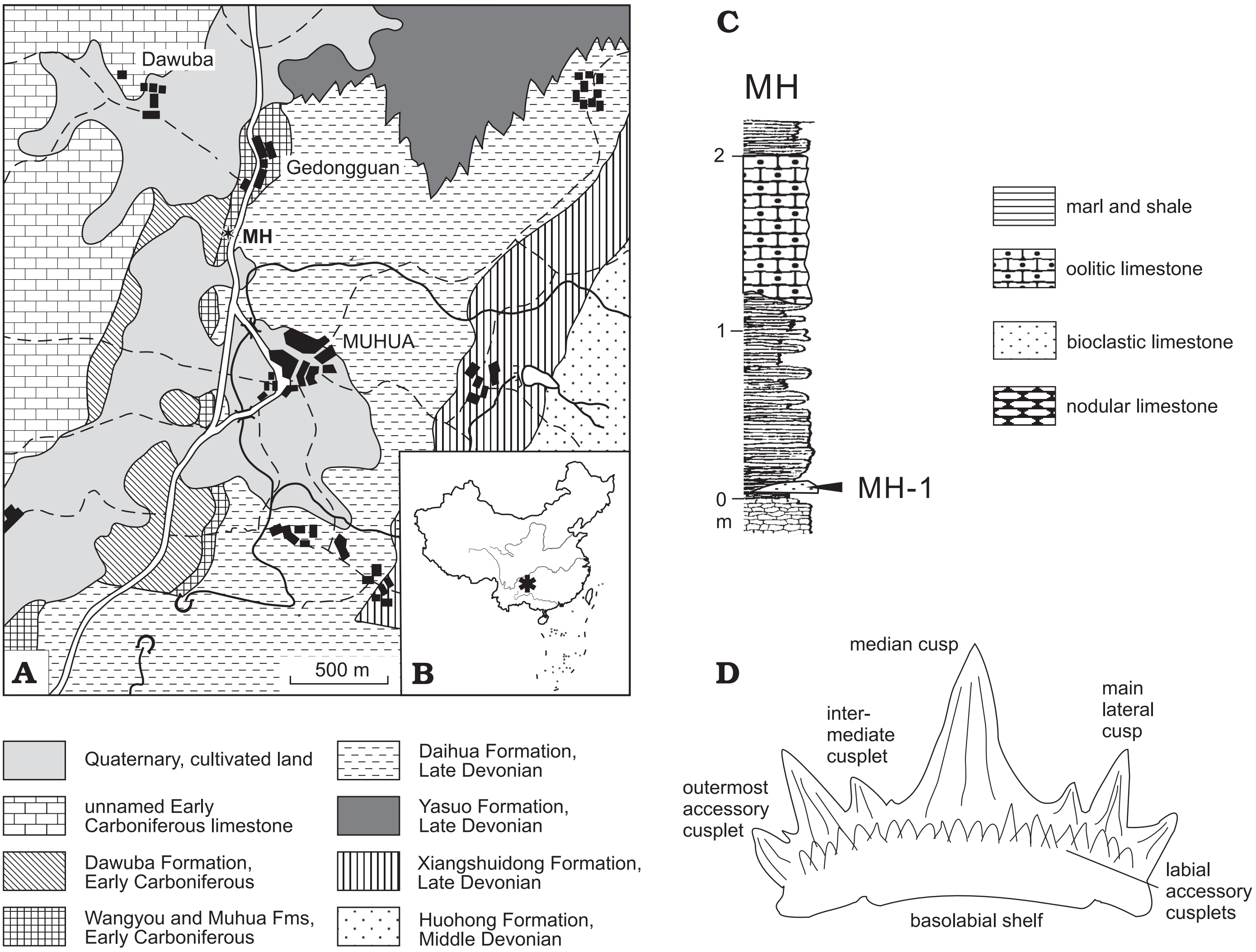

Fig. 1. **A**. Geology of the area of Muhua; location of the studied section (MH) marked with asterisk. **B**. Location of the Muhua locality in China. **C**. Stratigraphic column of the MH section with the position of the studied sample (MH-1). **D**. Major morphological terms of a cladodont tooth in labial view. A–C, courtesy of A. Baliński.

extends for about 1 m. Such lenses occur at various heights above the base of the Muhua Formation, within the basal marly sequence, in this and nearby outcrops (see Sun, Ma, et al. 2004: fig. 1). In Mu and M2 sections they are situated relatively high (1.3 m and almost 4 m above the base, respectively), but in MH the lens starts almost immediately on top of the underlying limestones of the Wangyou Formation. The lithology of the marls, as well as the conodonts found in this part of the Muhua Formation (mainly siphonodellids, some pseudopolygnathids) suggest the pelagic conditions of deposition. However, the invertebrate fauna of the detrital limestone lenses, and especially benthic ostracodes (Olempska 1999) and brachiopods (Baliński 1999; Sun, Baliński, et al. 2004; Sun, Ma, et al. 2004) indicate a rather shallow, carbonate platform environment. It is possible that the lenses are products of the slumping of partly consolidated carbonaceous material from submarine rises into nearby basins, similar to the crinoid limestone bodies in the Viséan of Ostrówka, Holy Cross Mountains, Poland (Szulczewski et al. 1996).

The taxonomic composition of the chondrichthyan assemblage (Table 1) corroborates this assumption (see discussion at the end). The preservation of the ichthyoliths is rather special. Some are preserved extremely well, with even delicate cusps untouched, but others are partly or completely devoid of basal tissue which looks as though it has been chemically dissolved; from others the outer layer of the crown has been removed. Many teeth and scales are covered with minute, clearly diagenetic crystallites. Interestingly, the occlusal surfaces may be worn, but few teeth are mechanically abraded all over by turbulence. This suggests that in most cases the ichthyoliths were quickly covered by sediment and diagenetic processes were responsible for their partial destruction. The perfect preservation of other delicate fossils suggests that, too. The brachiopod shells found in the sample are usually complete but silicified. All this shows that intensive recrystallisation and substitution took place. The specimens are generally black with grey or brownish enameloid, where preserved.

Table 1. Frequency of chondrichthyan teeth and tooth-plates in the sample MH-1 from Muhua.

Taxon		Number of specimens
Thrinacodus bicuspidatus		9
Stethacanthus sp.		10
Tamiobatis sp.		25
Protacrodus cf. *serra*		1
Protacrodus sp.		4
Protacrodontoidea gen. et sp. indet.		3
Cassisodus margaritae		4
Hybodontiformes gen. et sp. indet.		2
Euselachii gen. et sp. indet.		3
Chomatodus linearis		1
Chomatodus? *davisi*		4
Helodus coniculus		15
Diclitodus denshumani		1
Deltodus sp.		2
Chondrenchelys sp.		3
Chondrenchelyidae gen. et sp. indet.		1
Cristatodens sigmoidalis		5
Crushing teeth	Type 1	1
	Type 2	3
	Type 3	1
	Type 4	1
	Type 5	1
Total classified teeth		100
Unclassified fragments of crushing teeth		~10

Despite the partial destruction of several specimens, the material is of considerable value. There are numerous hitherto unknown forms among the examined teeth, some of which were described herein as new genera and species, but others, represented only by one or two specimens, are temporarily kept in open nomenclature. Further discoveries and comparative studies will reveal if they deserve their own specific names or belong within the range of heterodonty of already established taxa.

Institutional abbreviations.—BGS, British Geological Survey, Keyworth, England; BGS-GSE, British Geological Survey, Edinburgh, Scotland; BMNH, The Natural History Museum, London, England; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; IGPUW, Institute of Geology, University of Warsaw, Warsaw, Poland; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; NMNH, National Museum of Natural History (Smithsonian Institution), Washington, D.C., USA; NMS, National Museums of Scotland, Edinburgh, Scotland; PKUM, Geological Museum, Peking University, Beijing, China.

Morphological terms

Euselachian-type base.—This type of chondrichthyan tooth base occurs in Protacrodontidae, Hybodontiformes, and Orodontiformes, as well as in basal Eugeneodontiformes, Petalodontiformes, and Holocephali. As far as the phylogenetic relationships between the former and latter three groups are concerned, the question is highly controversial, but the close similarities of tooth-base structure in all these taxa is an obvious fact.

The euselachian-type teeth are wide (mesio-distally) and short (labio-lingually). Lingual extension, if it exists, is usually short, and devoid of articulation devices, i.e., buttons and basolabial projections. There is at least one, horizontal row of nutritive foramina both on the orolingual and aboral-labial faces of the base and an area absolutely devoid of foramina on the aboral-lingual face of the base. The position and number of horizontal rows of pores varies, but the main lingual horizontal row of foramina always lies just beneath the crown or it is separated from the latter only by a narrow groove. In a large number of specimens, these pores continue lingually and downwards as wide, often anastomosing, uncovered canals which give this part of the base a spongy appearance. Such uncovered canals are found less often in *Protacrodus* than in the other considered taxa.

Cladodont crown.—Relatively slender cusps, unfused; prominent median cusp; of the lateral cusps the outermost is the largest; outermost accessory cusplets rarely present.

Protacrodont crown.—Low, pyramidal cusps with basal parts fused, covered with coarse vertical ridges joining at the tips.

Systematic palaeontology

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Phoebodontiformes Ginter, Hairapetian, and Klug, 2002

Family Phoebodontidae Williams in Zangerl 1981

Genus *Thrinacodus* St. John and Worthen, 1875

Thrinacodus bicuspidatus sp. nov.

Fig. 2.

Holotype: Specimen PKUM02-0129, a tooth (Fig. 2B) from the MH section north of Muhua, Guizhou Province, southern China; sample MH-1, bioclastic limestone, Muhua Formation, Carboniferous, Mississippian, Tournaisian, *Siphonodella crenulata* conodont Zone.

Derivation of the name: Latin *bicuspidatus* = bicuspid.

Material.—Nine teeth.

Diagnosis.—A species of *Thrinacodus* whose dentition is composed at least partly of teeth with only two cusps in the crown. The species resembles *Thrinacodus ferox* (Turner, 1982) in the general tooth outline, the shape of the base and the strong crown asymmetry in the lateral teeth, but differs by the loss of one of the cusps.

Description.—Judging from the material from Muhua and elsewhere, and comparing them to the type series of *Th. ferox* (Turner 1982) and dentition models proposed by Duncan

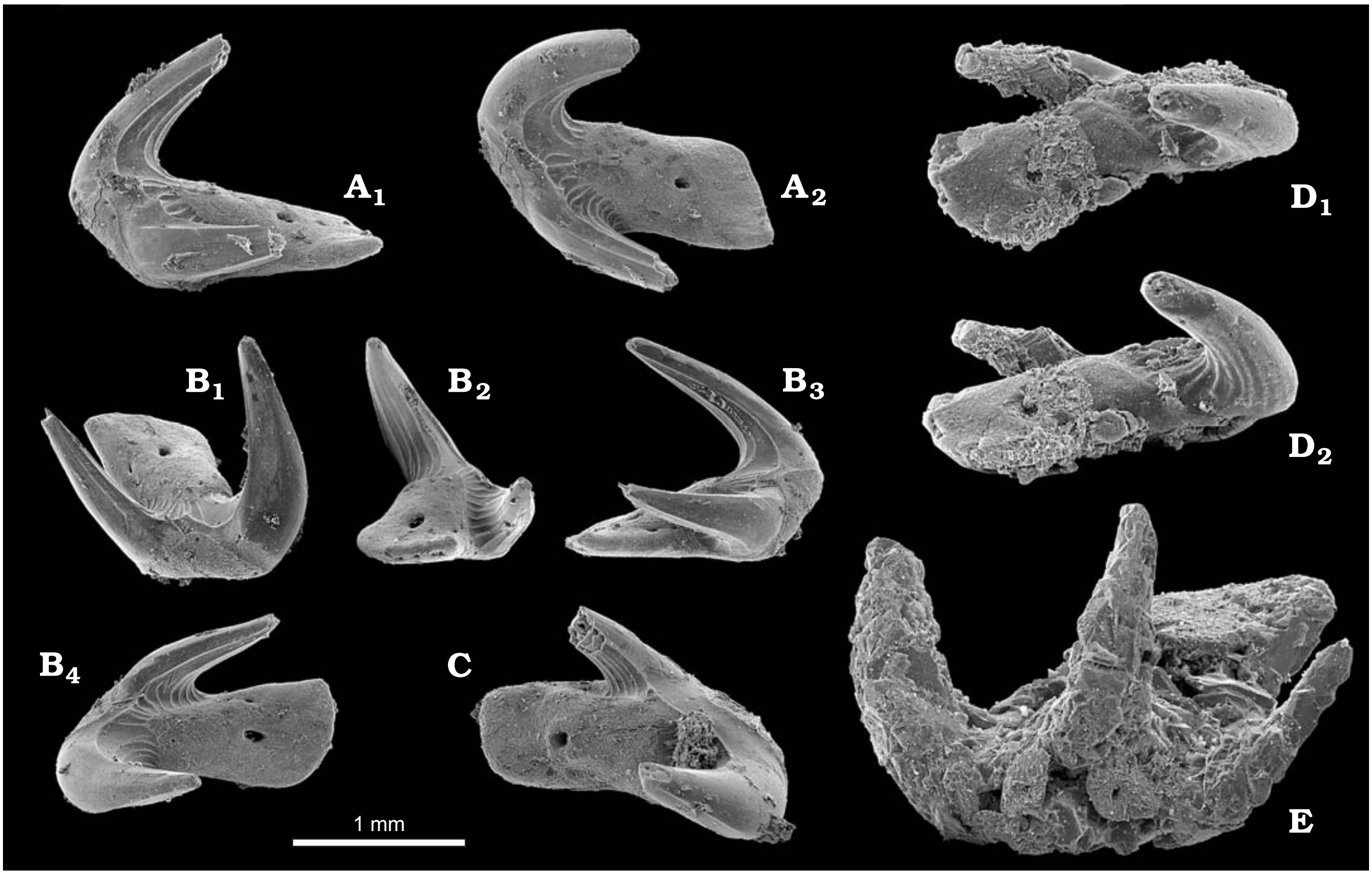

Fig. 2. Phoebodontiform chondrichthyan *Thrinacodus bicuspidatus* sp. nov. from sample MH-1, middle Tournaisian of Muhua, China. **A**. PKUM02-0128 in mesial (A_1) and oral (A_2) views. **B**. Holotype (PKUM02-0129) in labial (B_1), lingual (B_2), mesial (B_3), and oral (B_4) views. **C**. PKUM02-0130 in oral view. **D**. PKUM02-0131 in oral (D_1) and oblique distal (D_2) views. **E**. Tricuspid tooth (PKUM02-0132) in labial view.

