A new species of dercetid and the assessment of the phylogeny of the Enchodontoidei (Teleostei: Aulopiformes)

by

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ABSTRACT

The Enchodontoidei is an extinct suborder of a marine teleost order Aulopiformes. Most enchodontoids have been reported from deposits of the Late Cretaceous. One of the major groups in Enchodontoidei is the family Dercetidae, which is traditionally characterized by an elongate body, long snout, triradiate dermal scutes, and reduced neural spines. Despite the long history of the taxonomic studies since the early 19th century, the phylogenetic study of enchodontoids including dercetids has been performed only relatively recently. The Enchodontoidei was recovered as a paraphyletic group in previous studies, and the family Dercetidae was supported by a single synapomorphy, neural spines very reduced. The two newly discovered specimens from southern Alberta are here assigned to a new species of the genus *Dercetis*, which were mainly reported from Europe and the Middle East in previous studies. The new species is recovered as a sister to the other species of *Dercetis*, but the family Dercetidae is not supported as a monophyletic taxon. The preexisting character matrix is modified based on the assessment of 87 characters, and the analysis with a modified character matrix recovered a monophyletic Enchodontoidei supported by a single unambiguous synapomorphy, maxilla included in gape. Overall, the description of the new specimens provides new insights into the genus *Dercetis*, and the assessment of the preexisting characters suggests the urgent need for additional modifications of the matrix and revision of the character coding in some taxa.

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Chapter 1: Introduction

1.1 Taxonomic background

The Aulopiformes is an order of marine teleost fishes that is currently known from fifteen families with 261 species of extant members and many other extinct members mainly reported from the Cretaceous period (Nelson et al., 2016). The fifteen extant families are supported as monophyletic based on molecular and morphological studies (Baldwin and Johnson, 1996; Sato and Nakabo, 2002; Nelson et al., 2016), although the organization above the family level differs among the authors (four suborders in Sato and Nakabo (2002), three suborders in Davis (2010)). Some families include benthic species, such as the shallow-marine lizardfish (Synodontidae) and deep-sea tripodfish (Ipnopidae), whereas many other families contain pelagic to bathypelagic species, such as lancetfish (Alepisauridae) and telescopefish (Giganturidae) (Nelson et al., 2016).

Although these families vary greatly in morphology, they are currently united by several unique synapomorphies found in the branchial region (i.e., uncinate process of the second epibranchial elongate, absence of the cartilaginous condyle on the third pharyngobranchial for the articulation with the second epibranchial, presence of a fifth epibranchial) and also characterized by commonly shared features of the the axial skeleton (i.e., the medial processes of pelvic girdle joined medially by cartilage, epipleural bone series originating on vertebra two, one or more epipleural bones displaced dorsally into horizontal septum, absence of swim-bladder) (Rosen, 1973; Johnson, 1992; Patterson and Johnson, 1995; Baldwin and Johnson, 1996; Sato and Nakabo, 2002; Davis, 2010). Many families that are specialized in deep-sea habitats also show simultaneous hermaphroditism, which is one of the rarest reproductive strategies among vertebrate taxa (Davis and Fielitz, 2010).

1.2 Enchodontoidei

In addition to the extant members, Aulopiformes also includes many extinct taxa. The vast majority of these were described from Late Cretaceous marine deposits, although some have been reported from younger deposits, such as *Holosteus* from the Eocene and *Polymerichthys* from the Miocene (Uyeno, 1967; Davis and Fielitz, 2010; Marramà and Carnevale, 2017). In this thesis, I focus on the Cretaceous fossil taxa that are grouped together in the extinct suborder Enchodontoidei, of which the relationships among the groups have been debated for decades (Nelson, 1994; Fielitz, 2004; Silva and Gallo, 2011).

The taxonomy of the Enchodontoidei has been changed over time depending on the taxa included by different authors (summarized in Table 1-1). Berg (1940) only included the family Enchodontidae erected by Woodward (1901) in the suborder Enchodontoidei, which contained the genera *Apateodus*, *Cimolichthys*, *Enchodus*, *Eurypholis*, *Halec*, *Leptecodon*, *Pantopholis*, *Palaeolycus*, and '*Prionolepis'* (=*Aspidopleurus*). Later, Goody (1969) placed the suborder Enchodontoidei in the extant order Salmoniformes and included the families Enchodontidae (containing *Enchodus* and *Palaeolycus*) and Eurypholidae (containing *Eurypholis* and *Saurorhamphus*); he also included three other suborders, Ichthyotringoidei, Cimolichthoidei, and Halecoidei in the Salmoniformes. Nelson (1994) recognized Goody's (1969) four suborders as four superfamilies (Enchodontoidea, Cimolichthyoidea, Ichthyotringoidea, Halecoidea), and integrated them into a single suborder Enchodontoidei. The superfamily Enchodontoidea was included in the suborder Alepisauroidei by Fielitz (2004), based on morphological phylogenetic studies including a number of extant aulopiforms as well as *Cimolichthys, Enchodus*, *Eurypholis*, *Palaeolycus*, *Parenchodus*, *Rharbichthys*, and *Saurorhamphus*. Fielitz (2004) did not include other members of Nelson's (1994) Enchodontoidei, so in this study, I use the term

Enchodontoidei as a tentative suborder composed of the taxa that were included in Enchodontoidea by Fielitz (2004) and additional taxa mainly reported from Cretaceous marine deposits following several recent studies (Silva and Gallo, 2011; Díaz-Cruz et al., 2016; Vernygora et al., 2017; Alvarado-Ortega and Díaz-Cruz, 2020, Murray et al., 2022).

1.3 Dercetidae

One of the families traditionally included in Enchodontoidei is Dercetidae. The extinct family Dercetidae lived from the Late Cretaceous (Cenomanian) to the Paleocene (Danian). The family is generally characterized by an elongate body, long snout, short neural spines, and prominent triradiate scutes on the flank (Gallo et al., 2005; Vernygora et al., 2017). Historically, many fossil records of dercetids have been reported from the Eastern Tethys including Europe, North Africa, and the Middle East, whereas the number of reports from the Western Tethys and other western areas have been increasing only recently (Silva and Gallo, 2011, 2016). Currently, a few species are reported from North and South America (Blanco and Alvarado-Ortega, 2006; Figueiredo and Gallo, 2006; Vernygora et al., 2017; Alvarado-Ortega and Díaz-Cruz, 2020), and a few fragmentary specimens are known from the Western Interior Seaway (WIS) of Canada (Wilson and Chalifa, 1989; Wilson and Bruner, 2004). In the next chapter (Chapter 2), I describe the first well-articulated dercetid from the WIS, from Campanian deposits of southern Alberta, Canada.

The family Dercetidae was erected by Woodward (1901) and also described in his later work (Woodward, 1903). Although Pictet (1850) originally grouped together several species of dercetids, he used the term ‘Sclerodermis’ as a family name. Woodward (1903) considered dercetids to be members of the extant Notacanthiformes (halosaurs and spiny eels), but this idea was based only on superficial similarities in the morphology of the two groups, such as their long slender body and head. Goody (1969) placed Dercetidae within Cimolichthyoidei together with the family Cimolichthyidae, containing only *Cimolichthys,* based on several morphological characters, such as an elongate body and squamation restricted to prominent scutes on the flank. Later, Rosen (1973) erected the order Aulopiformes (including extant taxa) and placed all four of Goody's suborders as the basal members of the new suborder Alepisauroidei, but the interrelationships among those extinct members were left unresolved. Fielitz (2004) attempted a phylogenetic study of some extinct and extant members of Aulopiformes and concluded that some extinct taxa (i.e., *Cimolichthys, Enchodus*, *Eurypholis*, *Palaeolycus*, *Parenchodus*, *Rharbichthys*, and *Saurorhamphus*) together formed a monophyletic sister group to the extant Alepisauridae. Dercetidae was not included in Fielitz's (2004) study, but later phylogenetic studies (Gallo et al., 2005; Silva and Gallo, 2011) supported *Cimolichthys* as being more closely related to enchodontids (*Enchodus, Eurypholis, Palaeolycus*, *Saurorhamphus*) than Dercetidae. This scheme of relationships was followed in several later studies (Díaz-Cruz et al., 2016; Vernygora et al., 2017; Alvarado-Ortega and Díaz-Cruz, 2020), in which the monophyly of Dercetidae was supported by several characters including a shallow head, long snout, convoluted suture between hypurals 2+3, and triradiate scutes on the flank, although the first three characters can be homoplastic and are seen in non-dercetid members of Aulopiformes, and the morphology of the scutes varies within the group. In addition to these homoplastic characters, Vernygora et al. (2017) suggested that the single synapomorphy shared by dercetids is reduced neural spines, but a recent study by Alvarado-Ortega and Díaz-Cruz (2020) challenged the feature of reduced neural spines as a synapomorphy, instead suggesting the possibility of it being a homoplastic condition. Therefore, the monophyly of the family Dercetidae is currently weakly supported, and it is necessary to review all the phylogenetic studies of dercetids and their relatives. Here I tentatively follow the phylogenetic study of Alvarado-Ortega and Díaz-Cruz (2020), although the characters used in this data matrix are reassessed in Chapter 3. Based on the analysis of Alvarado-Ortega and Díaz-Cruz (2020), Dercetidae contains at least thirteen nominal genera (*Apuliadercetis, Benthesikyme, Brazilodercetis, Candelarhynchus, Caudadercetis, Cyranichthys, Dercetis, Dercetoides, Hastichthys, Nardodercetis, Ophidercetis, Pelargorhynchus,* and *Rhynchodercetis*), and there are five additional genera (*Kwangodercetis, Leccedercetis, Paradercetis*, *Scandiadercetis,* and *Stratodus*) that have been included in the family but excluded from the previous phylogenetic analyses (Casier, 1965; Taverne, 2005, 2008; Harrell, 2008). *Robertichthys* Blanco-Piñón and Alvarado-Ortega, 2005 is no longer considered a dercetid but probably belongs to Aspidorhynchidae, which is not even in Enchodontoidei (Díaz-Cruz et al., 2016).

1.4 Objectives of the thesis

The main focus of my thesis is describing new specimens of Dercetidae recovered from Upper Cretaceous deposits of southern Alberta. The new specimens are described and classified based on morphological characters, and a phylogenetic analysis is conducted using previous data matrices (Silva and Gallo, 2011; Díaz-Cruz et al., 2016; Vernygora et al., 2017; Alvarado-Ortega and Díaz-Cruz, 2020; Murray et al., 2022). These data matrices need to be revised because monophyly of the Enchodontoidei is not supported and monophyly of Dercetidae is only very weekly supported, and thus I will assess the characters used in the previous studies to provide an up-to-date phylogeny of the Enchodontoidei, including the family Dercetidae.

In sum, my objectives in the thesis are 1) to describe the new specimens and test whether they are grouped together with the Dercetidae, especially with the genus *Dercetis*, and 2) to assess the previous data matrices and provide a revised phylogeny of the Enchodontoidei. The newly described specimens and the revised phylogeny will update our knowledge of the Enchodontoidei and will provide the foundation for future studies of the extinct Aulopiformes.

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Table 1-1. The classification of the suborder Enchodontoidei by different authors.

Berg (1940)	Goody (1969)	Nelson (1994)	Fielitz (2004)
Enchodontoidei	Enchodontoidei	Enchodontoidei	Alepisauroidei
Enchodontidae	Enchodontidae	Enchodontoidea	Enchodontoidea
Apateodus	*Enchodus*	Enchodontidae	Enchodontidae
Cimolichthys	*Palaeolycus*	*Enchodus*	Enchodontinae
Enchodus	Eurypholidae	*Palaeolycus*	*Enchodus*
Eurypholis	*Eurypholis*	*Parenchodus*	Eurypholinae
Halec	*Saurorhamphus*	Eurypholidae	*Eurypholis*
Leptecodon		*Eurypholis*	*Saurorhamphus*
Pantopholis		*Saurorhamphus*	Palaeolycinae
Palaeolycus		Cimolichthyoidea	*Paleolycus*
'Prionolepis'		*Cimolichthys*	Rharbichthinae
		Benthesikyme	*Rharbichthys*
		Cyranichthys	
		Dercetis	
		Dercetoides	
		'Prionolepis'	
		Pelargophynchus	
		Rhynchodercetis	
		Stratodus	
		Ichthyotringoidea	
		Ichthyotringa	

  Apateodus

Halecoidea

  Halec

  Hemisaurida

  Phylactocephalus

Chapter 2: A large, new species of dercetid (Teleostei: Aulopiformes) from the Campanian Bearpaw Formation of Alberta, Canada.

2.1 Introduction

2.1.1 Background of the genus *Dercetis*

The extinct family Dercetidae is a major group placed in the extinct aulopiform suborder Enchodontoidei that lived from the Late Cretaceous (Cenomanian) to the Paleocene (Danian). The family was erected by Woodward (1901), but the included genera were named before the family was created. The genus *Dercetis* was first erected by Münster and Agassiz (1834). This enigmatic genus currently contains species that were previously assigned to several different genera (i.e., *Dercetis*, *Leptotrachelus*, *Benthesikyme*) since their first discovery in the early 19th century (Agassiz, 1834; Pictet, 1850; von der Marck, 1863; Woodward, 1901; Siegfried, 1966; Goody, 1969). In chronological order, *Dercetis scutatus* Münster and Agassiz, 1834, *Dercetis elongatus* Agassiz, 1835, *Dercetis triqueter* Pictet, 1850, *Dercetis tenuis* Pictet, 1850, and *Dercetis linguifer* Pictet, 1850 were named and described since the genus was first named in 1834 by Agassiz (1833-44). Subsequently, some additional species were assigned to this genus by several different authors, including *Dercetis reussi* Fritsch, 1878, *Dercetis latiscutatus* Woodward, 1903, *Dercetis maximus* Woodward, 1903, *Dercetis limhamnensis* Davis, 1890, *Dercetis rostralis* Signeux, 1954, *Dercetis ornatissimus* Caiser, 1965 and *Dercetis congolensis* 1965 (Fritsch, 1878; Woodward, 1903; Davis, 1890; Signeux, 1954; Caiser, 1965).

The genus *Leptotrachelus* was erected for the species *Leptotrachelus armatus* by von der Mark (1863) who recognized the difference in the length of the dorsal fin between *Dercetis* and *Leptotrachelus* (i.e., the dorsal fin is shorter in *Leptotrachelus*). Following this diagnosis, Pictet and Humbert (1866) reexamined Pictet's previous descriptions and synonymized *D. tenuis* with *D. triqueter* and moved it to *Leptotrachelus triqueter*, but retained *D. linguifer* as a valid species [later synonymized with *D. triquter* by Goody (1969)]. *Dercetis elongatus* was also once assigned to *Leptotrachelus* by Woodward (1901). There were several more species of *Leptotrachelus* described by different authors, including *L. hakelensis* Pictet and Humbert, 1866, *L. sagittatus* von der Mark, 1873, *L. longipinnis* Cope, 1878, *L. virgulatus* Cope, 1878, *L. gracilis* Davis, 1887, *L. serpentinus* Hay, 1903, and *L. gortanii* d'Erasmo, 1946 (Pictet and Humbert, 1866; von der Mark, 1873; Cope, 1878; Davis 1887; Hay, 1903: d'Erasmo, 1946). *Leptotrachelus hakelensis* was later assigned to a new genus *Rhynchodercetis* by Arambourg (1943). The generic name *Leptotrachelus* was used until White and Moy-Thomas (1940) replaced it with the new generic name *Benthesikyme* because the name *Leptotrachelus* was actually preoccupied by a genus of beetles.

Siegfried (1966) reexamined von der Marck's materials (*L. armatus* and *L. sagittatus*) and concluded that *Leptotrachelus* was a junior synonym of *Dercetis* because the shortness of the dorsal fin of *L. armatus* and *L. sagittatus* are due to their fragmentary condition in the specimens but not because of the nature of the fish. He also chose *D. elongatus* as the type species because the original type species, *D. scutatus,* was either lost or destroyed, and the description is not informative enough for comparison with other species today, and thus *D. scutatus* is considered to be a *nomen nudum* (Siegfried, 1966; Goody, 1969; Taverne, 2005).

The genus *Benthesikyme*, the replacement name for *Leptotrachelus*, was also considered a junior synonym of *Dercetis* until Taverne (2005) restored the name as a valid genus. Taverne (2005) conducted comprehensive research on every species ever assigned to this genus, and distinguished *Benthesikyme* from *Dercetis* by several distinctive characters such as *Benthesikyme* having an elongate first trunk vertebra which lacks neural and transverse processes, and the mesethmoid having pointed ends both anteriorly and posteriorly, whereas *Dercetis* has a first vertebra with neural and transverse processes and an anteriorly bifurcated mesethmoid. Following these emended diagnoses, *L. armatatus, L. gracilis*, and *D. rostralis* were assigned to *Benthsikyme armatatus, B. gracilis*, and *B. rostralis* respectively (Taverne, 2005).

Currently, only two nominal species, *D. elongatus* Agassiz, 1835 and *D. triqueter* Pictet, 1850 are considered valid in the genus *Dercetis* (summarized in Table 1). *Dercetis linguifer* is considered to be a junior synonym of *D. triqueter* as confirmed by Goody (1969). Although Goody (1969) confused *D. tenuis* and *D. linguifer* in his book, the fragmented abdominal region of *D. linguifer* was confirmed as being the same species as *D. triquter* (Goody, 1969). *Dercetis ornatissimus* and *L. gortanii* were placed in different genera, *Cyranichthys* and *Rhynchodercetis* respectively by Taverne (1987). Although Taverne (1987) did not reassess *D. congolensis* and did not reassign it to any other taxon, it differs from *D. ornatissimus* (= *Cyranichthys ornatissimus*) only by having a slightly stockier posterior region of the pterotic (Casier, 1965), so I here assume *D. congolensis* is closely related to the genus *Cyranichthys*. According to Taverne (2005), *L. sagittatus* is synonymized with *D. elongatus*, *L. virgulatus* is synonymized with *D. triqueter*, and *D. limhamnensis* is assigned to a new genus *Scandiadercetis*, while *L. serpentinus* is excluded from the genus *Dercetis* because of the vertebrae bearing two transverse processes diverging from the middle of the centra. Due to their incomplete conditions, *D. reussi*, *D. latiscutatus*, and *D. maximus* are left as genus incertae sedis, although *D. reussi* and *D. maximus* show unique morphology of their scutes or vertebrae (Taverne, 2005). I here follow the taxonomy of Taverne (2005).

Currently, specimens of *Dercetis* are known from several countries in Europe (Agassiz, 1833-1844; von der Marck, 1873; Ekrt et al., 2008; Taverne and Goolaerts, 2015), Lebanon (Pictet, 1850; Cope, 1878), Mexico (Alvarado-Ortega et al., 2020), and Canada (Wilson and Bruner, 2004), although the Canadian specimen was not fully described. Here, I describe two new specimens of a large *Dercetis* that were recently recovered from the Campanian Bearpaw Formation of Alberta. They show several characters that are considered to be diagnostic for this genus, such as the medio-parietal skull, anteriorly bifurcated mesethmoid, and single transverse processes on the vertebrae. The new specimens possess several unique characters which have not been reported previously for the any species of this genus. I therefore assign them to a new species.

2.1.2 Geological and faunal context

The two new specimens were collected from a commercial ammolite mine (Korite Mine). The mine samples the lower part of the Bearpaw Formation, and is located in the valley of the St. Mary's River, south of Lethbridge (Fig. 2-1). The Bearpaw Formation represents the last widespread marine deposits of the Western Interior Seaway (WIS), formed during the late Campanian to early Maastrichtian (Tsujita, 1995: Catuneanu et al., 1997). Because the specimens were collected together with commercial ammolite materials, their exact stratigraphic position is unknown. The Korite ammolites from the Lethbridge area are commonly explored and mined from two horizons within the Bearpaw Formation, Zone 4 and K Zone, where the horizons correlate with Muddy Unit 1 (*Baculites compressus* zone) and Muddy Unit 2 (*B. cuneatus* zone) respectively (Link and Childerhose, 1931; Tsujita, 1995; Mychaluk et al., 2001). Both units are dated with ^{40}Ar/^{39}Ar analyses as being in the middle of the upper Campanian, and the *B.*

cuneatus zone is estimated to be younger with the approximate age of 72.32–73.35 Ma (Izett et al., 1998; Cobban et al., 2006). The contact between the Bearpaw Formation and the underlying Dinosaur Park Formation in the Lethbridge area is dated around 74.8 Ma (Eberth, 2005), and thus, the specimens are no younger than 72.32 Ma and no older than 74.8 Ma.

Previously reported Bearpaw vertebrates include several species of marine reptiles (Sato, 2005; Konishi et al., 2014), marine turtles (Brinkman et al. 2006; Brinkman et al., 2015), various Chondrichthyes (Konishi et al., 2014; Cook et al., 2017), and a very few Osteichthyes known from gut contents of mosasaurids, such as small centra of an elopid fish cf. *Paratarpon* and the partial remains of an aulopiform fish *Ursichthys longiparietalis* (Konishi et al., 2011; Newbrey and Konishi, 2015). The occurrence of *Dercetis* was mentioned by Wilson and Bruner (2004), although the specimen they based this on was not fully described. There are also several undescribed specimens of *Enchodus* in the collection of the Royal Tyrrell Museum of Palaeontology (e.g., TMP 2019.043.0008, TMP 2020.043.0001).

2.2 Materials and Methods

The specimens were collected by Korite International Ltd. and are permanently housed in the collections of the Royal Tyrrell Museum of Palaeontology (TMP), Alberta, Canada. Specimen TMP 2001.042.0017 (Figs. 2-2, 2-3, 2-6, 2-7, 2-8) consists of two blocks (a, b) that were collected together in the field at the time of discovery of the specimen. The first block (TMP 2001.042.0017a) preserves the skull and the first 15 abdominal vertebrae. The second block (TMP 2001.042.0017b) contains 35 abdominal vertebrae with impressions of 17 additional centra, for a total of 52.

Specimen TMP 2017.021.0001 (Figs. 2-4, 2-5, 2-9) consists of four blocks (a-d) with some additional isolated fragments of teeth and vertebrae. The anterior block of the specimen (TMP2017.021.0001a) preserves the skull roof, occipital region, upper and lower jaws, median and pectoral fins, seven and a half centra, and four partial dermal scutes. The second block (TMP2017.021.0001b) preserves the axial skeleton with 12 vertebrae, more than 16 fragmented dermal scutes, several fin rays and intermuscular bones. TMP2017.021.0001c, the third block, includes the middle to posterior portion of the vertebral column with 11 vertebrae, and the articulated pelvic girdle and pelvic fin rays. The fourth block (TMP2017.021.0001d) contains only three and a half centra, but these preserve a unique expansion of the transverse processes. All four blocks were collected together from the same area and possess an identical morphology of the centra with relatively consistent size, so here I accept that they represent the same individual.

The preparation was done by Mark Mitchell, a preparator in TMP, using Micro Jack tools and pin vises. The specimens were examined using a Nikon SMZ1000 microscope. The holotype specimen (TMP 2001.042.0017) was also imaged using a GE HD750 64-slice medical CT scanner at Mayfair Diagnostics, Mayfair Place, Calgary, Canada. The specimen was scanned with a voltage of 120 kVp, a current of 265–500 modulated mA, and a resolution of 0.611 mm (512 matrix). The images were reconstructed and segmented using Dragonfly 2021.3 (software provided by Object Research Systems Inc, Canada). Photographs were taken using an Olympus E-M10II camera and an Olympus FE-370 8MP digital camera. Drawings were made by hand as well as using MediBang Paint Pro software.

2.2.1. Phylogenetic analysis

I used the data matrix from the most recent phylogenetic analysis for enchodontoids (Alvarado-Ortega and Díaz-Cruz, 2020; Murray et al., 2022). The matrix includes 87 characters and 38 ingroup taxa including the new Canadian species described here. Murray et al. (2022) used only a single outgroup, the extant aulopiform *Trachinocephalus*, in their analysis in order to recover a monophyletic Enchodontoidei in contrast to other authors (e.g. Alvarado-Ortega and Díaz-Cruz, 2020) who included three outgroups (with the addition of the stomiiform *Protostomias* and the probable myctophiform *Sardinioides*) which resulted in a paraphyletic Enchodontoidei in those analyses. Murray et al. (2022:fig. 7) did not recover a monophyletic Dercetidae, instead recovering the species normally placed in this family in a huge polytomy with other enchodontoids. Therefore, I here ran two analyses, the first (A) with three outgroups (*Protostomias, Sardinioides* and *Trachinocephalus*) and the second analysis (B) with a single outgroup (*Trachinocephalus*). Following previous studies, other Cretaceous aulopiform fishes that are poorly or incompletely preserved including *Calypsoichthys*, *Kwangodercetis, Paradercetis, Leccedercetis, Scandiadercetis, Ornatipholis*, *Ursichthys*, and *Stratodus* were excluded from the matrix, although potential dercetids (*Kwangodercetis, Paradercetis, Leccedercetis, Scandiadercetis* and *Stratodus*) are considered as comparative species in the diagnosis of the new taxon. All characters are unordered and of equal weight. I performed a maximum parsimony analysis in TNT 1.5 (Goloboff and Catalano, 2016) with the addition of data for *D. magnificus* sp. nov. (Appendix A.1). The most parsimonious trees were recovered from an heuristic (traditional) search using the tree bisection and reconnection (TBR) swapping algorithm with 1 random seed per 1000 replicates. The strict consensus tree was recovered from all of the most parsimonious trees. The consistency (CI) and retention (RI) indices were calculated in Mesquite ver. 3.6 (Maddison and Maddison, 2018). Bootstrap and Bremer support values were calculated in TNT 1.5 (Goloboff and Catalano, 2016).

2.2.2 Institutional Abbreviations

TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada.

2.2.3 Anatomical Abbreviations

aa, anguloarticular; **brst**, branchiostegal rays; **c**, centrum; **den**, dentary; **ect**, ectopterygoid; **end**, endopterygoid; **epn**, epineural; **epo**, epioccipital; **exo**, exoocipital, **f**, frontal; **hyo**, hyomandibula; **in**, intercalar; **lac**, lacrimal; **lp**, lateral process; **mes**, mesethmoid; **met**, metapterygoid; **mp**, median process; **mx**, maxilla; **na**, neural arch, **ns**; neural spine; **op**, opercle, **pa**, parietal; **pal**, palatine; **pcf**, pectoral fin ray; **pvf**, pelvic fin ray; **pop**, preopercle; **pto**, pterotic; **ptt**, posttemporal; **q**, quadrate; **scl**, sclerotic ring; **sph**, sphenotic; **soc**, supraoccipital; **sym**, symplectic; **tps**, transverse process

2.3 Systematic Palaeontology

Division TELEOSTEI Müller, 1845
Subdivision NEOTELEOSTEI Nelson, 1969
Order AULOPIFORMES Rosen, 1973
Suborder ENCHODONTOIDEI sensu Nelson, 1994
Family DERCETIDAE Woodward, 1901

Genus *DERCETIS* Münster and Agassiz, 1834

Included species (following Taverne, 2005)—The type species *Dercetis elongatus* Agassiz, 1835 from the Turonian of England, and *Dercetis triqueter* Pictet, 1850 from the Upper Senonian of Lebanon.

'*Dercetis' reussi*, '*D.' latiscutatus*, and '*D.' maximus* are excluded from *Dercetis* due to the incompleteness of the available material; they are left as genus incertae sedis. However, these taxa are clearly different from the new species described here, in that '*D.' maximus* possesses multiple spiny projections on the neural arches (Woodward, 1903:pl. xv, fig. 2), and '*D.' reussi* has a first abdominal centrum that is not extremely elongated (Fritsch, 1878:pl. ii, fig. 8; Taverne, 2005). '*Dercetis' latiscutatus* is too fragmentary to compare the osteological details with the new taxon, and it was left unassigned by Taverne (2005), therefore, it is also left as incertae sedis in this study and not used in the comparisons. As noted in the Introduction, *'D.' congolensis* is probably better placed in *Cyranichthys*, however it can also be distinguished from the new species by the frontal being narrower in front of the sphenotic. (Casier, 1965:fig. 7).

DERCETIS MAGNIFICUS sp. nov.

(Figs. 2-2 to 2-9)

Type Material—Holotype TMP 2001.042.0017, an incomplete specimen of a large individual with a slightly distorted skull and the anterior 15 vertebrae, and the posterior portion of the axial skeleton with at least 35 vertebrae preserved (Fig. 2-2). Paratype TMP 2017.021.0001a, b, c and d, four blocks of an incomplete specimen of a large individual (Figs. 2-

4, 2-5). The blocks contain a well-preserved skull roof and occipital region, jaws, vertebrae, median and paired fins, and dermal scutes.

