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New scolecodonts (polychaeta, annelida) from the Late Silurian of Yunnan, South China

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Abstract
Scolecodonts are the fossilised jaw apparatus of polychaetes, with fossil records dating back to the Late Cambrian. However, they are commonly found in Ordovician, Silurian and Devonian strata. Here, we describe three species—*Langeites* aff. *glaber, Langeites* sp., and *Oenonites* spp. from the Miaogao Formation in Yiliang, Yunnan, South China. A comparative morphological study on the maxillary apparatus of the family Paulinidae and the extant members of Eunicidae and Onuphidae was conducted. This study aims to evaluate evolutionary changes in the maxillary apparatus, particularly the first maxilla, within the eulabidognatha-type apparatus. To infer their palaeoecology, *Langeites* aff. *glaber* and *Langeites* sp. were compared with modern species of Eunicidae and Onuphidae based on their complex maxillary apparatus. The similarity between these fossil and extant taxa suggests that *Langeites* retained similar feeding habits over time. These scolecodonts represent a new record for the Late Silurian of South China, and extend the geographical range of the genus *Langeites*. As a genus restricted to the Silurian, *Langeites* has potential applications in stratigraphic correlation for the Late Ludlow to Early Pridoli.

Keywords Scolecodonts, Microfossil, Polychaeta, Silurian, South China

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Introduction

Scolecodonts, the pharyngeal structures of polychaetes (Annelida), are commonly preserved as microfossils due to their resistance to corrosion than soft tissues (Briggs & Kear, 1993). Early publications mistakenly identified them as fish teeth (Eichwald, 1854; Pander, 1856). Around the same time, Massalongo (1855) described annelids impressions from Tertiary deposits in Italy, preserving their jaws in situ. However, his findings remained largely unnoticed until Angelin later correctly identified them as polychaete jaws in correspondence with Hinde, Thorell, and Lindström (Bergman, 1989).

Scolecodonts have been traced back to the Late Cambrian (Williams et al., 1999) with the first Silurian record discovered by Hinde (1882) in the Wenlock Formation of Gotland, Sweden. Subsequent studies by Martinsson (1960) described two Silurian scolecodont assemblages from Sweden and used the apparatus taxonomy to name the materials. According to the available global records of Silurian scolecodonts, most known Silurian scolecodonts have been documented in Baltica and Laurentia, including Estonia, United States, Canada, British Isles, and Severnaya Zemlya (Eriksson et al., 2004). In contrast, fewer specimens have been recovered from Gondwana and its peripheral plates, including China, North Africa, and Australia (Eriksson et al., 2013).

Previous research on scolecodonts has focused on species descriptions (Bergman, 1989; Eriksson, 1997; Eriksson et al., 2012; Hints, 1998), biogeography distribution (Eriksson et al., 2013; Hints & Eriksson, 2007), taxonomic assemblages (Calner et al., 2008), and their relationship with Silurian biological events (Männik et al., 2024; Tonarova et al., 2012). However, relatively little attention has been paid to their paleoecology (Bergman, 1995; Hints & Tonarová, 2023).

Among polychaetes, members of Eunicida and Phyllodocida possess jaw apparatuses, and all known Silurian examples belong to the Eunicida (Paxton, 2009). Within this order, Paulinitidae is the only Palaeozoic family classified under Eulabidognatha (Paxton, 2009), with fossil occurrences ranging from the Late Ordovician to Carboniferous (Eriksson & Bitter, 2015). Paulinitidae is among the most common and widespread families of Silurian scolecodonts (Eriksson et al., 2012), and within this family, the genus *Langeites* is particularly common in the Ludlow–Pridoli (Hints et al., 2000; Männik et al., 2024). When Kielan-Jaworowska (1966) first established *Langeites*, only forceps-like first maxillae (MI) were known. Later Bergman (1989) incorporated second maxilla (MII) characteristics into *Langeites* when studying Paulinitidae from Gotland. Fossil occurrences of *Langeites* are predominantly known from the Baltic region (Bergman, 1989; Eriksson et al., 2012; Kielan-Jaworowska, 1966; Männik et al., 2024), Cornwallis and Baillie-Hamilton islands (Hints et al., 2000), and rare reports exist from South China. The only known records of *Langeites* in South China come from the Ordovician Taowan Group (Wang et al., 2008) and Devonian Pulai Formation (Ye, 1994). The Yiliang scolecodonts thus provide new insights into the details of morphology and distribution of *Langeites*.

Since scolecodonts serve as feeding apparatuses, their morphology is closely linked to dietary habits. A detailed comparison of the new jaw apparatuses from Yiliang with those of extant taxa was undertaken to infer the paleoecology of *Langeites* and reconstruct the morphological evolution of eulabidognatha-type jaw structures. Additionally, this study examines the stratigraphic and geographic distribution of *Langeites* in the Silurian, particularly *Langeites glaber*, and assesses its potential for biostratigraphic correlation.

Geology and age

The specimens described in this study originate from the Miaogao Formation at the Dadukou section, Yiliang County, Yunnan Province (E103°11 ′2.54", N24°55′ 58.90"), located in the southwestern part of the Yangtze Plate (Fig. 1A, B). The Miaogao Formation is approximately 60 m thick at the well-exposed section and is unconformably overlain by Quaternary deposits. It comprises a continuous succession of dolomitic limestone, limestone, and shale interbedded with fossiliferous limestones (Fig. 1C). Four fossiliferous limestones horizons have been identified from bottom to up, with the studied scolecodonts, along with abundant conodonts, brachiopods, gastropods, and rare fish scales, recovered from the third horizon of gray limestone.

The Miaogao Formation represents a highly fossiliferous Late Silurian unit within the Yangtze Plate, containing previously described brachiopods, tabulate corals, bivalves, nautiloids, trilobites (Rong & Yang, 1980; Rong et al., 2019), and vertebrates including *Ligulalepis*, *Kawalepis* and *Naxilepis* (Zhao & Zhu, 2014); as well as *Poracanthodes qujingensis* (Wang & Dong, 1989). Documented microfossils include *Ozarkodina crispa, Hindeodella pricilla* and *Frichonechella* (Rong et al., 1995; Wang, 1980), serving as key index fossils for regional stratigraphic correlation.

Based on lithological and fossil assemblages, the Miaogao Formation has been dated to the Late Ludlow–Early Pridoli (Rong et al., 2019; Wang et al., 2021, 2023). The Dadukou section yields an abundance of conodonts (*Ozarkodina crispa,* Fig. 2D–F) and a few of fish scales of *Poracanthodes qujingensis* (Fig. 2A, B), further supporting a Late Silurian (Ludlow–Pridoli) chronostratigraphic position.