(2003: fig. 3) we may presume that there are three general morphotypes of teeth in *Thrinacodus bicuspidatus* sp. nov.

The first, most common, which probably corresponds to lateral tooth families, has a bicuspid crown with both cusps curved lingually. The distal cusp is larger (see Ginter et al. 2002 for identification of sides in *Thrinacodus*), standing almost upright in the labial view; its distal divergence from the normal to basal plane does not exceed 10 degrees. The mesial cusp is smaller, clearly divergent mesially from the vertical position in the labial aspect, and also much more stronger directed lingually than the distal cusp. The cusps are smooth labially and ornamented with gentle subparallel cristae lingually. A weak lateral carina separates the two faces of the cusps. This carina connects the cusps, but in some specimens it forms a straight line (Fig. 2C, partly covered by dirt), and in others, the carinae of the two cusps join at the midline at an angle (Fig. 2A_1, B_1, B_4). In the latter case, there occur a few short cristae, on the lingual side of the medial area, which do not belong to any of the cusps.

The base is extended lingually, almost flat and thin lingually and thicker, with a low hump, nearer to the crown. The lateral margins of the base are almost parallel or the lingual part is wider. The distal lingual angle is oblique, and the mesial is acute. A large foramen occurs almost at the centre of the oral surface. There is a triangular attachment area on the labial side (Fig. 2B_1, B_3) devoid of enameloid, bearing a few minor foramina. Its shape corresponds to the route of the carina in the medial area.

The second tooth type (Fig. 2E), if correctly ascribed to this species, probably represents the anterior region of the jaw. It has a long base and three slender cusps of different sizes. Such teeth are commonly found among the dentition of *Th. ferox* (see e.g., Turner 1982: fig. 3F), but might also have been retained in *Th. bicuspidatus*. In such a case, based only on this type of tooth it is impossible to distinguish these two species.

The third form, not found in Muhua, but co-occurring with the first morphotype in a sample from the middle Tournaisian of Martin Spring (Nevada; Dr Charles A. Sandberg's collection, deposited at IGPUW) is tricuspid, compact, with short and thick cusps and a relatively short base. It resembles the teeth usually placed in the symphyseal (Turner 1982: figs. 2D, 3A, 5) or parasymphyseal (Duncan 2003: figs. 3A, B, 4) positions in the restorations of *Th. ferox* dentition.

Remarks.—The existence of bicuspid thrinacodonts in the Tournaisian of NW Australia was signalled by Ginter et al. (2002: 202), but this is the first time that such teeth have been illustrated and described. It was supposed by Ginter et al. (2002) that the disappearance of the mesial cusp was due to

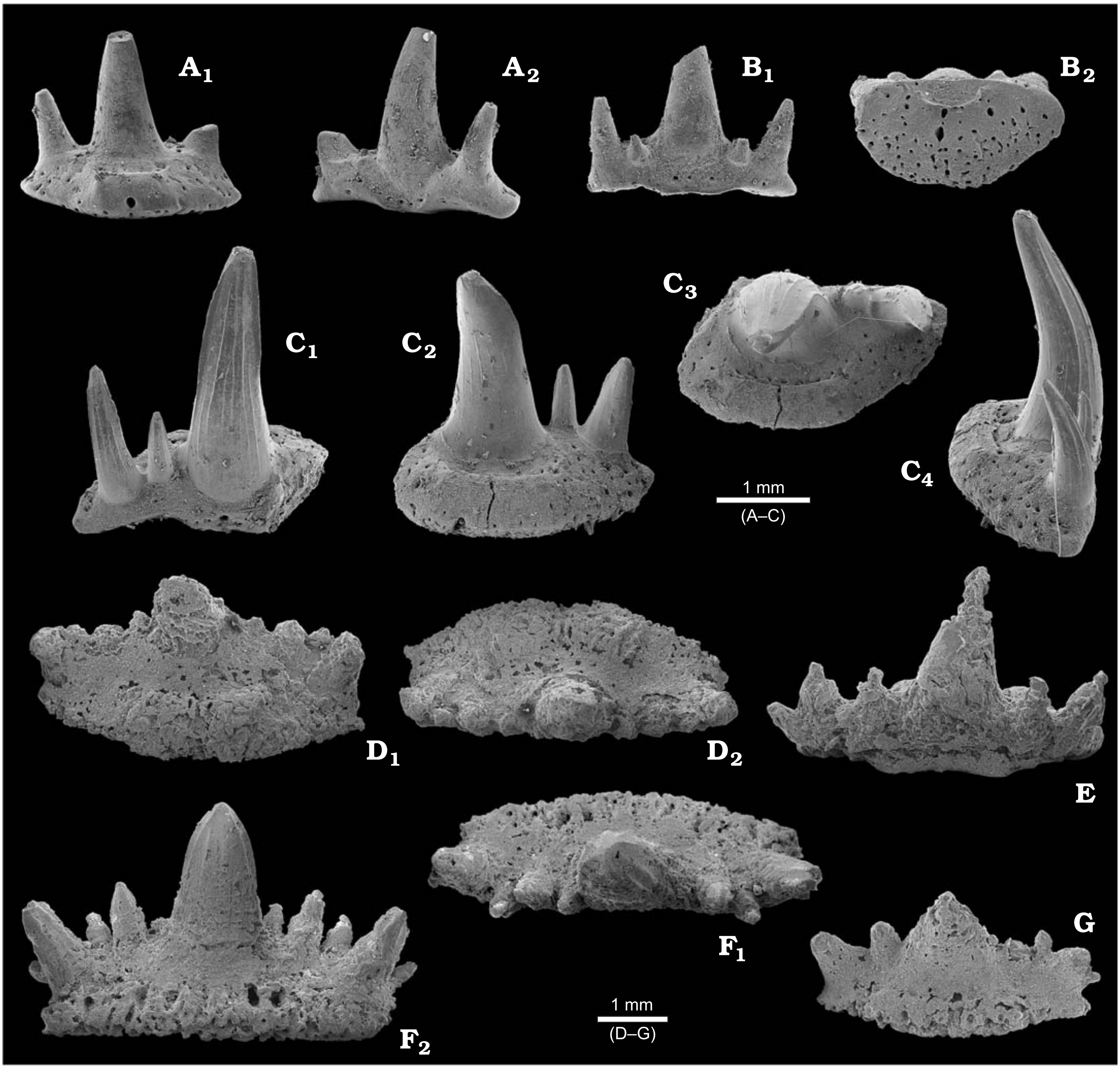

Fig. 3. Cladodont teeth from sample MH-1, middle Tournaisian of Muhua, China. **A**–**C**. *Stethacanthus* sp. **A**. PKUM02-0133 in lingual (A_1) and labial (A_2) views. **B**. PKUM02-0134 in labial (B_1) and aboral (B_2) views. **C**. PKUM02-0135 in labial (C_1), lingual (C_2), oral (C_3), and lateral (C_4) views. **D**–**G**. *Tamiobatis* sp. **D**. PKUM02-0136 in lingual (D_1) and oral (D_2) views. **E**. PKUM02-0137 in labial view. **F**. PKUM02-0138 in oral (F_1) and lingual (F_2) views. **G**. PKUM02-0139 in lingual view.

an advanced stage of crown rotation combined with size reduction of the mesial and central cusps in the lateral teeth of *Thrinacodus ferox*. However, the size difference and the angle between the distal and central cusps in the most asymmetrical teeth of the type series of *Th. ferox* (Turner 1982: fig. 2A–C; see also Ginter 2001: fig. 3D, E) is greater than between the two cusps of *Th. bicuspidatus* sp. nov., so in this aspect the asymmetry is more advanced in *Th. ferox*.

It is largely assumed that the bicuspid *Thrinacodus* teeth developed from tricuspid forms, but a controversy exists as to whether it was the lateral or central cusp that was lost in this process. Our preferred hypothesis is that the lateral (probably mesial) cusp became phylogenetically less involved in food aprehension due to the vertical torsion of the crown. Almost all of the clutching function was taken by the distal, enlarged cusp, with a minor help from the central one, and finally the mesial cusp became obsolete. However, an alternative opinion is presented by Vachik Hairapetian (personal communication 2006) who suggested, based on specimens of *Th. bicuspidatus* from Iran, that the central cusp was reduced due to the pressure from a cusp of the next tooth. In his concept, the angular connection of carinae and the presence of short cristae in the medial area are remnants of the suppressed central cusp.

Stratigraphic and geographic range.—Middle Tournaisian of southern China (Muhua), NW Australia (Canning Basin), Iran, and Nevada.

Order Symmoriiformes Zangerl, 1981

Family Stethacanthidae Lund, 1974

Genus *Stethacanthus* Newberry, 1889

Stethacanthus sp.

Fig. 3A–C.

Material.—10 teeth.

Description.—The stethacanthid teeth from Muhua are small (base width from 2 to 3 mm, median cusp height up to 2.5 mm) and display several features typical of *Stethacanthus*: separate bases of median and lateral cusps (this feature characteristic of all symmoriids); all the cusps rounded in cross-section at the base, only slightly compressed labio-lingually closer to the tip; dense but rather gentle striation of the cusps; compact and distinct articulation devices (orolingual button and basolabial projection) not wider than the base of the median cusp. The enameloid was removed from the crowns of the smaller teeth, but it remains on the larger, broken specimen, and an indistinct lateral carina is observable on the median cusp and on the outermost lateral cusp. The carina connects the lateral cusps, but apparently does not connect them with the median cusp. The teeth are generally five-cusped, but one of the smaller specimens was apparently four-cuspid (Fig. 3A), lacking one of the intermediate cusplets.

Remarks.—The most similar *Stethacanthus* teeth to those ones presented here are those associated with the spine-brush complex CMNH 8988 from the upper Famennian Cleveland Shale of Ohio. Williams (1985: pl. 15: 1) identified that specimen as *S. altonensis* (St. John and Worthen, 1875), but it seems that he had too inclusive a concept of that species. The teeth of true *S. altonensis* (*sensu* Lund 1974; compare also "*Akmonistion zangerli*" in Coates and Sequeira 2001), characteristic of the Upper Mississippian, have a much stronger and rounded median cusp and relatively shorter outer cusps.

The teeth of *Stethacanthus* sp. from Muhua differ from the otherwise similar teeth of *Denaea* Pruvost, 1922, by their shorter lingual bases, no sign of splitting of the button by the nutritive canal openings, and by their relatively thicker median cusp.

Order Ctenacanthiformes Glikman, 1964

Family Ctenacanthidae Dean, 1909

Genus *Tamiobatis* Eastman, 1897

Tamiobatis sp.

Fig. 3D–G.

Material.—Twenty five teeth.

Description.—Most specimens tentatively attributed here to *Tamiobatis* are in a very poor state of preservation. Crowns of all the teeth but one are completely devoid of enameloid and external layers of dentine; bases seem to be largely dissolved. Therefore, restoration of the real shape of these teeth and their classification is rather problematic.

It is evident that the crown is of cladodont design, with numerous lateral cusps. The best-preserved crown (Fig. 3F) is composed of a prominent, but relatively low median cusp and ten lateral cusps. On each side of the median cusp there are two larger cusps, two intermediate cusplets and an accessory cusplet in the outermost position. The median cusp, considerably compressed labio-lingually, is twice as high and three times as broad at the base as the highest lateral cusps and bears a few, rather coarse cristae on both faces and a lateral carina. Similar ornamentation apparently occurs on the largest lateral cusps. Most other teeth possess smaller number of lateral cusps, but the general pattern: smaller-larger-smaller cusplet is always present. Also in the majority of specimens (except Fig. 3D) the largest lateral cusp is flanked by the outermost accessory cusplet.

The base is short, laterally elongated, probably with typical ctenacanthoid articulation devices: laterally elongated, ridge-like button (Fig. $3D_1$) and a shelf-like basolabial projection wider than the base of the median cusp (Fig. 3E).

Remarks.—In the overall appearance and size, these teeth strongly resemble those of specimen CMNH 9280, *Tamiobatis vetustus* sensu Williams (1998) from the upper Famennian Cleveland Shale of Ohio. However, they clearly differ by the lack of a row of minute labial accessory cusplets, so characteristic of the referred specimen. Teeth of *T. wachsmuthi* (St. John and Worthen, 1875) from the Kinderhookian of Iowa lack such accessory cusplets (Fig. 10D), but they are about three times larger than the largest teeth of *Tamiobatis* sp. from Muhua and their median cusp is ornamented only at the base.

It must be noted here that the classification of *T. wachsmuthi* and certain other cladodonts such as *T. succinctus* (St. John and Worthen, 1875), and, consequently, the specimens from Muhua, ascribed to the genus *Tamiobatis* is based solely on the close resemblance (observed by Williams 1998) between the skulls of the partially articulated, tooth-bearing specimen CMNH 9280 and the type specimen of *T. vetustus* Eastman, 1897 (NMNH 1717, only neurocranium). Not all the authors agree with Williams' conclusions (see Maisey 2005).

Ctenacanthiformes gen. et sp. indet.

Fig. 9F.

Material.—One tooth.