Type Locality and Age— Bearpaw Formation in the valley of the St. Mary's River, south of Lethbridge, Canada, upper Campanian (Upper Cretaceous).

Etymology— From Latin word 'magnificus' (splendid, magnificent), in reference to the larger body size of the new species and the robust hyomandibula compared to other known species.

Diagnosis—The new species is included in the genus *Dercetis* based on the moderately elongate rostrum having a lower jaw slightly shorter than the upper jaw, mesethmoid anteriorly bifurcated and posteriorly acute, parietals not separated by the supraoccipital (medio-parietal skull), toothed premaxilla with an ascending process at the anterior end, toothed maxilla bulging anteriorly into the articular process for the premaxilla, axial skeleton with triradiate dermal scutes and vertebrae having a single pair of transverse processes. The new species is distingished from the currently valid species, *D. elongatus* and *D. triqueter*, by the parietal having a posterior margin extending beyond the supraoccipital, the maxilla tapering towards the posterior end, the maxilla bearing multiple tooth rows, the hyomandibula having an elongate anterior limb, and the very reduced neural spines with blunt tips.

Further differs from *D. triqueter*, but not *D. elongates*, by the first abdominal centrum being three times longer than deep, the lower jaw slightly shorter than the upper, and the dentary and scutes ornamented (in *D. triqueter* the first abdominal centrum is twice as long as deep, the lower jaw is equal in length to the upper, and the dentary and scutes without ornamentation; Woodward, 1901; Taverne, 2005). Further differs from *D. elongatus*, but resembles *D. triqueter*, in having a premaxilla that possesses larger teeth in more than one tooth row, whereas *D.*

elongatus has smaller teeth in a single tooth row (Taverne, 2005; Taverne and Goolaerts, 2015:fig. 3, 5).

2.4 Description

2.4.1 General remarks

The new species is much larger than any other species of *Dercetis* and even larger than any previously reported dercetids. The holotype (TMP 2001.042.0017a and b) and paratype (TMP 2017.021.0001a-d) are incomplete fish, both missing the caudal region, and therefore, standard length and total length cannot be measured directly from the fossils. However, based on the preserved portion of the skeleton, it is estimated that the living fish would have been more than one meter long. The fish has a shallow, elongate head and body with reduced neural spines on the vertebrae, similar to other dercetids.

The head length (HL) of the holotype (TMP 2001.042.0017) measured from the rostrum tip to the posterior margin of the preserved portion of the operculum is 332 mm. The head depth is 75.4 mm which is 22.7% of HL. The preorbital length is 160 mm (48.2% HL). In TMP 2001.042.0017a, the first block of the holotype, the anteriormost abdominal centrum is 31.2 mm and is about two times longer than the 15th centum, the posteriormost centrum in this block, which is 14.8 mm. The paratype (TMP 2017.021.0001) is slightly smaller than the holotype, with the head length being 275 mm. The head depth and preorbital length are difficult to determine due to their fragmentary condition of the skull. The average length of the centra is 20 ± 2 mm with the largest anterior centrum measuring 25 mm.

2.4.2 Skull roof

The skull in both specimens is exposed in dorsal view and preserves most of the elements (Figs. 2-3, 2-4). The frontal is elongate and the largest bone of the skull roof. The anterior half is triangular and tapered towards the anterior end. The posterior half is almost a trapezoid shape that expands laterally above the sphenotic and posteriorly contacts the parietal with a large interdigitating suture. The contact between the right and left frontals is a slightly sinuous suture, which ends where the posterior end of the mesethmoid inserts between the anterior portions of both frontals. The lateral edge of the frontal expands slightly above the orbit and contacts the lacrimal anterior to the orbit. The bone surface is highly ornamented, especially in the center of ossification, where the multiple striations with tubercles radiate out and extend to each end of the bone.

The parietal (Figs. 2-3, 2-4) is antero-posteriorly short and subtriangular in shape. The posterior edge extends beyond the occipital region and contacts the pterotic posterolaterally. The suture between the left and right parietals is interdigitating, although the notches are shallower than those of the suture between the frontal and parietal. The left and right parietals meet in the midline and are not separated by the supraoccipital, forming a medio-parietal skull. Striations and tuberculation are also observed on the bone surface, and the posterior edge is extensively ornamented with multiple rows of tubercles.

The pterotic (Figs. 2-3, 2-4) is elongated and extends posteriorly beyond the occiput. The posterior end also reaches past the parietal and projects beyond the supraoccipital. Dorsolaterally, the pterotic abuts the frontal and parietal, and the anterior end contacts the posterior expansion of the frontal. The holotype preserves the anteroventral portion of the pterotic that overlaps the partially preserved sphenotic. The posterior half is ornamented with more striations than the anterior half.

The mesethmoid (Fig. 2-3, 2-4, 2-6) is a single, median, elongate bone inserted between the left and right frontals. The anterior end has semicircular lateral projections, forming a bifurcated shape (Fig. 2-6). The paratype only preserves the partial anterior end, in which the bifurcation is observable by its impression. The posterior end is fragmented in both the holotype and the paratype, but the shape can be inferred by its contact with the frontals, which indicates that the bone has an acute posterior end. The bone surface is also covered by longitudinal striations.

2.4.3 Orbital region

The orbit is partially preserved in the holotype (Fig. 2-3). Very thin lamellar bones, identified as remains of the sclerotic ring, surround the orbit. The right lacrimal is also partially preserved and more or less trapezoidal in shape. The external surface of the lacrimal is highly ornamented with small ridges that resemble the patterning of the skull roof. The left lacrimal is attached to the lateral edge of the left frontal, although most of it is missing. The sphenotic is well preserved in TMP2017.021.0001a, and exposed in dorsal view. The sphenotic is smooth and projects laterally underneath the frontals. In the holotype, the right sphenotic is partially visible below the anterior end of the pterotic. The lacrimal is partially preserved and placed anterior to the orbit. The surface is highly ornamented with striations. Other infraorbital series are well preserved, with only fragments visible near the sclerotic ring of the holotype.

2.4.4 Upper jaws

The upper jaw is slightly longer than the lower and consists of a slender maxilla and a robust premaxilla. The right maxilla is exposed in lateral view in the holotype (Fig. 2-3) and the left maxilla is preserved in ventral view in the paratype (Fig. 2-4). Overall, the bone is thin and elongated, expands anteriorly to form the anterior articulation for the premaxilla, and tapers towards the posterior end. The surface of the bone is not ornamented. There are at least three tooth rows visible on the left maxilla of TMP2017.021.0001a (paratype). Maxillary teeth are slender, slightly curved with acrodin caps on the tip, and smaller than premaxillary teeth.

The premaxilla (Figs. 2-3, 2-4) is a robust triangular bone that extends for almost half the length of the skull. The bone tapers towards the anterior end, which then becomes slightly expanded and forms an ascending process that attaches to the mesethmoid medially. The bone surface bears multiple striations, especially around the anterior end. There is a long longitudinal ridge along the midline of the bone, with a small triangular notch at the termination of the ridge located posterior to the anterior expansion of the mesethmoid. The ridge extends posteriorly to the point where the anterior process of the maxilla enters the gape and overlaps the premaxilla. Premaxillary teeth are conical and slightly curved, with multiple tooth rows confirmed in the CT image (Appendix A.3).

2.4.5 Mandible

The mandible (Figs. 2-3, 2-4) is well-preserved in the holotype and partially preserved in the paratype, and consists of a long slender dentary and a large triangular anguloarticular. The posterior end of the upper limb of the dentary extends nearly to the posterior end of the mandible, whereas the anterior end tapers anteriorly and ends slightly behind the anterior tip of the rostrum. There are at least five tooth rows on the dentary with many small teeth; the second lateral tooth row bears a smaller number of large teeth. All teeth are slightly curved posteriorly. The mandibular sensory canal, visible in the CT image, shows its partially open condition, with the canal enclosed in the dentary but open in the angular. The anterior tip of the dentary bulges slightly ventrally, and presumably forms a mandibular symphysis.

The anguloarticular (Figs. 2-3, 2-4) is long, smooth, and shaped almost like an isosceles triangle, tapering towards the articular facet with the dentary. The bone has a shallow articular facet for the quadrate. A groove running along the lateral face of the anguloarticular demarcates a slender dorsal portion and broad ventral region (visible on TMP2017.0021.0001a). Specimen TMP2017.0021.0001a also preserves a small triangular left retroarticular that articulates with the posterior end of the anguloarticular.

2.4.6 Hyopalatine bones and branchial arches

The hyopalatine bones are well preserved in the holotype (Fig. 2-3, 2-7). The hyomandibula in lateral view presents a well-developed anterior head with minute striations presumably for muscle attachment (Fig. 2-7). The bone bends into a vertical orientation below the pterotic. A groove runs along the posterodorsal surface of the hyomandibula, which divides the bone into the articular facet for the opercle and the body of the hyomandibula that overlaps a small symplectic ventrally. The symplectic is narrow and covered dorsally by the hyomandibula, and the ventral end articulates with the quadrate. The quadrate is fan-shaped and contacts the anguloarticular anteriorly.

The palatine (Fig. 2-3) is a broad triangular bone covering almost the entire roof of the mouth in the preorbital portion and tapering towards the anterior end. The bone is slightly concave with a smooth dorsal surface. The ventral surface bears multiple tooth rows comprising teeth of various sizes. The articulation of the posterior end of the palatine with the anterior end of the ectopterygoid is posterior to the level of the lacrimal. The ectopterygoid is a narrow, flat bone that is angled and expanded below the orbit. The bone bears minute striations externally and a single tooth row internally. The endopterygoid is exposed laterally in the paratype and partially visible in the CT image of the holotype (Appendix A.4). It is broader than the ectopterygoid and expands posteriorly, almost reaching the quadrate. The posteroventral portion of the endopterygoid seems to be thinner and is not visible in the CT image. The presence of teeth also cannot not be confirmed because of the resolution of the CT image. The thin, triangular metapterygoid is exposed laterally in the holotype, and overlaps the endopterygoid externally. Only the dorsal portion is visible in the CT image, due to poor resolution.

There are five left branchiostegal rays visible in the paratype. The most ventral branchiostegal ray appears shorter than the others, but this may be due to preservation. All branchiostegal rays are thin and preserved ventral to the preopercle and the pectoral fin.

2.4.7 Occipital region

The occipital region in the paratype (Fig. 2-4) is better preserved than that of the holptype. The supraoccipital is a small bone with a very reduced crest, and it does not separate the parietals. The epioccipitals are located posterolateral to the supraoccipital and dorsal to the exoccipitals. The intercalars are positioned lateral to the exoccipitals. There are small spaces between the epioccipitals and intercalars, probably due to the fragmentary condition of the bones. The posttemporal fossa is not visible and so presumably is covered by the pterotic. The basioccipital is present, but the details of the morphology could not be examined due to poor resolution of the CT images.

2.4.8. Opercular bones

The opercular series is composed of a preopercle, opercle, subopercle and interopercle, all of which are preserved in the holotype (Fig. 2-3). The preopercle is well preserved in both the holotype and paratype (Figs. 2-3, 2-4). The vertical limb is elongated dorsally and extends along the ventral third of the hyomandibula, whereas the ventral limb projects anteriorly, forming a right angle with the dorsal limb. The details of a sensory canal on the preopercle are visible on the paratype, with many small sensory pores opening along the canal. The opercle is represented with only by the remains of the ventral portion of the bone, which contacts the subopercle. The interopercle is partially preserved between the preopercle, opercle and subopercle on the holotype. All bones of the opercular series are smooth and unornamented.

2.4.9. Vertebral column

Both the holotype and paratype preserve an incomplete series of vertebrae (Figs. 2-2, 2-5, 2-8). The first 15 abdominal vertebrae are well preserved in the first block of the holotype (TMP 2001.042.0017a), which also shows the detailed morphology of the unique neural arches and spines (Fig. 2-8). The neural arch extends from the anterior to the posterior ends of the centrum, and both the anterior and posterior ends project dorsally. There are minute pits on the lateral surface of the neural arches. The neural spine is not well developed and forms a blunt projection at the posterior end of the neural arch. The blunt and pitted nature of the neural arches of the holotype is confirmed in specimen TMP2017.0021.0001a (anterior part of the paratype), in which the area of the partial scutes is preserved. In more posterior vertebrae, the neural arch becomes smooth with no pits on the surface. The centrum is longer than high; this is particularly the case for the first centrum, which is almost three times as long as it is high. Centra are smooth in texture in the anterior abdominal vertebral column, whereas minute striations can be seen on the centra in the posterior part of the vertebral column.

A single, broad, transverse process projects from each centrum, and there is a small ridge in the middle of the process. Ribs are thin and attached to each process, although the rib articulation is only preserved in the anterior few vertebrae of the holotype. Several intermuscular bones identified as epineurals are well-developed and cover the vertebrae dorsally. Each epineural is thin, elongate and rod-like, overlapping the one behind. The epineurals cover almost the entire length of the preserved axial skeleton of the holotype and paratype except for some fragmentary blocks of isolated posterior vertebrae where they are absent or not preserved.

2.4.10 Fins and girdles

Fins and girdles are better preserved in the paratype (TMP 2017.021.0001). The pectoral girdle is not well preserved except for the left posttemporal, which is triangular and ornamented on the external surface. The left pectoral fin (Fig. 2-4) is partially preserved in lateral view in the first block of the paratype with the skull elements. A single unbranched fin ray and at least five branched rays are visible below the subopercle. The unbranched ray is unsegmented and appears smooth on its surface, whereas the branched rays show multiple segmentations, particularly on the posterior edge.

The segmentation is more prominent in the pelvic fin, which is composed of eight rays preserved together with the partial right lateral process of the pelvic girdle found in the posterior block of the paratype (TMP 2017.021.0001c; Fig. 2-9). The position of the pelvic girdles and fins is not clear, except that they are located farther posteriorly than the pectoral fins. The preserved portion of the pelvic girdle shows the paired median process (*sensu* Sato and Nakabo,

2002) where the right and left posterior portions meet at the midline. The left lateral process is more fragmentary than the right and the fin rays are not fully preserved (Fig. 2-9).

Dorsal fin rays are not well preserved in either specimens, and are obscured by a covering of fragmentary dorsolateral dermal scutes in the paratype (Fig. 2-5). Thin bundles of bones on top of the neural arch in TMP2017.021.0001a (anterior block of paratype) are identified as epineurals rather than dorsal fin rays because they are unsegmented and covered by scutes. The dorsal pterygiophores cannot be identified due to the fragmentary condition of the specimen. Anal fin rays are preserved but scattered on TMP2017.021.0001c (posterior block of paratype). Although the total number is difficult to determine, both unbranched and branched fin elements are present.

2.4.11 Dermal scutes

Several triradiate dermal scutes are prominently preserved in the paratype (Fig. 2-5). The holotype preserves a tiny fragment of a dorsolateral scute in the anterior block, and the posterior block preserves a series of small triradiate scutes along the dorsolateral and ventrolateral surfaces. TMP2017.021.0001b (the second block of the paratype) shows large, well-preserved, triradiate lateral scutes and a couple of fragmentary dorsolateral scutes; these latter seem to have a different shape from those dorsal to the neural arches in the first block of the paratype (TMP2017.021.0001a). The triradiate lateral scutes are highly ornamented on the external surface with ridges and tubercles. In addition to that ornamentation, there is a prominent median ridge running along the midline from the anterior to the posterior end of the scute, making the ornamentation dorsoventrally symmetrical. The inner surface of each scute is smooth and concave due to the median ridge projecting from the external side. The dorsolateral scutes dorsal to the neural arches also bear minute tubercles, but no ridges. The tubercles are smaller than those on the triradiate scutes, and the tubercles cover the surface almost up to the edges, whereas the tubercles on the triradiate lateral scutes do not reach the edges of the scutes. The number of rows of scutes is not completely clear, but there would have been at least two rows of scutes on each flank.

2.5 Results of the phylogenetic analysis

The heuristic analysis using three outgroups (analysis A: following e.g., Alvarado-Ortega and Díaz-Cruz, 2020) recovered 12 most parsimonious trees (MPTs), each with a length of 501 steps. The strict consensus of these trees was recovered with a consistency index (CI) of 0.1698 and retention index (RI) of 0.3818 (Fig. 11-1). On the other hand, the heuristic analysis using a single outgroup (analysis B: following Murray et al., 2022) recovered two MPTs. The strict consensus of the two MPTs of treelength 469 was recovered with CI of 0.2229 and RI of 0.5306. In both analyses, *Dercetis magnificus* sp. nov. was placed within a clade that includes (*Pelargorhynchus* + (*D. magnificus* sp. nov. + (*D. elongatus* + *D. triqueter*))), therefore *D. magnificus* sp. nov. is the sister to the other valid species of *Dercetis*.

In analysis A, most of the dercetid taxa are part of a large polytomy and monophyly of Dercetidae is not supported (Fig. 2-10). Only a clade of (*Hastichthys gracilis* + *H. totonacus*) was supported by a bootstrap value >50%, but the placement of the rest of the taxa was not strongly supported. Analysis B recovered a clade which is mostly composed of dercetid taxa, but it also included *Nardorex* and *Spinasctutichthys*, which were not previously placed in the Dercetidae (Fig. 2-11). In analysis B, the clade (*D. magnificus* sp. nov. + (*D. elongatus* + *D. triqueter*)) was united by three characters [10:1—anterior end of mesethmoid bifid; 37:1—

ascending process of the premaxilla present; 43:1—mandible teeth only curved]. *Pelargorhynchus* was recovered as sister to the *Dercetis* clade, and the clade (*Pelargorhynchus* + (*D. magnificus* sp. nov. + (*D. elongatus* + *D. triquester*))) was supported by several characters [4:1—skull roof ornamented with tubercles and ridges; 16:1—parietals short, 35:1—premaxilla ornamented; 45:1—equal tooth size on mandible; 50:1—mandible ornamented].

2.6 Discussion

2.6.1 Phylogeny

The difference in the results of the two analyses A and B is not only the consistency and retention indices but also the resolution and number of recovered monophyletic clades. I here focus on analysis B, which used the single outgroup *Trachinocephalus*, because this analysis found *Dercetis magnificus* sp. nov. to be grouped with members of Dercetidae, and that clade was recovered as monophyletic as in previous studies (e.g. Silva and Gallo, 2011; Vernygora et al., 2017; Alvarado-Ortega and Díaz-Cruz, 2020). Vernygora et al. (2017) suggested that Dercetidae is supported by a single synapomorphy, reduced neural spines (character 71), whereas the Implied Weighted Maximum Parsimony Analysis by Alvarado-Ortega and Díaz-Cruz (2020) found that the reduced neural spines may be a homoplastic condition although the monophyly of the family was supported by the Bayesian Inference analysis by the same authors. Unlike previous studies, analysis B did not recover a monophyletic family Dercetidae but instead recovered a clade with inclusion of *Nardorex* and *Spinascutichthys* (Fig. 2-11). Here I tentatively retain the family Dercetidae as a paraphyletic group, pending the more comprehensive review of current data matrices presented in the next chapter.

2.6.2 Temporal and geographic distributions

Dercetis magnificus sp. nov. is the first well-preserved *Dercetis* reported from Canada. The type species of the genus, *D. elongatus*, was found in the Turonian of England and the Campanian of Germany (Woodward, 1901; von der Marck, 1873), and the other species, *D. triqueter*, was reported from the Senonian of Lebanon and the Maastrichtian of Belgium and the Netherlands (Pictet, 1850; Tavern and Goolaerts, 2015).

Specimens possibly belonging to *Dercetis* have been reported from the Turonian of Czech Republic (Ekrt et al., 2008), the Turonian of Mexico (Alvarado-Ortega et al., 2020), and the Campanian of Canada (Wilson and Bruner, 2004). Both the Czech and Mexican specimens are quite small, with a head length of 30-50 mm, and the details of the cranial features cannot be fully compared to *D. magnificus* sp. nov. due to the nature of the preservation (Ekrt et al., 2008; Alvarado-Ortega et al., 2020). The other Canadian specimen was reported from the Bearpaw Formation of Lethbridge, Alberta, with no specimen number given (Wilson and Bruner, 2004), but I believe the specimen is UALVP 45921. UALVP 45921 is a three-dimensionally preserved partial skull roof and braincase, the length of the preserved portion of the skull being about 137 mm. The overall morphology of the skull roof and the pattern of the striations and tubercules on the bone surface is very similar to *D. magnificus* sp. nov. I here assign UALVP 45921 to *D. magnificus* sp. nov. not only because the skull is morphologically similar, but also because it was collected from the same area and formation.

In sum, the occurrence of the genus *Dercetis* is currently limited to the Late Cretaceous, and more specimens have been reported from the eastern Tethys (Europe, Lebanon) than the west area of the Tethys (Mexico, Canada). From the WIS, *D. magnificus* is the only reported species of the genus *Dercetis*, and is represented by both large (TMP2001.042.0017 and TMP2017.021.0001) and small (UALVP 45921) individuals.

2.6.3 Body size

The body size of the previously reported specimens of *Dercetis* was no larger than 60 cm. *Dercetis elongatus* was estimated by Woodward (1901) to probably attain 60 cm, although the specimens were not complete. The complete specimens of *D. triqueter* were reported to be 20 to 30 cm in total length (Woodward, 1901; Goody, 1969). Although the total length of *D. magnificus* sp. nov. cannot be measured, the length from the anterior tip of the rostrum to the posterior end of the 15th vertebrae of the holotype is about 57 cm, which indicates this fish had a much larger body size than any specimens that were previously reported.

The size of the new species indicates that at least some dercetids had the potential to reach a larger body sizes. There are several enchodontoids that can reach about 1-2 meters, such as *Enchodus*, *Cimolichthys*, and *Stratodus* (Michaut, 2012; Everhart, 2017). Especially, *Enchodus* shows various body sizes, encompassing both the larger species *E. petrosus* (estimated standard length (SL) > 1 m) and the smaller species *E. marchesettii* (SL < 18 cm) (Goody, 1969; Everhart, 2017). The deposits of the WIS, including the Bearpaw Formation, comprise sediments corresponding to an open marine environment where large fishes could survive. Although more materials are needed to investigate the growth series of dercetids, the new species expands our knowledge of size variation in *Dercetis* and other dercetid fishes.

2.7 Conclusion

The two new specimens (TMP 2001.042.0017 and TMP 2017.021.0001) were assigned to the new species of the genus *Dercetis* based on the observation of morphology and the internal anatomy provided by the CT image. The result of morphological phylogenetic analysis also supported the placement of the new species as a sister to the two species of *Dercetis*, *D. elongatus* and *D. triqueter*, which are currently valid as species of *Dercetis* defined by Taverne (2005). The reports of the genus *Dercetis* from the western area of the Tethys and the WIS were limited to a very small individual from Mexico (Alvarado-Ortega et al., 2020) and an incomplete braincase from Alberta, Canada (Wilson and Bruner, 2004), so the two new specimens provided the first detailed description of the species of *Dercetis* found in the western side of the Tethys. The incomplete specimen reported by Wilson and Bruner (2004) was also assigned to the same species to the newly described specimens based on the morphology of the skull roof. Finally, the two new specimens were larger than the any other previously reported *Dercetis*, which show a potential to attain the larger body size in the genus *Dercetis* and dercetids.

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Woodward, A. S. 1901. Catalogue of fossil fishes in the British Museum (Natural History). Part IV. Containing the actinopterygian Teleostomi of the suborders Isospondyli (in part), Ostariophysi, Apodes, Percesoces, Hemibranchii, Acanthopterygii, and Anacanthini. British Museum (Natural History), London, 636 pp.

Woodward, A. S. 1903. The fossil fishes of the English Chalk. Part II. Monograph of the Palaeontographical Society, pp. 57–96.

Table 2-1. A list of species have been placed in the genera *Dercetis, Leptotrachelus*, and *Benthesikyme* and the current taxonomy.

Species	Original work	Current status		Age	Location
D. scutatus	Münster and Agassiz, 1834	→ *nomen nudum*	(Siegfried, 1966)	Senonian	Westphalia, Germany
D. elongatus	Agassiz, 1837			Turonian	England
D. triqueter	Pictet, 1850			Upper Senonian	Sahel Alma, Lebanon
D. tenuis	Pictet, 1850	→ *D. triqueter*	(Pictet and Humbert, 1866)	Upper Senonian	Sahel Alma, Lebanon
D. linguifer	Pictet, 1850	→ *D. triqueter*	(Goody, 1969)	Upper Senonian	Sahel Alma, Lebanon
D. reussi	Fritsch, 1878	→ incertae sedis	(Taverne, 2005a)	Turonian	Bohemia, Czech Republic
D. limhamnensis	Davis, 1890	→ *Scandiadercetis limhamnensis*	(Taverne, 2005a)	Danian	Limhamn, Sweden
D. latiscutatus	Woodward, 1903	→ incertae sedis	(Taverne, 2005a)	Turonian	Kent, England
D. maximus	Woodward, 1903	→ incertae sedis	(Taverne, 2005a)	Coniancin - Santonian	Essex, England
D. rostralis	Signeux, 1954	→ *Benthesikyme rostralis*	(Taverne, 2005a)	Upper Senonian	Sahel Alma, Lebanon
D. ornatissimus	Casier, 1965	→ *Cyranichthys ornatissimus*	(Taverne, 1987)	Cenomanian	Kwango, D.R.Congo
D. congolensis	Casier, 1965	→ *Cyranichthys?*		Cenomanian	Kwango, D.R.Congo
L. armatus	von der Marck, 1863	→ *Benthesikyme armatus*	(Taverne, 2005a)	Campanian	Westphalia, Germany
L. hakelensis	Pictet and Humbert, 1866	→ *Rhynchodercetis hakelensis*	(Arambourg, 1943)	Middle Cenomanian	Hakel, Lebanon
L. sagittatus	von der Marck, 1873	→ *D. elongatus*	(Taverne, 2005a)	Campanian	Westphalia, Germany
L. longipinnis	Cope, 1878	→ *Benthesikyme gracilis*	(Taverne, 2005a)	Santonian	Sahel Alma, Lebanon
L. virgulatus	Cope, 1878	→ *D. triqueter*	(Taverne, 2005a)	Santonian	Sahel Alma, Lebanon
L. gracilis	Davis, 1887	→ *B. gracilis*	(Taverne, 2005a)	Upper Senonian	Sahel Alma, Lebanon
L. serpentinus	Hay, 1903	→ incertae sedis	(Taverne, 2005a)	Cenomanian	Hakel and Hajula, Lebanon
L. gortanii	Erasmus, 1946	→ *Rhynchodercetis gortanii*	(Taverne, 1987)	Lower Cenomanian	Comen, Slovenia

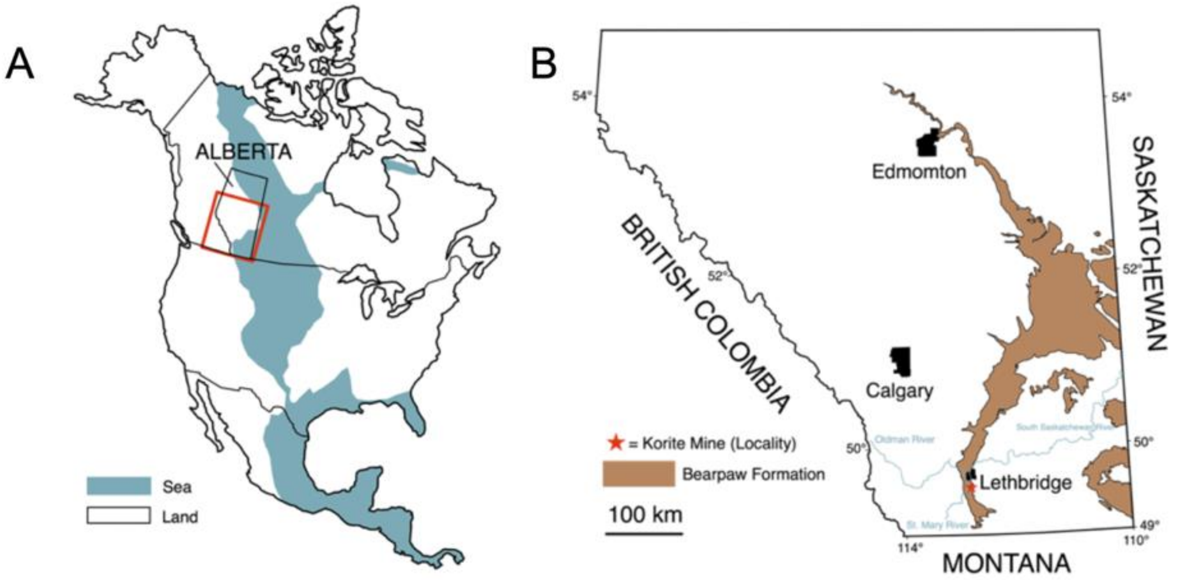

FIGURE 2-1. Location map of the locality. **A**, Drawing of the WIS during the late Campanian, modified from Scotese (2014). The box indicates the southern area of Alberta. **B,** Geological map of southern Alberta with the locality (Korite Mine) and the Bearpaw Formation, modified from Prior *et al*. (2013).