Materials and methods

Approximately 60 kg of fossiliferous limestone was collected from the Miaogao Formation at the Dadukou section, Yiliang County, Yunnan Province. To extract microfossils, the samples were treated with a 5% dilute acetic acid solution and collected with a piece of nylon fabric with a mesh size of 0.08 mm in diameter. The resulting residues were carefully examined under a Leica DFC450 microscope, and scolecodonts were manually picked for further study. The selected specimens were coated with a gold–palladium (Au/Pd) alloy under vacuum conditions and subsequently examined using a scanning electron microscope (VEGA3-TESCAN) to document their morphological details. Adobe Photoshop 2022 and CorelDRAW 2022 were used for image processing and figure preparation. A total of over 300 microfossils were recovered, primarily consisting of conodonts, brachiopods (Fig. 2G–I)

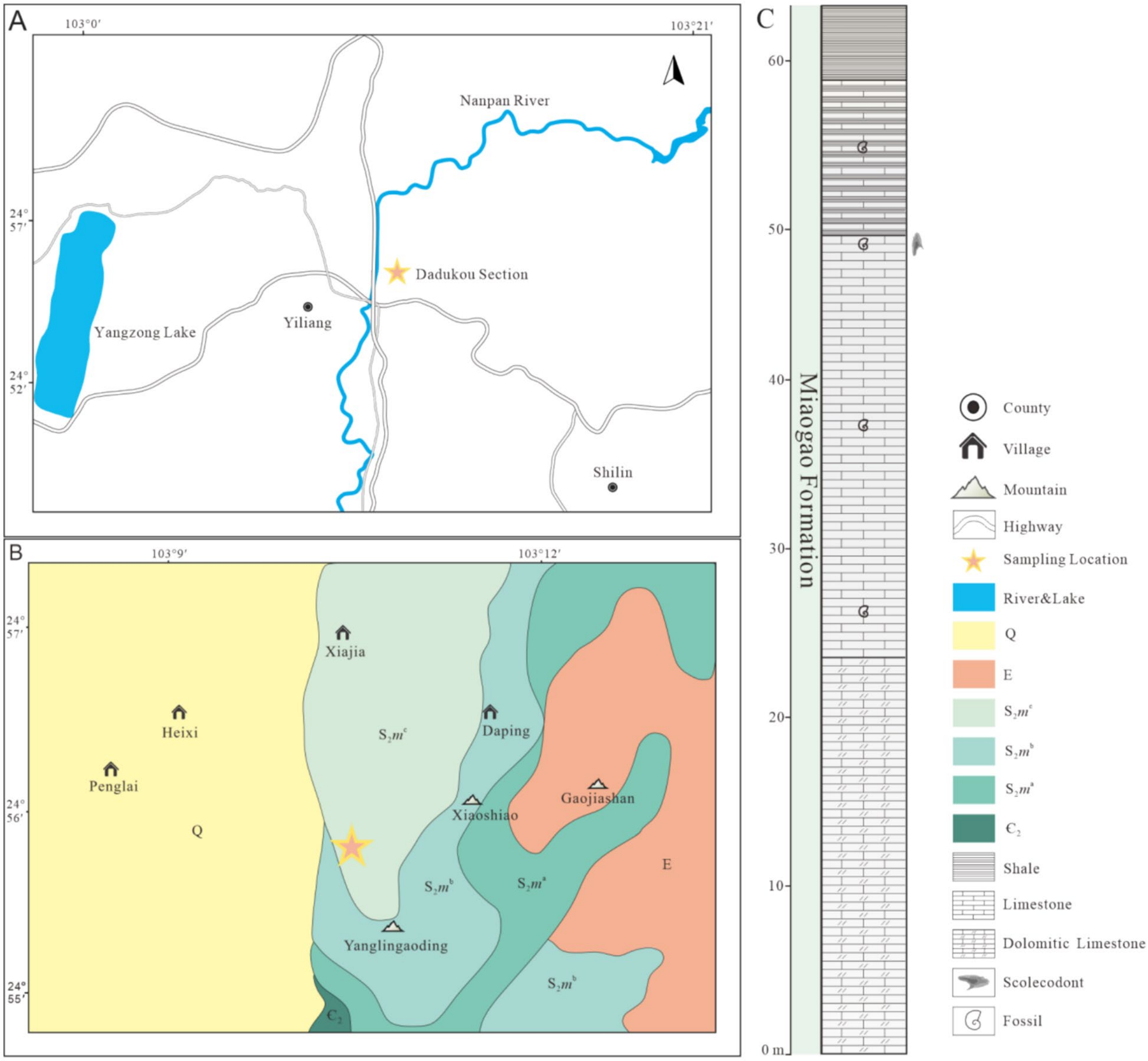

Fig. 1 Location and stratigraphy of the studied section in Yiliang, South China

and gastropods (Fig. 2C), along with a smaller number of scolecodonts (Fig. 3), and fish scales (Fig. 2A, B). Among these, 28 scolecodonts were identified and cataloged under specimen numbers YLSS01 to YLSS28. The collection includes: 15 first maxilla (MI), 10 second maxilla (MII), 2 fourth maxilla (MIV), and 1 unclassified jaw fragment. These specimens belong to two genera: *Langeites* and *Oenonites*. Additionally, several isolated jaw fragments were found, including: 5 MI (YLSS06 to YLSS10), 3 MII (YLSS18 to YLSS20), 1 unidentified maxilla (YLSS28). Due to their fragmentary preservation, these isolated specimens could not be definitively assigned to specific species. All studied specimens are housed in the Geological Innovation Team laboratory at Kunming University of Science and Technology.

Scolecodonts of the Miaogao formation from Yiliang

The scolecodont assemblage from Yiliang includes first (MI), second (MII), and fourth (MIV) maxillae, which are generally fragile and often fragmentary. However, several well-preserved first and second maxillae were identified, allowing taxonomic classification within the families Paulinitidae and Polychaetaspidae. Paulinitid maxillae are significantly more abundant in this assemblage than polychaetaspid maxillae.