Description.—The only known tooth of this probably yet undescribed shark is a moderately large cladodont (width of base 14 mm, height at the median cusp 7.5 mm, originally possibly about 10 mm) with three lateral cusps on each side of the prominent median cusp. The second pair of lateral

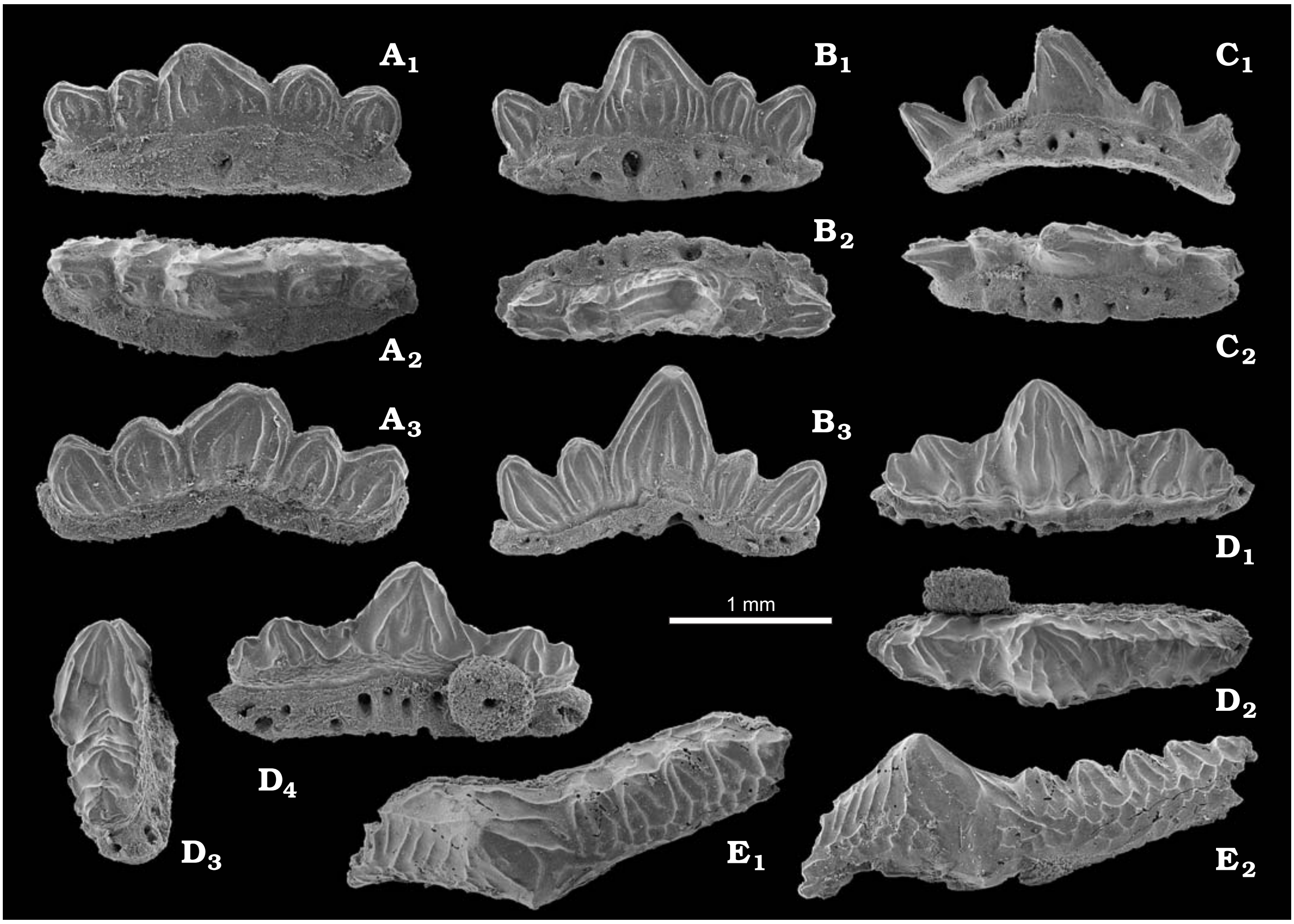

Fig. 4. Protacrodont teeth from sample MH-1, middle Tournaisian of Muhua, China. **A**, **B**. *Protacrodus* sp. **A**. PKUM02-0140 in lingual (A_1), oral (A_2), and labial (A_3) views. **B**. PKUM02-0141 in lingual (B_1), oral (B_2), and labial (B_3) views. **C**. *Protacrodus* cf. *serra* Ginter, Hairapetian, and Klug, 2002, PKUM02-0142 in lingual (C_1) and oral (C_2) views. **D**, **E**. Protacrodontidae? gen et sp. indet. **D**. PKUM02-0143 in labial (D_1), oral (D_2), lateral (D_3), and lingual (D_4) views. **E**. PKUM02-0144 in oral (E_1) and labial (E_2) views.

cusps is the highest. The segments of the base below the median cusp and that below of the main lateral cusps are in line, but the intermediate and outermost cusplets are placed more labially (Fig. 9F_2). There is a trace of a minute accessory denticle at the base of one of the intermediate cusplets (Fig. 9F_3). The labial face of all the cusps is ornamented by a few vertical cristae; on the median cusp, they probably do not reach the tip. The lingual face seems to be completely smooth, but as the lingual part of the base is broken (Fig. 9F_1), this may be a result of post-mortem abrasion.

The complete shape of the base is unknown, but the wavy outline of the labial rim is fairly well preserved. There is a basolabial depression below the median cusp and two rounded prominences, situated below the intermediate cusplets, are framing it. On the aboral side of the base, there probably were two rounded projections (Fig. 9F_4), similar to those observed in the Pennsylvanian ctenacanthid *Glikmanius occidentalis* (Leidy, 1859), but in the specimen from Muhua these are preserved only as vague swellings.

Remarks.—Hitherto, no other shark teeth presenting all of the above-mentioned features have been recorded. The teeth of *Glikmanius* do have a deep basolabial depression, two basolabial prominences and labially produced intermediate cusplets, but the outermost pair of smaller accessory cusplets is absent. Such cusplets are typical of *Tamiobatis*, but the latter has a generally straight basolabial rim and multiple intermediate cusplets of variable height (see above).

The tooth closest in its characteristics to the specimen described here was found among the dentition of a lower Viséan shark recently found in Glencartholm, Scotland (NMS 2000.14.2; Fig. 10F). That very large tooth (base width about 40 mm) possesses an outermost pair of accessory cusplets placed similarly to the cladodont from Muhua and displays similar proportions between the cusps. However, it has a shelf-like basolabial projection (as in *Ctenacanthus*, see Williams 2001) instead of two separate prominences, its basolabial depression is shallow, and all the cusps appear to be positioned more in line than in the Chinese specimen.

It is worth noting here that the Scottish shark may represent a well known ctenacanthiform species, *Goodrichthys* *eskdalensis* (Moy-Thomas, 1936). The holotype of *Goodrichthys*, also from the Viséan of Glencartholm, has damaged teeth, but careful comparison of the available fragments with the teeth exposed in NMS 2000.14.2 reveals several common features (Ginter 2007). We therefore tentatively suggest that morphologically, the tooth under study occupies an intermediate position between *Goodrichthys* and *Glikmanius* and can arguably be attributed to the Ctenacanthiformes.

Cohort Euselachii Hay, 1902

Superfamily Protacrodontoidea Zangerl, 1981

Family Protacrodontidae Cappetta, Duffin, and Zidek, 1993

Genus *Protacrodus* Jaekel, 1925

Protacrodus sp.

Fig. 4A, B.

Material.—Four teeth.

Description.—These protacrodont teeth are characterised by a pentacuspid crown with a prominent, labio-lingually compressed median cusp, about twice as high as the lateral cusps (Fig. $4B_3$) or a little less (Fig. $4A_3$). All the lateral cusps may either be equal to each other or the outermost are the largest. All the cusps are rounded in both the labial and lingual views and ornamented on both sides with two generations of cristae: the outer, concentric and parallel to the cusps margins and the inner, more vertical ones, often branching basally. The base is perforated by a single large nutritive canal whose openings are situated submedially on the lingual and baso-labial faces. It is uncertain whether the other, minute foramina particularly visible in Fig. $4B_1$ were open on the surface before fossilisation.

In the rounded shape of the cusps and the form of cristae, *Protacrodus* sp. is similar to *P. aequalis* Ivanov, 1996, but the crown of the latter is characterised by only three cusps of virtually the same size.

Protacrodus cf. *serra* Ginter, Hairapetian, and Klug, 2002

Fig. 4C.

Material.—One tooth.

Description.—The only tooth of this type has five largely separate cusps in the crown which is strongly compressed labio-lingually. The base of this specimen is arched. Such specimens can be found among the material of *P. serra* from the type area and horizon (upper Famennian of the Anti-Atlas; compare Ginter et al. 2002: pl. 11: 1).

Protacrodontidae? gen. et sp. indet.

Figs. 4D, E, 6C

Material.—Three teeth.

Description.—We present here three rather different crushing teeth. The two larger specimens are extremely elongated mesio-distally with one or two major, pyramidal cusps and a series of smaller lateral, largely fused cusps of similar size. The crown is ornamented with coarse, wavy cristae directed towards the apices of the cusps or vertical in the areas where no cusp can be distinguished. A peculiar festoon-like ornamentation, in some places forming honeycomb cells, covers the crown-base interface. The base is typically euselachian.

The largest tooth (Fig. 6C; mesio-distal dimension of preserved part about 7 mm) has extensively fused lateral cusps, forming together a long ridge, lowering laterally, whereas the tips of the cusps in the smaller tooth (Fig. 4E; about 3 mm) are clearly discernible and the major cusp seems to be more prominent. The larger tooth is almost straight, but the mesio-distal axis of the smaller one turns about 20° at the major cusp.

The side with two major cusps in the largest tooth is apparently complete. If so, the tooth is extremely asymmetrical. The same side in the smaller tooth is broken, so it is impossible to say whether there was only one (preserved) major cusp or two, as in the other specimen, and if the tooth continued further.

The third, smallest tooth (Fig. 4D; 2.4 mm mesiodistally) is virtually symmetrical, like typical protacrodont teeth. The lateral cusps, present on both sides, are fused up to the two-thirds of their height. The crown ornamentation is almost identical to that in the second tooth. The characteristic festoon-like sculpture near the base is very delicate on the lingual face, and on the labial face it shows only as a double, wavy line.

Remarks.—The festoon-like (or "coarse reticulate" *sensu* Long and Hairapetian 2000) pattern of ornamentation of the basal part of the crown is common in several Famennian protacrodontids. Long and Hairapetian (2000) presented it as a diagnostic feature of the genus *Dalmehodus*; it also occurs in crushing teeth from Utah (Ginter 2001: fig. 6D, E, H), on the lingual side of several teeth of *Deihim mansureae* from Iran (Ginter et al. 2002: text fig. 10G), and on one of the Moroccan teeth referred to as "Protacrodontidae cf. *Deihim mansureae*" by Ginter et al. (2002: pl. 6: J). The latter authors suggested it to be merely a result of intersection between vertical cristae and the growth lines of the crown, but whereas in the case of the teeth from Utah and the labial side of the smallest tooth from Muhua this appears to be true, there are also specimens (e.g., Fig. 4E) in which the relation of this sculpture to the coronal cristae is less obvious.

If our identification of the three described teeth as belonging to the same species is correct, this would mean that the level of heterodonty is very high here. The third, symmetrical tooth could represent the anterior part of the dentition, the second, longer tooth could come from the anterolateral tooth families and the first tooth with fused cusps could be situated in the posterior position, as a "molar". Judging from the positions of teeth within the dentition of the upper Pennsylvanian *Hamiltonichthys* (Maisey 1989: figs. 26, 27), it can be assumed that the shorter part in asymmetrical teeth is directed mesially and the longer branch—distally. The symmetrical teeth in *Hamiltonichthys* occur on the shorter side of asymmetrical ones.

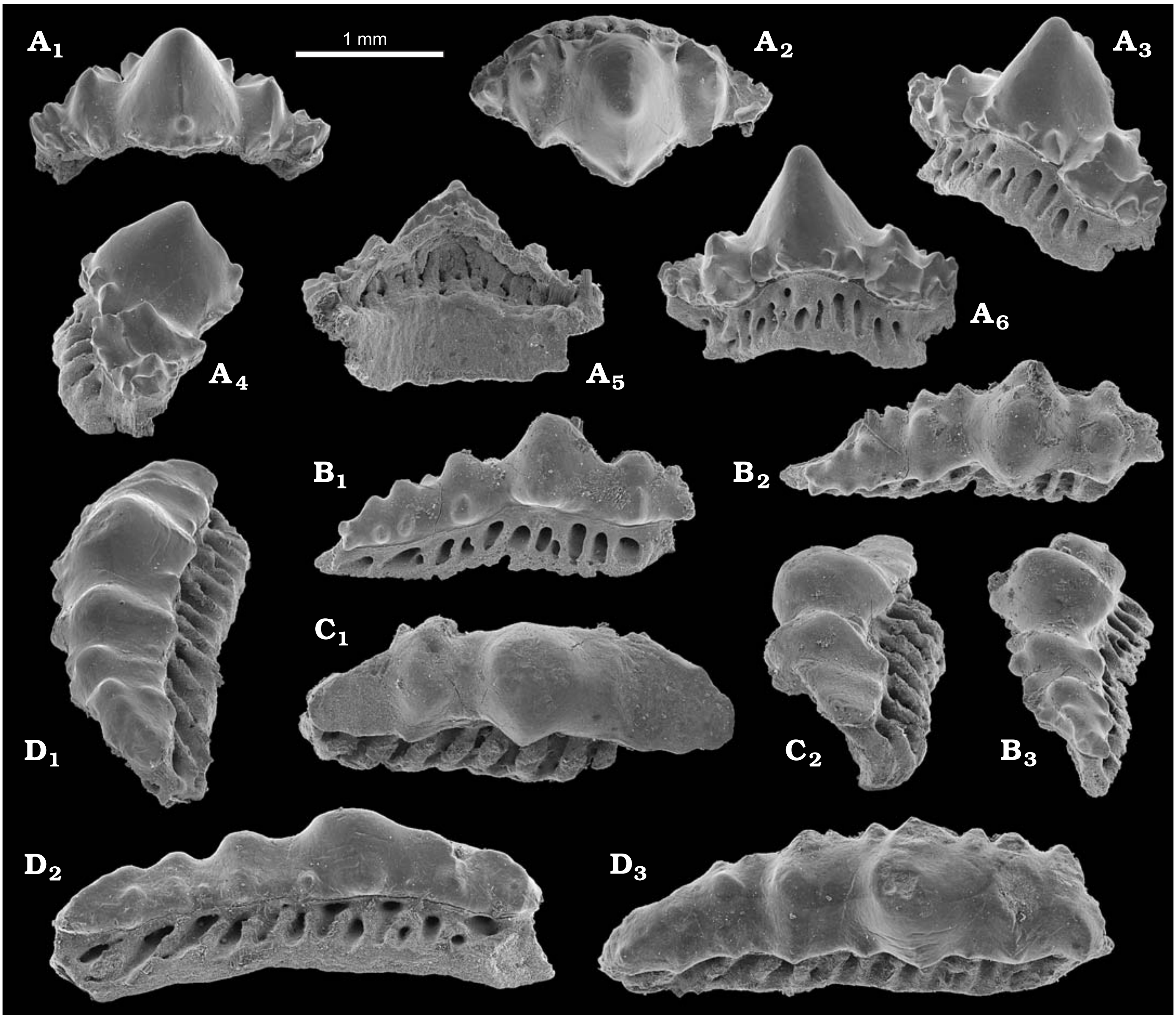

Fig. 5. Hybodontiform chondrichthyan *Cassisodus margaritae* gen. et sp. nov. from sample MH-1, middle Tournaisian of Muhua, China. **A**. Anterior tooth, holotype (PKUM02-0145) in labial (A_1), oral (A_2), lateral/lingual (A_3), lateral (A_4), aboral (A_5), and lingual (A_6) views. **B**–**D**. Lateral teeth. **B**. PKUM02-0146 in lingual (B_1), oral (B_2), and lateral (B_3) views. **C**. PKUM02-0147 in oral (C_1) and lateral (C_2) views. **D**. PKUM02-0148 in lateral (D_1), lingual (D_2), and oral (D_3) views.