FIGURE 2-2. The two blocks of TMP2001.042.0017. **A**, TMP2001.042.0017a, anterior block of the holotype. **B**, TMP2001.042.0017b, the posterior block of the holotype. The scale bar = 5 cm.

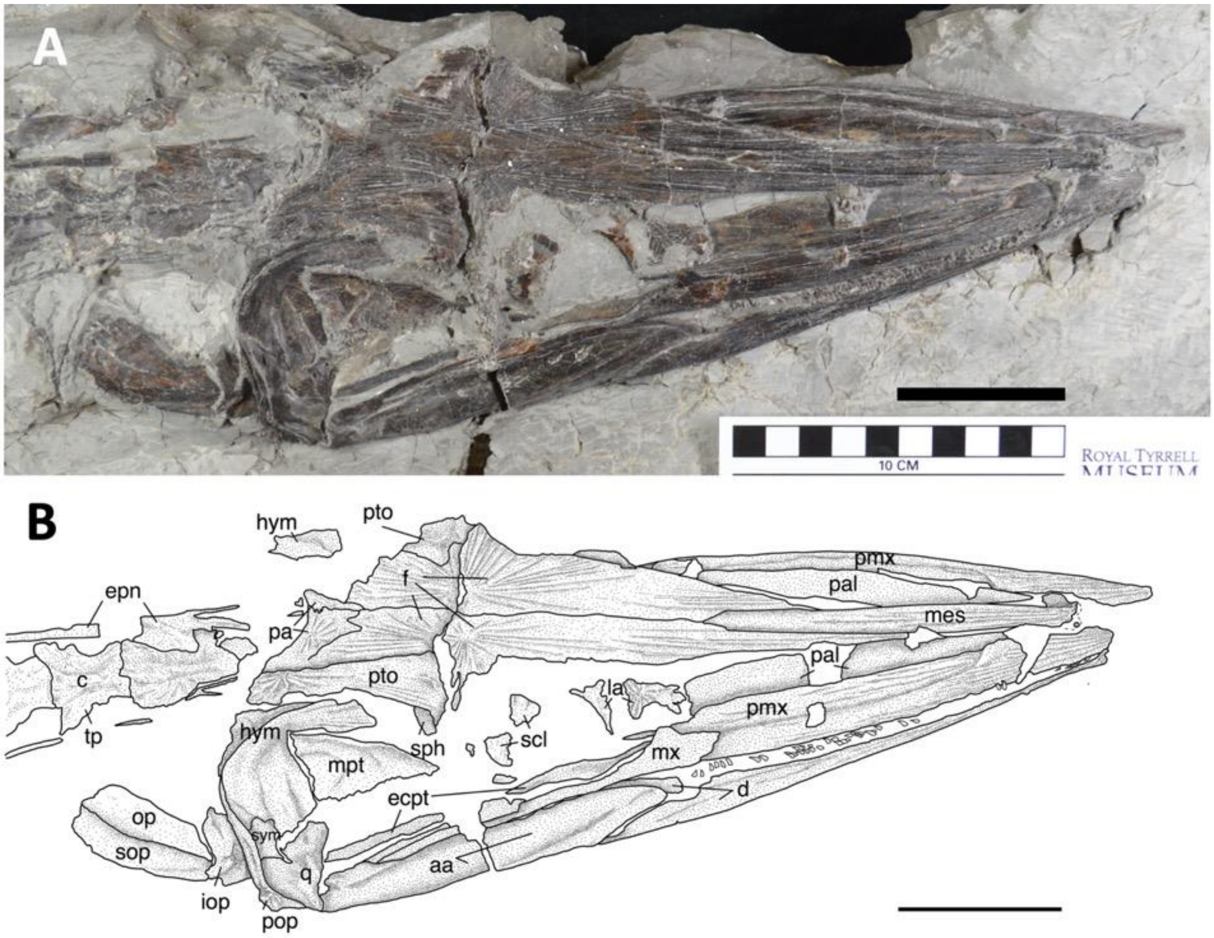

FIGURE 2-3. A, The dorsolateral view of the skull of the holotype (TMP2001.042.0017a). **B**, The interpretation of the skull of the holotype (TMP2001.042.0017a). The scale bar = 5 cm.

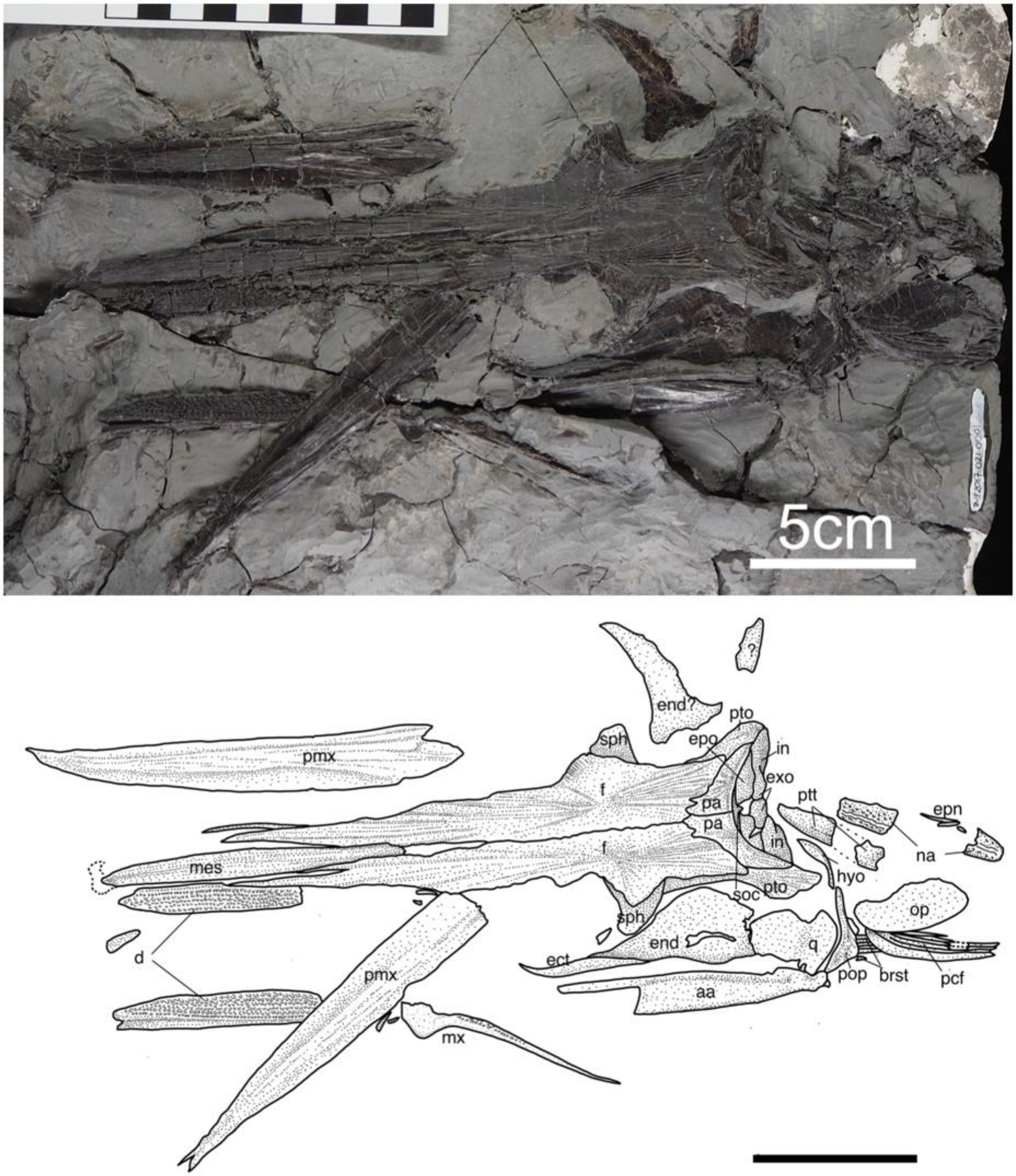

FIGURE 2-4. The dorsal view of the skull portion on the TMP2017.021.0001a (the first block of the paratype). The scale bar = 5 cm.

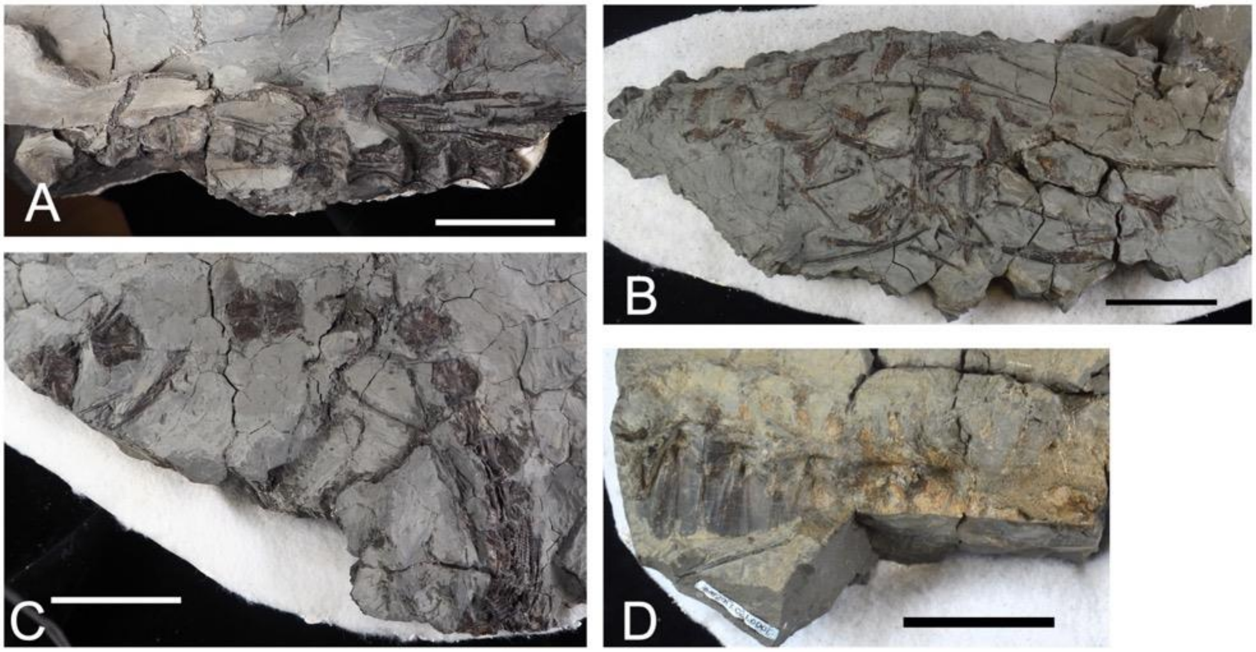

FIGURE 2-5. The four blocks of the TMP2017.021.0001a-d. **A**, The vertebrae and scutes on the first block (TMP2017.021.0001a—the skull on the same block is in figure 2-4). **B**, The triradiate lateral scutes and scattered fin rays on the second block (TMP2017.021.0001b). **C**, The posterior abdominal vertebrae and the pelvic fins on the third block (TMP2017.021.0001c). **D**, The broad expansion of transverse processes on the fourth block (TMP2017.021.0001d). The all scale bars = 5 cm.

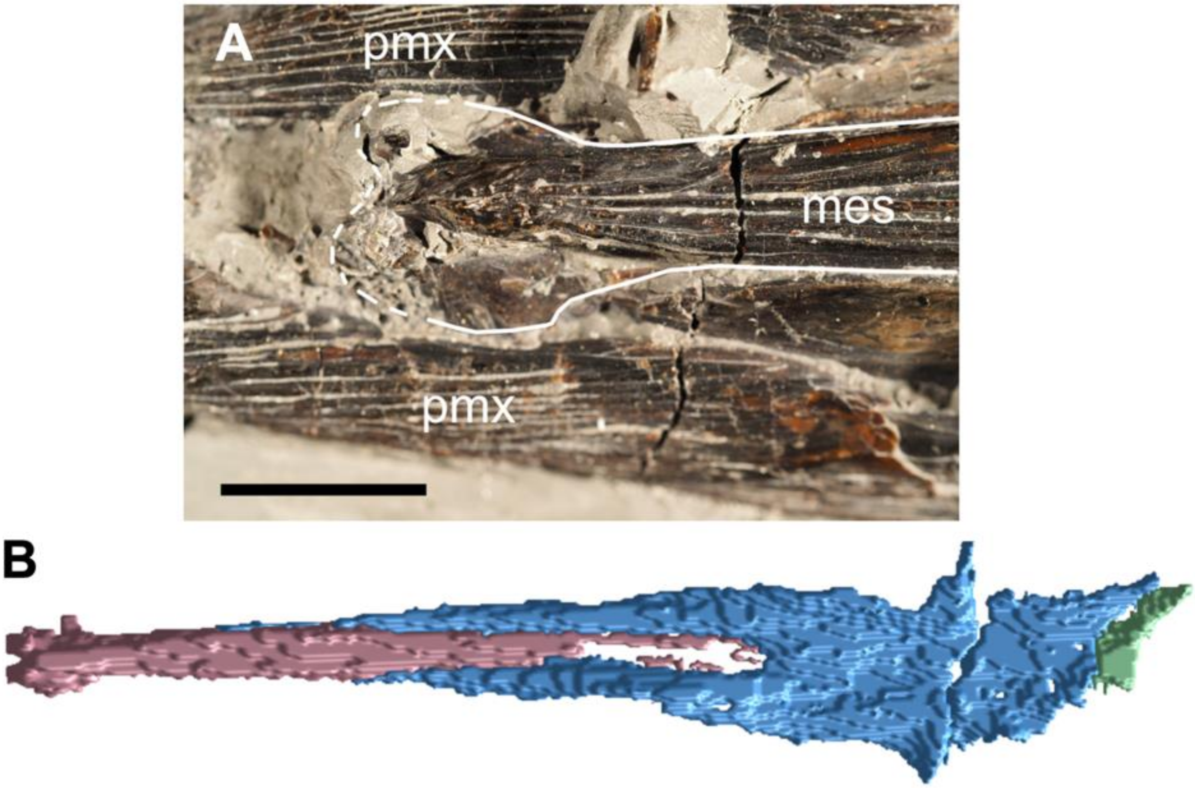

FIGURE 2-6. **A**, The anterior end of the mesethmoid of the holotype (TMP2001.042.0017) showing the bifid extremity. **B**, The reconstructed skull roof from the CT image with the mesethmoid (pink), frontals (blue), and partial parietals (green). Anterior is to the left. The scale bar = 1 cm.

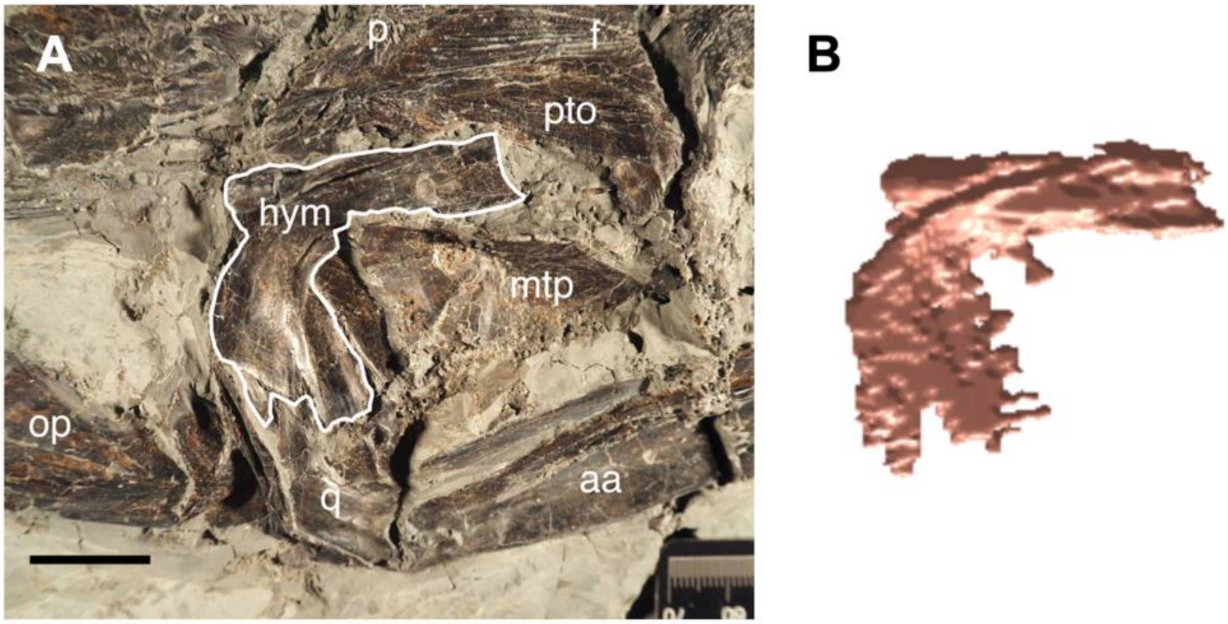

FIGURE 2-7. **A**, The left hyomandibula of the holotype (TMP2001.042.0017a) is outlined with the white line. **B**, The same left hyomandibula reconstructed from the CT image. The scale bar = 2 cm.

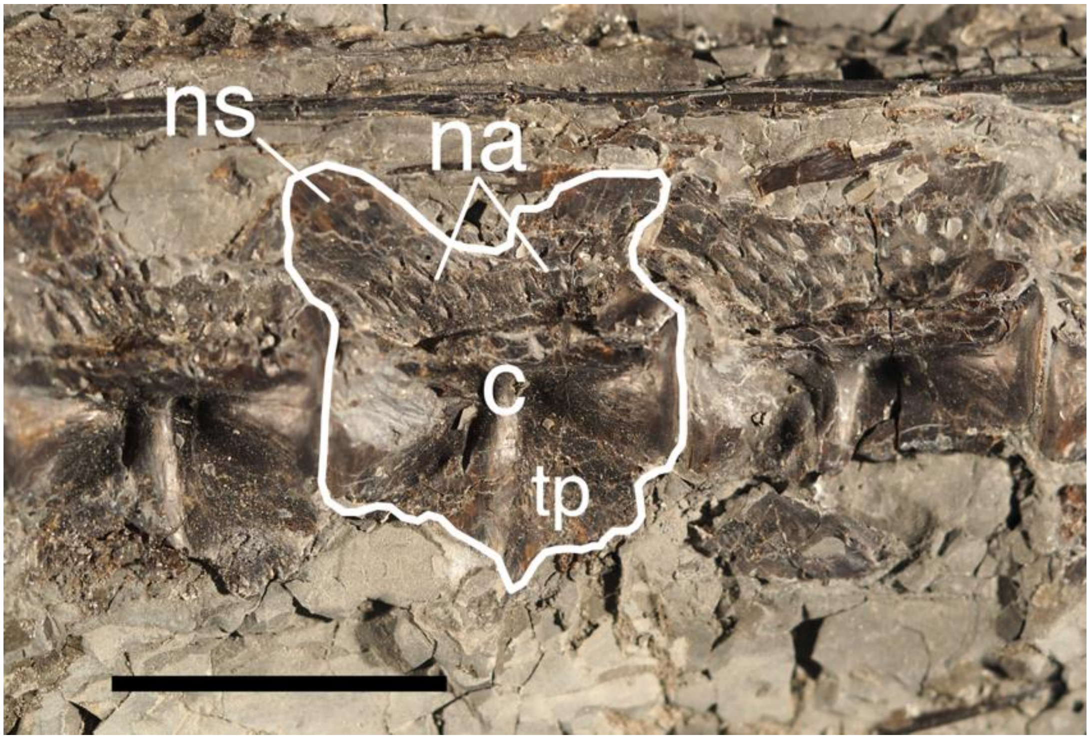

FIGURE 2-8. The third, fourth, and fifth anterior abdominal vertebrae of the holotype (TMP2001.042.0017a). The fourth vertebra is outlined with white line to show the blunt neural spine. Anterior is to the right The scale bar = 2 cm.

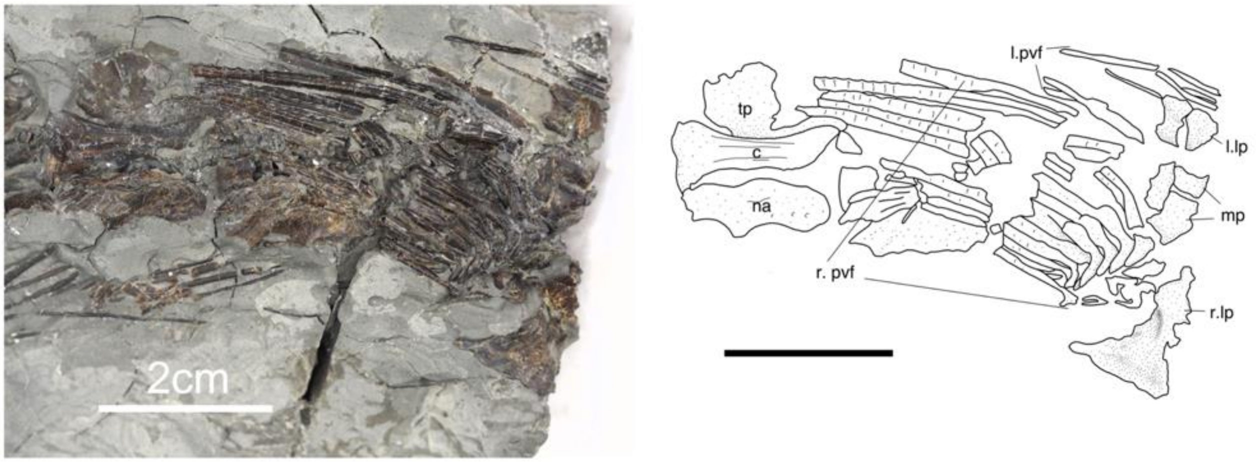

FIGURE 2-9. The pelvic girdle and fin rays on the TMP2017.021.0001c. Anterior to the right.

The scale bars = 2 cm.

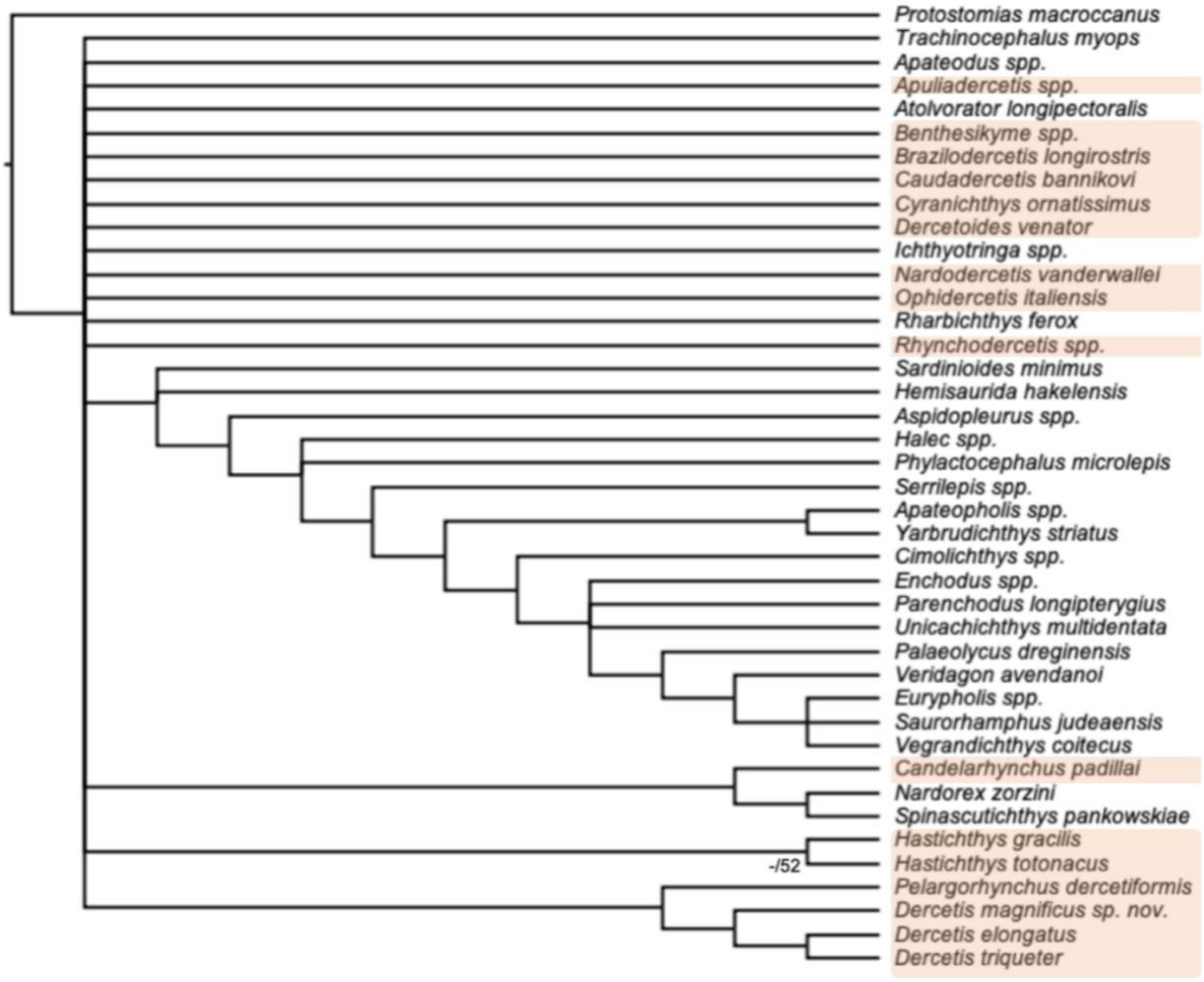

FIGURE 2-10. The results of phylogenetic analysis (A) of the enchodontoids with *Dercetis magnificus* sp. nov. Three outgroups (*Protostomias*, *Sardinioides*, and *Trachinocephalus*) were used. The strict consensus of 12 most parsimonious trees (MPTs) of treelength 501 (CI = 0.1698, RI = 0.3818). Values at the node indicates Bremer/Bootstrap (>50%) values. Taxa that previously have been assigned to Dercetidae are highlighted in color.