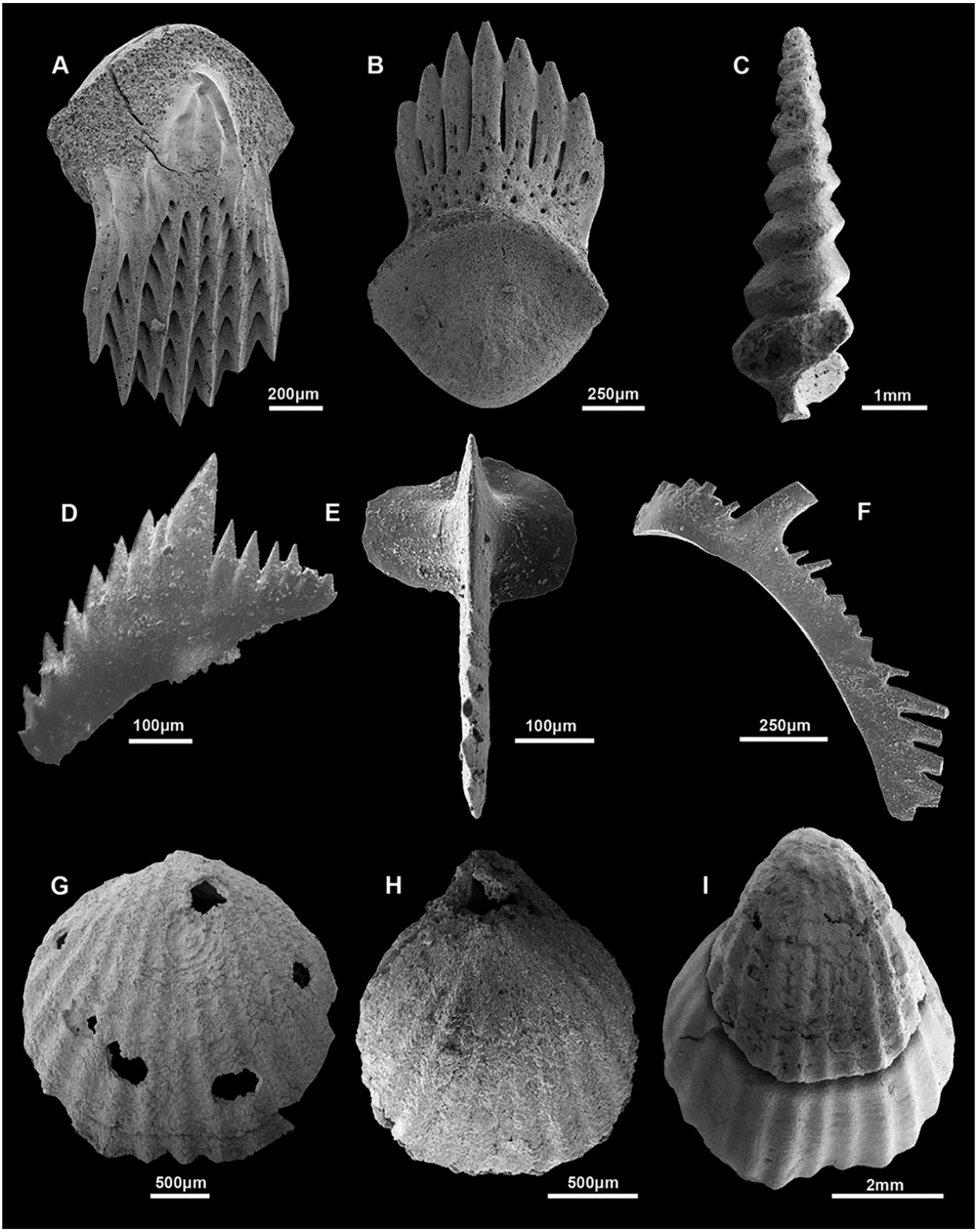

Fig. 2 **A**, **B** *Poracanthodes qujingensis* (YLSP01): **A** Dorsal side, **B** Ventral side. **C** Gastropoda, *Hormotoma* sp. (YLSC01). **D**–**F** *Ozarkodina crispa*: **D** YLSC001, lateral view; **E** YLSC002, oral view; **F**. YLSC003, lateral view. **G**–**I** Brachiopoda, *Proathyris* sp. (YLSB01–YLSB03)

(See figure on next page.)

Fig. 3 **A**–**H** *Langeites* aff. *glaber*: **A** Right MI (YLSS01) with nine sub-distal denticles (arrowed), ventral side, **B** Right MI (YLSS01), dorsal side; **C**, **D** Right MII, YLSS11, **C** Dorsal side, **D** Ventral side; **E** Right MIV (YLSS21), ventral side; **F** Left MIV (YLSS22), ventral side; **G** Detail of (**A**), showing the fine denticles; **H** Detail of (**D**), showing the ligament rim. **I**–**N** *Langeites* sp.: **I**–**J** Right MI, YLSS02, **I** Ventral side, **J** Dorsal side; **K** Right MII (YLSS12), ventral side; **L** Left MII (YLSS13), dorsal side; **M** Detail of (**I**), showing sub-terminal denticles; **N** Detail of (**J**), showing undenticulated ridge. **O**–**S** *Oenonites* spp.: **O** Left MI (YLSS23), dorsal side; **P** Left MI (YLSS24), ventral side; **Q** YLSS25, posterior part of MI; **R** YLSS26, posterior part of MI; **S** Detail of (**R**), showing triangular denticles

A total of 14 paulinitid maxillae were recovered, including first maxillae (YLSS01–YLSS05, Tables S1–S5), second maxillae (YLSS11–YLSS17, Tables S11–S17), and fourth maxillae (YLSS21–YLSS22, Tables S21, S22). The first maxillae range from 0.46 mm to 2.40 mm in length and 0.16 mm to 0.53 mm in width, and the second maxillae measure 0.72 mm to 3.96 mm in length and 0.32 mm to 0.82 mm in width (see Supplementary Tables for more information), indicating that they may represent different species or developmental stages. Some specimens display denticles along the inner margin, although they are not well preserved in all cases. The unique morphology of right MI and right MII confirms their assignment to the genus *Langeites*. Additionally, two well-preserved fourth maxillae were identified, showing a visible myocoele opening and clear denticles along the inner margin. According to their size and morphology, these MIV specimens likely represent left and right counterparts of the same species.

Polychaetaspid jaws are relatively rare in this assemblage. Only five first maxillae (YLSS23–YLSS27, Tables S23–S27) were recovered, ranging from 0.69 mm to 3.96 mm in length and 0.43 mm to 0.99 mm in width. These specimens exhibit 4 to 16 denticles along the inner margin. On the basis of available material, determination at the species level was difficult. These specimens exhibit a large, hooked fang, characteristic of *Oenonites*. However, due to the limited number of specimens and their preservation state, species-level identification was not possible.

Several isolated and incomplete jaw fragments were also found, including 5 first maxillae (YLSS06–YLSS10, Tables S6–S10), 3 second maxillae (YLSS18–YLSS20, Tables S18–S20) and 1 unidentified maxilla (YLSS28, Table S28). The poor preservation of these specimens precluded definitive taxonomic classification.

Morphology and systematic classification of Eunicida

The classification of jaw apparatuses in Eunicida is based on the number, relative position, arrangement, and shape of jaw elements (Edgar, 1984; Paxton, 2009). Early studies by Ehlers (1868) grouped all polychaete jaws with short and wide carriers under Labidognatha. Later, Kielan-Jaworowska (1966) introduced a four-type classification: Placognatha, Ctenognatha, Labidognatha, and Prionognatha. This system was further refined by Paxton (2009) who added two additional types: Symmetrognatha and Eulabidognatha. Today, it is widely acknowledged that there are six distinct types of jaw apparatuses: Placognatha, Ctenognatha, Labidognatha, Prionognatha, Symmetrognatha, and Eulabidognatha (Koroleva & Tzetlin, 2024; Paxton, 2009; Paxton & Eriksson, 2012; Shcherbakov et al., 2022; Suttner & Hints, 2010; Tzetlin et al., 2020; Zanol et al., 2021). To investigate changes in the maxillary apparatus over time, a comparative analysis of these six jaw types was conducted.

Placognatha (Fig. 4A–C): Late Cambrian to Permian (e.g., *Xanioprion walliseri*, Fig. 4C). Placognatha-type apparatuses are the oldest and most primitive, characterized by symmetrical plates with a single dentate ridge (Kielan-Jaworowska, 1962; Paxton, 2009; Williams et al., 1999). The apparatuses exhibit asymmetrical maxillae by the Middle Ordovician (e.g., *Pistoprion tanstans*, Fig. 4B).

Ctenognatha (Fig. 4D–G): Late Cambrian to present (e.g., *Archaeoprion quadricristatus*, Fig. 4F; *Tetraprion pozaryskae*, Fig. 4G). Today, only the family Dorvilleidae (Fig. 4D, E) remains (Paxton, 2009). Ctenognatha-type apparatuses (Fig. 4D–G) exhibit a transition from symmetrical to subsymmetrical jaws.