Superfamily Hybodontoidea Zangerl, 1981

Family indet.

Genus *Cassisodus* nov.

Type species: *Cassisodus margaritae* sp. nov.

Derivation of the name: Latin *cassis* = helmet; Greek *'odous* = tooth.

Diagnosis.—Teeth with euselachian bases and crowns composed of a prominent median cusp and two to four lateral cusps on each side. All the cusps smooth, rounded in cross section, slightly compressed mesio-distally, provided with at least one accessory cusplet on both lingual and labial sides. The lateral rami of the crown gradually narrowing and lowering outwards, and gently curved linguad.

The overall appearance of the teeth and especially the labial overhang of the main cusp, with its accessory cusplet, resemble *Lissodus* Brough, 1935. However, the occurrence of accessory cusplets on both sides of lateral cusps is unique of *Cassisodus*.

Cassisodus margaritae sp. nov.

Fig. 5.

1996 *Lissodus* sp.; Ivanov 1996: fig. 7A, B.

Holotype: Specimen PKUM02-0145 (Fig. 5A) from the MH section north of Muhua, Guizhou Province, southern China; sample MH-1, bioclastic limestone, Carboniferous, Mississippian, Tournaisian, *Siphonodella crenulata* conodont Zone.

Derivation of the name: Latin *margarita* = pearl, a girl's name.

Material.—Four teeth.

Diagnosis.—As for genus.

Description.—As in the case of other euselachian and euchondrocephalan sharks' teeth in the collection, a considerable degree of heterodonty is observed in the dentition of *Cassisodus margaritae* sp. nov. Fortunately, in this case the characteristic distribution of accessory labial and lingual cusplets on the lateral cusps makes the identification easier. Among the four teeth assigned here to this species, there is one (Fig. 5A) rather narrow (2 mm mesio-distally), very well preserved tooth, possibly representing anterior, clutching part of the dentition, and three wider (up to 4 mm mesio-distally), crushing, partly damaged lateral(?) teeth (Fig. 5B–D).

The width/length (mesio-distal/labio-lingual) ratio of the first tooth (holotype, Fig. 5A) is about 2. The size of the median cusp is roughly double that of the lateral cusps. The lateral cusps are closely packed and their mesio-distal compression is stronger than in the other specimens. Each lateral cusp forms a group with one labial accessory cusp and up to two cusplets on the lingual side. The accessory cusplets are connected with the tips of lateral cusps by labio-lingual carinas. Similar carinas may connect accessory cusplets of the adjacent groups (Fig. 5A_3, A_6, right side). There are four accessory cusplets at the base of the lingual side of the median cusp, symmetrically placed towards the midline, and a single cusplet on the labial side. The lingual part of the base is relatively extensive. It seems to be narrower than the crown, but this is probably an illusion, caused by the fragments broken off symmetrically. In the aboral view, the labial, porous and the lingual, smooth, parts are distinctly separated.

The other three, wider teeth (Fig. 5B–D; original width/length ratio about 3.5) are partly broken and their crowns appear to be polished, either by wear or by post-mortem abrasion. They are so similar to each other, save for the size, that we suspect they come from the same tooth family. The smallest of them (Fig. 5B) is in the best shape. The median cusp is only twice as large as the nearest lateral cusps. The lateral cusps are more widely spaced and the labial accessory cusplets, apparently not belonging to any cusp+cusplets group, occur between them (Fig. 5B_1). There are at least three groups of cusplets on each side. The lateral ends of the tooth are very narrow, almost pointed.

Remarks.—*Cassisodus margaritae* sp. nov. shares several general features with basal holocephalians, such as *Helodus*: shape and vascularisation of the base (euselachian-type), and differentiation of teeth (anterior narrower with high median part, posterior very wide with lower crowns). However, it differs clearly by the lack of tubular dentine (orthotrabeculine *sensu* Zangerl et al. 1993) and by having developed instead a very sophisticated ornamentation. Owing to these differences, it more closely resembles Famennian forms such as *Deihim* Ginter, Hairapetian, and Klug, 2002, which is also a supposedly highly heterodont taxon. As mentioned in the diagnosis, the strong labial overhang of the crown, supported by the accessory cusplet, makes the teeth of *C. margaritae* look like those of *Lissodus*.

Stratigraphic and geographic range.—Middle Tournaisian of southern China (Muhua), Viséan of southern Urals (Sikaza).

Hybodontoidea gen. et sp. indet.

Fig. 6A.

Material.—One complete tooth and one crown.

Description.—The crown of the complete tooth is composed of three largely fused cusps, of which the median, pyramidal in shape, is the highest. The crown is provided with a prominent labial peg, similar to that of *Lissodus*. On the lingual face of each lateral cusp there is a strong vertical ridge, widening downwards. A similar, bifurcating ridge is also present on the lingual face of the median cusp.

The most remarkable feature of this tooth is its very deep (twice as deep as the crown height), subrectangular base, slightly directed linguad. It is generally of the euselachian type, with a spongy structure.

Euselachii gen. et sp. indet.

Fig. 6D.

Material.—One complete tooth and two fragments.

Description.—The well preserved tooth is relatively large (base width above 6 mm), with a thick euselachian-type base and a virtually symmetrical crown of the shape intermediate between cladodont and protacrodont. Altogether, there are nine cusps in the crown, standing upright in the lateral view. The prominent median cusp is pyramidal, showing protacrodont-like, coarse cristae (also present in the lateral cusps), but its relative height is greater than that in typical protacrodonts. Of the lateral cusps, the outermost are the largest and divergent from the midline, these two features distinguishing them from typical hybodonts (see Agassiz 1833-43: vol. 3: 178). The intermediate cusplets are largely fused, at least up to two thirds of their height. The middle of the three is the highest.

Remarks.—The intermediate morphology of the crown combined with the euselachian base as well as the lack of comparable specimens in the literature preclude any definitive classification of these teeth at the moment. In fact, there are many similar, unnamed cladodont-protacrodont teeth dispersed in the Palaeozoic collections all over the world. It is probable that the taxa to which they belonged are situated close to the point of ctenacanthiform-euselachian divergence.

Subclass Euchondrocephali Lund and Grogan, 1997

Order Petalodontiformes Zangerl, 1981

Genus *Chomatodus* Agassiz, 1838

Chomatodus linearis (Agassiz, 1838)

Fig. 6B.

Material.—One tooth.

Description.—The tooth crown is in a form of a mesio-distally elongated bar (mesio-distal dimension 5 mm, average

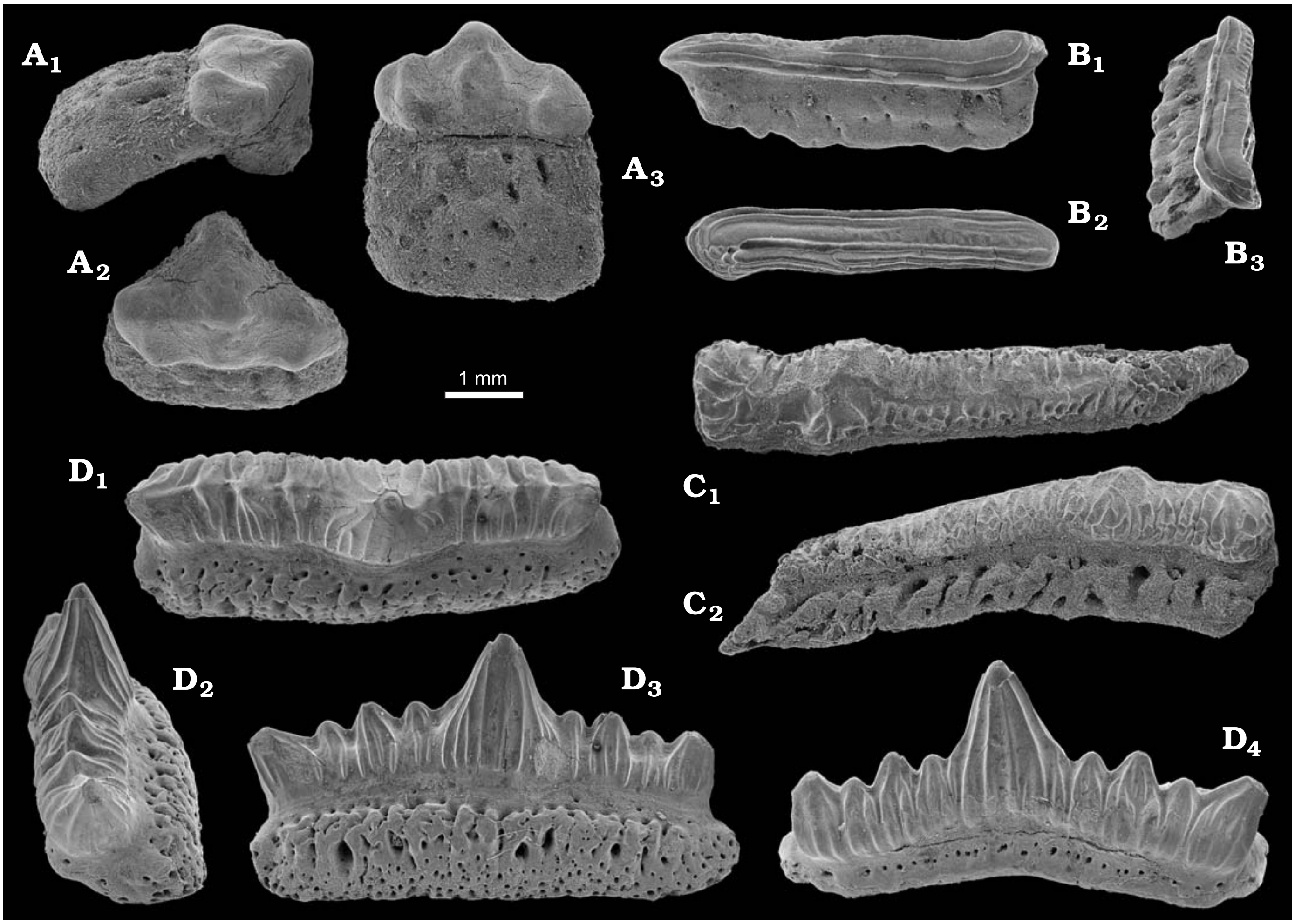

Fig. 6. Euselachian and petalodontiform teeth from sample MH-1, middle Tournaisian of Muhua, China. **A**. Hybodontiformes gen. et sp. indet., PKUM02-0149 in lateral (A_1), oral (A_2), and lingual (A_3) views. **B**. *Chomatodus linearis* (Agassiz, 1838), PKUM02-0150 in lingual (B_1), oral (B_2), and lateral (B_3) views. **C**. Protacrodontidae? gen. et sp. indet., PKUM02-0151 in oral (C_1) and lingual (C_2) views. **D**. Euselachii gen. et sp. indet., PKUM02-0152 in oral (D_1), lateral (D_2), lingual (D_3), and labial (D_4) views.

labio-lingual dimension 0.8 mm) with rounded ends, slightly upturned at one end. It is composed of a low central ridge, surrounded by concentric growth layers. Some traces of tubular dentine can be observed in the worn part of the ridge (e.g., Fig. 6B2 right). The base is shorter and narrower than the crown, more than 1 mm deep, almost vertical, and perforated with numerous narrow canals.

Remarks.—The teeth of this type, albeit much larger, have already been described in the mid-19th century by Agassiz (1833–43) and Newberry and Worthen (1866). The specimens from the Carboniferous Limestone in the vicinity of Bristol, originally illustrated as *Psammodus linearis* by Agassiz (vol. 3: pl. 12: 5–13), but subsequently translated to the genus *Chomatodus* in the text volume (Agassiz 1833–43, vol. 3: 108) differ, in addition to the size, by the better differentiated and higher central ridge, less conspicuous concentric growth lines (compare Fig. 10G), and the lack of an upturned end.