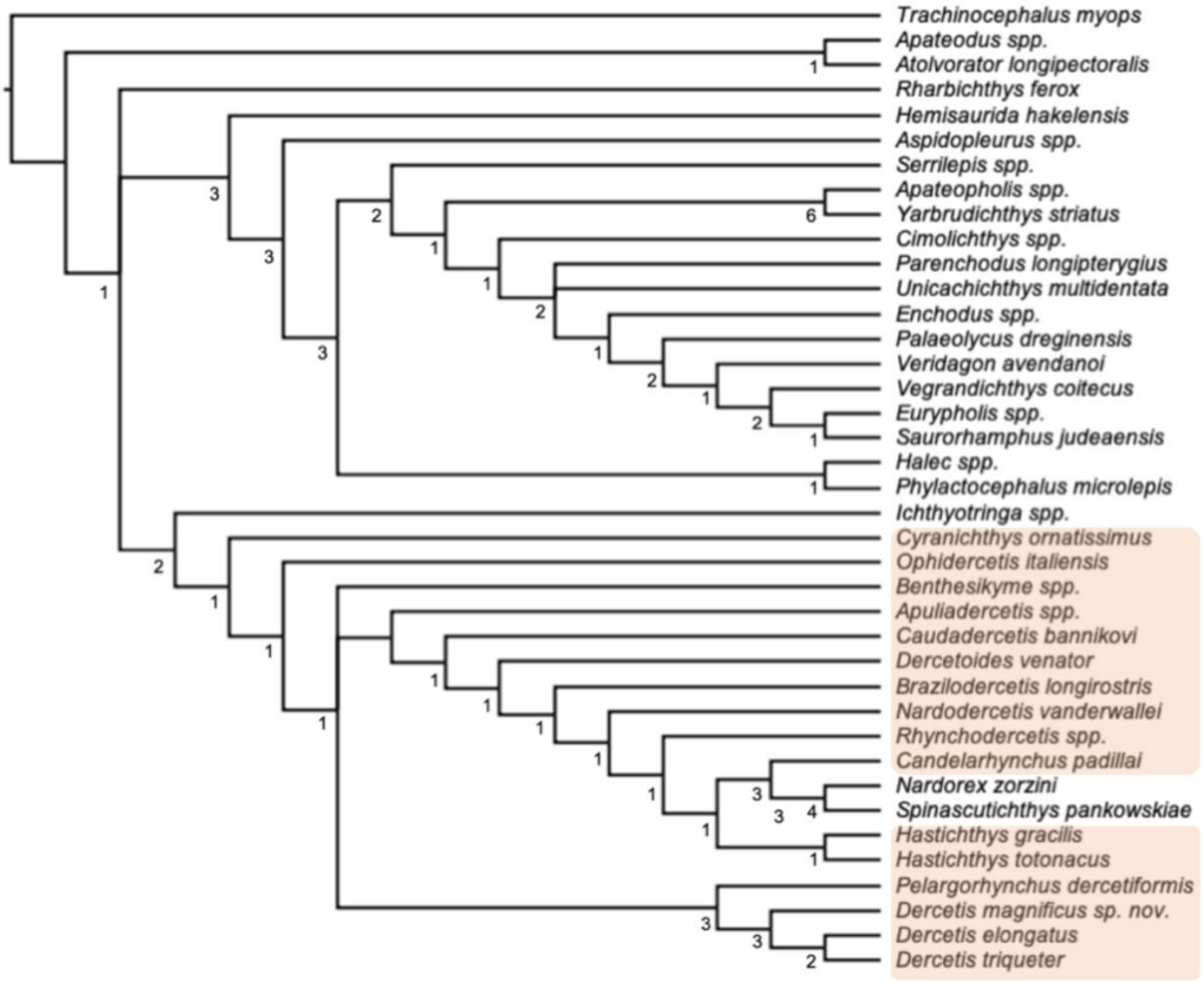

FIGURE 2-11. The result of phylogenetic analysis (B) of the enchodontoids with *Dercetis magnificus* sp. nov. A single outgroup (*Trachinocephalus*) was used. The strict consensus of 2 most parsimonious trees (MPTs) of treelength 469 (CI = 0.2229, RI = 0.5313). Values at the node indicates Bremer/Bootstrap (>50%) values. Taxa that previously have been assigned to Dercetidae are highlighted in color.

Chapter 3: Phylogeny of the Enchodontoidei

3.1 Introduction

Enchodontoids have been studied by many authors since the early 20th century (e.g. Woodward, 1901; Berg, 1940; Arambourg, 1954; Goody, 1969), although most of these studies focused on descriptive work with only a few on phylogenetic relationships until recently. The placement of the group within the wider diversity of teleosts was often based on the overall similarities of the body form and the skull morphology and this resulted in many different assignments of the group by different authors. For example, Woodward (1901, 1903) suggested a potential relationship between his family Enchodontidae, such as *Apateodus* and *Enchodus*, and the living alepisaurids, such as lancetfish (*Alepisaurus*) and sabertooth fish (*Evermannella*), but he considered the family Dercetidae to be related to the living members of Notacanthiformes (deep-sea eel-shaped fishes) rather than to alepisaurid fishes. In contrast, Goody (1969) placed all the enchodontoid fishes in the order Salmoniformes based on superficial morphological features, such as an elongate body and a toothed maxilla. Although both studies included detailed descriptive work, the taxonomy was not based on the synapomorphies and was not explicitly tested.

Rosen (1973) first attempted to examine the phylogenetic relationships of enchodontoids with extant members of the Aulopiformes, the order he erected in the same work (Rosen, 1973), and placed fifteen fossil taxa (*Ichthyotringa, Apadeodus, Apateopholis, Cimolichthys, Dercetis, Rhynchodercetis, Pelargochynchus, 'Prionolepis', Enchodus, Palaeolucus, Eurypholis, Saurorhamphus, Halec, Phylactocephalus, Hemisaurida*) as basal members of his suborder Alepisauroidei, alongside the extant superfamilies Alepisauroidea and Synodontoidea [although the current understanding of the Alepisauroidei does not include Rosen's (1973) Synodontoidea except the family Giganturidae (Davis, 2010; Nelson, 2016)]. Rosen (1973) also proposed that two other *incertae sedis* taxa, *Sardinius* and *Volcichthys*, were primitive members of his Synodontoidea. The 59 character states Rosen constructed (1973:tables 1-4) were based on Goody's (1969) work and were used to summarize the features of fifteen enchodontoids, but no parsimony analysis was performed nor were the relationships tested (Rosen, 1973:tables 1-4).

Several subsequent phylogenetic studies of Aulopiformes mainly focused on the extant taxa. Baldwin and Johnson (1996) conducted a comprehensive parsimony analysis of 43 extant aulopiform genera with 118 morphological characters that included the detailed features of the branchial arches and supported monophyly of the order. The monophyly of the Aulopiformes was also supported by Sato and Nakabo (2002) who integrated the previous studies of extant aulopiforms (e.g., Johnson, 1982; Okiyama, 1984, 1988; Baldwin and Johnson, 1996) and tested their relationships with a modified dataset containing 101 characters. Finally, Davis (2010) performed a molecular and total evidence analysis with 139 morphological characters from the previous studies and DNA data, and suggested that monophyly of the Aulopiformes was strongly supported. In this thesis, I use the classification of Nelson et al. (2016), which follows the analysis of Davis (2010), for the interrelationships among the extant families.

The systematics of the extinct taxa, on the other hand, were discussed by several authors, but many studies focused on limited numbers of species or groups (Chalifa, 1989a, b; Taverne, 1991; Fielitz, 2004; Gallo et al., 2005). Chalifa (1989a) described two genera, *Yabrudichthys* and *Serrilepis*, and placed them in the Enchodontoidei based on several synapomorphies, such as a long, strut-like maxilla and reduced supramaxilla, although this placement was not tested. Chalifa (1989b) also examined the family Dercetidae from the phylogenetic point of view with the proposed interrelationships of four genera (*Dercetis*, *Pelargorhynchus*, *Dercetoides*, *Rhynchodercetis*) based on fifteen characters. Taverne (1991) followed Chalifa's (1989) study and constructed 33 'primitive' characters and 40 derived character states to determine dercetid phylogeny. Neither Chalifa (1989b) nor Taverne (1991) performed a parsimony analysis, but the characters they constructed were carried over in later phylogenetic studies.

Gallo et al. (2005) first attempted a parsimony analysis of the Dercetidae with new and modified characters from Chalifa (1989b) and Taverne (1991). A total of 52 characters and thirteen genera (six non-dercetids and seven dercetids) were used to test the monophyly of the Dercetidae, which was supported by two synapomorphies, absence of the opercular ridge and reduced neural spines (Gallo et al., 2005). However, they included a limited number of other enchodontoid fishes because the main focus of the study was the phylogenetic position of the Dercetidae.

Fielitz (2004) conducted a parsimony analysis to investigate the phylogenetic position of the family Enchodontidae within the extant aulopiform fishes. He used fifteen enchodontoid species and eight species of extant aulopiforms with two extant outgroups (Fielitz, 2004). The 87 morphological characters he used were constructed based either on those of Baldwin and Johnson (1996) or Fielitz (1999). The results suggested that the enchodontoids (*Cimolichthys* + Enchodontidae *sensu* Fielitz (2004)) had a sister relationship with alepisaurid fishes (*Alepisaurus* and *Omosudis*), supporting the alepisaurid-enchodontoid hypothesis proposed by Woodward (1901) and Rosen (1973). However, none of the members of the Dercetidae was included in this study, and thus only the families Enchodontidae and *Cimolichthys* are currently placed in the superfamily Alepisauroidea (Nelson et al., 2016).

A more inclusive parsimony analysis of enchodontoids was attempted by Silva and Gallo (2011). Their study included 33 enchodontoid genera with three outgroups (the possible stomiiform *Protostomias*, the probable myctophiform *Sardinioides*, and the aulopiform *Trachinocephalus*) and used 87 characters, of which 21 were new and 66 modified from Chalifa (1989b), Taverne (1991), Baldwin and Johnson (1996), Fielitz (2004), and Gallo et al. (2005). Enchodontoidei was recovered as a paraphyletic group, although the monophyly of the family Enchodontidae was supported by a single synapomorphy, the presence of middorsal scutes, and the family Dercetidae was also supported by a single synapomorphy, reduced neural spines (Silva and Gallo, 2011).

Beckett et al. (2017) conducted comparative studies based on the gill morphology of some enchodontoids and various extant species, and placed some enchodontoids into different extant groups, although the number of examined extinct species was limited to six taxa. They placed the genera *Halec* and *Apateodus* in the suborder Alepisauroidei, with *Halec* assigned to the family Alepisauridae and *Apateodus* to the family Paralepididae (Beckett et al., 2017). However, the gill structure is often not preserved in the fossil record, and they did not include major enchodontoid families such as Enchodontidae and Dercetidae. They also did not used the matrix from Silva and Gallo (2011) and some later studies, so the monophyly of the Enchodontoidei was not tested (Beckett et al., 2017).

Based on the character matrix constructed by Silva and Gallo (2011), six more taxa were added with several new discoveries (Díaz-Cruz et al., 2016; Vernygora et al., 2017; Díaz-Cruz et al., 2019a, b, 2020a; Alvarado-Ortega and Díaz-Cruz, 2020; Murray et al., 2022). In the most recent study by Murray et al. (2022), the monophyly of the Enchodontoidei was not tested, but the interrelationships among the 36 extinct taxa were examined. Their analysis did not even recover a monophyletic Dercetidae, and the family Enchodontidae was only weakly supported, without any unambiguous synapomorphies (Murray et al., 2022). In this chapter, I will assess the characters of the existing matrix and test the monophyly of the Enchodontoidei and Dercetidae.

3.2 Materials and Methods

I will perform two analyses to compare the results generated from a single matrix before and after modifications have been applied. The first analysis is done by using the matrix without any modification of characters and character states. The second analysis is done by using the matrix following modification of some characters and character states.

The characters assessed are those used in the most updated matrix (Murray et al., 2022; see Appendix B.1), consisting of 87 morphological characters originally used by Silva and Gallo (2011). The modified character matrix was constructed with Mesquite ver. 3.6 (Maddison and Maddison, 2018). Characters were coded for each taxon based on descriptions from the literature and personal observation. All characters are unordered and of equal weight.

A total of 39 ingroup taxa are included in the modified matrix. The additional taxa in this study are the new species described in Chapter 2 and the genus *Stratodus*, which was excluded from previous studies. The coding of *Stratodus* is based on SDSM 81334, comprising a partial skull and nearly complete postcranial skeleton. Following Chapter 2, the genus *Dercetis* is coded as two separate species, *D. elongatus* and *D. triqueter*.

The extant aulopiform *Trachinocephalus* (Synodontoidei) is used as an outgroup. Moreover, two more extant aulopiforms, *Lestidium* (Alepisauroidei), and *Lestrolepis* (Alepisauroidei), are added to test the relationships of extinct and extant Aulopiformes. Specimens of those two additional taxa were borrowed from the Kanagawa Prefectural Museum of Natural History, Kanagawa, Japan (*Lestidium prolixum*—KPM-NI 65354/65355, *Lestrolepis japonica*— KPM-NI 65352/65353) and cleared and stained following the protocol of Taylor and Van Dyke (1985).

Both previously included extinct outgroup taxa, *Protostomias* and *Sardinioides*, have histories controversial taxonomic histories. The genus *Protostomias* was traditionally classified in the Stomiiformes (Arambourg, 1954). Fink (1985) proposed the exclusion of this genus from the Stomiiformes and suggested more systematic work was needed, whereas later Taverne (1992) revised the description of *Protostomias* and retained the genus in the Stomiiformes. On the other hand, the placement of the genus *Sardinioides* is a bit more complicated. *Sardinioides* includes several species reported from Germany, UK, and Lebanon, and the species included in the previous studies are the Lebanese species, *S. minimus*, described and placed in Myctophiformes by Goody (1969). Other German and British species were also assigned to Myctophiformes until Beckett (2017) placed the British species, *S. illustrans*, in the Aulopiformes based on the synapomorphy found on the gill arch. Rosen (1973) did not assign *S. minimus* (*Cassandra minimus*) in his comparative study, and thus, the placement of *S. minimus* is not fully understood. Therefore, here I only use probable stomiiform *Protostomias* for the extinct outgroup taxon.

A maximum parsimony analysis was performed in TNT 1.5 (Goloboff and Catalano, 2016). The most parsimonious trees were recovered from an heuristic (traditional) search using the tree bisection and reconnection (TBR) swapping algorithm with 1 random seed per 1000 replicates. All of the most parsimonious trees were used to form the strict consensus tree. The consistency index (CI) and retention index (RI) were calculated in Mesquite ver. 3.6 (Maddison and Maddison, 2018). Bootstrap and Bremer support values were calculated in TNT 1.5 (Goloboff and Catalano, 2016).

3.3 Character assessment

The existing character matrix (Appendix B.1) comprises 87 characters from seven different studies (Chalifa, 1989b; Taverne, 1991; Baldwin and Johnson, 1996; Fielitz, 2004; Gallo et al., 2005; Silva and Gallo, 2011). The original source of each character is indicated for reference. The 87 characters were modified and integrated by Silva and Gallo (2011), and the character coding of most of taxa were also done by Silva and Gallo (2011) except the taxa added later (Díaz-Cruz et al., 2016; Vernygora et al., 2017; Díaz-Cruz et al., 2019a, b, 2020a; Alvarado-Ortega and Díaz-Cruz, 2020; Murray et al., 2022).

3.3.1 Review and comments on each character

Character 1: Body length: (Chalifa, 1989b; modified by Gallo et al., 2005)

Body length was used as a classic diagnosis for the Dercetidae that typically have a very elongate body (Woodward, 1901). Chalifa (1989b) divided the body length into two conditions, very elongate and slightly elongate, to distinguish Dercetidae from *Cimolichthys* and '*Prionolepis*,' and Gallo et al. (2005) later proposed three conditions based on the ratio between the depth and the length of the body [0: slightly elongate— body depth to length ratio less than or equal to 1:10; 1: elongate—from 1:11 to 1:15; 2: very elongate—higher than 1:15]. However, the proportion of the head to standard length is not considered here, although it varies among taxa that share the same body length states. For example, both *Ichthyotringa* and *Palaeolycus* are coded as having an elongate body [1: ratio 1.11 to 1.15], but the head length of *Ichthyotringa* is more than one-third standard length (Taverne, 2006; Fielitz and González-Rodríguez, 2008), whereas the head length of *Palaeolycus* is less than one-third of standard length (von der Marck, 1863). Therefore, the character of the ratio between the body depth and length may contain taxa that possess different head to body proportion. I do not modify this character here because I focus on monophyly of Enchodontoidei and Dercetidae in this thesis, and I do not have access the measure the body proportion of each taxon.

Character 2: Head height (Chalifa, 1989b; modified by Gallo et al., 2005)

The head height, in other words, head depth, was often considered together with the head length, and the taxa with elongate heads have often been described as having a shallow head (e.g., Woodward, 1901; Goody, 1969). Chalifa (1989b) thought the shallow head is seen in dercetids, *Cimilichthys*, and '*Prionolepis*,' whereas Gallo et al. (2005) defined a low head ([1] the head length more than four times of the greatest height of the head) and a deep head ([0] the head length four times or less than the greatest height of the head), and both *Cimilichthys*, and '*Prionolepis*'(=*Aspidopleurus*) were coded as having state 0 [deep head]. From this definition by Gallo et al. (2005), all dercetids, *Ichthyotringa*, *Saurorhamphus*, and *Spinascutichthys* possess state 1 [low head]. *Vegrandichthys*, a long-snouted enchodontoid, was coded as state 1 [low head] in the existing matrix, but the head depth is less than four times head length (Díaz-Cruz et al., 2020a), and so this taxon should be coded as state [deep head] according to the definitions of Gallo et al. (2005).

Character 3: Snout length (Taverne, 1991; modified in Gallo et al., 2005)

A very elongate snout was thought to be the plesiomorphic condition for dercetids by Taverne (1991). Gallo et al. (2005) delimited the long snout as being two times or longer than the length of the orbit. The long snout is seen in all dercetids, several enchodontoids, and some extant members (*Lestidium* and *Lestrolepis*) in this study. However, the proportion of the snout length (= preorbital length) to the head length was not considered by Gallo et al. (2005). I leave this character with current definition by Gallo et al. (2005) until I have access to actual specimens of each taxon for measuring the preorbital length.

Character 4: Dermal pattern on skull roof (Gallo et al., 2005)

The presence of ornamentation on the skull roof was noted by several authors (e.g., Goody, 1969; Chalifa, 1989b), but it was not considered from the phylogenetic point of view. Taverne (2006) recognized the smooth condition of the dermal bones is the plesiomorphic state of enchodontoids. Gallo et al. (2005) divided the character into four states [0: smooth; 1: only with tubercles; 2: only with ridges; 3: tubercles + ridges] but found that the ornamentation pattern did not define any clade. The pattern can also vary within the same genus, for example, *Dercetis triqueter* has state 1 [only with tubercles], whereas *D. elongatus* and *D. magnificus sp. nov.* show state 3 [tubercles + ridges]. Gallo et al. (2005) presumably followed Fielitz (2004) for constructing multiple states for ornamentation of the dermal bones, but these were later simplified to either ‘smooth’ or ‘ornamented’ for other dermal bones by Silva and Gallo (2011). Here, I will modify this character state from four states [0: smooth; 1: only with tubercles; 2: only with ridges; 3: tubercles + ridges] to two states [0: smooth; 1: ornamented] to make it consistent with character states of other dermal bones.

Character 5: Vomerine teeth (Fielitz, 2004)

Fielitz (2004) pointed out that vomerine teeth are found in *Cimolichthys* and *Eurypholis*. Taverne (2006) found large teeth on the vomer in *Ichthyotringa* (although this taxon was coded as [0: absent] in the preexisting matrix), and several newly discovered genera of enchodontoids, such as *Apuliadercetis*, *Aspidopleurus, Nardorex*, and *Unicachichthys*, were also confirmed to possess vomerine teeth (Taverne, 2004; Alvarado-Ortega and Porras-Múzquiz, 2012; Díaz-Cruz et al., 2016, 2021).

Character 6: Number of teeth on dermopalatine (Fielitz, 2004)

Having a single dermopalatine tooth [coded as 2: single] was considered a synapomorphy of the family Enchodontidae (*seusu* Fielitz (2004), including *Enchodus, Eurypholis, Parenchodus, Rharbichthys, Saurorhamphus*), but later studies showed this character does not support the clade as currently constituted (Silva and Gallo, 2011; Díaz-Cruz et al., 2016). Only *Spinascutichthys* and *Yabrudichthys* were confirmed to be lacking the palatal teeth [state 1: none], whereas most of the other enchodontoids possess multiple teeth on the palatine [state 0: two or more].

Character 7: Dermopalatine length (Fielitz, 2004)

This character was also constructed by Fielitz (2004) to define his Enchodontidae with two states [0: at least twice as long relative to the longest dermopalatine tooth; 1: as long as or shorter than the longest dermopalatine tooth]. Silva and Gallo (2011) rephrased these states as [0: twice or more times longer than its tooth; 1: equal-sized or shorter than its tooth], although the meaning of the character is the same. *Enchodus, Eurypholis, Rharbichthys,* and *Saurorhamphus* possess state [1], and irregularly, *Ophidercetis*, a member of Dercetidae, is also coded as state [1]. However, the preservation of the palatine in *Ophidercetis* (depicted in Taverne, 2005a: fig. 4) is not good compared to other species, such as *Enchodus* and *Eurypholis*, and the character coding of *Ophidercetis* by Silva and Gallo (2011) is not based on the actual observation, so more specimens of *Ophidercetis* and will be needed to truly confirm the length of the dermopalatine.

Character 8: Antorbital (Silva and Gallo, 2011)

The presence of the antorbital was confirmed in *Atolvorator, Candelarhynchus, Serrilepis,* and *Phylactocephalus* among the ingroup taxa, but most of the other members are coded as missing data. This character varies among the extant aulopiforms according to previous studies (Rosen, 1973; Johnson et al., 1996; Sato and Nakabo, 2002) and among the outgroup taxa in this study (*Trachinocephalus* [0: present]; *Lestidium* and *Lestrolepis* [1: absent]).

Character 9: Nasal (Silva and Gallo, 2011)

The presence of the nasal [0] is confirmed only in a few ingroup taxa*, Brazilodercetis, Hastichthys, Ophidercetis,Rharbichthys, Rhynchodercetis,* and *Veridagon*. Other taxa are either lacking the nasal [state 1] or missing data. *Atolvorator* is also coded as missing data, although the original description of the holotype noted the presence of the nasal (Gallo and Coelho, 2008).

Character 10: Anterior extremity of mesethmoid (Taverne 1991)

The morphology of the anterior extremity of the mesethmoid was used to define the primitive and derived condition in dercetids by Taverne (1991). He thought the bifurcated anterior end, seen in *Dercetis*, was the primitive state, whereas the other dercetids have an acute anterior end of the mesethmoid (Taverne, 1991). Gallo et al. (2005) pointed out that the bifurcated anterior end is an autapomorphy of *Dercetis*, whereas Silva and Gallo (2011) found this state in the probable myctophiform *Sardinioides* and *Nardorex* as well as *Dercetis* and suggested that this is the homoplastic condition. Comparing those three taxa, the mesethmoid is a rod-like, long bone in *Dercetis*, whereas *Sardinioides* and *Nardrex* have a broad and short bone, with the lateral expansion thickened ventrally in *Sardinioides* (Goody, 1969; Taverne, 2004, 2005a) although the end is bifurcated in all of these taxa. Thus, the homology of the anterior bifurcation of the mesethmoid is questionable and could have evolved separately in each taxon.

Character 11: Posterior extremity of mesethmoid (Taverne, 1991; modified by Silva and Gallo, 2011)

The bifurcation of the posterior end of the mesethmoid was also thought by Taverne (1991) to be the derived condition in dercetids. Primitive dercetids and other enchodontoids possess a mesethmoid with a simple, acute posterior end, so this character was divided into two conditions (states): acute or bifid. Silva and Gallo (2011) modified the character into three states [bifid (0); acute (1); straight (2)] without coding the last state [straight (2)] in any taxon. The only genus tentatively coded as [straight (2)] is *Spinascutichthys*, coded by Murray et al. (2022), but this was a tentative coding because the posterior end of the mesethmoid of *Spinascutichthys* is neither acute nor bifid. The state [straight (2)] was not fully explained when it was modified by Silva and Gallo (2011), and the reason why Taverne (1991) created this character was to highlight the bifid condition in derived dercetids. *Cimolichthys* and *Phylactocephalus* also possess a bifurcated posterior end of the mesethmoid, although they are not considered members of Dercetidae (Goody, 1969).

Character 12: Autosphenotic spine (Gallo et al., 2005)

Gallo et al. (2005) created two states [0: straight; 1: posteriorly curved] for the morphology of the spine on the autosphenotic, and found the posteriorly curved autosphenotic spine to be a synapomorphy uniting two genera, *Rhynchodercetis* and *Hastichthys*. Currently, this state is also found in *Atolvorator* and *Spinascutichthys* (Silva and Gallo, 2011; Murray et al., 2022).

Character 13: Suture between frontals (Silva and Gallo, 2011)

The suture between the right and left frontals are markedly sinuous [state 1] in some taxa, such as *Apateodus* and *Atolvorator*, and slightly sinuous [state 0] in many other taxa (Silva and Gallo, 2011). However, this character was not clearly explained by those authors when they added it to the matrix, and the delimitation of the states is subjective.

Character 14: Posterior border of frontal (Gallo et al., 2005)

Gallo et al. (2005) created two states for the level reached by the posterior extent of the frontal [0: behind the autosphenotic spine; 1: at the level of the autosphenotic spine] and coded *Dercetoides* and *Hastichthys* as state [1]. However, they also mentioned *Ichthyotringa* is polymorphic, possessing both states within the genus (Gallo et al., 2005). Also, in later studies *Hastichthys* was re-coded as state [0] (Vernygora et al., 2017; Alvarado-Ortega Díaz-Cruz, 2020), and this character no longer supports any clade.

Character 15: Shape of the posterior border of the orbit (Gallo et al., 2005)

A concave post-orbital border [state 0] is found in most of the taxa, whereas a convex post-orbital border [state 1] is found only in a few taxa, *Apuliadercetis, Ichthyotringa, Nardorex, Rhynchodercetis* and *Hastichthys*. The definition of the states was not fully explained by Gallo et al. (2005), but they coded state 1 [convex post-orbital border] in *Ichthyotringa* and *Rhynchodercetis*, of which their posterior border of the orbit appears to be concave due to the anteiorly projected sphenotic (e.g. *Ichthyotringa africana* in Taverne (2006:fig 3)).

16. Parietal length (Taverne, 1991, modified in Gallo et al., 2005)

The length of the parietal has been described with two states [0: long (length equal or larger than its height); 1: short (length smaller than its height)] proposed by Gallo et al. (2005). Originally, Taverne (1991) considered the long parietal to be the primitive state, but Gallo et al. (2005) suggested that the long parietal is found in more derived taxa.

17. Supraorbital sensory canal in the skull roof (Fielitz, 2004)

Silva and Gallo (2011) noted this character was used by Fielitz (2004), but I found it was not discussed in Fielitz (2004) but instead was described in some taxa by Goody (1969). Only six ingroup taxa (*Atolvorator, Aspidopleurus, Eurypholis, Parenchodus, Unicachichthys,* and *Saurorhampus*) possess an exposed supraorbital sensory canal [state 1], and other taxa have the supraorbital sensory canal enclosed in the frontal bone [state 0].

18. Extension of the supraoccipital (Gallo et al., 2005)

The supraoccipital is a single median bone behind the skull roof forming the mid-dorsal part of the occiput. A supraoccipital that does not separate the parietals [state 0] is described as the medio-parietal condition, whereas the supraoccipital separating the left and right parietals forms a latero-parietal skull (Rosen, 1973; Taverne, 1991). Taverne (1991) suggested that the medio-parietal condition might be the primitive state among dercetids, but recent finds show variation within the dercetids, such as *Scandiadercetis* having an intermediate condition of the parietals that are separated by the supraoccipital in the posterior half but meet one another in the midline in the anterior half (Taverne, 2005a), although *Scandiadercetis* was not included in this study because of the incomplete nature of the specimen.

19. Supraoccipital crest (Taverne, 1991)

A distinct crest on the supraoccipital is absent [state 1] in a few taxa (*Pelargorhynchus, Rharbichthys, Unicachichthys,* and *Spinascutichthys*). *Benthesykime* was also coded as [state 1: absent] in the preexisting study, but Taverne (1991) noted this genus is primitive among dercetids and shares the plesiomorphic state of the supraoccipital crest, which is present [state 0]. I leave *Benthesykime* as the preexisting state [1] until I have access to the actual specimens.

20. Supraoccipital with two well-delimited regions (Silva and Gallo, 2011)

The unique morphology of the supraoccipital which is divided into anterior and posterior regions forming two clearly delimited regions is only present in *Nardorex* (Taverne, 2004). Currently, the state [1: present] is an autapomorphy of *Nardorex* and, therefore, is not useful to find relationships among the enchodontoids.

21. Extension of pterotic (Chalifa, 1989b)

Chalifa (1989b) believed the projection of the pterotic beyond the occiput [state 1] to be a synapomorphy of some derived dercetids. However, the extended pterotic is found in many ingroup taxa not just dercetids. Most of the dercetid taxa possess state [1], except *Candelarhynchus* and *Nardodercetis*, in which the pterotic is not projecting beyond the occiput [state 0], so the extended pterotic may be a plesiomorphic state for dercetids with some taxa having a reversal.

22. Dilatator fossa (Silva and Gallo, 2011)

The dilatator fossa, a shallow concavity on the skull roof for muscle attachment, is formed by the sphenotic, pterotic and frontal bones. Silva and Gallo (2011) created two states [0: unroofed; 1: roofed] but without giving a full description. Goody (1969: figs. 21, 32, 34, 37 etc.) depicted the dilatator fossa in his figures, but the states also were not fully described. *Cimolichthys, Candelarhynchus, Phylactocephalus, Vegrandichthys,* and *Spinascutichthys* have state [1], although none of them are united by this character. Many ingroup taxa are coded as missing data for this character because of the preservation of the fossil material.

23. Exposition of the post-temporal fossa (Chalifa, 1989b; modified in Gallo et al., 2005; Silva and Gallo, 2011)

The posttemporal fossa can be covered by the pterotic and epiotic bones [0: roofed] or exposed dorsally on the pterotic [1: unroofed]. Gallo et al. (2005) created three states [0: roofed; 1: partially roofed; 2: unroofed] because *Cimolichthys* exhibits an intermediate condition [1: partially roofed] based on Goody's (1969) description. Later, Silva and Gallo (2011) excluded the intermediate state from this character and coded *Cimolichthys* as state 0 [roofed] . Taverne (1991) argued that the roofed posttemporal fossa is the primitive condition in dercetids.