Symmetrognatha (Fig. 4H–K): Early Ordovician to present (e.g., *Kadriorgaspis kaisae*, Fig. 4K). Symmetrognatha-type apparatuses are distinguished by their four paired elements, with MI exhibiting a dentate, forceps-like, or conical shape (Paxton, 2009).

Prionognatha (Fig. 4L–M): Middle Ordovician to present. Currently, only the family Oenoidae is extant (e.g., *Oenone fulgida*; Fig. 4L). Prionognatha-type apparatuses introduce jaw asymmetry, a key feature in later forms, with species like *Atraktoprion major* (Fig. 4M) displaying a basal plate fused with the right MI (Paxton, 2009; Shcherbakov et al., 2022; Szaniawski & Wrona, 1973; Underhay & Williams, 1995).

Labidognatha (Fig. 4N–O): Middle Ordovician to Cretaceous (e.g., *Oenonites wyszogrodensis*, Fig. 4O). Labidognatha-type apparatuses are asymmetrical, having 5 pairs of elements in 2 rows (Edgar, 1984; Paxton, 2009; Struck et al., 2006). The basal plate is also fused with the

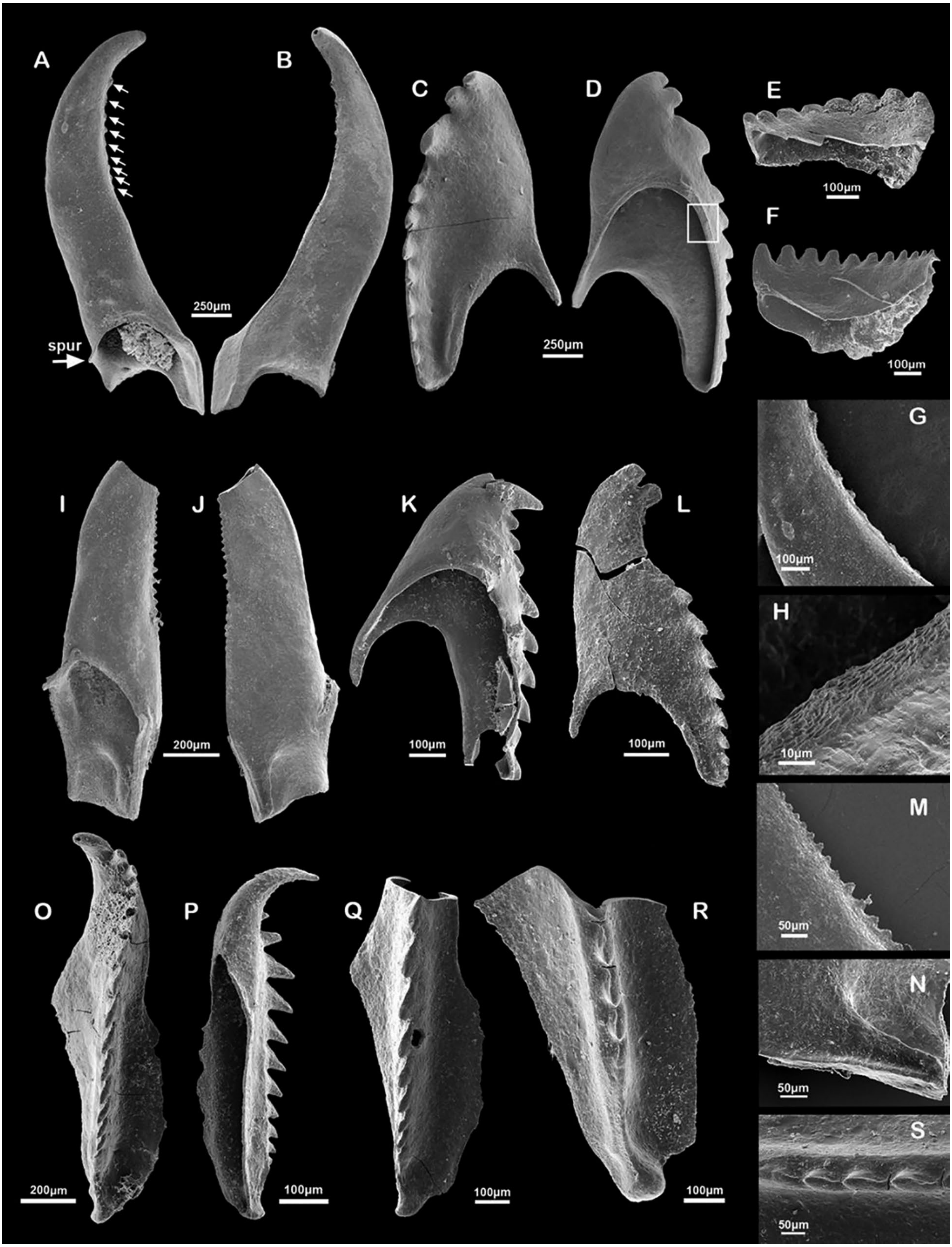

Fig. 3 (See legend on previous page.)