Newberry and Worthen (1866) followed Agassiz in calling such teeth *Chomatodus*, but they introduced eight new species based on the material from the Mississippian and Coal Measures of Iowa and Illinois. We consider the differences between these specimens and the type material insufficient for creating new taxa, with an exception, perhaps, for *Chomatodus cultellus* and *Ch. pusillus* with a very sharp crest in the place of the central ridge (Newberry and Worthen 1866: pl. 3: 13 and 14, respectively). The latter authors, probably correctly, placed *Chomatodus* within the Petalodontidae based on "crown having homologous parts of *Petalodus*" (Newberry and Worthen 1866: 34), apparently meaning the concentric growth lines around the central part of the crown. Woodward (1889) went further, attributing *Chomatodus linearis* partly to *Petalodus* itself and partly to *Helodus*. However, such identification is untenable in the light of modern understanding of the latter two genera.

Despite the obvious differences between the Chinese tooth and the type material we consider them as conspecific. The smaller size and different proportions of the crown parts suggest that the tooth under description comes from a very young individual. The British and American specimens were collected as macrofossils and do not cover all the size range within the species; they probably represent only adult forms.

Chomatodus davisi (Woodward, 1889) comb. nov.

Fig. 9D.

1875 *Chomatodus insignis* (Leidy sp.); St. John and Worthen 1875: pl. 10a: 5.

1889 *Petalodus davisii* sp. nov.; Woodward 1889: 46.

Material.—Two fairly complete teeth and two fragments.

Description.—The two more complete teeth are extremely elongated mesio-distally (2.5 mm) and flattened labio-lingually. They have blade-like crowns, labially convex and lingually concave. The crown of the first tooth (Fig. 9D) is of virtually equal height throughout. The crown of the second, higher tooth (Fig. 9E) is asymmetrical: it slopes down gently distally (?) and on the higher, mesial (?) end it is rounded in lingual view and ends rather abruptly. The outer layer of the crown seems to be partly diagenetically modified and partly removed, especially at the crown-base interface in the higher tooth. Therefore, almost no trace of ornamentation can be observed, save for the lingual face of the distal part of the larger tooth (Fig. 9E$_3$, right) where a few vague vertical ripples have remained. It is difficult to say what kind of a mineral tissue builds the crown, but it is possible that at least the highest part of the blade in the larger tooth contains tubular dentine.

The vascularisation of the base is composed of interchanging vertical grooves and canals. The aboral side is flat and narrow, slightly arched, and devoid of foramina. The canals and grooves on the labial side are situated in a horizontal furrow, in which the lingual part of the base could fit. Owing to that feature, the crowns of teeth in a file were packed closely one after another, forming a pavement of blades.

Remarks.—The highest of the teeth described herein is similar to a form referred to by Woodward (1889) as *Petalodus davisi* (Fig. 10C; Viséan of Armagh, Northern Ireland). The asymmetrical shape of the crown, the vertical ripples on the upper blade, and the canal-groove interchange in the base are the main common features. However, "*P.*" *davisi* from Armagh displays a partly broken, but still clear growth line, separating the crown from the base, in the manner of *Chomatodus* or other petalodontiforms. Unfortunately, that region is damaged in the larger Chinese tooth and nothing like a growth line can be observed in the smaller tooth. Some help comes from a tiny, elongated fragment, which presents an evident horizontal ridge between the base and the crown. If that fragment really belongs to the same species as the other teeth that probably means that the latter lost that ridge during fossilisation. The general shape of the teeth described herein more resemble that of *Chomatodus* than that of *Petalodus* sensu stricto, and that is why we tentatively propose a new combination, *Chomatodus davisi*, for Woodward's (1889) taxon.

Yet another species, *Chomatodus incrassatus* (St. John and Worthen 1875, pl. 10: 18) possesses an asymmetrical crown, very similar to that of the larger tooth from Muhua, and the characteristic form of the base with a labial furrow. However, there are apparently two growth lines on the lingual and three on the labial sides of *Ch. incrassatus* and the teeth are much smaller than *Ch. davisi*, so it is impossible to decide at the moment whether these two are conspecific. If so, *Ch. davisi* would be a junior synonym.

The long and low tooth from the Viséan St. Louis Limestone of St. Louis, Missouri, referred to as "*Chomatodus insignis* (Leidy sp.)" by St. John and Worthen (1875, see especially pl. 10a: 5b) resembles the first tooth of the described above (Fig. 9D). Unfortunately, we had no opportunity to see Leidy's original (*Palaeobates insignis* Leidy, 1857) and evaluate St. John and Worthen's identification; Woodward (1889: 48; see also Hay 1902: 280) considered it doubtful. Thus, we have decided to use, at least temporarily, the name *Ch. davisi* for the specimens from Muhua.

Superorder Holocephali Bonaparte, 1841

Order Helodontiformes Patterson, 1965

Family Helodontidae Patterson, 1965

Genus *Diclitodus* Davis, 1883

Diclitodus denshumani (Newberry and Worthen, 1866)

Fig. 7A.

1866 *Helodus denshumani* sp. nov.; Newberry and Worthen 1866: 76, pl. 4: 21.

Material.—One tooth.

Description.—The crown of *Diclitodus denshumani* is convex labially and concave lingually. Its lingual/lateral ends slope down at 45° and are gently crenulated. The biting edge is almost horizontal, with lateral corners only slightly higher than the median part. The base is strongly expanded lingually and excavated at the lingual end. The orolingual side of the base is perforated with numerous nutritive canals and grooves. Width of the tooth is 1.5 mm.

Remarks.—An almost identical tooth was described by Newberry and Worthen (1866: pl. 4: 21a–c) from the Viséan Keokuk Limestone of Illinois as *Helodus denshumani*; although the illustrations are somewhat confusing, the description and diagrammatic sketch of the lateral view leave no doubt. However, as the tooth is much different from the specimens typically referred to as *Helodus*, and, on the other hand, resembles the type specimen of *Diclitodus scitulus* Davis, 1883 (BMNH P.49629; Fig. 10A) from the Carboniferous Limestone of Yorkshire, it should be included in *Diclitodus*. *D. scitulus* is much larger (7 mm wide) than *D. denshumani* and shows more prominent lateral corners of the crown, but the exposed labial part of the holotype (the rest is embedded in limestone) reveals a similar shape of the base.

Based on indirect reasoning, it was suggested (Woodward, unpublished notes, fide Stahl 1999: 54) that *Diclitodus* is a symphyseal tooth of a helodontiform. Such a position could explain the extreme rarity of such forms in comparison to other bradyodont teeth and tooth-plates. This being the case, it is quite possible that *Diclitodus* sp. is in fact a symphyseal tooth of the next described species, *Helodus*

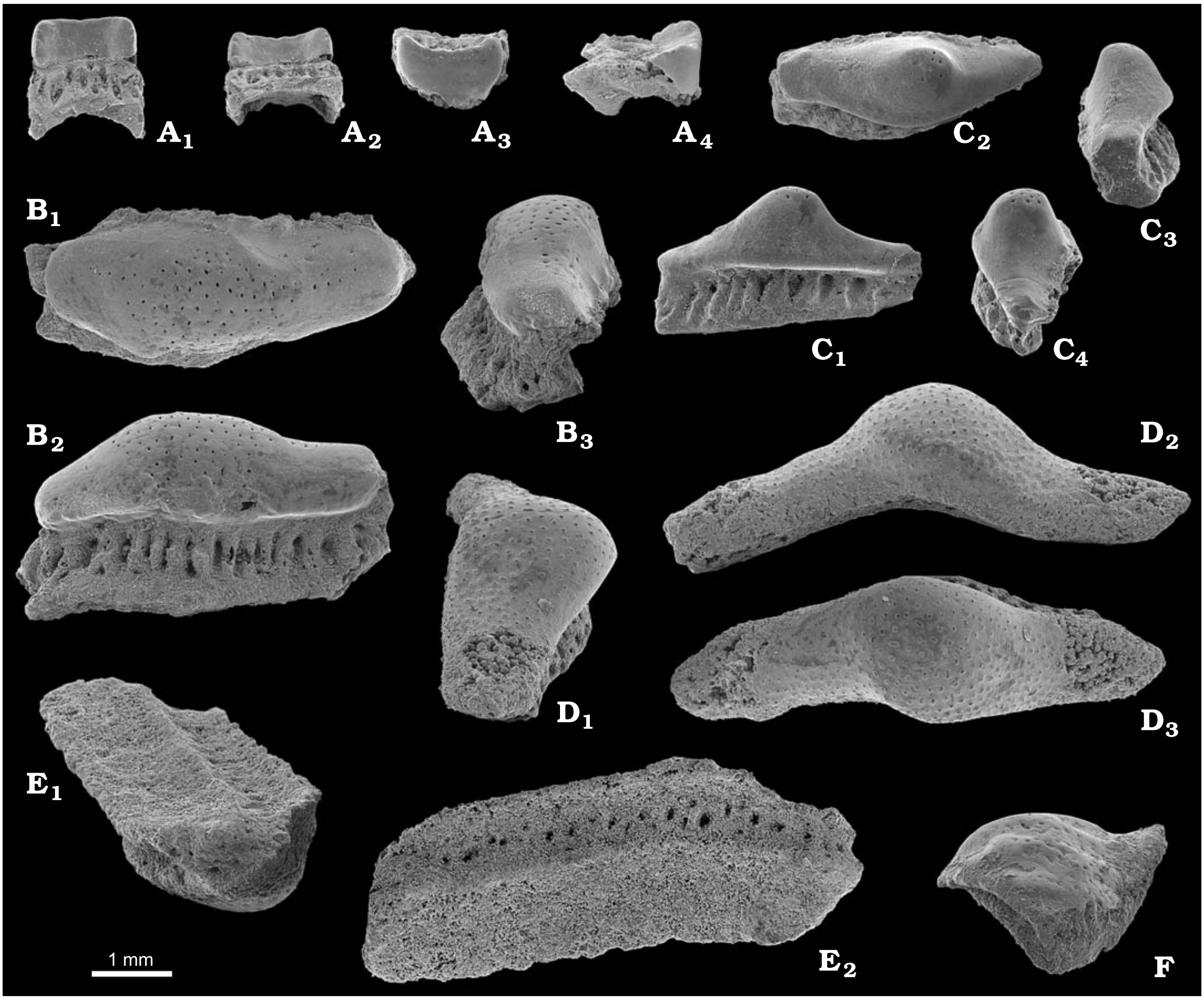

Fig. 7. Holocephalian dental elements from sample MH-1, middle Tournaisian of Muhua, China. **A**. *Diclitodus denshumani* (Newberry and Worthen, 1866), PKUM02-0153, in lingual (A_1), lingual/aboral (A_2), labial (A_3), and lateral (A_4) views. **B–E**. *Helodus coniculus* Newberry and Worthen, 1866. **B**. PKUM02-0154 in oral (B_1) lingual (B_2), and lateral (B_3) views. **C**. PKUM02-0155 in lingual (C_1), oral (C_2), and two lateral (C_3, C_4) views. **D**. PKUM02-0156 in lateral (D_1), labial (D_2), and oral (D_3) views. **E**. PKUM02-0157 in aboral/lateral (E_1) and aboral (E_2) views. **F**. *Deltodus* cf. *sublaevis* (Agassiz, 1838), tooth plate (PKUM02-0158) in labial view.

coniculus, and, consequently, represents the genus *Helodus*, as originally proposed.

Genus *Helodus* Agassiz, 1838

Helodus coniculus St. John and Worthen, 1866

Fig. 7B–E.

Material.—Fifteen teeth.

Description.—We include in this species several isolated holocephalian teeth of different crown shapes, considering that the variety may reflect heterodonty typical of crushing-grinding dentitions. The crowns are composed of a central, bulbous structure which is relatively high, almost pointed (Fig. 7C), to dome-like, semi-spherical (Fig. 7D), to low, broad, elongated mesio-distally (Fig. 7B). The crowns are slightly asymmetrical. The mesial and distal branches differ in length and breadth, and slope down from the central part outwards at different angles. The whole crown is covered with a thick layer of tubular dentine, but the tubule openings in better preserved specimens are exposed on the surface only in the areas most subject to wear (see especially Fig. 7C_1).

The base is of a typical euselachian type, with canals and grooves on the lingual side, canal openings in the aboral-labial concavity and a broad, flat aboral-lingual surface (Fig. 7E).

Remarks.—Judging from such articulated specimens of basal holocephalians' dentition as *Psephodus magnus* Traquair (1885: figs. 1, 2; Ginter and Piechota 2004: fig. 3H; NMS