24. Orbitosphenoid (Taverne, 1991)

The orbitoshenoid is a small, median bone that separates the two orbits and was thought to be absent in enchodontoids by Rosen (1973). However, currently seven taxa are coded as having the orbitosphenoid present [state 1], although many other taxa are coded as missing data due to the fragmentary condition of the specimens. Taverne (1991) argued that the absence of the orbitosphenoid is primitive in dercetids.

25. Basisphenoid (Taverne, 1991)

The basisphenoid is a single, median endochondral bone forming a part of the floor of a braincase and is present in most teleosts with a few exceptions (Arratia, 1997). The presence of the basisphenoid [state 0] is only found in a few dercetids (*Apuliadercetis, Candelarhynchus*, and *Hastichthys*), as well as *Ichthyotringa*, and *Atolvorator* in the ingroup. Many other taxa are coded as missing data for this character, which is difficult to determine in fossil material.

26. Supraorbital (Chalifa, 1989b)

The supraorbital bones are present [state 0] in five of the ingroup taxa (*Apateodus, Atolvorator, Cimolichthys, Halec*, and *Serrilepis*), whereas most of the other taxa show an absence of the supraorbitals [state 1]. Chalifa (1989b) thought the absence [state 1] was the plesiomorphic state in dercetids, and the existing phylogeny agrees with this.

27. Lachrymal shape (Gallo et al., 2005; modified in Silva and Gallo, 2011)

The character for the shape of the lacrimal (lachrymal, or first infraorbital) was first added to the phylogenetic study by Gallo et al. (2005). They created two states [0: trapezoidal; 1: rod-shaped] with only *Brazilodercetis* coded as [1] and only two taxa, *Eurypholis* and *Saurorhamphus*, coded as [0]. All other taxa in their study were coded as missing data due to the poor preservation of the lacrimal. Later, Silva and Gallo (2011) added two more states and analyzed the character with a total of four states [0: subtriangular; 1: suboval; 2: trapezoidal; 3: rod-shaped]. In the ingroup taxa, the subtriangular shape [0] is seen in *Spinascutichthys* and *Serrilepis*, and the suboval shape [1] is only seen in *Hastichthys*. The rod-shaped lacrimal is found in *Apuliadercetis*, *Brazilodercetis*, and *Nardorex*, although they do not form a clade. Alvarado-Ortega and Díaz-Cruz (2020) modified state for *Candelarhynchus* to ‘not applicable’, but *Candelarhynchus* possesses a lacrimal (= infraorbital 1), and I agree with Vernygora et al. (2017) that the shape is trapezoidal [state 2]. Arratia (1997) noted that most teleosts have an infraorbital 1 that is broader than infraorbital 2, with the exception of Osteoglossomorpha which has a tube-like narrow infraorbital 1. Thus, the broader lacrimal (e.g. state 1 [subtriangular]; state 2 [trapezoidal] could be a plesiomorphic state, although the homology of each shape is questionable. I leave this character as preexisting states because many ingroup taxa are coded as missing data due to the lack of preservation and wait modifying the states until additional specimens with better preserved lacrimal are found.

28. Position of the mandibular suspensorium (Gallo et al., 2005; modified by Silva and Gallo, 2011)

In most of the ingroup taxa, the mandibular suspensorium is positioned vertically [state 1]. An anteriorly inclined suspensorium is found in some dercetids and some non-dercetid taxa. The inclination of the hyomandibular varies among the extant aulopiforms, with some taxa having the hyomandibular rotated and lying almost parallel to the body axis (Baldwin and Johnson, 1996). This rotation is accompanying with an elongation of the ectopterygoid and reduction of the endopterygoid (Sulak, 1977; Baldwin and Johnson, 1996). Thus, the orientation of the suspensorium in the extinct taxa could also be related to the nature of several bones in the suspensorium, which I cannot determine here because of the limited access to each taxon.

29. Ectopterygoid (Taverne, 1991)

The ectopterygoid is toothed [state 1] in almost all ingroup taxa except some dercetids. Taverne (2006) noted that the presence of the ectopterygoid teeth to be a plesiomorphic state for enchodontoids and extant alepisauroids do no possess the extopterygoid teeth [state 0]. There are a few extant aulopiform taxa, such as synodontoids, that possess ectopterygoid teeth, but most of other genera have lost the ectopterygoid teeth (Baldwin and Johnson, 1996). Some dercetids (*Apuliadercetis*, *Brazilodercetis*. *Dercetoides*, and *Nardodercetis*) and *Yabrudichthys* are coded as state 0 [ectpterygoid toothless], whereas most of the ingroup taxa are coded as state 1 [ectopterygoid toothed].

30. Endopterygoid (Taverne, 1991)

The endopterygoid (= entopterygoid) is toothed [state 1] in many non-dercetid taxa. Among dercetids, *Benthesykime, Dercetis, Ophidercetis*, and *Hastichthys* have teeth on the endopterygoid. In *Cimolichthys* and *Dercetis*, the teeth are tiny and form a large tooth plate

(Goody, 1969). Numerous small teeth are also found on the endopterygoid in *Enchodus*, although the bone is narrower than that of *Cimolichthys* and *Dercetis* (Fielitz, 2002). In extant aulopiforms, the presence of endopterygoid teeth is also limited to a few taxa, and the majority of other members lack endopterygoid teeth (Baldwin and Johnson, 1996).

31. Placement of articular facet for the hyomandibula (Fielitz, 2004)

Fielitz (2004) found that the facet on the skull roof for articulation of the hyomandibular is ventral to the dilatator fossa [state 1] in *Eurypholis, Saurorhamphus*, and one species of *Enchodus* (*E. gracilis*), whereas the facet is posteroventral to the dilatator fossa in *Cimolichthys* and other species of *Enchodus* (e.g., *E. petrosus* and *E. gladiolus*). There are more taxa that possess the ventrally oriented facet in the current matrix, but this character can be polymorphic within a genus, as shown by the species of *Enchodus* (Fielitz, 2004).

32. Number of articular facets for the hyomandibula (Silva and Gallo, 2011)

Silva and Gallo (2011) divided the number of articular facets into two states [0: a continuous facet; 1: two facets]. A continuous facet [state 0] is seen in all dercetids except a few taxa which are coded as missing data.

33. Premaxilla (Taverne, 1991)

The premaxilla is toothed [state 0] in almost all taxa except some dercetids and *Spinascutichthys*. Taverne (1991) considered the presence of teeth [state 0] to be the primitive condition in dercetids. In many extant aulopiforms, the premaxilla is the dominant tooth-bearing bone of the upper jaw (Baldwin and Johnson, 1996).

34. Posterior extension of the premaxilla (Gallo et al., 2005)

The premaxilla posteriorly reaches the orbit [state 0] in many non-dercetid taxa, whereas the premaxilla does not reach the orbit [state1] in most dercetids except *Pelargorhynchus*. Gallo et al. (2005) coded both *Dercetis* and *Pelargorhynchus* as having state [0: not reaching the orbit], but Silva and Gallo (2011) later re-coded the state in *Dercetis* to [1: reaching the orbit]. The premaxilla-orbit position of *Pelargorhynchus* was not discussed by Silva and Gallo (2011), so this species needs to be revisited to confirm the state because all other dercetid members have the opposite state [1].

35. Dermal pattern on premaxilla (Siva and Gallo, 2011)

The character of ornamentation of the premaxilla was added by Silva and Gallo (2001) with two states [0: smooth, 1: ornamented]. Many dercetids have a smooth [state 0] surface on the premaxilla except a few taxa (*Candelarhynchus, Hastichthys*, and *Pelargorhynchus*). *Dercetis* shows a polymorphic condition with *D. elongatus* having an ornamented premaxilla and *D. triqueter* having a smooth premaxilla. *Dercetis magnificus sp. nov.* also shows the premaxilla ornamented with multiple striations (Chapter 2). Thus, the presence or absence of ornamentation can show intrageneric variation.

36. Fenestra in the premaxilla (Siva and Gallo, 2011).

The fenestra in the anterior end of the premaxilla [state 1: present] is found in some enchodontids (*Enchodus, Eurypholis, Palaeolycus, Veridagon, Vegrandichthys,* and *Saurorhamphus*). *Atolvorator* is coded as missing data, although the original description of the holotype noted the possible fenestra on the premaxilla (Gallo and Coelho, 2008). No dercetids possess the premaxillary fenestra. In the extant members, the family Paralepididae (Alepisauroidei) shows the premaxilla with a fenestra, as seen in both *Lestidium* and *Lestrolepis* in this study.

37. Ascending process of the premaxilla (Siva and Gallo, 2011)

An ascending process on the anterior symphysial part of the premaxilla is present [state 1] in *Dercetis, Ophidercetis, Nardorex, Eurypholis, Parenchodus, Rharbichthys*, and *Unicachichthys*. *Apuliadercetis* was also coded as [1], but the newly discovered species (*A. gonzalezae*) appears to have the state [0: absent] (Díaz-Cruz et al., 2021). Taverne (1991) thought that the presence of the small ascending process on the premaxilla was the primitive condition in dercetids.

38. Maxillary teeth (Taverne, 1991)

Teeth present on the maxilla [state 1] is seen in most of the dercetids and many non-dercetids. The possible family Enchodontidae (*Enchodus, Parenchodus, Palaeolycus, Veridagon, Vegrandichthys, Unicachichthys,* and *Saurorhamphus*) have a toothless [0] maxilla. *Cimolichthys* was previously thought to have a toothless maxilla, but the recent study of the internal skull anatomy by Díaz-Cruz et al. (2020b) confirmed the presence of maxillary teeth in *Cimolichthys*.

39. Placement of the maxilla (Gallo et al., 2005)

A unique placement of the maxilla has been considered to be a synapomorphy of enchodontoids (Rosen, 1973; Nelson, 1994; Fielitz, 2004). Fieliz (2004) first attempted the phylogenetic study including the character of maxilla with three states [0: excluded from gape of jaw; 1: included in gape and is toothed; 2: included in gape, but teeth absent], and his analysis resulted in the state 2 [maxilla included in gape but lacking teeth] is a plesiomorphic condition in enchodontoids. However, he also found the reversion of the state from 2 [maxilla included in gape but lacking teeth] to the state 1 [maxilla included in gape and is toothed] and concluded that this character was not recodered as a unique and unreversed synapomorphy. Taverne (1991) also suggested that having a toothed maxilla included in the gape is the primitive condition in dercetids. Gallo et al. (2005) separated out the states of the maxillar being toothed or not and the placement of the maxilla; they created different states [0: position of maxilla over the premaxilla; 1: behind the premaxilla] without discussing the inclusion or exclusion of the maxilla from gape.

40. Teeth on upper jaw (Gallo et al., 2005; modified by Silva and Gallo, 2011)

Gallo et al. (2005) created three states for the condition of the upper jaw teeth [0: straight; 1: curved + straight; 2: curved] to distinguish *Brazilodercetis* with state [1] from other enchodontoids. Silva and Gallo (2011) added one more state and used a total of four states [0: only straight; 1: absent; 2: curved + straight; 3: only curved] because one of their outgroups, *Protostomias*, lacks upper jaw teeth. However, the delimitation of the character was not fully described by either Gallo et al. (2005) or Silva and Gallo (2011), and absence of the upper jaw teeth in *Protostomias* is redundant with the characters of absence of the premaxillary and maxillary teeth, causing triple weight of these characters in that taxon.

41. Supramaxilla (Chalifa, 1989b)

Chalifa (1989b) assumed that the absence of the supramaxilla [state 0] was a plesiomorphic state in dercetids. As presented by Chalifa (1989b), the supramaxilla is absent in all dercetids in the existing matrix. Absence of the supramaxilla was also confirmed in *Ichthyotringa* by Taverne (2006). Many non-dercetid taxa have a supramaxilla present [state 1]. Arratia (1997) noted that presence of the supramaxilla is a relatively advanced feature in actinopterygians, although it is lost in certain groups of teleosts. In extant aulopiforms, both conditions can be found with some having two supramaxillae and some having a reduced supramaxilla (Nelson et al., 2016).

42. Mandible length (Taverne, 1991)

Taverne (1991) argued that the mandible being shorter than the snout length [state 1] is the derived state in dercetids. A shorter mandible is seen in *Brazilodercetis, Candelarhynchus, Nardodercetis, Rhynchodercetis*, and *Hastichthys*, whereas all other taxa are coded as the mandible length equal to the snout length [state 0]. However, certain taxa, such as *Eurypholis*, and *Spinascutichthys*, possess a mandible that is actually longer than the snout (Goody, 1969; Murray et al., 2022; personal observation). *Saurorhamphus* and *Vegrandichthys* seem to have a mandible longer than the snout by the original descritions (Chalifa, 1985; Díaz-Cruz et al., 2020).

43. Teeth on mandible (Gallo et al., 2005)

Similar to the upper jaw teeth (character 40), Gallo et al. (2005) created three states for the condition of the mandibular teeth [0: only straight; 1: only curved; 2: curved + straight].

These states were also not fully explained by those authors, and this character does not support any clade.

44. Teeth size on upper jaw (Gallo et al., 2005; modified in Silva and Gallo, 2011)

This character was also created by Gallo et al. (2005) and was coded as state 1 [teeth of different height] only in '*Prionolepis*', *Cyranichthys*, and *Brazilodercetis*, with other taxa coded as having teeth of the same height [state 0]. Later, Silva and Gallo (2011) added the condition 'teeth absent' to state [0] such that state 0 became 'absent or with same height'. Again, this state is repetitive for *Protostomias* in which the upper jaw lacks teeth.

45. Teeth size on mandible (Gallo et al., 2005)

Teeth of varying height [state 0] are found in many non-dercetid taxa whereas many dercetids were coded to have teeth of similar height [state 1] in the preexisting matrix. The new species of *Apuliadercetis* shows the mandible with teeth of equal size and height [state 1] in contrast to the preexisting coding of this genus of Díaz-Cruz et al. (2021). *Cyranichthys* was coded as having state [0] in the preexisting matrix, but in fact, the mandible of this taxon is unknown (Casier, 1965). *Enchodus* is a typical example for state [1], with the large conical teeth placed in the inner row on the dentary and numerous small teeth located on the external margin of the dentary (Goody, 1969).

46. Rows of teeth on upper jaw (Gallo et al., 2005)

Only a few taxa in the ingroup, *Dercetis, Stratodus,* and *Aspidopleurus*, show two or more tooth rows [state 1] on the upper jaw. All other taxa possess a single row of teeth on the upper jaw [state 0]. *Dercetis* exhibits a polymorphic state within the genus, with *D. elongatus* having a single row, and *D. triqueter* and *D. magnificus sp. nov.* having multiple tooth rows. In extant aulopiforms, the synodontoid *Trachinocephalus* possesses numerous rows of teeth on the upper jaw. *Protostomias* lacks upper jaw teeth, and so cannot be coded for this character.

47. Rows of teeth on mandible (Gallo et al., 2005)

Unlike the upper jaw, number of tooth rows on the lower jaw show more variation. Many non-dercetid taxa have two or more rows of teeth [state 1]. *Eurypholis* was coded as state [0: single row], but *E. boisseieri* possesses two rows of mandibular teeth (Goody, 1969; personal observation). The specimen of *Stratodus* included in this study (SDSM 81334) does not preserve either lower jaw, but the holotype of *Stratodus* (AMNH 1753) shows multiple rows of teeth on the probable dentary so I coded as state 1 [two or more rows].

48. Anteroventral prongs on dentary (Fielitz, 2004)

The presence of anteroventral prongs on the dentary [state 1] was proposed by Fielitz (2004) to characterize *Enchodus, Eurypholis,* and *Saurorhamphus*, although *Eurypholis* and *Saurorhamphus* were coded as lacking the prongs [state 0] in later studies. Díaz-Cruz et al. (2016) suggested the presence of anteroventral prongs was a synapomorphy of the Enchodontidae including some additional taxa (*Unicachichthys* and *Parenchodus*), whereas the newly reported enchodontoid *Spinascutichthys* also possesses the anteroventral prongs but was not recovered as a member of the family Enchodontidae (Murray et al., 2022).

49. Mandibular sensory canal (Fielitz, 2004)

Fielitz (2004) divided the character of the mandibular sensory canal into three states [0: enclosed by bone; 1: partially open; 2: open] based on the extant synodontoid *Synodus* having state [0], the alepisauroid *Alepisaurus* with state [1], and *Enchodus* with state [2]. In the preexisting matrix, species of *Hastichthys* were coded in different ways within the genus, with *H. gracilis* having an open canal and *H. totonacus* having an enclosed canal. *Dercetis magnificus* sp. nov. shows state 1 [partially open], whereas other two species of *Dercetis* are coded as state 2 [open]. Thus, this character shows intergeneric variations in some genera. Also, *Enchodus* was coded as state [1: partially open] in the preexisting matrix, although the original study by Fielitz (2004) coded it as having state [2: open], and I agree with Fielitz (2004) by personal observation.

50. Mandibular dermal pattern (Fielitz, 2004; modified by Silva and Gallo, 2011)

Fielitz (2004) proposed four states for the mandibular dermal pattern [0: absent; 1: present as ridges; 2: present as ridges with tubercles; 3: present as tubercles]. Later, Silva and Gallo (2011) simplified the states into two states [0: smooth; 1: ornamented]. Many non-dercetid taxa show the presence of ornamentation on the mandible, whereas within Dercetidae, only *Dercetis, Dercetoides,* and *Pelargorhynchus* have the ornamentation. Moreover, *Dercetis* shows an intrageneric variation with *D. elongatus* and *D. magnificus sp. nov.* having ornamentation and *D. triqueter* having a smooth mandible.

51. Flange on anguloarticular (Gallo et al., 2005)

An anguloarticular flange is present [state 0] in most dercetids except *Hastichthys* and two species of *Dercetis*. In non-dercetid taxa, both presence [state 0] and absence [state 1] of the flange are found and both states are homoplastic.

52. Quadrate-mandibular articulation (Fielitz, 2004)

The character of the quadrate-mandibular articulation in *Eurypholis* and *Saurorhamphus* was noted by Goody (1969), and Fielitz (2004) incorporated the character in his phylogenetic study. Fielitz (2004) created two states [0: the articulation between the quadrate and mandible is visible in lateral view; 1: the articulation is hidden] and coded both *Eurypholis* and *Saurorhamphus* as having state [1]. However, this state is only shared by these two genera, and the hidden articulation is a result of the "vertical upgrowth of bone from the lateral face" of the anguloarticular (Goody, 1969:109, fig. 45). Arratia (1997) noted that a well-developed postarticular process in the lower jaw can be found in some basal teleosts (elopomorphs, osteoglossomorphs), so the development of the posterior portion of the anguloarticular in *Eurypholis* and *Saurorhamphus* noted by Goody (1969) might be a similar structure to Arratia's (1997) the developed postarticular process. If so, then the primitive state of this character might be presence of the process, i.e., a hidden quadrate-mandibular articulation.

53. Articular facet for the quadrate (Siva and Gallo, 2011)

Most dercetids have a shallow articular facet for the quadrate [state 0], whereas many non-dercetids possess a deep facet for the articulation [state 1]. This character was not fully explained by Silva and Gallo (2011) and the shallow articular facet can be the result of having a shallow head, because many shallow-headed taxa were coded as having state [0].

54. Retroarticular process (Goody, 1969)

This character was added by Silva and Gallo (2011) mentioning that it was adapted from Goody (1969). However, the definition of the retroarticular process was not fully explained by Silva and Gallo (2011). Based on the description of a retroarticular process used in Goody (1969), I assume this character indicates the process behind the articular condyle for the quadrate that curves around the condyle posteriorly. In the preexisting matrix, the retroarticular process is present [state 0] in most of the taxa except *Apateopholis, Cimolichthys, Candelarhynchus, Rhynchodercetis, Saurorhamphus*, and *Spinascutichthys*. In the previously known species of *Dercetis*, the retroarticular process is coded as 1 [absent] in the preexisting matrix, but the new species possesses a retroarticular process that curves behind the articular condyle. The absence of the retroarticular process can be an artifact due to the small size of the previously known species of *Dercetis* or intrageneric variation.

55. Ornamentation of the infraorbital bones (Siva and Gallo, 2011)

The infraorbital bones are not preserved in all taxa, but they are ornamented [state 1] in *Apuliadercetis, Eurypholis, Parenchodus, Serrilepis* and *Saurorhamphus*. The infraorbitals in these fish are usually small, and not well-preserved, except for infraorbital 1 (= lacrimal) and may be hard to see in small specimens. Therefore, many taxa are coded as missing data for this character in the matrix.

56. Preopercle shape (Gallo et al., 2005; modified by Silva and Gallo, 2011)

The shape of the preopercle was first included in the phylogenetic analysis by Gallo et al. (2005) with four states [1: triangular; 2: crescent-shaped; 3: rod-shaped; 4: pipe-shaped]. Silva and Gallo (2011) added a fifth state [0: L-shaped] for coding the condition in *Nardorex*.

However, states [4] and [0] are each only found in a single taxon, therefore interpreted as an autapomorphy, and the majority of the taxa are coded as having state [1]. The delimitation of the shapes was not clear, and state [0: L-shaped] in *Nardorex* is the result of the preopercle having a well-developed posteroventral spine (Taverne, 2004), which is redundant with character 58 (below) and also seen in other taxa, such as *Eurypholis* and *Saurorhamphus* (Goody, 1969).

57. Preopercular dermal pattern (Fielitz, 2004; Silva and Gallo, 2011)

Fielitz (2004) created four states for the dermal pattern on the preopercle, and Silva and Gallo (2011) simplified the states into two conditions [0: smooth; 1: ornamented]. The preopercular is smooth in dercetids and some non-dercetids. The taxa that were previously assigned to Enchodontidae all possess an ornamented preopercle [state 1].

58. Posteroventral spine on the preopercle (Siva and Gallo, 2011)

A well-developed, posteroventral spine on the preopercle [state 1] is found in *Apateopholis, Eurypholis, Hemisaurida, Nardorex, Saurorhamphus, Spinascutichthys, Unicachichthys,* and *Yabrudichthys.* As mentioned above (character 56), *Nardorex* has been double weighted for this feature by the well-developed spine and posteriorly L-shaped preopercle (Taverne, 2004). In all other taxa, the posteroventral spine of the preopercle is either absent or reduced [state 0].

59. Dimensions of the opercle (Gallo et al., 2005)

Many dercetids show an opercular that is longer than the height [state 1]. Among non-dercetid taxa, *Nardorex, Spinascutichthys,* and *Yabrudichthys* also have state [1].

60. Opercular crest (Gallo et al., 2005)

The crest on the opercle is absent [state 0] in dercetids, and Gallo et al. (2005) suggested the absence of the opercular crest is a synapomorphy of the family Dercetidae. However, Silva and Gallo (2011) pointed out that the absence of the opercular crest is also found in *Atolvorator, Hemisaurida, Nardorex,* and *Rharbichthys*. *Apateodus* was coded as having state [1: crest present] in the preexisting matrix, but the external view of the opercle appears to be smooth without any crest (Goody 1969; Newbrey and Konishi, 2015), and specimens of that taxon that Silva and Gallo (2011:507) cited do not preserve the opercle (confirmed in photographs of the specimens in the digital portal of the Natural History Museum, London). Therefore, the character coding of *Apateodus* is questionable.

61. Spine on posterior border of the opercle (Gallo et al., 2005)

The spine on the posterior border of the opercle is present [state 1] only in a few of the ingroup taxa, *Eurypholis, Saurorhamphus* and *Spinascutichthys*. The extant aulopiforms *Lestidium* and *Lestrolepis* also show state [1], but the other extant aulopiform *Trachinocephalus* has state [0: absent], so this character varies among the extant groups.

62. Opercular and subopercular dermal pattern (Fielitz, 2004; modified by Silva and Gallo, 2011)

The states of dermal patterns for the opercle and subopercle created by Fielitz (2004) were simplified into two states [0: smooth; 1: ornamented] by Silva and Gallo (2011). Most dercetids except *Dercetoides* have smooth [state 0] opercular and subopercular bones, whereas many enchodontid taxa exhibit a highly ornamented opercle and subopercle (Fielitz, 2004). The opercle in *Dercetoides* has a smooth dorsal portion and ridged ventral portion, and is much less ornamented compared to the dermal pattern seen in *Enchodus* or *Eurypholis*, which have opercles ridged with tubercles (Chalifa, 1989b; Goody, 1969). I leave this character and the state of *Dercetoides* without modification until I can confirm the nature of the specimens.

63. Interopercle (Chalifa, 1989b)

The interopercle is present [state 0] in most dercetids except *Pelargorhynchus*. Chalifa (1989b) thought the absence of the interopercle [state 1] is more primitive because the interopercle is commonly seen in teleosts. Fielitz (2004) also noted the absence of the interopercle is shared among taxa in his Enchodontidae, and the preexisting matrix agrees with the state [1] found in all enchodontids, such as *Enchodus* and *Eurypholis*.

64. Mesocoracoid (Taverne, 1991)

The mesocoracoid is present [state 1] in *Apateodus, Apateopholis, Ichthyotringa, Halec, Serrilepis,* and *Yabrudichthys*. Taverne (1991) assumed that the absence of the mesocoracoid [state 0] is the plesiomorphic condition for dercetids, and this agrees with the existing matrix.

65. Scapula and coracoid (Taverne, 1991)

The scapula and coracoid are separate elements [state 0] in most of the taxa. A co-ossified scapulo-coracoid [state 1] is found in *Aspidopleurus, Dercetoides, Parenchodus,* and *Serrilepis*. *Spinascutichthys* was coded as [1: co-ossified] by Murray et al. (2022) but they stated that these bones were not preserved, and, therefore, this character should have been coded as missing data. Taverne (1991) noted that having a separate scapula and coracoid is the primitive condition in dercetids. In the extant aulopiforms, the scapula and coracoid are not co-ossified but are connected by cartilage (Baldwin and Johnson, 1996; Sato and Nakabo, 2002). Thus, the taxa with a co-ossified scapula-coracoid might have independently developed their condition, because the taxa with this feature do not form a clade.

66. Supraneurals (Fielitz, 2004)

The supraneurals are present [state 0] in most of the taxa that can be coded for this character. The supraneurals are absent [state 1] in *Atolvorator, Ichthyotringa,* and *Parenchodus*, but many dercetids are coded as missing data due to the fragmentary preservation of the specimens.

67. Total number of vertebrae (Gallo et al., 2005; modified by Silva and Gallo, 2011)

The total number of vertebrae was first used in a comparative study by Chalifa (1989b). The delimitation of the states used by Chalifa (1989b) is 60-80 vertebrae in dercetids, 50-60 in *Cimolichthys*, and 45 in '*Prionolepis*'. Gallo et al. (2005) simply delimited the numbers into two states [0: more than 45; 1: equal to or less than 45]. Silva and Gallo (2011) modified the states to [0: more than 50; 1: equal to or less than 50]. Currently, among ingroup taxa, all dercetids, *Cimolichthys* and *Palaeolycus* have more than 50 vertebrae [state 0]. *Atolvorator* was coded as [0: more than 50] in the previous data matrix, but the total number of vertebrae is 47 as confirmed in Gallo and Coelho (2008).

68. Number of caudal vertebrae (Silva and Gallo, 2011)

The number of caudal vertebrae was added as a character by Silva and Gallo (2011) with two states [0: more than 20; 1: equal to or less than 20]. However, the delimitation was not based on previous studies, and a traditional diagnostic character of dercetids is that the caudal vertebrae number approximately 25-30 (Goody, 1969; Chalifa, 1989b). With the current states, many non-dercetid ingroup taxa have state [0] in addition to dercetids.

69. Ribs (Silva and Gallo, 2011)

This character was created by (Silva and Gallo, 2011) and divided into two states [0: ribs extending to the pelvic fin origin; 1: ribs surpassing the pelvic fin origin], although the definition of the states were not explained. Most of the taxa except *Apateopholis, Parenchodus, Rharbichthys,* and *Yabrudichthys* are coded as state [1], but there are also some taxa with missing data.

70. Transverse processes on the vertebrae (Chalifa, 1989b)

Chalifa (1989b) noted that two pairs of transverse processes on each vertebra [state 1] are found in *Rhynchodercetis* and *Dercetoides*. Rosen (1973) pointed out the presence of two pairs of transverse processes is similar to the condition in the extant aulopiforms. Chalifa (1989b) also assumed the state [1] is the derived condition among dercetids. Currently, additional dercetid taxa (*Apuliadercetis, Brazilodercetis, Caudadercetis, Nardodercetis,* and *Hastichthys*) and *Parenchodus* are coded as having state [1]. However, the transverse processes in *Parenchodus* were not fully described in the original study (Raab and Chalifa, 1987), and the reconstruction of the skeleton does not show the clear bifurcation of the transverse processes.