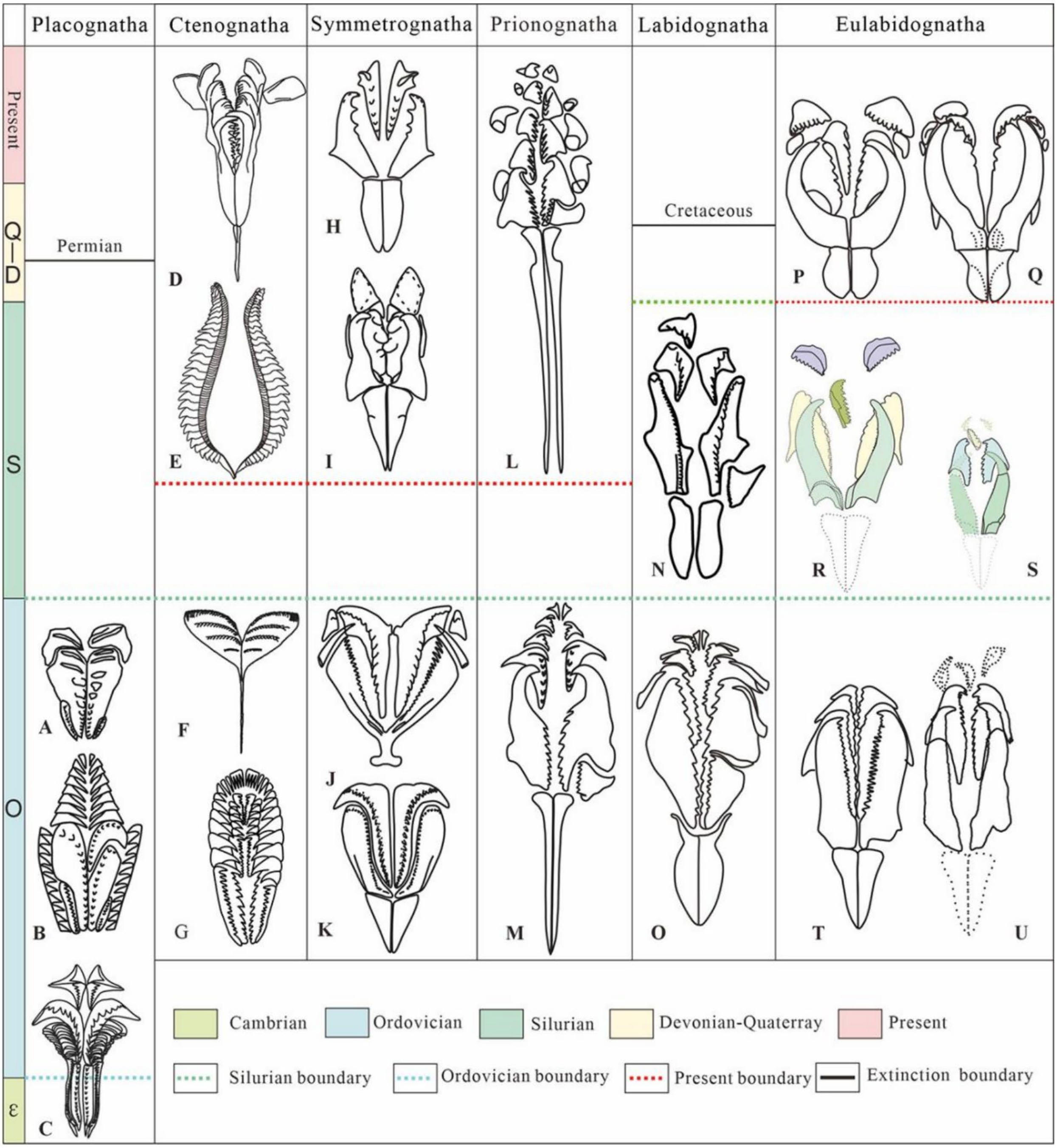

Fig. 4 Different types of maxillary apparatus in Eunicida. **A**–**C**. Placognatha: **A**. *Rhytiprion magnus* (Rhytiprionidae; from Eriksson et al., 2004), **B**. *Pistoprion tanstans* (Mochtyellidae; from Paxton, 2009), **C**. *Xanioprion walliseri* (Xanioprionidae; modified Whittle et al., 2008). **D**–**G**. Ctenognath: **D**. *Ophryotrocha mammillata* (Dorvilleidae, from Zanol et al., 2021), **E**. *Dorvillea australiensis* (Dorvilleidae, from Paxton, 2009), **F**. *Archaeoprion quadricristatus* (Archaeoprionidae, from Mierzejewski & Mierzejewska, 1975), G. *Tetraprion pozaryskae* (Tetraprionidae; from Eriksson et al., 2004). **H**–**K**. Symmetrognatha: **H**. *Palurites jurassicus* (Hartmaniellidae; from Paxton, 2009), **I**. *Augeneria* sp. (Lumbrineridae; from Zanol et al., 2021), **J**. *Conjungaspis minutus* (Conjungaspidae; from Hints, 1999), **K**. *Kadriorgaspis kaisae* (Conjungaspidae; from Paxton, 2009). **L**–**M**. Prionognatha: **L**. *Oenone fulgida* (Oenonidae, from Kielan-Jaworowska, 1966), **M**. *Atraktoprion major* (Atraktoprionidae; from Kielan-Jaworowska, 1966). **N**–**O**. Labidognatha: **N**. *Megaramphoprion magnus* (Ramphoprionidae, from Eriksson, 2001), **O**. *Oenonites wyszogrodensis* (Polychaetaspidae, from Paxton, 2009). **P**–**U**. Eulabidognatha: **P**, *Paradiopatra fragosa* (Onuphidae, from Zanol et al., 2021), **Q**. *Eunice roussaei* (Eunicidae, from Zanol et al., 2021), **R**. *Langeites* aff. *glaber* (Paulinitidae), **S**. *Langeites* sp. (Paulinitidae), **T**. *Kettnerites* (*Aeolus*) *sisyphi klasaardensis* (Paulinitidae, from Bergman, 1989), **U**. *Kingnites diamondi* (Paulinitidae, from Eriksson et al., 2012)

right MI, where is consistent with prionognaths (Paxton, 2009).

Eulabidognatha (Fig. 4P–U): Late Ordovician to present (e.g., *Kettnerites* (*Aeolus*) *sisyphi klasaardensis*, Fig. 4T; *Langeites* aff. *glaber*, Fig. 4R). There are two extant families, the Eunicidae and Onuphidae. Eulabidognatha-type apparatuses characterized by dentate to forceps-like MI, a highly reduced right MI fused (Paxton, 2009). Among Palaeozoic Paulinitidae, the right MI and right MII are considered the most diagnostic elements for taxonomic classification (Bergman, 1989). Asymmetrical MIII and MIV features are extremely difficult to distinguish (Bergman, 1989).

The following terminology of descriptive terms in this study is after Bergman (1989).

Systematic palaeontology

Phylum Annelida Lamarck, 1809.

Class Polychaeta Grube, 1850.

Order Eunicida Dales, 1963.

Superfamily Eunicea Grube, 1852.

Family Paulinitidae Lange, 1947.

Genus *Langeites* Kielan-Jaworowska, 1966

Type species *Langeites glaber* Kielan-Jaworowska, 1966

Langeites aff. *glaber.*

(Fig. 3A–H).

Material. YLSS01, right MI (Fig. 3A–B, G); YLSS11, right MII (Fig. 3C, D, H); YLSS21, right MIV (Fig. 3E); YLSS22, left MIV (Fig. 3F).

Description. Eulabidognatha-type apparatus consisting of right MI, right MII, left MIV and right MIV are known; carriers and precise relationships of elements in apparatus are unknown.

Right MI, dorsal side: Length 2.4 mm, width about 1/5 of the length. The inner and outer margins are almost parallel, but the jaw tapers anteriorly with a well-developed, dorsolaterally directed, slender fang. The inner margin is slightly curved and only a few sub-distal denticles spread along from the posterior most of the arch to the middle part (Fig. 3G). Subsequently, the inner margin to the undenticulated ridge has no denticles. The basal furrow is short and shallow oriented parallel to outer margin of basal portion.

Ventral side: There is no discernible difference between the inner and outer margins. A very short distinct spur exists on the posterior outer part, but is not visible in dorsal view. The ventral side features nine sub-distal denticles along the inner margin. The crescent-shaped myocoele opening is narrow, slightly enclosed, representing about one-quarter of its jaw length. The opening is surrounded by a narrow rim.

Right MII, dorsal side: Length 3.96 mm, width about half of the length. Two very large pre-cuspidal denticles of almost equal size are followed by a large, triangular, and slanting cusp, which in turn is followed by about 13 intermediate denticles. The shank is moderately to fairly short with a blunt angle. The ramus is needle-shaped, long, and narrow.

Ventral side: The crescent-shaped myocoele opening is wide, slightly enclosed, representing about half of the jaw length. The opening is surrounded by a narrow ligament rim (Fig. 3H).

Right MIV, ventral side: Length 0.7 mm, and width half of the length. Comb-like jaw with a slightly curled inner margin. It bears 11 densely spaced denticles along the inner margin, with the size gradually decreasing from the anterior to the posterior. The myocoele opening is open and extends from the posteriormost to anteriormost, occupying the whole jaw length.

Left MIV, ventral side: Length about 0.5 mm, width half of the length. Incomplete jaw with the open myocoele opening occupying the whole jaw length. Almost a mirror image of the ventral side of the right MIV, except that 8 densely spaced denticles along the inner margin.