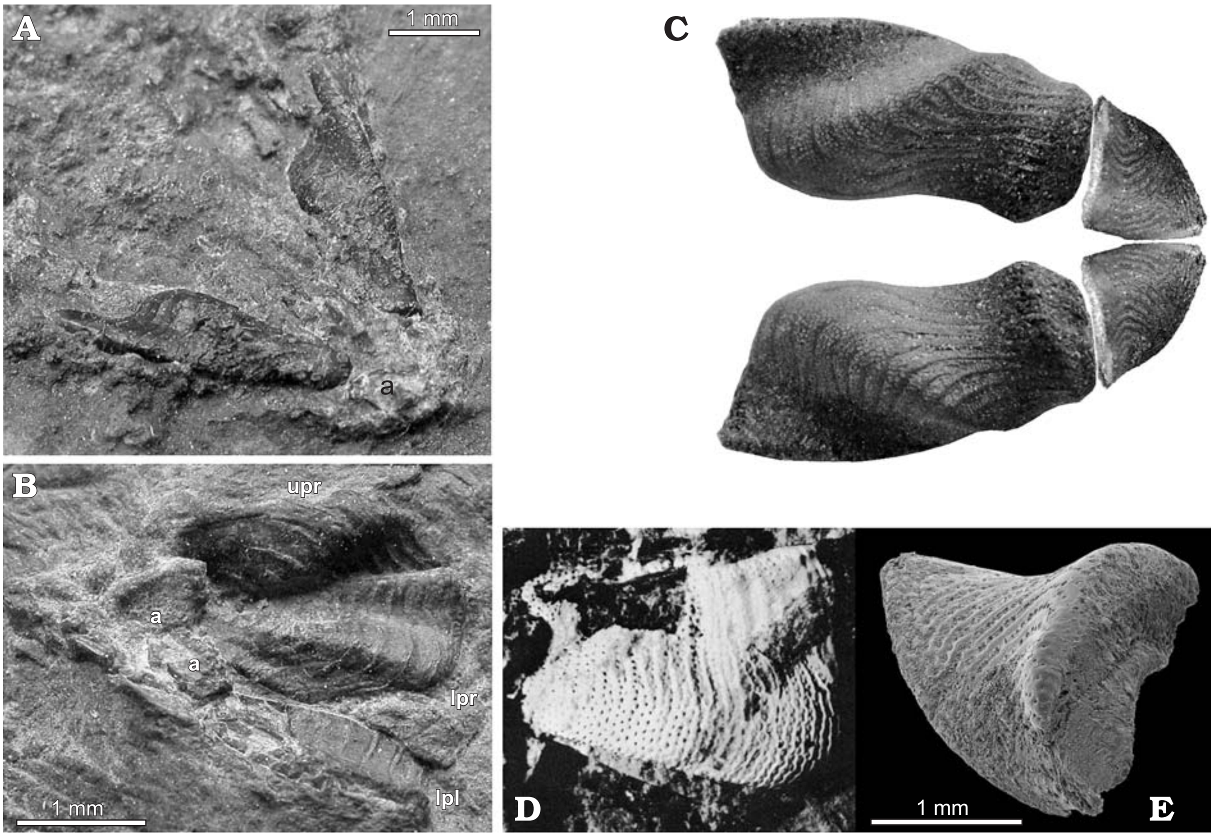

Fig. 8. Chondrenchelyid dental elements. **A**, **B**. *Chondrenchelys problematica* Traquair, 1888, from the lower Viséan of Glencartholm, Dumfriesshire, Scotland. **A**. Anterior part of NMS 2002.68.1, showing a jaw with two well preserved posterior tooth-plates and remnants of anterior plates. **B**. Tooth plates of BGS-GSE 13328. Abbreviations: a, anterior plates; upr, right upper posterior plate; lpr, right lower posterior plate; lpl, left lower posterior plate. **C**. Computer-generated restoration of the upper (?) dentition in *Chondrenchelys* sp. from MH-1; anterior to the right, not to scale. **D**. *Harpagofututor volsellorhinus* Lund, 1982, from the Serpukhovian of Bear Gulch, Montana, upper posterior plate of CM 27324b (from Lund 1982). **E**. Anterior tooth plate of *Chondrenchelys* sp. (PKUM02-0160) from MH-1.

1950.38.51) it seems probable that the narrow and high teeth of the crushing-clutching type in *Helodus coniculus* (Fig. 7C) were situated in the anterior region of jaw. Such teeth are in fact the only ones corresponding to the type specimen (Newberry and Worthen 1866: pl. 4: 19; see also Stahl 1999: fig. 52). The rest of teeth probably formed a crushing-grinding pavement in the lateral and posterior regions.

Order Cochliodontiformes Obruchev, 1953

Family Cochliodontidae Owen, 1867

Genus *Deltodus* Morris and Roberts, 1862 (ex Agassiz ms. 1859)

Deltodus sp.

Fig. 7F.

Material.—Two incomplete tooth-plates.

Description.—The plates have a wavy shape with the main, convex part covered with a few vague ridges made of tubular dentine, and a triangular lateral wing. The specimens resemble to some extent the tooth-plates of *Deltodus sublaevis* Agassiz, 1838 (Fig. 10E), but their state of preservation precludes the precise identification.

Order Chondrenchelyiformes Patterson, 1965

Family Chondrenchelyidae Berg, 1940

Genus *Chondrenchelys* Traquair, 1888

Chondrenchelys sp.

Figs. 8E, 9A, B.

Material.—Three tooth-plates.

Description.—There are tooth plates of two kinds in the studied material: one large plate, elongated antero-posteriorly (Fig. 9A), and two smaller, triangular plates (Figs. 8E, 9B); one of the latter is partly destroyed. All the plates have smooth, concave aboral surfaces and wavy oral surfaces, ornamented with concentric ridges separated by areas with numerous minute pores.

On the larger plate, the centre of the ridges is situated in the anterolabial region (identification of sides is based on articulated specimens of *Chondrenchelys problematica* Traquair, 1888, from Scotland; Fig. 8A, B). The primary ridges are more densely packed anteriorly. Posteriorly, the spaces between them become so wide that in a few instances secondary ridges are added. Thus, in the anterior part there are 13 ridges and posteriorly their number increases to 17. There

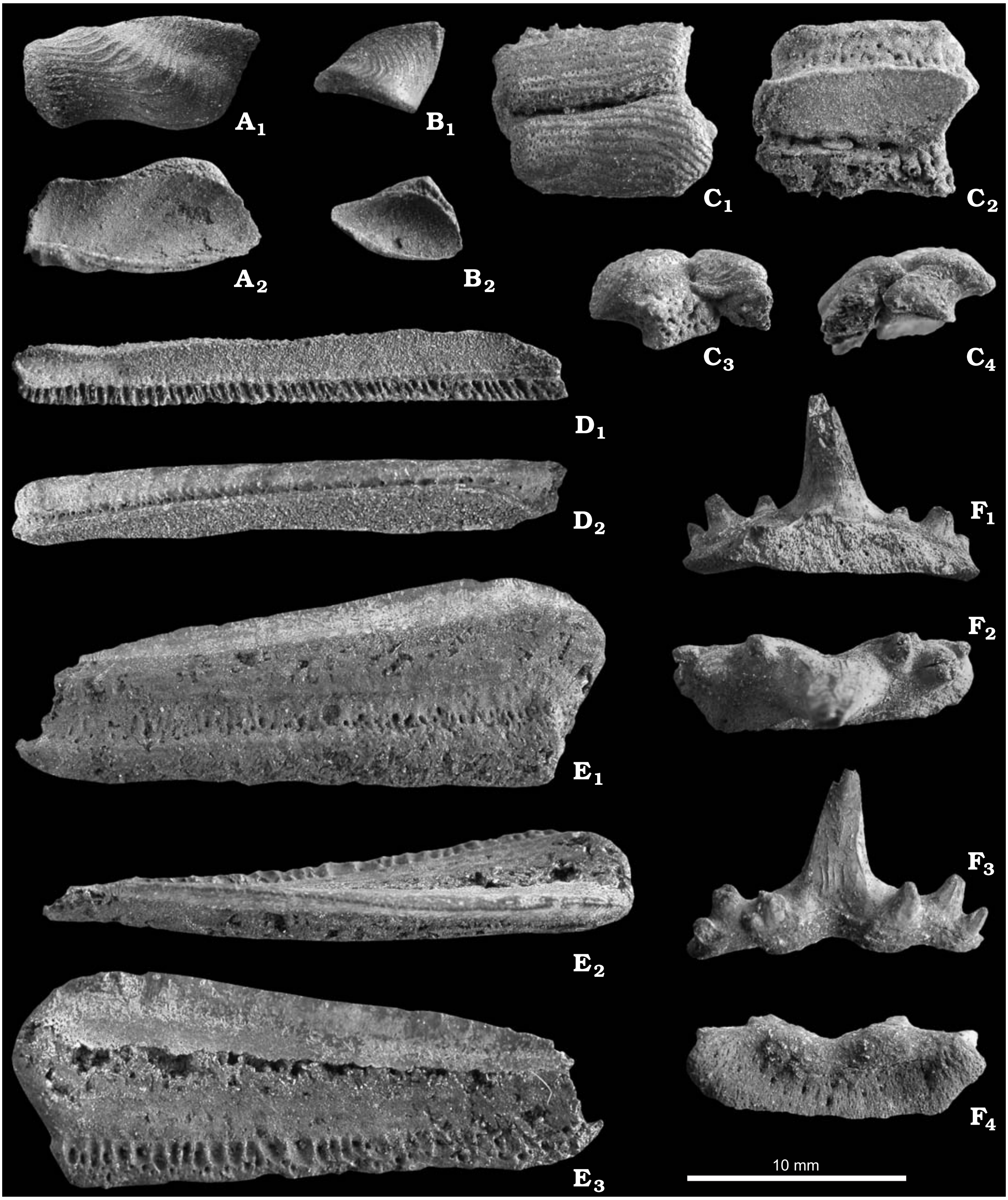

Fig. 9. Chondrichthyan teeth and tooth plates from sample MH-1, middle Tournaisian of Muhua, China. **A**, **B**. *Chondrenchelys* sp. **A**. Posterior toothplate (PKUM02-0159) in oral (A_1) and aboral (A_2) views. **B**. Anterior toothplate (PKUM02-0160) in oblique oral (B_1) and aboral (B_2) views. **C**. Chondrenchelyidae gen. et sp. indet., two overlapping teeth of a tooth family (PKUM02-0161) in oral (C_1), aboral (C_2), and two lateral (C_3, C_4) views. **D**, **E**. *Chomatodus davisi* (Woodward, 1889). **D**. Low tooth (PKUM02-0162) in lingual (D_1) and oral/labial (D_2) views. **E**. High tooth (PKUM02-0163) in labial(E_1), oral (E_2), and lingual (E_3) views. **F**. Ctenacanthiformes gen. et sp. indet., tooth (PKUM02-0164) in lingual (F_1), oral (F_2), labial (F_3), and aboral (F_4) views; lingual base broken.

is a major sella in the middle of the plate, directed antero-labio-posterolingually, framed by two sinuses. The anterior and posterolabial margins of the oral surface are upturned.

On the smaller plates, the growth centre is probably placed posterolabially (in this case the sides are identified based on *Harpagofututor volsellorhinus* Lund, 1982, a chondrenchelyid from Montana). There are about 14 ridges in the posterior part and two to three added at the anterior corner. The oral surface is gently concave, with the posterior and anterolabial margins upturned.

Remarks.—The larger tooth plate is very similar to the posterior plates of *Chondrenchelys problematica* from the lower Viséan of Glencartholm, Dumfriesshire, Scotland, but it is impossible to decide at the moment, whether it represents an upper or lower pair (compare Fig. 8B). The smaller plates are probably anteriors. Unfortunately, none of the specimens of *Chondrenchelys* examined by Lund (1982: text-figs. 4D, 5F) and by us showed the oral view of anterior plates, so the comparison is problematic in this case. The outline of the smaller plates from Muhua is comparable to the anterior plates of *H. volsellorhinus* from the Serpukhovian of Bear Gulch in Montana (Lund 1982: pl. 2: 4, 5), but their ornamentation (radiating ridges with coarse nodes in *Harpagofututor*) is different. Interestingly, the sculpture of the posterior plates in *H. volsellorhinus* and that of Chinese material is almost identical (compare Fig. 8D and E). On the other hand, the plates of *C. problematica* do not show pores between ridges. This may be only a matter of preservation, because the tubules in tubular dentine are originally covered by a thin outer mineral layer (pallial dentine), often partly or completely removed during fossilisation. Nevertheless, because of this difference and inability to compare anterior tooth plates, we leave our material in open nomenclature.

Chondrenchelyidae gen. et sp. indet.

Fig. 9C.

Material.—Two teeth of a tooth-file.

Description.—The crowns of the teeth are rectangular with rounded corners, convex, each resembling a loaf of bread in oral view. The surface is ornamented with concentric ridges whose growth centre is situated labially. Spaces between the ridges are perforated with numerous pores, similarly to the tooth plates of *Chondrenchelys* sp. The bases are of the euselachian type, thick, with a broad basolingual surface devoid of foramina. The tooth bases are overlapping, clearly showing the mode of attachment between the teeth in a tooth

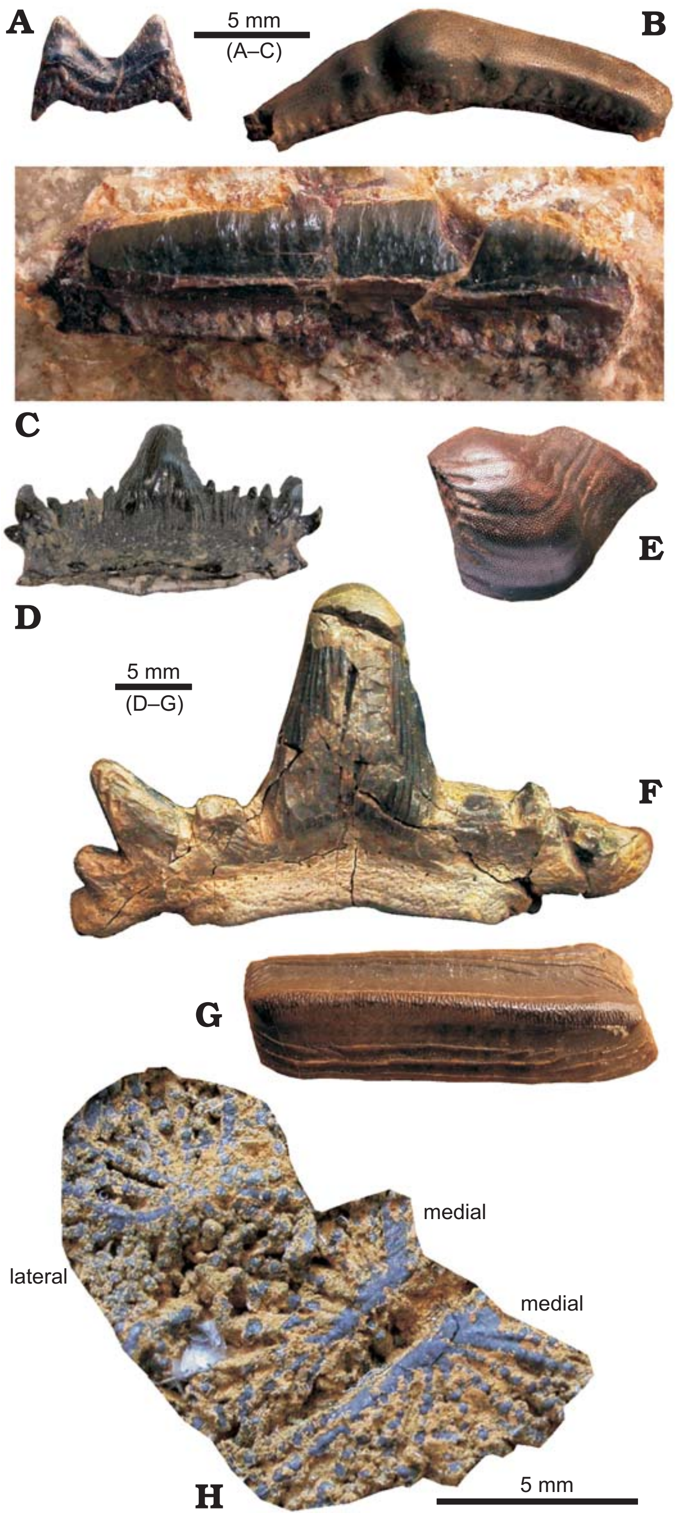

Fig. 10. Reference specimens from Laurussia. **A**. *Diclitodus scitulus* Davis, 1883, holotype (BMNH P.49629), from the Carboniferous Limestone, Richmond, Yorkshire, England, in labial view. **B**. "?*Psephodus laevissimus*", specimen BMNH P.9914, from the Lower Limestone shales bone bed, Avon Gorge near Bristol, in oral view. **C**. *Chomatodus davisi* (Woodward, 1889), a specimen of the type series (BMNH P.2656), from the Viséan Mountain Limestone of Armagh, Northern Ireland, in lingual view. **D**. *Tamiobatis wachsmuthi* (St. John and Worthen, 1875), a specimen of the type series (MCZ 6371), from the Kinderhookian of Burlington, Iowa, in labial view. **E**. *Deltodus sublaevis* (Agassiz, 1838), specimen BGS 5964, from the Viséan Mountain Limestone of Armagh, Northern Ireland, in oral view (left side broken). **F**. ?*Goodrichthys eskdalensis* (Moy-Thomas, 1936), a tooth from the specimen NMS 2000.14.2, from the lower Viséan of Glencartholm, Dumfriesshire, Scotland, in labial view. **G**. *Chomatodus linearis* (Agassiz, 1838), specimen BMNH P.2653, from the Lower Carboniferous Yoredale Beds, Richmond, Yorkshire, England, in oral view. **H**. *Sibyrhynchus denisoni* Zangerl and Case, 1973 (FMNH PF6408), palatal tooth plates.