71. Neural spines (Chalifa, 1989b)

The reduction of the neural spines [state 1] has been proposed as a synapomorphy for Dercetidae by many authors (Chalifa, 1989b; Taverne, 1991; Gallo et al., 2005; Vernygora et al., 2017). Silva and Gallo (2011) qualified the condition of the spines to the two states [0: well-developed (their length surpassing the length of the vertebral centrum); 1: very reduced (their length equal to or less than half of the length of the vertebral centrum)]. All members that were previously assigned to dercetids exhibit state [1: very reduced].

72. Neural spines bifid in the abdominal region (Silva and Gallo, 2011)

Bifid abdominal neural spines [state 0] are found in some taxa, such as *Candelarhynchus, Nardorex, Rharbichthys, Veridagon, Parenchodus* and *Unicachichthys.* The neural spines in *Rhynchodercetis* appear to be bifid in the abdominal region (Gallo et al., 2005:fig. 12), although it is coded as missing data in the preexisting matrix.

73. Distribution of epipleurals (Silva and Gallo, 2011)

The series of epipleurals were reported by Silva and Gallo (2011) to extend to more than a half of the body [state 0] in most of the taxa except *Apateopholis, Aspidopleurus, Parenchodus, Phylactocephalus,* and *Veridagon* in which the epipleurals extending up to half of the body [state 1]. The definition of the character and states was not explained by Silva and Gallo (2011), but I assume that state 0 [extend to more than a half of the body] indicates the epipleural series is present on the vertebrae for almost the whole of the axial skeleton, as such a condition occurs in *Dercetis*. The description of *Apateopholis* by Goody (1969) mentioned both epipleurals and epineurals occur on the first 33 vertebrae of a total of 40 vertebrae, which might also qualify as extending more than a half of the body [0], but I leave the state [1: extending up to half of the body] as coded by Silva and Gallo (2011) because I do not have access the actual specimen.

74. Distribution of epineurals (Silva and Gallo, 2011)

The series of epineural bones also extend to more than a half of the body [state 0] in almost all taxa. Only *Aspidopleurus* and *Phylactocephalus* are coded as the epineurals extending up to half of the body [state 1], because the epineurals do not occur in the posterior half of the body.

75. Position of the pectoral fin (Baldwin and Johnson, 1996)

The pectoral fin is positioned high on the side of the body [state 0: (last fin-ray placed at the level of the ventral border of the opercle or a little above)] in many dercetids. Many other non-dercetids possess state [1: low (last fin-ray placed below the level of the ventral border of the opercle)] except *Eurypholis, Saurorhamphus, Spinascutichthys,* and *Vegrandichthys*. In extant aulopiforms, many alepisauroids have pectoral fins positioned low on the body, and the lower position is thought to be more primitive in teleosts (Baldwin and Johnson, 1996).

76. Orientation of the pectoral fin base (Baldwin and Johnson, 1996; modified in Silva and Gallo, 2011)

The pectoral fins are inserted horizontally [state 1] in the extant alepisauroids, whereas many other extant aulopiforms have a vertical orientation of the fins [state 0] (Baldwin and Johnson, 1996). In ingroup taxa, many dercetids show state [0], and many non-dercetids show state [1]. There are a few taxa that exhibit state [2: inclined], such as *Atolvorator, Apateopholis,* and *Nardodercetis*.

77. Origin of the pelvic fin (Taverne, 1991)

The origin of the pelvic fin is opposite or posterior to the dorsal fin [state 1] in many ingroup taxa. Taverne (1991) thought that state [1] is the plesiomorphic condition in dercetids, although *Nardodercetis* and *Ophidercetis* are coded as state [0: pelvic fin origin anterior to the dorsal fin] by Silva and Gallo (2011) mentioning that they based on the description by Taverne (2005a, b), although both specimens are incompletely preserved.

78. Dorsal fin length (Gallo et al., 2005; modified by Silva and Gallo, 2011)

The character for length of the dorsal fin was divided into two states by Gallo et al. (2005) [0: short (less than 30 rays); 1: long (more than 30 rays)]. Silva and Gallo (2011) modified the delimitation of the states to [0: short (less than 20 rays); 1 long (more than 20 rays)]. The long dorsal fin [state 1] is found in a relatively limited number of taxa, such as *Cyranichthys, Dercetis, Ophidercetis, Parenchodus, Rhynchodercetis, Stratodus,* and *Yabrudichthys*.

79. Shape of the first proximal pterygiophore of the dorsal fin (Fielitz, 2004)

The shape of the first pterygiophore is different from the remaining pterygiophores in the dorsal fin [state 0] in most of the taxa, except *Serrilepis, Spinascutichthys* and *Yabrudichthys*, which exhibit state [1: all equal in shape]. In extant aulopiforms, evermanellids have a broad triangular first pterygiophore, whereas the rest of the aulopiforms do not show any specialization of the first pterygiophore (Baldwin and Johnson, 1996).

80. Anal fin length (Silva and Gallo, 2011)

The anal fin is short [state 0: up to 15 rays] in many ingroup taxa, whereas the anal fin is long [state 1: more than 15 rays] in *Benthesykime, Caudadercetis, Enchodus, Ophidercetis, Nardorex, Palaeolycus, Parenchodus, Saurorhamphus, Spinascutichthys,* and *Veridagon*. There is intergeneric variation in *Hastichthys*, with *Hastichthys gracilis* having a long fin [state 1], and *H. totonacus* with a short [state 0] anal fin. The number of fin rays can vary among the other genera, such as *Enchodus* ranging from 16 to 20 anal fin rays depending on species (Goody, 1969; Chalifa, 1989a).

81. Anal fin edge (Baldwin and Johnson, 1996; modified by Silva and Gallo, 2011)

The anal fin has a serrated edge [state 1] only in *Caudadercetis* and *Rharbichthys*; the rest of the ingroup taxa have state [0: not serrated]. This character was created by Baldwin and Johnson (1996) to distinguish alepisauroids with state [1] from other aulopiforms. The original character states were [0: external margin of anal fin not indented; 1: indented] (Baldwin and Johnson, 1996). The description of the states as modified by Silva and Gallo (2011) [0: not serrated; 1: serrated] can be confusing for interpretation of the specimens.

82. Fusion of hypurals (Silva and Gallo, 2011)

The fusion of hypurals [state 1] is seen in many dercetids, *Cimolichthys, Parenchodus, Serrilepis, Spinascutichthys, Unicachichthys, Veridagon,* and *Yabrudichthys*. In other taxa, the hypurals are separate and coded as state 0 [free] in the preexisting matrix. Some taxa are coded as unknown for this feature.

83. Contact between hypurals 2 and 3 (Chalifa, 1989b)

Chalifa (1989b) believed that the presence of the convoluted suture between hypurals 2 and 3 [state 1] was a derived character in some dercetids. Vernygora et al. (2017) also suggested that state [1] delimits a major dercetid clade, although it is not found in all dercetid members. Other non-dercetid taxa have state [0: separate hypurals 2 and 3]. For the newly added genus *Stratodus*, a convoluted suture was found to be present between hypurals 2 and 3 in specimen SDSM 81334.

84. Body scales (Chalifa, 1989b)

This character is the presence or absence of general fish body scales, not the scutes (characters below). The body scales are present [state 0] in several taxa, *Aspidopleurus, Ichthyotringa, Halec, Pelargorhynchus, Phylactocephalus, Saurorhamphus,* and *Serrilepis*. Chalifa (1989b) used the character 'scales' in her comparative study, but apparently was referring to the dermal scutes found in many taxa. In extant aulopiforms, body scales are absent [state 1] in evermanellids, alepisaurids, and paralepidids, whereas synodontoids are covered by scales (Baldwin and Johnson, 1996).

85. Flank scutes (Gallo et al., 2005; modified by Silva and Gallo, 2011)

Traditionally, dercetids were characterized by the presence of dermal scutes on the flank which are often triradiate in form (Woodward, 1901; Goody, 1969; Taverne, 1991). Gallo et al.

(2005) created four states for the flank scutes [0: absent; 1: triangular; 2: cordiform; 3: tripartite], and Silva and Gallo (2011) added a fifth state [4: rectangular]. However, the morphology of the scutes is highly variable and difficult to code. For example, *Eurypholis, Ophidercetis, Vegrandichthys,* and *Saurorhamphus* are all coded as [1: triangular], but the scutes in *Ophidercetis* are very different from those in *Saurorhamphus* (Chalifa, 1989b:fig. 3; Taverne, 2005a:fig 8). Similarly, *Cimolichthys* and *Pelargorhynchus* are both coded as [2: cordiform], but the scutes in *Cimolichthys* are not cordifom at all but rather hexagonal in shape (Woodward, 1903:pl. xii) or rhomboid shape (personal observation). *Cyranichthys* is coded as state 1 [triangular] in the preexisting matrix, but the scutes described by Taverne and Goolaerts (2015:fig. 15) is rather triradiate. The recently added species *Spinascutichthys* was coded as missing data because none of the morphologies listed in the states fit the unique shape of the scutes in *Spinascutichthys*. State [4: rectangular] is an autapomorphy of *Rharbichthys*, so this state is not useful in the parsimony analysis.

86. Number of rows of scutes on flanks (Taverne, 1991)

Taverne (1991) proposed the presence of two or more rows of scutes on the flanks [state 2] to be the primitive state for dercetids. State [2] is found in *Cimolichthys, Stratodus*, and some dercetids (*Cyranichthys, Brazilodercetis, Dercetis, Ophidercetis,* and *Pelargorhynchus*). A single row of flank scutes [state 1] is found in some dercetids (*Apuliadercetis, Dercetoides, Nardodercetis, Rhynchodercetis,* and *Hastichthys*) and non-dercetids (*Eurypholis, Rharbichthys, Saurorhamphus, Spinascutichthys, Veridagon,* and *Vegrandichthys*). The state [0: absent] is redundant with character 85 state [0], absence of flank scutes.

87. Middorsal scutes (Gallo et al., 2005)

The presence of middorsal scutes [state 1] is suggested to be a possible synapomophy of Enchodontidae (Díaz-Cruz et al., 2016). *Spinascutichthys* is the only genus outside of the enchodontid clade with state [1], although it shares some other enchodontid features, such as the presence of the anteroventral prongs on dentary (Murray et al., 2022). All other taxa are coded as [0: absent].

3.3.2 Summary of the modification of characters/character states

Modified characters are summarized below with the original character/states and the new character/states indicated.

Character 4

The ornamentation of the other dermal bones was simplified to two states either ‘smooth’ or ‘ornamented’ by Silva and Gallo (2011). Thus, this character should be consistent with the states of other dermal bones.

Original—Dermal pattern on skull roof [0] smooth; [1] only with tubercles; [2] only with ridges; [3] tubercles + ridges

Modified—Dermal pattern on skull roof [0] smooth; [1] ornamented

Character 11

The addition of the state 2 [straight] was not fully explained by Silva and Gallo (2011), and only *Spinascutichthys* is coded as state 2. I integrated the states 1 [acute] and 2 [straight] to accommodate the mesethmoid of *Spinascutichthys* of which the anterior end is neither bifid nor acute.

Original—Posterior extremity of mesethmoid: [0] bifid; [1] acute; [2] straight

Modified— Posterior extremity of mesethmoid: [0] bifid; [1] not bifid (acute or straight)

Character 39

The inclusion of the maxilla in gape has been proposed to be a synapomorphy of Enchodontoidei by many authors (Rosen, 1973; Nelson, 1994; Fielitz, 2004). I replace the states created by Gallo et al. (2005) which did not take into account the inclusion or exclusion of maxilla from gape.

Original—Placement of the maxilla: [0] over the premaxilla; [1] behind the premaxilla

Modified— Placement of the maxilla: [0] excluded from gape; [1] included in gape

Character 42

I add the third state of mandible which is longer than the snout length to accommodate the nature of this state in *Spinascutichthys* and possible other taxa such as *Eurypholis*.

Original—Mandible length: [0] equal to snout length; [1] shorter than the snout

Modified—Mandible length: [0] equal to snout length; [1] shorter than the snout; [2] longer than the snout

Character 52

I rephrase the character to indicate the nature of the character found in anguloarticular, which expands posteriorly and overlaps the articular condyle for the quadrate.

Original—Quadrate-mandibular articulation: [0] exposed; [1] hidden

Modified—Extension of the posterior end of anguloarticular: [0] absent; [1] present

Character 85

I modify the state 2 [triangular] and 4 [rectangular] to [polygonal] because the lateral scutes found in *Eurypholis, Saurorhamphus*, and *Vegrandichthys* are rather rectangular shape although they are coded as state 2 [triangular] in the preexisting matrix. But the rectangular shape [4] is coded only in *Rharbichthys*, which Silva and Gallo (2011) indicated the different morphology from those in state [2: triangular]. The new state [polygonal] can accommodate both the rectangular lateral scutes of *Eurypholis* and *Rharbichthys* as well as rhomboid lateral scutes of *Cimolichthys* and latelal scutes *Spinascutichthys* which radiates five to six directions).

Original—Flank scutes: [0] absent; [1] triangular; [2] cordiform; [3] tripartite; [4] rectangular

Modified— Flank scutes: [0] absent; [1] cordiform; [2] triradiate (radiating to three directions); [3] polygonal (radiating more than three directions—rhomboid, rectangular, pentagonal, hexagonal)

3.3.3 Exclusion of characters/character states

Some characters are excluded from the new analysis based on their lack of usefulness. Characters found in only one taxon are autapomorphies, which are not informative in cladistic analyses.

Character 20

Supraoccipital with two well-delimited regions—only found in *Nardorex*

3.3.4 Changes to character coding

In the analysis with modified characters, some character states have been modified from the previously coded states or missing data for some of the taxa. The original data matrix is based on Murray et al. (2022). In this thesis, except for the taxa clearly measured or described in the literature, I only modify the states of taxa I personally observed, although there are some taxa that need to be revisited, such as *Apateodus* and *Ichthyotringa*.

Candelarhynchus

Originally, character 27 was coded as 2 [lacrimal shape trapezoidal] by Vernygora et al. (2017). Alvarado-Ortega and Díaz-Cruz (2020) re-coded as ‘not applicable’, but *Candelarhynchus* has a lacrimal which I agree with Vernygora et al. (2017) is trapezoidal shape.

Character 27: Lachrymal shape [n/a to 2]

Cyranichthys

The mandible of *Cyranichthys* has not been reported (Casier, 1965; Taverne and Goolaerts, 2015). Also, the lateral scutes appears to be triradiate based on the depiction by Taverne and Goolaerts, 2015:fig. 15)

Character 45: Teeth size on mandible [0 to ?]

Character 85: Flank scutes [1 to 3]

Enchodus

Many missing data of *Enchodus* in the preexisting matrix were filled in based on personal observation of specimens AMHN FF 1837, FF 3859, FF 6418, FF 19473; FHSM VP 409, VP 2939, VP 6611, and confirmation with previous studies (Goody, 1969; Chalifa, 1989c; Fielitz, 2004; Fielitz and González-Rodríguez, 2016). Character 49 and 68 were modified from the preexisting matrix also based on the personal observation and description from previous studies above.

Character 5: Vomerine teeth [? to 0]

Character 7: Dermopalatine length [? to 1]

Character 15: Shape of the post-orbital border [? to 0]

Character 19: Supraoccipital crest [? to 0]

Character 33: Premaxilla [? to 0]

Character 34: Posterior extension of premaxilla [? to 0]

Character 35: Dermal pattern on premaxilla [? to 1]

Character 36: Fenestra in the premaxilla [? to 1]

Character 46: Rows of teeth on upper jaw [? to 0]

Character 49: Mandibular sensory canal [1 to 2]

Character 68: Number of caudal vertebrae [1 to 0]

Character 78: Dorsal fin length [? to 0]

Character 83: Contact between hypurals 2-3 [? to 0]

Eurypholis

More than two rows of teeth were confirmed by personal observation of the specimens AMNH FF 3615, FF 3625, FF 14030, and by Goody (1969).

Character 47: Rows of teeth on mandible [0 to 1]

Ophidercetis

The original description by Taverne (2005a) was used by Silva and Gallo (2011) to code character 85: flank scutes. They coded *Ophidercetis* as having state 1 [triangular] probably based on figure 8 in Taverne (2005a). However, later Taverne and Goolaerts (2015:fig. 10) described the lateral scutes of a new specimen of *Ophidercetis*, which appears to be cordiform shape.

Character 85: Flank scutes [1 to 2]

Vegrandichthys

I follow the definition by Gallo et al. (2005) for character 2—a low head ([1] the head length more than four times of the greatest height of the head) and a deep head ([0] the head length four times or less than the greatest height of the head). Based on the description by Díaz-Cruz et al. (2020a), *Vegrandichthys* should have been coded as a deep head [0] because the head length is less than four times of the height of the head.

Character 2: Head height [1 to 0]

Spinascutichthys (Murray et al., 2022)

Murray et al. (2022) did not code character 15 because the states were not clearly defined by previous studies. Based on the coding by Gallo et al. (2005), I code 0 [posterior border of the orbit concave] in *Spinascutichthys* because the sphenotic is not projecting anteriorly, which is state 1 [posterior border of the orbit convex] as in *Ichthyotringa*. Also, the scapula and coracoid were not preserved well enough to determine the state for character 65, so I here re-code the state to missing data.

Character 15: Shape of the posterior border of the orbit [? to 0]

Character 65: Scapula and coracoid [1 to ?]

3.4 Results

3.4.1 Analysis without modification of characters/character states

The 24 most parsimonious trees (MPTs) were recovered from the analysis of 87 characters without modification of characters or character states (Appendix B.1). The strict consensus tree was created from all 24 MPTs of treelength of 506, and has a consistency index (CI) of 0.1729 and retention index (RI) of 0.4192 (Fig. 3-1). The extinct Enchodontoidei was not recovered as monophyletic because the extant outgroups (*Trachinocephalus, Lestidium,* and *Lestrolepis*) were placed within a polytomy with the ingroup taxa. Most of the taxa that were previously assigned to the family Dercetidae were placed in a clade supported by character 71:1[neural spines very reduced], but this character state [71:1] was also found in *Candelarhynchus*, which was excluded from the clade. The presence of triradiate scutes [85:3] were also found in the dercetid clade but some members had different morphologies of scutes and therefore different states for this character [85:0, absent in *Caudadercetis*, 85:1, triangular in *Ophidercetis* and *Cyranichthys*, 85:2, cordiform in *Pelargorhynchus*]. In fact, *Ophidercetis* and *Cyranichthys* are confirmed not to have triangular scutes but rather possess cordiform shaped scutes in *Ophidercetis* and triradiate scutes in *Cyranichthys* (Taverne and Goolaerts, 2015), and both states were modified in the next analysis. Although most dercetids were recovered in a monophyletic group, there was no unambiguous synapomorphy to support the clade.

The family Enchodontidae was proposed by Díaz-Cruz et al. (2016) to have two synapomorphies [48-1: anteroventral prongs present on the dentary; 87-1: middorsal scutes present], but neither of these two supported the monophyly of this family. The middorsal scutes are present in *Enchodus, Eurypholis, Palaeolycus, Parenchodus, Veridagon, Vegrandichthys, Unicachichthys, Saurorhamphus,* and *Spinascutichthys*. Only *Spinascutichthys* falls outside of the clade formed by the rest of the eight taxa, so having middorsal scutes is homoplastic for Enchodontidae and *Spinascutichthys* in this analysis.

3.4.2 Analysis with modified character matrix

The 86 characters as modified (Appendix B.2) were run in a new parsimony analysis. Three most parsimonious trees were recovered, and all were used to form the strict consensus tree with treelength of 490, CI of 0.1653 and RI of 0.3955 (Fig. 3-2). This time, the extant designated outgroups were recovered outside of the ingroup, forming a sister clade to a huge polytomy of the extinct taxa, which here are considered as Enchodontoidei. All enchodontoids except those with missing data share a single character state 38:1 [maxilla included in gape], which excludes the extant taxa from the clade of extinct ingroups.

However, the resolution within the extinct clade turned out to be lower than in the previous analysis. Most dercetids did not form a clade as found in the first analysis, except a small clade of (*Cyranichthys* + (*Pelargorhynchus* + (*Dercetis elongatus*, *D. triqueter*, *D. megnificus* sp. nov., *Stratodus*))) supported by several characters [4:1 skull roof ornamented; 49:1 mandible ornamented; 69:0 single transverse process; 77:1 long dorsal fin; 85: two or more rows of lateral scutes]. The three species of *Dercetis* and *Stratodus* form a polytomy, in which several characters were shared to support the group of *Dercetis* and *Stratodus*, although no unambiguous synapomorphy was found. One of the modified characters, flank scutes with a triradiate shape [83:2] did not support a dercetid clade as was found in the first analysis, but instead was recovered as a plesiomorphic state of all enchodontoids, although there are many reversals of the states. The reduced neural spines [70:1] did not support the familiy Dercetidae, instead only supporting a smaller clade of dercetid taxa (*Cyranichthys* + (*Pelargorhynchus* + (*Dercetis elongatus*, *D. triqueter*, *D. megnificus* sp. nov., *Stratodus*))). On the other hand, other enchodontoids except *Apateodus, Atolvorator, Ichthyotringa*, and *Rharbichthys* were recovered as a monophyletic clade supported by the opposite state of character 70 [0: neural spines well developed]. A monophyletic family Enchodontidae was weakly supported by several characters, such as character 86:1 [middorsal scutes present].

3.5 Discussion

The monophyly of the suborder Enchodontoidei was supported by the analysis with modification of characters and character states of some taxa, although the supporting value of both CI and RI are still low. The extinct suborder Enchodontoidei was supported by a single unambiguous synapomorphy, maxilla included in gape [38:1], and this agrees with several authors (Rosen, 1973; Nelson, 1994; Fielitz, 2004), although the interrelationships within Enchodontoidei was not recovered well, with many dercetid taxa recovered in a polytomy with other enchodontoid menbers. Fielitz (2004) defined the placement of the maxilla with three states [0: excluded from gape of jaw; 1: included in gape and is toothed; 2: included in gape, but teeth absent]. The state [1: included in gape and is toothed] supported his enchodontoid clade, but there were reversals in some taxa [from state 1 to 2] because he constructed the character to include maxillary teeth which caused reversals, and thus he did not find this character to be an unambiguous synapomorphy which should be unique and unreversed. In this study, I coded the maxillary teeth and the placement of the maxilla separately because the loss of teeth is related to the tooth germ layer, and the exclusion of the maxilla is a result of the extension of the premaxilla which completely forms the gape. Therefore, the two are not necessarily correlated.

The family Dercetidae was, however, not recovered as monophyletic in the analysis with modified character matrix. Alvarado-Ortega and Díaz-Cruz et al. (2020) challenged the monophyly of the family because their parsimony analysis did not result in a clade of the traditional taxa included in Dercetidae . Here, the analysis with modified characters showed that the family Dercetidae was also not supported and a previous unambiguous synapomorphy, neural spines very reduced [71:1 (in the original matrix), 70:1 (in the modified matrix)] was recovered as an ancestral condition of all enchodontoids. The ancestral condition of reduced neural arch [71:1 (in the original matrix), 70:1 (in the modified matrix)] retained in a small clade of (*Cyranichthys* + (*Pelargorhynchus* + (*Dercetis elongatus*, *D. triqueter*, *D. megnificus* sp. nov., *Stratodus*))), but it was not recovered as a synapomorphy with other dercetids.

One of the modified characters, presence of triradiate flank scutes [85:3 (in the original matrix), 84: 2(in the modified matrix)], that supported a monophyletic dercetid clade found in the first analysis did not recover a monophyly of dercetids but supported a clade of (*Cyranichthys* + (*Pelargorhynchus* + (*Dercetis elongatus*, *D. triqueter*, *D. megnificus* sp. nov., *Stratodus*))) with a reversion in *Pelargorhynchus* [2 to 1]. The presence of triradiate scutes has traditionally been used as a character of the Dercetidae (Woodward, 1901; Goody, 1996; Taverne, 1991), however, flank scutes are also present in other enchodontoids, such as *Cimolichthys* and *Eurypholis*, and the morphology of scutes varies among those taxa. Gallo et al. (2005) and Silva and Gallo (2011) classified the shape of the scutes in several states, but adding various morphologies to a single state made it difficult to code and sometimes caused miscoding. For example, *Spinascutichthys* was coded as n/a in this character because none of the scute shapes was applicable (Murray et al., 2022). There was a miscoding in the origical matrix for *Ophidercetis*, in which scutes were coded as triangular, but the state "triangular" was originally created for the scutes of *Eurypholis* and *Saurorhamphus* (Gallo et al., 2005), which do not resemble the scutes of *Ophidercetis* at all. Although they do not form a clade, all of *Spinascutichthys, Ophidercetis, Eurypholis* and *Saurorhamphus* were coded as [83:3 flank scutes polygonal] in the modified analysis to avoid any confusion. Other character modifications or addition of new characters found in dercetids taxa will be needed to resolve the monophyletic dercetid clade.

The family Enchodontidae was not supported by any unambiguous synapomorphies even after modifying the matrix. The clade (*Enchodus, Palaeolycus* + (*Unicachichthys* + (*Parenchodus* + *Veridagon*)) + ((*Vegrandichthys* + (*Eurypholis* + *Saurorhamphus*)))) was weakly supported by the least homoplastic character [85:1 middorsal scutes present], although the state was also found in *Spinascutichthys*. Testing monophyly of the family Enchodontidae was not carried out in this study because the objective of the thesis focused on testing the suborder Enchodontoidei and the family Dercetidae. More systematic works will be needed to resolve the monophyly of the Enchodontidae.

3.6 Conclusion

A phylogenetic analysis of the suborder Enchodontoidei was performed in this chapter. A total of 86 characters with six modified characters ended up being used in the revised analysis. The Enchodontoidei was supported as monophyletic based on a single unambiguous character, maxilla included in gape, which follows the previous hypothesis proposed by many authors

(Rosen, 1973; Nelson, 1994; Fielitz, 2004). The choice of outgroups and modification of six characters helped in recovering a monophyletic group, although a more inclusive study with other extant members and reexamination of some taxa, such as *Sardinioides* spp., *Apateodus* spp., *Ichthyotringa* spp., and other incomplete specimens of which the character states were not modified in this thesis, are needed for better resolution in a future study.

The family Dercetidae was not recovered in the analysis with the modified matrix. The triradiate scutes were recovered as a plesiomorphic state of the family, although some taxa have reversed states. The new species, *Dercetis magnificus*, was recovered in a polytomy with the other two species of *Dercetis*, *D. elongatus* and *D. triqueter*, and *Stratodus*. The family Enchodontidae was also not supported by any unambiguous synapomorphy. Further study with additional modification of characters and states, addition of new characters, and correction of the character coding will be needed to test the monophyly of Dercetidae and Enchodontidae.