Comparisons. Both of the MI and MII of *Langeites* aff. *glaber* are similar to those of *L. glaber*, particularly in the MII. However, the MI of *L.* aff. *glaber* bears a small and dorsolaterally directed fang. MIV of *L. glaber* are absent. Compared with *L. siciliensis* (Corradini & Olivieri, 1974), the right MIV of *L.* aff. *glaber* has a different shape, denticles, and myocoele opening. The right MIV of *L. siciliensis* is quadrangular with 6–10 tapering denticles, while that of *L.* aff. *glaber* is comb-like with 11 short and blunt denticles. The myocoele opening of *L.* aff. *glaber* is wide open from the posteriormost to anteriormost, while that of *L. siciliensis* closes at the anterior and posterior edges.

Remarks. The right MI, right MII, and MIV of *L.* aff. *glaber* are well-preserved, particularly the MIV, which has received little attention in previous studies. Here, we infer the location of the two MIV based on the size relationships and MIV of *L. siciliensis* (Corradini & Olivieri, 1974). The MI and MII are the most informative elements in revealing the similarities and differences between extinct and extant maxillae (Bergman, 1989; Paxton & Eriksson, 2012). Although the MI and MII of *L.* aff. *glaber* are similar to those of *L. glaber,* there are still differences in the denticulation, inner margin, and bending direction.

Stratigraphic Occurrence. Dadukou section, Yiliang County, Yunnan Province, China; Late Ludlow to Early Pridoli, Miaogao Formation.

Langeites sp.

(Fig. 3I–N).

Material. YLSS02, right MI (Fig. 3I, J, M, N); YLSS12, right MII (Fig. 3 K); YLSS13, left MII (Fig. 3L).

Description. Eulabidognatha-type apparatus, consisting of right MI, right MII, and left MII, are documented; the carriers and precise relationships of elements in apparatus remain unknown.

Right MI, dorsal side: Length about 1.55 mm, width about 0.35 mm. Due to the damage of the anterior-most part, the length/width ratio is uncertain. The inner and outer margins are near-parallel. The inner margin is covered with 18 knob-like sub-terminal, densely spaced denticles, occupying about half of the well-preserved jaw length. The denticles are almost equal in size except for the posteriormost ones, which increase in size (Fig. 3M). The undenticulated ridge is almost straight, with a length of approximately 0.23 mm (Fig. 3N). The basal angle is approximately 18° and the basal furrow is narrow and deep.

Ventral side: The ovoid-shaped myocoele opening is wide and slightly enclosed, representing about half of the jaw length. The opening is surrounded by a narrow rim (Fig. 3I).

Right MII, ventral side: Conical element with a length of 0.8 mm and width of more than half the length. One pre-cuspidal denticle is followed by a large, tall triangular cusp (Fig. 3K). The three sloped-backward intermediate denticles are small and sub-triangular. The six post-cuspidal denticles are sharp and triangular. The shank end is broken. The crescent-shaped myocele opening is relatively narrow, slightly enclosed, representing about 0.6 of the jaw length. The needle-shaped ramus is medium length and narrow with a posteriorly oriented, pointed extremity.

Left MII, dorsal side: Length about 0.73 mm, width half of the length. Almost a mirror image of the ventral side of the right MII, except that the element has a double equal-sized cusp and eight small post-cuspidal denticles along the inner margin (Fig. 3L). The shank is narrow and bluntly ended.

Comparison. Although the right MI is poorly preserved on the fang, the basal portion and the denticles on the inner margin are well preserved. The MI of *Langeites* sp. are similar to those depicted for *L.* aff. *glaber* and *L. glaber* in shape, but differ in denticulation and size. *L.* sp. is much smaller than others and is distinguished from *L.* aff. *glaber* and *L. glaber* by the densely spaced denticles along the inner margin.

Stratigraphic Occurrence. Dadukou section, Yiliang County, Yunnan Province, China; Late Ludlow to Early Pridoli, Miaogao Formation.

Family Polychaetaspidae Kielan-Jaworowska, 1966.

Genus *Oenonites* Hinde,1879.

Type species *Oenonites curvidens* Hinde,1879.

Oenonites spp.

(Fig. 3O–S).

Material. YLSS23–YLSS24, left MI (Fig. 3O, P); YLSS25–YLSS27, incomplete MI (Fig. 3Q–S, Tables S25–S27).

Description. Labidognatha-type apparatus, only consisting of MI, are documented. Two of the MIs are well-preserved and are assigned to the left MI based on the direction of the fang (Fig. 3O, P). These MIs vary in size and display ventral and dorsal features, respectively.

Left MI, dorsal side (Fig. 3O): Narrow and elongate jaw. Length about 1.39 mm, width slightly less than 1/3 of the length. Greatest width at mid-length. Outer margin slightly concave to straight. At about mid-length, there is a well-pronounced ramus which points slightly postero-dextrally. Posterior of the ramus, the outer face tapers strongly and becomes hidden by the posteriormost denticles. The anteriormost denticle is developed as a large, long, and hooked fang. A series of 16–18 small, tightly packed, and slanted denticles decrease in size posteriorly, approximately the 7–11th denticles are slightly larger than the surrounding ones. Anterior of the cove, inner face very narrow. The inner margin follows the dentary in the anterior part of the jaw, but at approximately mid-length, it turns right and then posteriorly.

Left MI, ventral side (Fig. 3P): Myocoele opening extends for more than 0.9 of the jaw length. The anteriormost denticle is developed as a large, long, and hooked fang. A series of more than 10 small, tightly packed, and slanted denticles decrease in size posteriorly, approximately the 2nd–4th denticles are slightly larger than the surrounding ones. The myocoele opening exhibits a long and narrow ligament rim.

Remarks. Despite the determination at the species level being impossible because of the state of preservation, all of them are assigned to *Oenonites* based on the preserved fang, the triangular denticles and the inner and outer faces, with at least two species present. The two left MIs differ in denticulation and size. Posterior of the cove, the outer face of one incomplete MI (Fig. 3R) exhibits greater width compared to others than others (Fig. 3O, Q). Thus, the specimens were assigned to *Oenonites* spp.

Stratigraphic Occurrence. Dadukou section, Yiliang County, Yunnan Province, China; Late Ludlow to Early Pridoli, Miaogao Formation.

Results

Comparative analysis of the right MI in Silurian Paulinitidae

To evaluate the taxonomic placement of the Yiliang scolecodonts, a comparative morphological analysis of the right first maxilla (MI) was conducted. This analysis considered key features such as size, basal angle, denticles, basal plate, outer and inner margins, fang and undenticulated ridge. Among Silurian Paulinitidae, five representative genera—*Gotlandites*, *Hindenites*, *Kettnerites*,