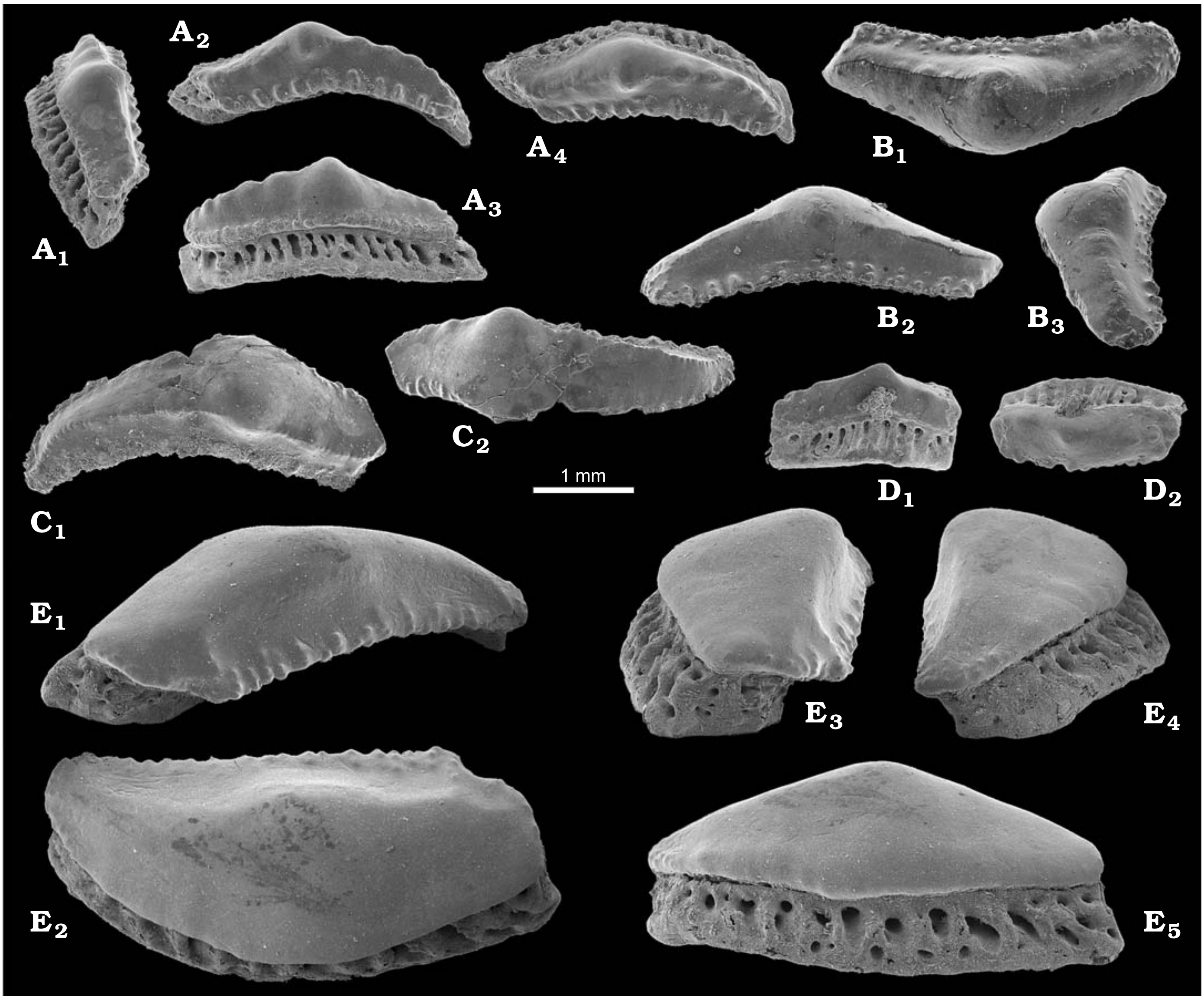

Fig. 11. Teeth of Euchondrocephali incertae sedis from sample MH-1, middle Tournaisian of Muhua, China. **A**–**D**. *Cristatodens sigmoidalis* gen. et sp. nov. **A**. Holotype (PKUM02-0165) in lateral (A_1), labial (A_2), lingual (A_3), and oral (A_4) views. **B**. Crown of PKUM02-0166 in oral (B_1) labial (B_2), and lateral (B_3) views. **C**. Crown of PKUM02-0167 in oral (C_1) and lingual? (C_2) views. **D**. Small tooth (PKUM02-0168) in lingual (D_1) and oral (D_2) views. **E**. ?*Cristatodens sigmoidalis*, PKUM02-0169 in oblique labial (E_1), oral (E_2), lateral (E_3), opposite lateral (E_4), and lingual (E_5) views.

family. Although the basolingual surface of the more lingual tooth is damaged, it is evident that these surfaces in subsequent teeth formed together a uniform, concave, almost completely smooth surface.

Remarks.—Assignment of this specimen to the Chondrenchelyidae is provisional and based only on the similarity of ornamentation of occlusal surfaces. Thus far nothing alike was recorded from the members of this family. However, this type of dentition could represent an intermediate, basal form of the group in which not all the teeth have been transformed into tooth plates, but are already strongly attached to each other. These loaf-like teeth resemble the flat teeth in *Psephodus magnus* (Traquair 1885: figs. 1, 2), which coexist in the same dentition with narrow, *Helodus*-like teeth on one side and broad, sturdy tooth plates on the other. However, because of their size it is unlikely that the teeth under description could occur together with the plates of *Chondrenchelys* sp.

Order uncertain

Family uncertain

Genus *Cristatodens* nov.

Type species: *Cristatodens sigmoidalis* sp. nov.

Derivation of the name: Latin *cristatus* = crested, *dens* = tooth.

Diagnosis.—Teeth with euselachian bases and crowns composed of almost completely fused cusps forming a crest, decreasing laterally. Lingual side of the crown convex and smooth, labial side slightly concave or straight, crenulated at the base.

The upper part of the crown is slightly similar to that of *Venustodus* St. John and Worthen, 1875, but it lacks concentric growth lines, typical of the latter genus and other petalodontiforms.

Cristatodens sigmoidalis sp. nov.

Fig. 11A–D, ?E.

Holotype: Specimen PKUM02-0165, a tooth (Fig. 11A) from the MH section north of Muhua, Guizhou Province, southern China; sample MH-1, bioclastic limestone, Carboniferous, Mississippian, Tournaisian, *Siphonodella crenulata* conodont Zone.

Derivation of the name: Latin *sigmoidalis* = sigmoidal, from the outline of the crown.

Material.—Three teeth and two crowns.

Diagnosis.—*Cristatodens* in which the occlusal crest is sigmoidal in oral view.

Description.—The crown is composed of almost completely fused cusps; only the tips are distinguishable. The median cusp is the largest and thickest, rounded in cross section. The crest formed by the lateral cusps decreases outwards. On one side (it is difficult to determine if it is mesial or distal), it gently turns linguad, but on the other it first goes straight and at the lateral end it turns labiad. The crown is smooth save for the basal rim which is regularly crenulated. Crenulations are stronger on the labial face. The internal structure of the crown, and especially the presence or absence of the tubular dentine, is unknown.

The euselachian-type base is of the same width or only slightly wider (mesio-distally) than the crown. Its lingual margin is convex in oral view, parallel to the lingual rim of the crown. The lateral margins are straight and directed labio-lingually.

The average width of the larger teeth is 3.5–5 mm. In the smaller specimen (2.5 mm; Fig. 11D) sigmoidality of the occlusal crest is only indistinctly marked.

There is a single, larger tooth (6.2 mm; Fig. 11E) with a similar base shape, and the outline and crenulation of the crown, but without a differentiated median cusp and sigmoidal occlusal crest. It is only provisionally attributed here to this species.

Remarks.—The only comparable tooth from elsewhere is the specimen BMNH P.9914, from the Mississippian of Avon near Bristol, labeled as ?*Psephodus laevissimus* (Fig. 10B). It is particularly similar to the tooth illustrated here in Fig. 11B, but much larger (width about 20 mm). Its crown is built of tubular dentine. It is likely that BMNH P.9914 and *Cristatodens sigmoidalis* are conspecific, despite the size difference, but more material is required to confirm this assumption.

Unidentified chondrichthyan crushing teeth

Most of the teeth presented in this section probably belong to the Euchondrocephali, some also may represent Euselachii. However, because of the poor representation of these forms in the sample and the lack of comparative material, we temporarily refrain from attributing them to any of the above-mentioned groups.

Crushing tooth Type 1

Fig. 12A.

Material.—One tooth.

The tooth has a compact crushing crown whose lingual margin is straight and the labial side convex, provided with a narrow labial peg. There is a low prominence at the centre of the crown and two similar higher points on both lateral sides. A vermicular ornament covers the labial face of the crown. The base is narrower than the crown, also bearing a labial peg.

Crushing tooth Type 2

Fig. 12B–D.

Material.—Three teeth.

The crown in these teeth is elongated mesio-distally, provided with a distinct basolabial margin and a weak labial peg. Some traces of a mesio-distal occlusal crest are visible (Fig. $12D_1$, left). The median portion of the crown is somewhat higher than the lateral parts. The upper layer of the crown is built of tubular dentine. The base is deep, typically euselachian, equal in width or slightly narrower than the crown. The width of the teeth is variable, from 1.5 to 4 mm.

Crushing tooth Type 3

Fig. 12E.

Material.—One tooth.

The tooth crown is oval, composed of tubular dentine, with almost the whole labial margin upturned. The euselachian-type base has a broad, strongly arched lingual extension, widening lingually.

Crushing tooth Type 4

Fig. 12F.

Material.—One tooth.

Only a part of this bar-like tooth is preserved. Labial and lingual margins of the crown are parallel to each other, the labial margin bearing heavy crenulation. The crown is very low, with only an indistinct prominence in the median? region. The base is typically euselachian, with almost no lingual extension.

Crushing tooth Type 5

Fig. 12G.

Material.—One tooth.