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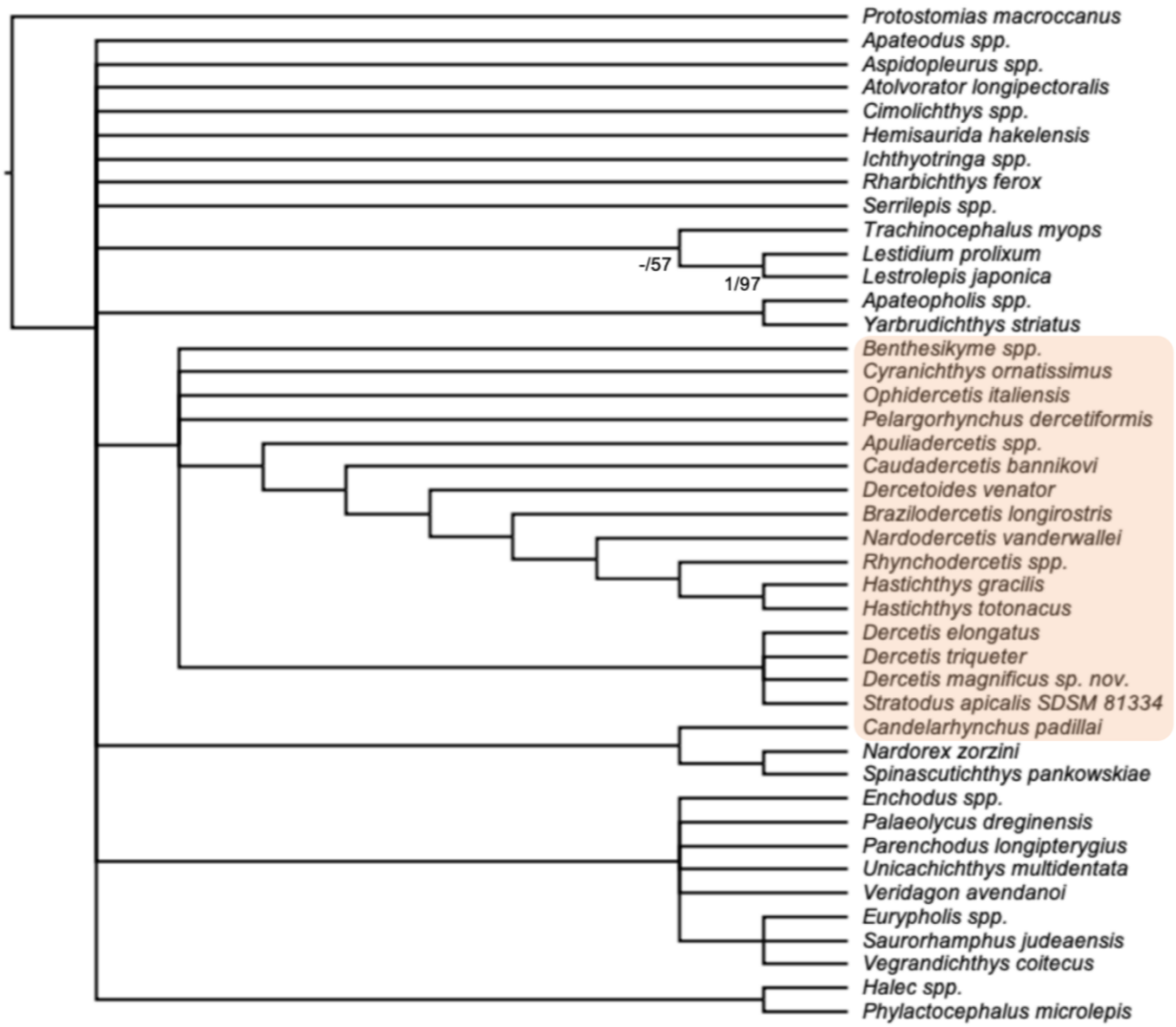

FIGURE 3-1. The result of the analysis without character modification. The strict consensus tree of 24 most parsimonious trees with treelength of 506 obtained from the analysis with 87 characters without modification (CI = 0.1729; RI = 0.4192). The Bremer/Bootstrap values with only 50%> bootstrap values are indicated. Taxa that previously have been assigned to Dercetidae are highlighted in color.

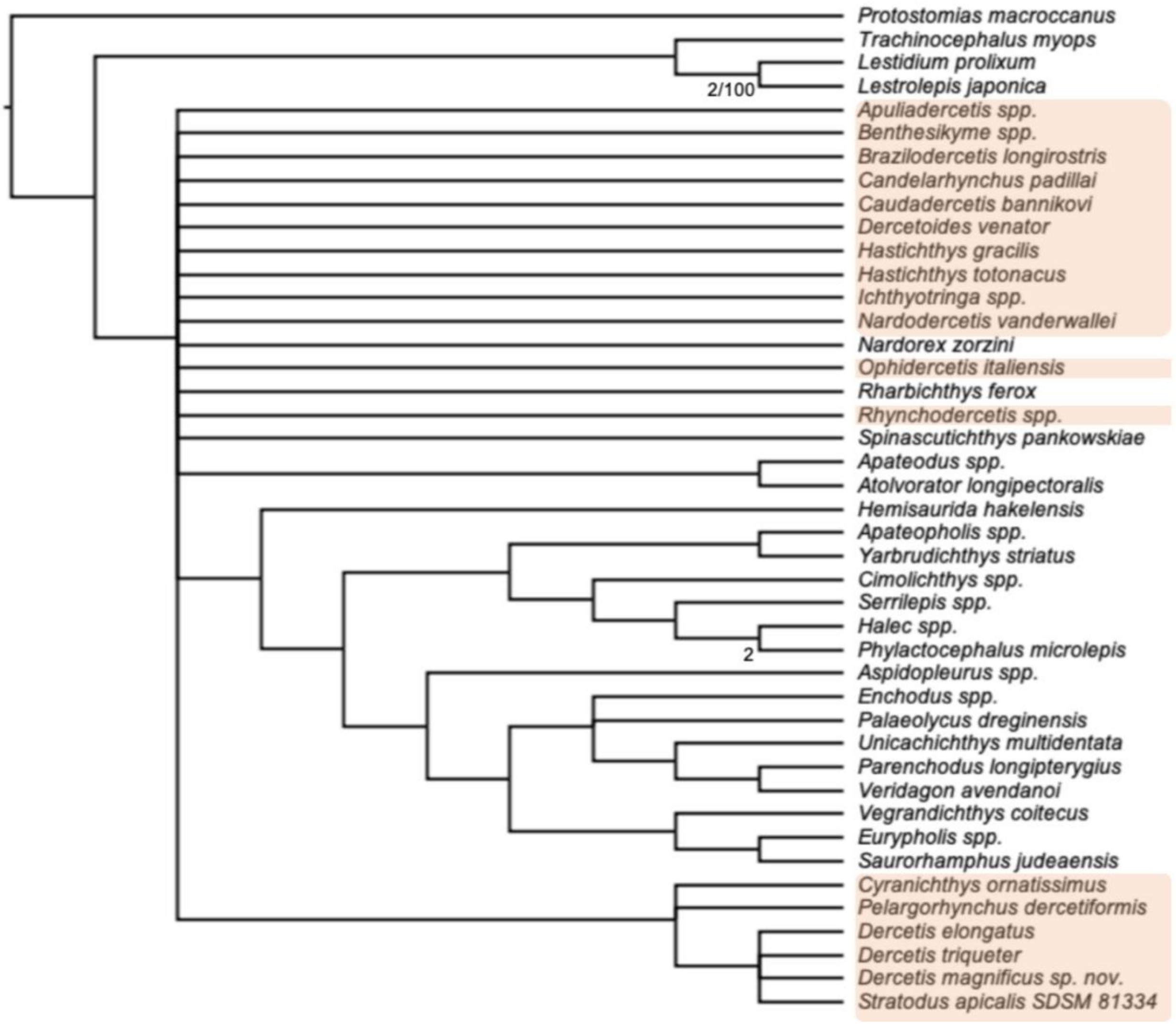

FIGURE 3-2. The result of the analysis with character modification. The strict consensus tree of 10 most parsimonious trees with treelength of 490 obtained from the analysis with modified 86 characters (CI = 0.1653; RI = 0.3955). The Bremer/Bootstrap values with only 50%> bootstrap values are indicated. Taxa that previously have been assigned to Dercetidae are highlighted in color.

Chapter 4: Conclusions and Future research

4.1 General conclusion

In this thesis, the main objectives were 1) to describe the new specimens of dercetid, and 2) to test monophyly of the family Dercetidae and the suborder Enchodontoidei by assessing the preexisting character matrix. In Chapter 2, I described two newly discovered specimens from the Bearpaw Formation of Alberta and assigned them to the new species of the genus *Dercetis*. The new specimens are larger than any other specimens that were previously reported as *Dercetis* and provided anatomical detail particularly on the cranial region. In addition to the large body size, the new species is described as the first well-preserved *Dercetis* from the Western Interior Seaway as well as the western area of the Tethys, whereas the reports of the other two species of *Dercetis* are restricted to the eastern Tethys (Woodward, 1901; Taverne, 2005). The result of the phylogenetic analysis using a character matrix from previous studies (Alvarado-Ortega and Díaz-Cruz, 2020; Murray et al., 2022) recovered the new species, *D. magnificus* sp. nov. as a sister to the two previously known species of *Dercetis*, *D. elongatus* and *D. triqueter*. However, they were recovered in a polytomy together with *Stratodus apicalis* in the analysis with a modified character matrix performed in Chapter 3, which needs to be reanalyzed in future studies with better resolution.

In Chapter 3, I assessed a total of 87 preexisting characters and ended up modifying six characters and character states. In some taxa, such as *Apateodus*, *Atolvorator*, and *Ichthyotringa*, there were potential missing data or miscoded data that need to be recoded. The analysis with modified characters/states and some changes to coding in several taxa recovered monophyly of the suborder Enchodontoidei supported by a single unambiguous synapomorphy—maxilla included in gape. This character was modified from Gallo et al. (2005) character 39 [placement of maxilla 0: over the premaxilla; 1: behind the premaxilla] to the new character 38 (in the modified matrix) [position of maxilla 0: excluded from gape; 1: included in gape]. The inclusion of the maxilla in the gape was suggested as a synapomorphy by multiple authors (Rosen, 1973; Nelson, 1994; Fielitz, 2004) and this study supported their hypothesis. The monophyletic family Dercetidae, however, was not supported in the modified analysis possibly due to the low resolution of the recovered trees. The very reduced neural arches was suggested as a single synapomorphy of Dercetidae (Vernygora et al., 2017; Alvarado-Ortega and Díaz-Cruz, 2020); however, the result did not even recover the previous monophyletic clade but placed most of the dercetids in a polytomy with other enchodontoids. More examination of the specimens that were previously assigned to Dercetidae will be needed to construct the characters/states that possibly support the clade. Although the modified analysis resulted in a lower supporting value, the assessment of each character in the preexisting matrix provided a basis for the additional modifications in a future phylogenetic study.

4.2 Limitations and future research

A limitation in this thesis was mainly the limited access to the specimens. The extant aulopiforms are mostly adapted to deep-seas and it is not easy to obtain comparative specimens. In this thesis, only three extant members of aulopiform taxa were included in the modified matrix, so future studies will require more extant taxa to be included to increase the reliability of the relationships between extant and extinct taxa. Also, the study in Chapter 3 did not include *Sardinioides* as an outgroup because of the uncertain placement of the genus (Rosen, 1973; Beckett et al., 2017). In fact, *Sardinioides illustrans* was assigned to the Aulopiformes based on the unique synapomorphy found on the gill arch (Beckett et al., 2017). *Sardinioides minimus* was recovered as part of the ingroup in the previous studies (Silva and Gallo, 2011; Alvarado-Ortega and Díaz-Cruz et al., 2020), so a revised systematic work of species of *Sardinioides* is needed for more reliable assignment of this genus.

In this thesis, I focused only on the Enchodontoidei that mainly lived in the Cretaceous and did not consider other extinct aulopiform fossils that were reported from younger deposits in the phylogenetic analysis, such as *Holosteus* from the Eocene and *Polymerichthys* from the Miocene (Uyeno, 1967; Marramà and Carnevale, 2017). The addition of those younger extinct taxa would provide more information regarding the relationships between the extinct and extant Aulopiformes.

There were several more characters that could be modified or removed, such as the shape of the preopercle that included redundant states (e.g., L-shaped) with the other preopercle character (posteroventral spine developed). Several taxa also showed polymorphism or intrageneric variation in some characters, such as the dermal ornamentation of the dentary present in *Dercetis elongatus* and *D. magnificus* sp. nov. but absent in *D. triqueter*. Those characters/states as well as other potential modifications can be performed in future studies, but require access to each specimen, and the revision of coding will also be required in some taxa. Further, there are other possible characters to be added, such as the detailed morphology of the vertebrae among the Enchodontoidei, but the limited access to actual specimens of all taxa in this thesis prevented me from adding an extra character. Further character assessment remains until the future when I actually observe the specimens and can assess possible additional characters.

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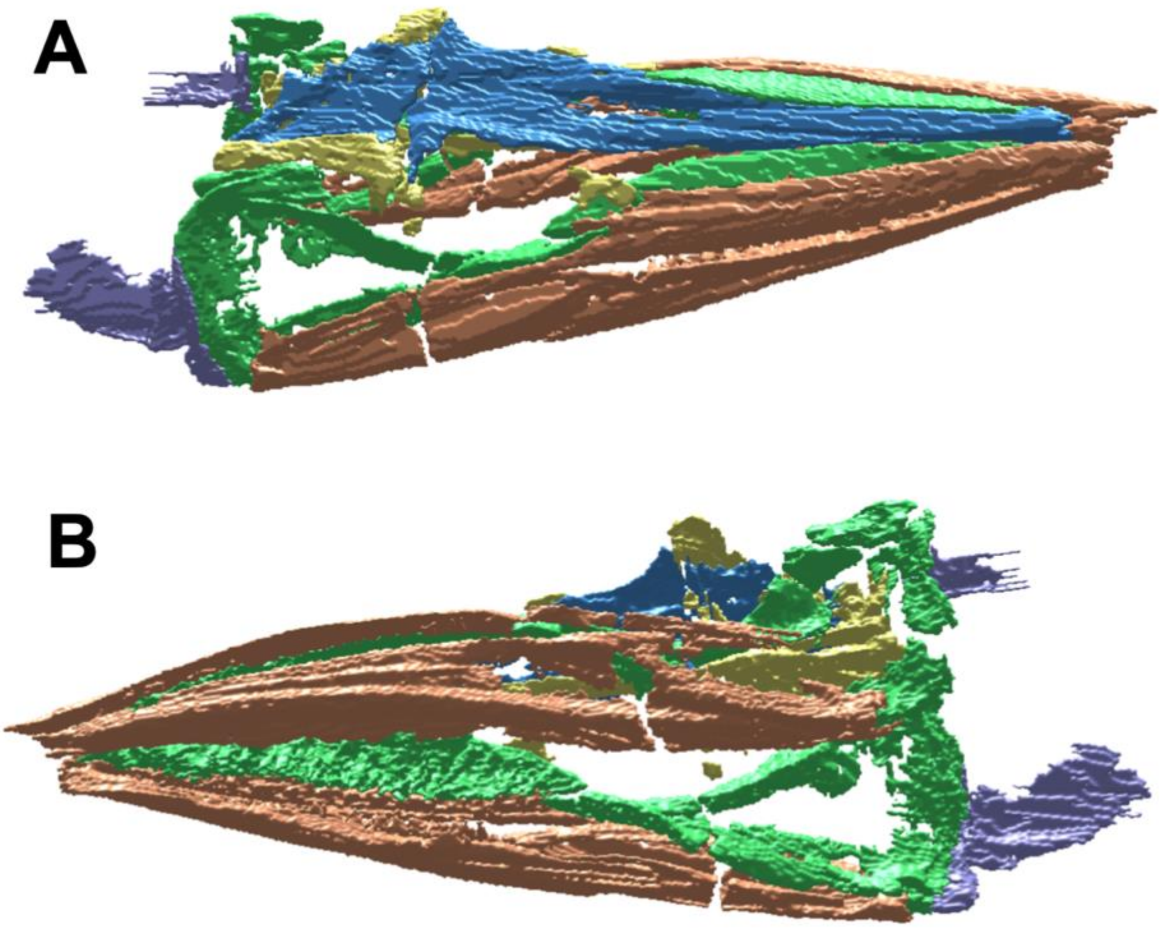
APPENDIX A: Chapter 2 “A large, new species of dercetid (Teleostei: Aulopiformes) from the Campanian Bearpaw Formation of Alberta, Canada.”

A.1 The data matrix modified from Murray et al. (2022) with addition of the *Dercetis magnificus* sp. nov.

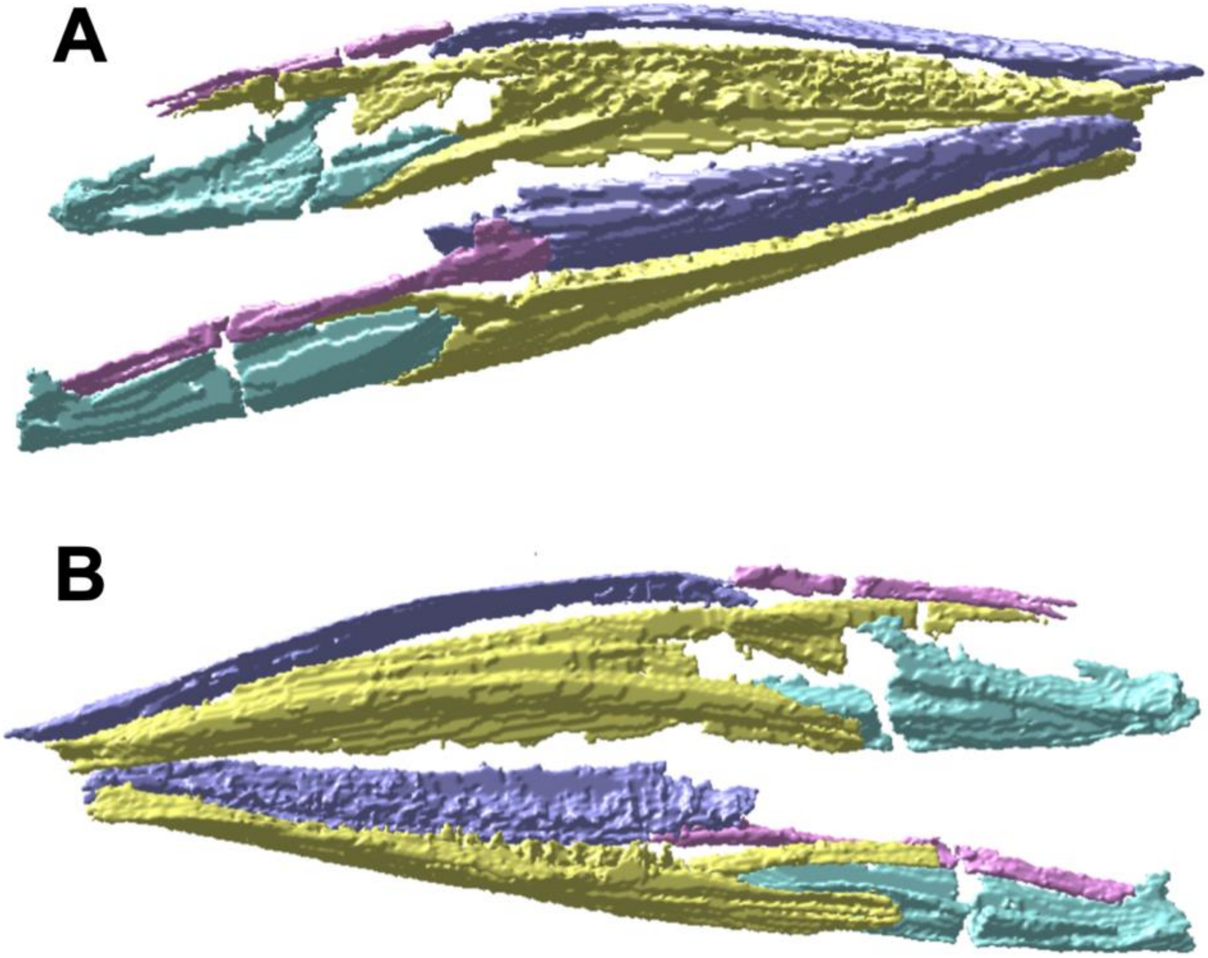
	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Sardinioides minimus	0	0	0	0	0	0	0	0	?	1	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	1	?	0	?	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0
Protostomias macroccanus	0	0	0	0	0	1	0	0	0	0	0	0	?	0	0	0	0	1	0	0	1	?	1	?	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
Trachinocephalus myops	0	0	0	3	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	?	0	0	0	1	?	2	0	0	2	1
Apateodus spp.	?	0	0	0	0	0	0	?	?	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	?	0	?	?	1	1	1	0	0	1	0	0	0	0	0	0	0	0	2	0
Apateopholis spp.	0	0	1	1	?	0	0	?	?	0	?	0	0	0	0	1	?	1	?	0	0	0	1	1	1	?	?	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Apuliadercetis spp.	2	1	1	0	1	0	0	?	?	0	0	0	0	1	1	0	0	0	0	0	1	?	0	?	0	1	3	1	0	0	1	0	0	1	0	0	1	1	1	2	0	0	0	1
Aspidopleurus spp.	0	0	0	3	1	0	0	?	?	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1
Atolvorator longipectoralis	0	0	0	0	0	?	?	0	?	?	?	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	2	0	1	1	0	0	0	1	0	?	0	1	0	0	1	0	0	0
Benthesikyme spp.	2	?	1	0	?	0	0	?	?	0	1	?	0	0	0	0	?	0	1	0	1	?	0	?	?	1	?	?	1	1	?	?	0	1	0	0	0	1	1	3	0	?	?	1
Brazilodercetis longirostris	?	1	1	2	?	0	0	?	0	0	1	0	0	0	0	0	0	0	0	0	1	?	1	?	?	1	3	0	0	0	1	0	1	1	0	0	0	1	1	2	0	1	1	1
Candelarhynchus padillai	?	1	1	0	?	?	?	0	1	?	1	?	?	1	?	0	0	0	0	0	0	1	0	0	0	?	-	1	?	?	0	0	1	1	1	0	0	1	1	0	0	1	0	0
Caudadercetis bannikovi	2	1	1	0	?	0	0	?	?	0	0	?	?	?	0	0	0	1	?	?	1	?	1	?	?	?	?	1	?	0	1	0	0	?	0	0	?	?	?	2	?	0	2	1
Cimolichthys spp.	0	0	0	2	1	0	0	?	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	?	1	1	1	0	1	0	0	1	0	0	0	0	0	1	0	2	0
Cyranichthys ornatissimus	1	1	1	2	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0	0	1	?	0	?	?	1	?	?	?	?	?	?	0	1	0	0	?	0	1	0	0	?	?	1
Dercetoides venator	2	1	1	1	?	?	?	?	1	0	0	0	?	1	0	1	0	1	0	0	1	0	1	?	?	1	?	0	0	0	1	0	0	1	0	0	?	1	1	3	0	0	1	0
Enchodus spp.	0	0	0	3	?	2	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0	?	?	?	?	?	?	1	1	?	1	0	?	?	?	?	?	0	0	0	1	0	0	1
Eurypholis spp.	0	0	0	1	1	2	1	?	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	2	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0	2	0
Halec spp.	0	0	0	1	0	0	0	?	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	?	?	0	?	1	1	1	1	1	0	0	1	0	0	1	0	2	1	0	1	1
Hastichthys gracilis	2	1	1	0	?	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	?	0	0	?	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	1	0	0
Hastichthys totonacus	2	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	?	0	0	0	1	1	1	1	?	?	0	1	1	1	0	0	1	1	0	0	1	0	0
Hemisaurida hakelensis	0	0	0	0	0	0	0	?	1	?	1	0	?	1	0	?	?	?	?	0	0	0	?	?	?	1	?	0	1	1	1	1	0	0	0	0	0	1	0	3	1	0	1	1
Ichthyotringa spp.	1	1	1	0	0	0	0	1	?	0	?	0	0	0	1	0	?	0	0	0	0	?	0	0	0	?	?	1	1	1	?	0	0	1	0	0	0	1	0	0	?	0	2	0
Nardodercetis vanderwallei	2	1	1	0	0	0	0	?	?	0	0	?	0	0	0	1	0	1	?	0	0	?	?	?	?	1	?	0	0	0	?	0	1	1	0	0	?	1	0	0	0	1	0	0
Nardorex zorzini	?	0	0	2	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	1	0	?	0	1	?	1	3	1	1	?	?	?	0	0	0	0	1	0	1	3	0	0	0	0
Ophidercetis italiensis	2	1	1	0	?	2	1	?	0	0	1	0	0	0	0	0	0	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	0	0	1	1	1	2	0	0	2	1
Pelargorhynchus dercetiformis	1	1	1	3	?	?	?	?	?	0	0	0	0	0	0	1	0	1	1	0	1	?	1	?	?	1	?	1	1	?	?	?	0	0	1	0	0	1	1	0	0	0	2	0
Palaeolycus dreginensis	1	0	0	2	?	2	1	?	1	?	?	0	?	1	0	?	?	1	?	?	1	?	1	?	?	?	?	1	1	0	?	?	0	0	0	1	0	0	1	0	?	0	0	1
Parenchodus longipterygius	0	0	0	3	?	2	?	1	?	0	1	0	1	1	0	1	1	1	0	0	1	0	1	0	?	1	?	0	1	1	?	1	0	0	1	0	1	0	0	3	0	0	2	1
Rharbichthys ferox	0	0	0	2	?	2	1	?	0	0	1	0	?	0	0	0	?	1	1	0	0	?	0	?	?	?	?	1	?	1	1	0	0	1	0	0	1	1	0	0	0	0	2	1
Rhynchodercetis spp.	2	1	1	0	0	0	0	?	0	0	0	1	0	0	1	1	0	1	0	0	1	?	1	?	?	1	?	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0
Saurorhamphus judeaensis	1	1	1	1	?	0	0	?	1	0	1	0	0	0	0	1	1	1	0	0	1	?	0	1	1	1	2	1	1	?	1	0	0	0	1	1	?	0	1	3	0	0	0	0
Serrilepis spp.	0	0	0	3	0	0	0	0	?	0	1	0	1	0	0	1	0	0	0	0	1	?	1	1	1	0	0	1	1	1	?	0	0	1	1	0	?	1	0	3	1	0	1	0
Phylactocephalus microlepis	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	0	0	1	1	?	?	?	?	1	1	?	0	1	0	0	1	0	0	1	0	2	1	0	1	1
Unicachichthys multidentata	0	0	0	3	1	0	0	?	?	?	?	?	0	?	?	?	1	?	1	?	0	?	?	?	?	1	?	1	1	?	?	?	0	0	1	?	1	0	1	2	1	0	0	1
Vegrandichthys coitecus	0	1	1	1	?	0	1	?	?	0	?	0	0	0	0	1	0	1	?	?	?	1	?	?	?	?	?	0	?	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1
Veridagon avendanoi	0	0	0	2	?	0	?	?	0	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	0	0	?	1	0	0	1	3	1	0	2	1
Yarbrudichthys striatus	0	0	1	1	0	1	0	1	?	?	?	0	0	0	0	?	?	?	?	0	1	0	1	0	?	?	?	0	0	0	?	1	0	1	0	0	?	1	?	0	0	0	0	0
Spinascutichthys pankowskiae	1	1	1	0	0	1	?	1	1	?	2	1	0	0	?	1	0	1	1	0	0	1	0	1	1	1	0	1	1	0	1	0	1	1	0	0	0	0	1	3	0	0	1	0
Dercetis elongatus	2	1	1	3	0	0	0	?	?	1	1	0	0	0	0	1	0	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	1	0	1	1	1	2	0	0	1	1
Dercetis triqueter	2	1	1	1	0	0	0	?	?	1	1	0	0	0	0	?	0	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	0	0	1	1	1	2	0	0	1	1
Dercetis magnificus sp. nov.	?	1	1	3	0	0	0	?	?	1	1	0	0	0	0	1	0	0	0	0	1	?	0	1	1	1	2	1	1	0	1	0	0	1	1	0	1	1	1	2	0	0	1	1