Table 1 Summarized right MI of typical species of Silurian scolecodonts

Species	*Gotlandites slitensis*	*Hindenites angustus*	*Kettnerites (Aeolus) microdentatus*	*Lanceolatites gracilis*	*Langeites glaber*	*Langeites* aff. *glaber*	*Langeites* sp.
Length/mm	0.83–1.85	0.29–1.08	0.36–1.05	0.36–1.18	0.62–3.1	2.4	1.50
Width (*length)	0.3	0.33	0.25–0.33	0.2	1/5	0.22	0.23
Basal angle/°	30–35	5	20–30	30–40	/	/	≈18
Denticles	9–15	12–19	≈40	15–20	10–16	9	≥ 18
Basal plate	skew, rectangular	long	/	/	rectangular	/	rectangular
Basal portion	/	/	fairly wide	fused to the jaw or triangular	/	/	fused to the jaw
Out margin	a reversed 's' shaped	/	more or less pronounced concavity	smoothly wavy with a distinct median concavity	arcuate	convex	almost straight
Fang	strongly developed	/	sickle-shaped	narrow and pointed	outwards	sickle-shaped	/
Inner margin	convex	/	almost straight	medially concave	nearly straight to concave	concave	nearly straight
Undenticulated ridge	forms the posterior sharp tip of the jaw	long, 03*length	high and narrow	conspicuously pointed tip	/	elongated, 0.6*length	pronounced, 0.3*length
Shank	/	/	almost triangular with a pointed proximity	wide posteriorly, fairly blunt-ended	/	/	/

All descriptions of MI of *Gotlandites slitensis*, *Hindenites angustus*, *Kettnerites* (*Aeolus*) *microdentatus*, *Lanceolatites gracilis* and *Langeites glaber* were obtained from Bergman (1989). Slash lines indicate unknown morphological features

Lanceolatites, and *Langeites*—were selected for comparison with the species of *Langeites* from Yiliang (Table 1).

The right MI of *Langeites* is significantly larger than those of other genera. *Langeites* exhibits fewer, shorter denticles than *Kettnerites,* which has approximately 40 fine denticles*. Hindenites* and *Gotlandites* have an elongated basal plate, whereas *Langeites* lacks the basal plate. *Kettnerites* and *Langeites* display a slightly concave outer margin, while *Gotlandites* has a reversed 'S' shape outer margin. *Hindenites* and *Kettnerites* bears triangular serrated denticles along the inner margin*,* whereas *Langeites* possesses a concave inner margin with small knob-like denticles. The fang in *Langeites* is slender, differing from the sickle-shaped fang of *Kettnerites*. The undenticulated ridge in *Langeites* and *Hindenites* is elongated, but short and pointed in *Gotlandites*, and while high and narrow in *Kettnerites*. These differences confirm that *Langeites* is morphologically distinct from other Paulinitidae.

Intra-genus variation in the right MI of Yiliang *Langeites*

Compared with the type specimen *Langeites glaber*, the MI of the Yiliang species were basically the same in length/width ratio, basal plate, outer margin, and undenticulated ridge, but they were different from those of *L. glaber* in fine denticles, inner margin, and fang. *Langeites* aff. *glaber* has a few of sub-distal knob-like denticles, which only cover one-quarter of the entire inner margin. *Langeites* sp. has numerous small denticles, which are distributed along the inner margin.

Among the Yiliang *Langeites*, *L.* aff. *glaber* has a larger MI than *L.* sp. *L.* sp. has numerous, smaller denticles along the entire inner margin, compared with *L.* aff. *glaber*. On the basis of observing different ontogenetic stages in extant eunicidans, it should be noticed that the larval and juvenile MI show different features (Paxton & Eriksson, 2012). The small size and fine denticles of *L.* sp. resemble the juvenile maxillae of modern Eunicidae (e.g., *Diopatra aciculata*), suggesting that *L.* sp. represents an early developmental stage of *Langeites.* The MI of *L.* aff. *glaber* and *L.* sp. document jaw development in *Langeites.*

Comparison of fossil and extant Eunicida maxillary apparatus

To assess evolutionary trends, the maxillary apparatus of *Langeites* was compared with modern eunicidan taxa, specifically Eunicidae (e.g., *Eunice roussaei*) and Onuphidae (e.g., *Diopatra* spp.). Among the extant taxa, the maxillary apparatus structure of Eunicida is the most complex, with short carriers, four to five toothed plates on the right side, and five to six toothed plates on the left (Clemo & Dorgan, 2017). MIII are absent on the right side, while the MIV are larger on this side compared with those on the left in Eunicida (Paxton, 2000). Both *L.* aff. *glaber* and *L.* sp. have forceps-like MI with sub-distal/sub-terminal denticles on the inner margins and conical to plate-like MII; these features bear resemblance to those found in extant Eunicidae (e.g. *Eunice roussaei*) and Onuphidae (e.g., *Diopatra* spp.).

Comparative analysis of the maxillary apparatus between scolecodonts and extant Eunicida revealed an increased jaw asymmetry throughout the evolution of jaw apparatuses. The early Ordovician scolecodonts (e.g., *Xanioprion walliseri,* Fig. 4C; *Tetraprion pozaryskae*, Fig. 4G) had symmetrical maxillae. Whereas, the maxillae of the Silurian and Devonian scolecodonts became increasingly asymmetrical, including labidognatha-type (e.g., *Megaramphoprion magnus*, Fig. 4N), prionognatha-type (e.g., *Atraktoprion major*, Fig. 4M) and eulabidognatha-type apparatuses (e.g., *Kettnerites* (*Aeolus*) *sisyphi klasaardensis*, Fig. 4T). Today, polychaetous annelids with asymmetric eulabidognatha-type apparatuses (Fig. 4P, Q) remain dominant among living polychaetous annelids (Parry et al., 2019; Paxton, 2009). This asymmetry is particularly evident in *Langeites*, where the right MI and right MII differ significantly in size and shape, a feature retained in modern Eunicidae (Paxton & Eriksson, 2012).

During the evolution of the eulabidognatha-type apparatus, notable changes in MI are evident over time, including the alterations in shape and microstructure, such as denticles along the inner margin decrease in size and some may eventually disappear (Fig. 4). The earliest eunicidan jaw apparatuses featured densely spaced denticles along the inner margin (e.g., *K.* (*Aeolus*) *sisyphi klasaardensis*, Fig. 4T) (Bergman, 1989). By the Silurian, *Langeites* exhibited a forceps-like MI with fewer denticles (e.g., *L.* aff. *glaber*, Fig. 4R), a trend that continued into extant Eunicidae and Onuphidae, where denticles are often absent (e.g., *Eunice roussaei*, Fig. 4Q; *Diopatra* spp, Clemo & Dorgan, 2017; *Paradiopatra fragosa*, Fig. 4P) (Paxton & Eriksson, 2012). Interestingly, morphological changes in MI are pronounced during ontogeny in living polychaetous annelids (Paxton & Eriksson, 2012), which supports evolutionary trends observed in the eulabidognatha-type apparatus. The presence of sub-terminal denticles in *Langeites* sp. but not in *L.* aff. *glaber* supports the hypothesis that denticle loss occurred through ontogeny and evolutionary time.

Discussion

The microfossil assemblage from Yiliang contains abundant conodonts, brachiopods, and gastropods, but a small number of scolecodonts and fish scales. The scolecodont assemblage from Yiliang exhibits low diversity, with only two identified genera, *Langeites* and *Oenonites*. This contrasts with more diverse Silurian polychaete faunas found in regions such as the Baltic area (Eriksson & Von Bitter, 2015), Arctic Canada (Hints et al., 2000), and the Prague Basin (Tonarová et al., 2012). Given the preservation and the small number of available specimens, more materials that reveal the diversity of the Yiliang fauna of polychaetes are necessary in the future.