This is the most unusual tooth in the collection, because it is extremely elongated mesio-distally. Its preserved part is over 13 mm wide, whereas its labio-lingual dimension does not reach 2 mm even in the thickest (median) part. The crown is composed of a rounded median prominence (about 1.5 mm high) and low wings gradually lowering laterally. The outer layer of the crown tissue is largely damaged, so only some better preserved parts suggest that it might have been orna-

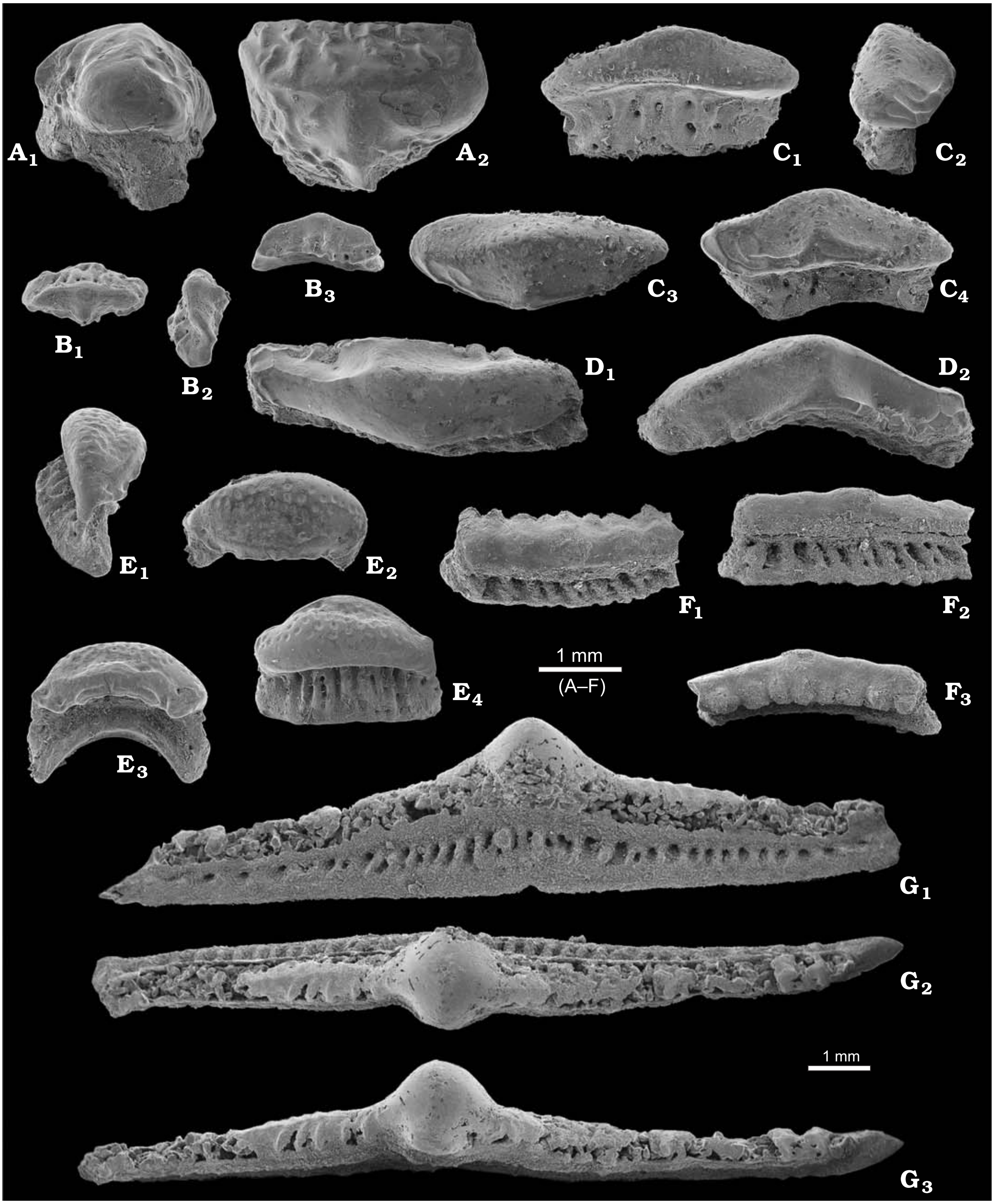

Fig. 12. Unidentified chondrichthyan crushing teeth from sample MH-1, middle Tournaisian of Muhua, China. **A**. Type 1, PKUM02-0170 in lateral (A_1) and oral (A_2) views. **B**–**D**. Type 2. **B**. Small tooth (PKUM02-0171) in oral (B_1), lateral (B_2), and labial (B_3) views. **C**. PKUM02-0172 in lingual (C_1), lateral (C_2), oral (C_3), and labial (C_4) views. **D**. PKUM02-0173 in oral (D_1) and labial (D_2) views. **E**. Type 3, PKUM02-0174 in lateral (E_1), oral (E_2), labial (E_3), and lingual (E_4) views. **F**. Type 4, PKUM02-0175 in oral (F_1), lingual (F_2), and labial (F_3) views. **G**. Type 5, PKUM02-0176 in lingual (G_1), oral (G_2), and labial (G_3) views.

mented with labio-lingual ridges. No trace of tubular dentine was found. The base is also of the euselachian type, with almost no lingual extension.

Chondrichthyan scales

Three types of growing chondrichthyan scales, protacrodont, ctenacanth, and hybodont (see Gross 1938; Reif 1978), were identified in the material from Muhua.

The protacrodont scales (Fig. 13A, B) are characterised by flat crowns, rounded anteriorly and pointed posteriorly, composed of several generations of odontodes closely attached to each other. Each new generation of odontodes grows around the older part of the crown. The neck of the scale is perforated with minute foramina. The upper margin of the base is diamond-shaped and the main body of the base is semi-spherical. All these features make this type of scales resemble acanthodian scales, the fact already noted by Gross (1938) in his description of the body cover of *Protacrodus vetustus* Jaekel, 1925, from the Frasnian of Bad Wildungen.

The ctenacanth scales (Fig. 13C–F; name given by Reif 1978 based mainly on scales of a ctenacanthiform "*Ctenacanthus*" *costellatus* Traquair, 1884 from the Mississippian of Scotland) are the most common shark scales in Devonian and Carboniferous rocks. They were found not only associated with ctenacanths, but also with more primitive sharks' teeth, such as *Phoebodus* (Ginter and Turner 1999). The crown is less compact than that of the protacrodont type. The odontodes grow more or less parallel and the outline of the crown is variable, from small and rounded to extremely elongated laterally. The base is smaller than the crown, from diamond-shaped to rounded, to elliptical, with a flat or concave basal surface.

The hybodont scales (Fig. 13G; the term based by Reif 1978 mainly on articulated specimens of *Hybodus delabechei* from the Jurassic of Lyme Regis in England) are characterised by the crowns with odontodes standing upright and only their upper parts turned posteriorly, if at all. The crowns of scales from Muhua are compressed laterally, there are pores in the neck, and the bases are rounded and flat.

Problematic plates

Fig. 13K, L.

Two polygonal plates were found, ornamented with rows of tubercles radiating from the centre. One of the plates (Fig. 13K) is symmetrical, in the shape of a knight's shield, pointed at one end and bifurcated and depressed at the other. The other plate (Fig. 13L) has a more irregular shape and the tubercles are relatively larger. It is difficult to propose the assignment of these plates. However, the symmetrical plate (probably worn in the central area) reveals some similarity to the mandibular or palatal tooth plates of Iniopterygii, and particularly of *Sibyrhynchus* Zangerl and Case, 1973 (Fig. 10H). If the identification is correct, it could be one of lateral plates, and the bifurcated part would be directed towards the midline of the palate and contact with one of the paired median plates.

Discussion

The assemblage of chondrichthyan microremains from the Tournaisian of Muhua is very diverse. This is not unusual of the Mississippian shallow water facies, since even greater diversity is observed in the collection described by St. John and Worthen (1875, 1883) mainly from the outcrops lying close to each other along the Mississippi valley. What is specific for the Muhua fauna is that these 22 taxa, belonging to at least eight orders, come from a small limestone lens, precisely dated by conodonts. This allows us to treat the whole association as a representation of a chondrichthyan community very restricted in time and space.

The majority of the fauna consists of teeth with euselachian-type bases, and of these most are crushing forms, perhaps except for the teeth referred to here as "Euselachii gen. et sp. indet.", which display a curious combination of euselachian base and an almost cladodont crown. The abundance of crushing dental elements is natural, because the invertebrate fauna of MH-1 is rich in brachiopods (Baliński 1999) and other shelly fossils, a typical prey of durophagous fish. The variability of shapes of crushing and grinding teeth and tooth plates is a result of strong monognathic and dignathic heterodonty, but it also reflects high taxonomic diversity. It is a perfect example of the postulated explosive radiation of chondrichthyans after the extinction of placoderms at the end of the Devonian which emptied the niches on shallow water platforms. Chondrichthyan teeth with crushing crowns and euselachian bases are known from rocks much older than the Devonian–Carboniferous boundary (probably the oldest is *Orodus devonicus* Hussakof and Bryant, 1918, from the upper Givetian/lower Frasnian Conodont Bed, Eighteen Mile Creek, New York), but even in the richest samples from the Iranian Platform (Ginter et al. 2002) the number of species is much smaller compared to that in Muhua. Moreover, sample MH-1 yields representatives of several groups unknown from the Devonian, such as Petalodontiformes and Chondrenchelyidae.

Regarding sharks with more primitive, clutching dentitions, *Thrinacodus*, *Stethacanthus*, and *Tamiobatis* might have preyed on small actinopterygians, conodonts, and other unarmoured organisms swimming above the bottom. We have only one piece of evidence of a larger predator which might have threatened the thriving benthic chondrichthyan community: the *Goodrichthys*-like ctenacanthiform tooth.

It is interesting that a lot of species recorded from Muhua, not only stethacanthids or ctenacanthiforms whose body size and shape suggest that they were good swimmers and hunters, but also such minute durophagous bottom dwellers as *Chondrenchelys*, have their counterparts (if not members of the same species) in the distant regions of Laurussia. This shows that there were no significant barriers in Mississippian

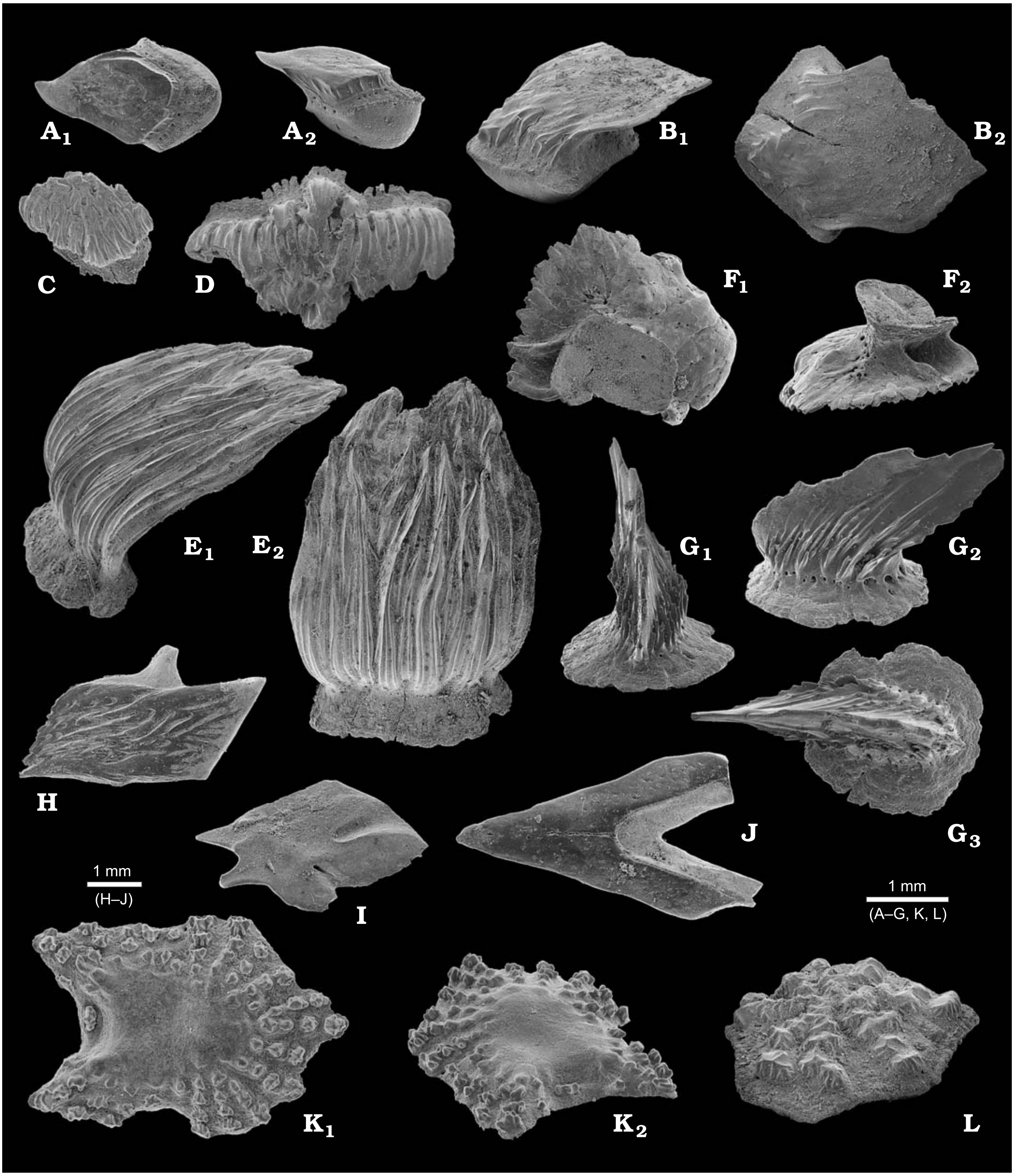

Fig. 13. Fish scales and problematic plates from sample MH-1, middle Tournaisian of Muhua, China. **A**, **B**. Protacrodont chondrichthyan scales. **A**. PKUM02-0177 in coronal (A_1) and lateral (A_2) views. **B**. PKUM02-0178 in lateral (B_1) and coronal (B_2) views. **C**–**F**. Ctenacanth chondrichthyan scales. **C**. PKUM02-0179 in coronal view. **D**. PKUM02-0180 in coronal view. **E**. PKUM02-0181 in lateral (E_1) and anterior coronal (E_2) views. **F**. PKUM02-0182 in basal (F_1) and oblique basal (F_2) views. **G**. Hybodont chondrichthyan scale (PKUM02-0183) in anterior (G_1), lateral (G_2), and coronal (G_3) views. **H**–**J**. Actinopterygian scales. **H**. Body scale (PKUM02-0184) in external view. **I**. Body scale (PKUM02-0185) in oblique basal view. **J**. Fulcral scale (PKUM02-0186) in external view. **K**, **L**. Problematic plates. **K**. PKUM02-0187 in oral (K_1) and oblique (K_2) views. **L**. PKUM02-0188 in oblique view.

seas between shallow water areas and the species could disperse, sooner or later, finding suitable conditions on their way. *Thrinacodus bicuspidatus* sp. nov. occurs virtually simultaneously in Muhua, Canning Basin, Iran, and Nevada and probably goes extinct before the end of the Tournaisian. However, several other species (among them *Chomatodus linearis*, *Ch. davisi*, *Helodus coniculus*, *Diclitodus denshumani*) are unknown from the Tournaisian outside Muhua. They are apparently absent from the Kinderhookian (Tournaisian: Hastarian) of the North American mid-continent, but appear in the upper Osagean (lower Viséan) Burlington and Keokuk Limestones of the same area and, a few of them, were recorded from the Mountain Limestone (upper Viséan) of Northern Ireland.

The assemblage from Muhua is yet another evidence that, in order to restore the true stratigraphic and biogeographic picture of Palaeozoic chondrichthyan faunas, studies of disarticulated remains, especially teeth, are indispensable. Focusing on articulated specimens alone, leaves gaps in our knowledge which may be filled only by careful analysis and comparison of ichthyoliths.

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