The most common genera in the Silurian recorded are *Kettnerites*, *Oenonites*, *Mochtyella*, *Pistoprion*, *Vistulella*, *Protarabellites*, *Kalloprion,* and *Leptoprion* (Eriksson et al., 2013), e.g., the Baltic area (Eriksson & Von Bitter, 2015), Siberia, Arctic Canada (Eriksson & Von Bitter, 2015) and British Isles (Hints et al., 2000), and Prague Basin (Tonarova et al., 2012; Berke et al., 2022). *Langeites*, as a common genus, is mainly restricted to the Silurian (Eriksson et al., 2013). Among these, *L. glaber* occurs in Late Silurian samples from Poland (Kielan-Jaworowska, 1966), Late Ludlow samples from the Hemse and Sundre beddings of Gotland (Bergman, 1989), and Pridoli samples from the Read Bay section of Canadian Arctic Archipelago (Hints et al., 2000). Another upper Carboniferous to lower Permian material from Sicily, Italy, was assigned to *Langeites* and named a new species, *L. siciliensis* (Olivieri et al. 1973), but it was considered as a new genus, *Brochosogenys*, by Colbath (1987). To sum up, previous records of *Langeites* were recorded in both Baltica and Laurentia during Late Ludlow to Early Pridoli. The discovery of *Langeites* in South China significantly expands its known range and suggests a broader paleogeographic distribution than previously recognized. Additionally, *Langeites glaber* is a known biostratigraphic marker for the Late Ludlow–Early Pridoli, and its occurrence in the Miaogao Formation strengthens its potential as a stratigraphic tool for Silurian correlation.

Interestingly, the diverse polychaete assemblage from the Late Silurian Kopanina Formation of the Prague Basin contains at least 16 genera, including *Kettnerites, Oenonites,* and *Pistoprion* as common genera (Tonarova et al., 2012), while *Langeites* is missing from this assemblage. The absence of *Langeites* in the Kopanina Formation of the Prague Basin, may indicate that it had specific environmental preferences. However, further research is required to confirm this observation. The distribution of Silurian scolecodonts is influenced by the conditions of the sediment (Bergman, 1989; Eriksson et al., 2013). During the Silurian, South China was situated near the equator (Golonka et al., 2023), with supposedly warmer water conditions compared with the Prague Basin. The discovery of *Langeites* in South China supports the hypothesis that its distribution may have been influenced by ocean temperature and sedimentary environments.

Kozur (1970) and Paxton (2009) proposed that the fossil jaws of Paulinitidae may be the common ancestors of the extant Eunicidae (e.g., *Eunice roussaei*) and Onuphidae (e.g., *Diopatra* spp.). According to the comparison between *Langeites* and the extant taxa of Eunicida, both jaws are very similar. These comparisons indicate that *Langeites* likely had feeding habits similar to modern Eunicidae and Onuphidae, supporting its role as a predatory or omnivorous marine benthic polychaete. These evolutionary changes in MI and MII structure provide further evidence that Paulinitidae may be ancestral to modern Eunicidae and Onuphidae, supporting the hypothesis proposed by Kozur (1970) and Paxton (2009).

Diopatra is a tube-dwelling omnivore that feeds on invertebrates, protists, algae (Berke, 2022; Mangum et al., 1968), and other accessible food (Jumars et al., 2015). Comparative studies of extant taxa suggest that modern *Diopatra* spp. use their MI to grasp prey and interlock their maxillae to secure food (Clemo & Dorgan, 2017), a function likely shared by *Langeites*. The forceps-like MI and complex maxillary apparatus of *L.* aff. *glaber* and *L.* sp. indicate an ability to capture and process a variety of food sources, including small invertebrates, protists, or algae. And the presence of interlocking MI and MII in *Langeites* resembles the jaw mechanics of modern predatory polychaetes, supporting its role as a mobile, active feeder. The loss of denticles in more derived taxa suggests an evolutionary shift towards grasping and tearing soft-bodied prey rather than processing hard-shelled organisms.

According to Clemo and Dorgan (2017), an important morphological distinction between the jaws of herbivorous or omnivorous *Diopatra* spp. and carnivorous *Lumbrineris* spp. is the asymmetric third maxilla of *Diopatra* spp. The third maxilla may be beneficial for efficiently fracturing larger pieces of food, such as macroalgae and other food items within reach of their tubes. Thus, asymmetry of scolecodont jaw apparatuses during evolution may be closely related to the diet of ancient scolecodonts. That is, the changes in jaw apparatuses from symmetry to asymmetry may indicate the significant changes in diet and feeding behavior throughout the evolution of scolecodonts. Additionally, the presence of sub-terminal denticles in *Langeites* sp. but not in *L.* aff. *glaber* suggests ontogenetic changes in feeding adaptations, similar to those observed in modern Eunicidae (Paxton & Eriksson, 2012).

Diopatra are also found in the guts of multiple epibenthic fishes (Berke, 2022; Vega et al., 2023). Fossil vertebrate remains found alongside *Langeites* in the Miaogao Formation (e.g., *Poracanthodes qujingensis* and conodonts, Fig. 2) suggest that it may have been part of a marine food web where vertebrates preyed on polychaetes. The association of *Langeites* with brachiopods, gastropods, and corals suggests that it may have lived in a warm, shallow marine environment, similar to modern Eunicida, which prefer neritic habitats (Zanol et al., 2021).

Conclusion

This study documents three species of scolecodonts from the Miaogao Formation, Yiliang, Yunnan, South China, providing new insights into the diversity, morphology, and paleoecology of Silurian polychaetes. *Langeites* aff. *glaber* is characterised by a forceps-like right MI with sub-distal denticles along the inner margin and a right MII with two large pre-cuspidal denticles, a triangular cusp, and 13 intermediate denticles. The MI of *L.* sp. is much smaller than that of *L.* aff. *glaber* with more numerous and densely spaced denticles, likely representing a juvenile form of *Langeites*. A comparative analysis of *Langeites* and extant Eunicida (Eunicidae and Onuphidae) reveals notable evolutionary trends in the maxillary apparatus, including: (1) reduction in denticle number from densely spaced (Ordovician) to fewer, widely spaced (Silurian) to absent (modern taxa); (2) increased jaw asymmetry, supporting a transition toward specialized feeding adaptations. Functional similarities between *Langeites* and modern predatory polychaetes, indicating a consistent feeding strategy over evolutionary time. The presence of *Langeites* in South China significantly expands its known geographic range. As a genus restricted to the Late Ludlow–Early Pridoli, *Langeites* holds potential for biostratigraphic correlation. Its occurrence in the Miaogao Formation strengthens its use as a stratigraphic marker for the Late Silurian. These findings enhance our understanding of Silurian polychaete paleoecology and evolutionary history, but further studies with additional fossil material are needed to refine its taxonomy, biogeography, and ecological interactions.

Supplementary Information

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Additional file 1.

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Author contributions
D.G. designed the research, selected microfossil specimens, prepared the figures and tables. C.S. led the fieldwork, described the specimens and analysed

the results. All authors contributed to the writing of the manuscript, revised and approved the final version of the manuscript.

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Data availability
All data during this study are provided in the text, figures, tables and supplementary tables. Specimens of scolecodonts (numbered YLSS01 to YLSS28) are housed in the Geological Innovation Team laboratory, Kunming University of Science and Technology. These data are available via Cen Shen [cshen@kmust.edu.cn] at Kunming University of Science and Technology.

Declarations

Ethics approval and consent to participate
Not applicable.

Competing interests
The authors declare no competing interests.

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