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
Sardinioides minimus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0
Protostomias macroccanus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	?	0	1	0	0	0	?	0	0	0	0	0	0	0	?	0	1	0	0	0	1	0	0	0
Trachinocephalus myops	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Apateodus spp.	0	0	0	0	2	0	0	0	1	0	0	3	0	0	0	1	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Apateopholis spp.	1	0	0	0	2	0	1	0	0	1	?	1	1	1	0	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	?	0	1	0	0	0
Apuliadercetis spp.	0	0	0	0	2	0	0	0	0	0	1	1	0	0	1	0	0	0	0	?	0	0	0	0	1	1	1	1	0	0	1	2	1	0	0	0	0	1	0	1	3	1	0
Aspidopleurus spp.	1	1	1	0	0	0	0	0	0	?	?	1	1	0	0	1	0	0	1	?	1	0	1	0	1	0	0	1	1	1	1	2	1	0	0	0	0	0	0	0	0	0	0
Atolvorator longipectoralis	0	0	1	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	?	?	0	0	1	0	0	0
Benthesikyme spp.	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	0	0	?	?	?	?	0	?	0	1	?	1	3	?	0
Brazilodercetis longirostris	1	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	1	3	2	?
Candelarhynchus padillai	1	?	?	0	2	0	1	0	0	1	0	2	0	0	1	0	0	0	0	?	0	?	?	?	1	0	1	0	?	?	0	2	1	0	?	?	?	?	?	1	0	0	0
Caudadercetis bannikovi	0	0	0	0	2	0	0	0	0	0	?	1	0	?	0	0	0	0	?	?	0	?	0	0	1	1	1	1	?	0	0	0	1	?	0	1	1	1	1	1	0	0	0
Cimolichthys spp.	0	0	1	0	2	1	0	0	0	1	?	1	0	0	0	1	0	1	1	?	?	0	0	0	?	0	0	1	0	?	1	?	1	0	?	0	?	1	0	1	2	2	0
Cyranichthys ornatissimus	0	0	?	?	?	?	?	?	?	?	?	1	0	0	1	0	0	0	?	0	?	?	?	?	?	0	1	?	?	?	?	?	1	1	?	?	?	?	?	1	1	2	0
Dercetoides venator	1	0	1	0	2	1	0	0	0	0	?	3	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	3	1	0
Enchodus spp.	0	?	1	1	1	0	?	0	1	0	?	1	1	0	0	1	0	1	1	0	0	0	1	1	1	?	0	1	0	0	1	2	1	?	?	1	0	0	?	1	0	0	1
Eurypholis spp.	0	0	0	0	0	1	0	1	1	?	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Halec spp.	0	0	1	0	0	1	0	0	0	?	?	1	1	0	0	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Hastichthys gracilis	1	0	1	0	2	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	?	0	0	0	1	1	1	1	0	0	?	0	1	0	0	1	0	1	1	1	3	1	0
Hastichthys totonacus	1	0	1	0	0	0	1	0	0	0	?	1	0	0	1	0	0	0	0	?	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	3	1	?
Hemisaurida hakelensis	1	0	0	0	2	0	0	0	0	1	?	2	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	2	1	0	0	0	0	0	0	1	0	0	0
Ichthyotringa spp.	0	0	1	0	?	0	1	0	0	1	?	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Nardodercetis vanderwallei	1	0	0	0	2	0	0	0	0	0	0	?	?	?	1	?	0	0	?	0	0	0	0	0	1	1	1	1	0	0	1	1	0	?	?	0	0	0	1	1	3	1	0
Nardorex zorzini	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	?	1	0	0	0	0	0	1	0	0	0	0	1	?	?	?	1	0	0	0
Ophidercetis italiensis	0	0	1	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	0	0	0	2	0	1	0	1	0	?	?	1	1	2	0
Pelargorhynchus dercetiformis	1	0	0	0	?	1	?	0	0	?	?	1	?	0	0	0	?	0	1	0	?	?	0	?	?	0	1	1	?	?	1	?	1	1	?	0	?	?	?	0	2	2	0
Palaeolycus dreginensis	0	0	1	0	1	1	1	0	1	0	?	?	1	0	0	1	0	1	1	0	?	0	0	0	1	?	0	1	0	0	1	2	0	0	0	1	0	?	?	1	0	0	1
Parenchodus longipterygius	0	0	1	1	2	1	1	0	1	0	1	1	1	0	0	1	0	1	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	1	0	1	0	1	0	1	0	0	1
Rharbichthys ferox	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	?	0	0	0	0	1	2	1	0	0	0	1	0	0	1	4	1	0
Rhynchodercetis spp.	1	0	0	0	0	0	0	0	0	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?	0	0	0	2	1	1	0	0	0	1	1	1	3	1	0
Saurorhamphus judeaensis	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	2	0	0	0	1	0	0	0	0	1	1	1
Serrilepis spp.	1	0	1	0	?	1	1	0	1	0	1	1	1	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0
Phylactocephalus microlepis	1	0	0	0	2	1	0	0	0	0	?	1	1	0	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Unicachichthys multidentata	0	0	1	1	2	1	?	0	1	0	?	1	1	1	0	1	0	1	1	?	?	0	1	1	1	?	0	0	0	0	1	2	1	0	0	0	0	1	0	1	0	0	1
Vegrandichthys coitecus	0	0	1	0	0	1	1	0	1	0	?	1	1	0	0	1	?	1	1	?	?	0	?	?	?	?	0	?	?	?	0	2	0	0	?	?	?	?	?	1	1	1	1
Veridagon avendanoi	0	0	0	1	0	1	1	0	1	0	?	1	1	0	0	1	?	1	1	?	?	0	1	0	1	?	0	0	1	0	1	2	0	0	0	1	0	1	0	1	2	1	1
Yarbrudichthys striatus	0	0	0	0	?	1	1	0	1	0	?	1	1	1	1	?	0	0	1	1	0	0	1	0	0	?	0	1	0	0	1	2	1	1	1	0	0	1	0	1	0	0	0
Spinascutichthys pankowskiae	0	0	0	1	0	0	1	0	0	1	0	2	0	1	1	1	1	0	1	?	1	?	1	0	?	0	?	?	?	?	0	0	0	0	1	1	0	1	?	1	?	1	1
Dercetis elongatus	1	0	1	0	2	1	1	0	0	1	?	1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	1	1	0	0	0	0	1	?	0	?	?	?	?	1	3	2	0
Dercetis triqueter	1	1	1	0	2	0	1	0	0	1	?	1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	1	0	1	3	2	0
Dercetis magnificus sp. nov.	1	1	1	0	1	1	0	0	0	0	?	0	0	0	?	?	?	0	0	?	?	?	0	?	?	0	1	1	0	0	1	0	?	?	?	?	?	?	?	1	3	2	0

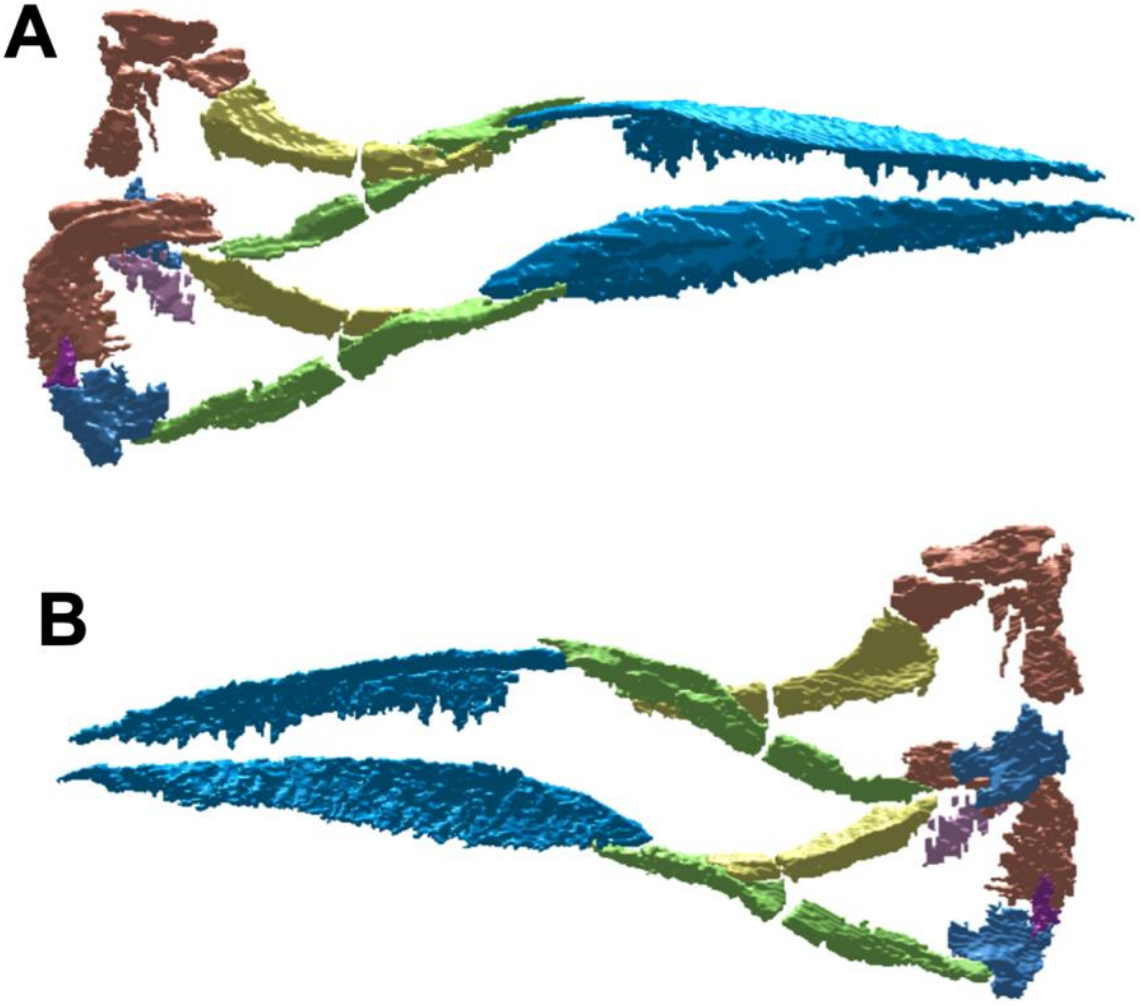
A.2 The reconstruction from the CT images of the head of the holotype. **A**, Right dorsolateral view. **B**, Left ventrolateral view. **Blue** = frontal, parietal, mesethmoid; **Green** = palatine, ectopterygoid, endopterygoid, metapterygoid, quadrate, symplectic, hyomandibula; **Orange** = premaxilla, maxilla, dentary, anguloarticular; **Purple** = opercle, subopercle, interopercle; **Yellow** = lacrimal, sphenotic, pterotic, prootic, pterosphenoid, parasphenoid, basioccipital, supraoccipital, epioccipital.



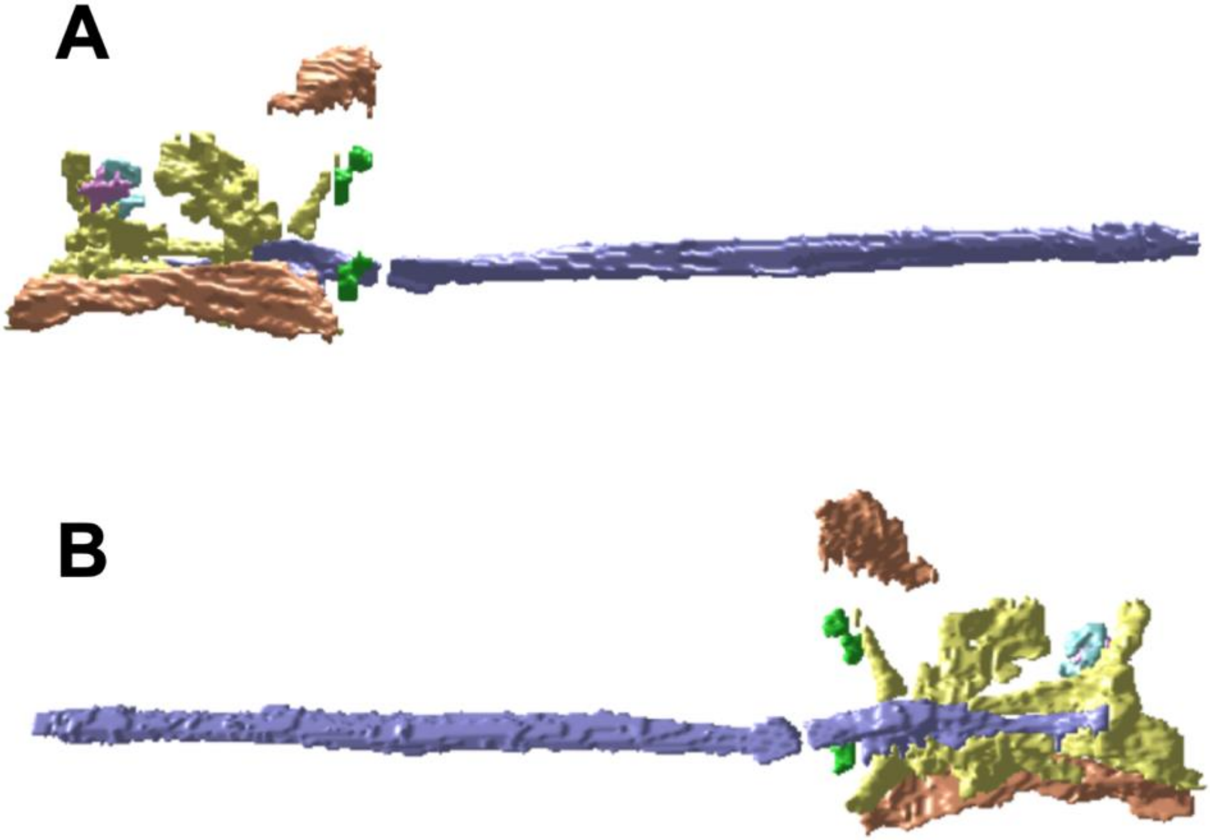
A.3 The reconstruction from the CT images of the upper and lower jaws. **A**, Right dorsolateral view. **B**, Left ventrolateral view. **Purple** = premaxilla; **Pink** = maxilla; **Yellow** = dentary; **Blue** = anguloarticular.



A.4 The reconstruction from the CT images of the hyopalatine bones. **A**, Right dorsolateral view. **B**, Left ventrolateral view. **Orange** = hyomandibula; **Blue** = palatine; **Green** = ectopterygoid; **Yellow** = endopterygoid; **Pink** = metapterygoid; **Purple** = symplectic.



A.5 The reconstruction from the CT images of the neurocraniam. **A**, Right dorsolateral view. **B**, Ventral view. **Orange** = pterotic; **Yellow** = prootic, basioccipital; **Blue** = epioccipital; **Green** = pterosphenoid; **Pink** = supraoccipital; **Purple** = parasphenoid.



APPENDIX B: Chapter 3 “Phylogeny of the Enchodontoidei”

B.1 Characters and states from the previous studies based on the most recent work (Murray et al., 2022).

1. Body length: [0] slightly elongate (lesser than or equal to 1:10); [1] elongate (from 1:11 to 1:15); [2] very elongate (higher than 1:15).
2. Head height: [0] deep; [1] low.
3. Snout length: [0] short; [1] long.
4. Dermal pattern on skull roof: [0] smooth; [1] only with tubercles; [2] only with ridges; [3] tubercles + ridges.
5. Vomerine teeth: [0] absent; [1] present.
6. Number of teeth on dermopalatine: [0] two or more; [1] none; [2] single.
7. Dermopalatine length: [0] twice or more times longer than its tooth; [1] equal-sized or shorter than its tooth.
8. Antorbital: [0] present; [1] absent.
9. Nasal: [0] present; [1] absent.
10. Anterior extremity of mesethmoid: [0] acute; [1] bifid.
11. Posterior extremity of mesethmoid: [0] bifid; [1] acute; [2] straight.
12. Autosphenotic spine: [0] straight; [1] posteriorly curved.
13. Suture between frontals: [0] slightly sinuous; [1] markedly sinuous.
14. Posterior border of frontal: [0] behind the autosphenotic spine; [1] at the level of the autosphenotic spine.
15. Shape of the posterior border of the orbit: [0] concave; [1] convex.
16. Parietal length: [0] long (length equal or larger than its height); [1] short (length smaller than its height).
17. Supraorbital sensory canal in the skull roof: [0] covered; [1] exposed.
18. Extension of the supraoccipital: [0] not separating parietals; [1] separating parietals.
19. Supraoccipital crest: [0] present; [1] absent.
20. Supraoccipital with two well-delimited regions: [0] absent; [1] present.

21. Extension of pterotic: [0] not projecting backwards beyond the level of occiput; [1] projecting beyond the occiput.
22. Dilatator fossa: [0] unroofed; [1] roofed.
23. Exposition of the post-temporal fossa: [0] roofed; [1] unroofed.
24. Orbitosphenoid: [0] present; [1] absent.
25. Basisphenoid: [0] present; [1] absent.
26. Supraorbital: [0] present; [1] absent.
27. Lachrymal shape: [0] subtriangular; [1] suboval; [2] trapezoidal; [3] rod-shaped.
28. Position of the mandibular suspensorium: [0] inclined; [1] vertical.
29. Ectopterygoid: [0] toothless; [1] toothed.
30. Endopterygoid: [0] toothless; [1] toothed.
31. Placement of articular facet for the hyomandibula: [0] posteroventral; [1] ventral.
32. Number of articular facets for the hyomandibula: [0] a continuous facet; [1] two facets.
33. Premaxilla: [0] toothed; [1] toothless.
34. Posterior extension of the premaxilla: [0] reaching the orbit; [1] not reaching the orbit.
35. Dermal pattern on premaxilla: [0] smooth, [1] ornamented.
36. Fenestra in the premaxilla: [0] absent; [1] present.
37. Ascending process of the premaxilla: [0] absent; [1] present.
38. Maxilla: [0] toothless; [1] toothed.
39. Placement of the maxilla: [0] over the premaxilla; [1] behind the premaxilla.
40. Teeth on upper jaw: [0] only straight; [1] absent; [2] curved + straight; [3] only curved.
41. Supramaxilla: [0] absent; [1] present.
42. Mandible length: [0] equal to the snout; [1] shorter than the snout.
43. Teeth on mandible: [0] only straight; [1] only curved; [2] curved + straight.
44. Teeth size on upper jaw: [0] absent or with same height; [1] with different height.
45. Teeth size on mandible: [0] different height; [1] equal height.
46. Rows of teeth on upper jaw: [0] single; [1] two or more.
47. Rows of teeth on mandible: [0] single; [1] two or more.
48. Anteroventral prongs on dentary: [0] absent; [1] present.
49. Mandibular sensory canal: [0] enclosed by bone; [1] partially open; [2] open.
50. Mandibular dermal pattern: [0] smooth, [1] ornamented.

51. Flange on anguloarticular: [0] present; [1] absent.
52. Quadrate-mandibular articulation: [0] exposed; [1] hidden.
53. Articular facet for the quadrate: [0] shallow; [1] deep.
54. Retroarticular process: [0] present, [1] absent.
55. Ornamentation in the infraorbital bones: [0] smooth, [1] ornamented.
56. Preopercle shape: [0] L-shaped; [1] triangular; [2] crescent-shaped; [3] rod-shaped; [4] pipe-shaped.
57. Preopercular dermal pattern: [0] smooth; [1] ornamented.
58. Posteroventral spine in the preopercle: [0] absent or reduced, [1] well-developed.
59. Dimension of the opercle: [0] deeper than long; [1] longer than deep.
60. Opercle crest: [0] absent; [1] present.
61. Spine on posterior border of the opercle: [0] absent; [1] present.
62. Opercular and subopercular dermal pattern: [0] smooth; [1] ornamented.
63. Interopercle: [0] present; [1] absent.
64. Mesocoracoid: [0] absent; [1] present.
65. Scapula and coracoid: [0] individualized; [1] co-ossified.
66. Supraneurals: [0] present; [1] absent.
67. Total number of vertebrae: [0] more than 50; [1] equal or minus than 50.
68. Number of caudal vertebrae: [0] more than 20; [1] equal or minus than 20.
69. Ribs: [0] extending to the pelvic fin origin; [1] surpassing the pelvic fin origin.
70. Transverse processes: [0] one pair; [1] two pairs.
71. Neural spines: [0] well-developed (their length surpassing the length of the vertebral centrum); [1] very reduced (their length equal or minus than half of the length of the vertebral centrum).
72. Neural spines bifid in the abdominal region: [0] present; [1] absent.
73. Distribution of epipleurals: [0] extending to more than a half of the body; [1] up to half of the body.
74. Distribution of epineurals: [0] extending to more than a half of the body; [1] up to half of the body.

75. Position of the pectoral fin: [0] high (last fin-ray placed at the level of the ventral border of the opercle or a little above); [1] low (last fin-ray placed below the level of the ventral border of the opercle).
76. Orientation of the pectoral fin base: [0] vertical; [1] horizontal; [2] inclined.
77. Origin of the pelvic fin: [0] anterior to the dorsal fin; [1] opposite or posterior to the dorsal fin.
78. Dorsal fin length: [0] short (lesser than 20 rays); [1] long (more than 20 rays).
79. Shape of the first proximal pterygiophore of the dorsal fin: [0] different from the remnants; [1] all equal in shape.
80. Anal fin length: [0] short (up to 15 rays); [1] long (more than 15 rays).
81. Anal fin edge: [0] not serrated; [1] serrated.
82. Fusion of hypurals: [0] free; [1] fused.
83. Contact between hypurals 2-3: [0] free; [1] with convoluted suture.
84. Body scales: [0] present; [1] absent.
85. Flank scutes: [0] absent; [1] triangular; [2] cordiform; [3] tripartite; [4] rectangular.
86. Number of rows of scutes on flanks: [0] absent; [1] single; [2] two or more.
87. Middorsal scutes: [0] absent; [1] present.

B.2 Characters and states modified from the previous studies. The modified characters and states are bolded.

1. Body length: [0] slightly elongate (lesser than or equal to 1:10); [1] elongate (from 1:11 to 1:15); [2] very elongate (higher than 1:15).
2. Head height: [0] deep; [1] low.
3. Snout length: [0] short; [1] long.
4. **Dermal pattern on skull roof: [0] smooth; [1] ornamented.**
5. Vomerine teeth: [0] absent; [1] present.
6. Number of teeth on dermopalatine: [0] two or more; [1] none; [2] single.
7. Dermopalatine length: [0] twice or more times longer than its tooth; [1] equal-sized or shorter than its tooth.
8. Antorbital: [0] present; [1] absent.
9. Nasal: [0] present; [1] absent.
10. Anterior extremity of mesethmoid: [0] acute; [1] bifid.
11. **Posterior extremity of mesethmoid: [0] bifid; [1] not-bifid (acute or straight)**.
12. Autosphenotic spine: [0] straight; [1] posteriorly curved.
13. Suture between frontals: [0] slightly sinuous; [1] markedly sinuous.
14. Posterior border of frontal: [0] behind the autosphenotic spine; [1] at the level of the autosphenotic spine.
15. Shape of the posterior border of the orbit: [0] concave; [1] convex.
16. Parietal length: [0] long (length equal or larger than its height); [1] short (length smaller than its height).
17. Supraorbital sensory canal in the skull roof: [0] covered; [1] exposed.
18. Extension of the supraoccipital: [0] not separating parietals; [1] separating parietals.
19. Supraoccipital crest: [0] present; [1] absent.
20. Extension of pterotic: [0] not projecting backwards beyond the level of occiput; [1] projecting beyond the occiput.
21. Dilatator fossa: [0] unroofed; [1] roofed.
22. Exposition of the post-temporal fossa: [0] roofed; [1] unroofed.

23. Orbitosphenoid: [0] present; [1] absent.
24. Basisphenoid: [0] present; [1] absent.
25. Supraorbital: [0] present; [1] absent.
26. Lachrymal shape: [0] subtriangular; [1] suboval; [2] trapezoidal; [3] rod-shaped.
27. Position of the mandibular suspensorium: [0] inclined; [1] vertical.
28. Ectopterygoid tooth: [0] absent [1] present.
29. Endopterygoid tooth: [0] absent [1] present.
30. Placement of articular facet for the hyomandibula: [0] posteroventral; [1] ventral.
31. Number of articular facets for the hyomandibula: [0] a continuous facet; [1] two facets.
32. Premaxillary tooth: [0] present; [1] absent.
33. Posterior extension of the premaxilla: [0] reaching the orbit; [1] not reaching the orbit.
34. Dermal pattern on premaxilla: [0] smooth, [1] ornamented.
35. Fenestra on the premaxilla: [0] absent; [1] present.
36. Ascending process of the premaxilla: [0] absent; [1] present.
37. Maxillary tooth: [0] absent; [1] present.
38. Position of the maxilla: [0] excluded from gape; [1] included in gape.
39. Teeth on upper jaw: [0] only straight; [1] absent; [2] curved + straight; [3] only curved.
40. Supramaxilla: [0] absent; [1] present.
41. Mandible length: [0] equal to the snout; [1] shorter than the snout; [2] longer than the snout.
42. Teeth on mandible: [0] only straight; [1] only curved; [2] curved + straight.
43. Teeth size on upper jaw: [0] absent or with same height; [1] with different height.
44. Teeth size on mandible: [0] different height; [1] equal height.
45. Number of rows of teeth on upper jaw: [0] single; [1] two or more.
46. Number of rows of teeth on mandible: [0] single; [1] two or more.
47. Anteroventral prongs on dentary: [0] absent; [1] present.
48. Mandibular sensory canal: [0] enclosed by bone; [1] partially open; [2] open.
49. Mandibular dermal pattern: [0] smooth, [1] ornamented.
50. Flange on anguloarticular: [0] present; [1] absent.
51. Extension of the posterior end of anguloarticular: [0] absent; [1] present.
52. Articular facet for the quadrate: [0] shallow; [1] deep.

53. Retroarticular process: [0] present, [1] absent.

54. Ornamentation in the infraorbital bones: [0] smooth, [1] ornamented.

55. Preopercular shape: [0] L-shaped; [1] triangular; [2] crescent-shaped; [3] rod-shaped; [4] pipe-shaped.

56. Preopercular dermal pattern: [0] smooth; [1] ornamented.

57. Posteroventral spine on the preopercle: [0] absent or reduced, [1] well-developed.

58. Dimension of the opercle: [0] deeper than long; [1] longer than deep.

59. Opercular crest: [0] absent; [1] present.

60. Spine on posterior border of the opercle: [0] absent; [1] present.

61. Opercular and subopercular dermal pattern: [0] smooth; [1] ornamented.

62. Interopercle: [0] present; [1] absent.

63. Mesocoracoid: [0] absent; [1] present.

64. Scapula and coracoid: [0] individualized; [1] co-ossified.

65. Supraneurals: [0] present; [1] absent.

66. Total number of vertebrae: [0] more than 50; [1] equal or minus than 50.

67. Number of caudal vertebrae: [0] more than 20; [1] equal or minus than 20.

68. Ribs: [0] extending to the pelvic fin origin; [1] surpassing the pelvic fin origin.

69. Transverse processes: [0] one pair; [1] two pairs.

70. Neural spines: [0] well-developed (their length surpassing the length of the vertebral centrum); [1] very reduced (their length equal or minus than half of the length of the vertebral centrum).

71. Neural spines bifid in the abdominal region: [0] present; [1] absent.

72. Distribution of epipleurals: [0] extending to more than a half of the body; [1] up to half of the body.

73. Distribution of epineurals: [0] extending to more than a half of the body; [1] up to half of the body.

74. Position of the pectoral fin: [0] high (last fin-ray placed at the level of the ventral border of the opercle or a little above); [1] low (last fin-ray placed below the level of the ventral border of the opercle).

75. Orientation of the pectoral fin base: [0] vertical; [1] horizontal; [2] inclined.

76. Origin of the pelvic fin: [0] anterior to the dorsal fin; [1] opposite or posterior to the dorsal fin.
77. Dorsal fin length: [0] short (lesser than 20 rays); [1] long (more than 20 rays).
78. Shape of the first proximal pterygiophore of the dorsal fin: [0] different from the remnants; [1] all equal in shape.
79. Anal fin length: [0] short (up to 15 rays); [1] long (more than 15 rays).
80. Anal fin edge: [0] not serrated; [1] serrated.
81. Fusion of hypurals: [0] free; [1] fused.
82. Contact between hypurals 2-3: [0] free; [1] with convoluted suture.
83. Body scales: [0] present; [1] absent.
84. **Flank scutes: [0] absent; [1] cordiform; [2] triradiate (radiating to three direcitons); [3] polygonal (radiating to more than three directions, such as rhomboid, rectangular, pentagonal, hexagonal).**
85. Number of rows of scutes on flanks: [0] absent; [1] single; [2] two or more.
86. Middorsal scutes: [0] absent; [1] present.

B.3 The preexisting character matrix based on Alvarado-Ortega and Díaz-Cruz (2020) and Murray et al. (2022) with addition of *Dercetis magnificus* sp. nov. and *Stratodus apicalis*.

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
Protostomias macroccanus	0	0	0	0	0	1	0	0	0	0	0	0	?	0	0	0	0	1	0	0	1	?	1	?	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	?	0	1	0	0	0	?	0	0	0	0	0	0	0	?	0	1	0	0	0	1	0	0	0
Trachinocephalus myops	0	0	0	3	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	?	0	0	0	1	?	2	0	0	2	1	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lestidium prolixum	1	0	1	3	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	3	0	0	2	1	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	?	0	0	1	0	0	0
Lestrolepis japonica	1	0	1	2	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	3	1	0	2	1	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
Apateodus spp.	?	0	0	0	0	0	0	?	?	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	?	0	?	?	1	1	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	1	0	0	3	0	0	0	1	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Apateopholis spp.	0	0	1	1	?	0	0	?	?	0	?	0	0	0	0	1	?	1	?	0	0	0	1	1	1	?	?	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2	0	1	0	0	1	?	1	1	1	0	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	?	0	1	0	0	0
Apuliadercetis spp.	2	1	1	0	1	0	0	?	?	0	0	0	0	1	1	0	0	0	0	0	1	?	0	?	0	1	3	1	0	0	1	0	0	1	0	0	1	1	1	2	0	0	0	1	0	0	0	0	2	0	0	0	0	0	1	1	0	0	1	0	0	0	0	?	0	0	0	0	1	1	1	1	0	0	1	2	1	0	0	0	0	1	0	1	3	1	0
Aspidopleurus spp.	0	0	0	3	1	0	0	?	?	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	?	?	1	1	0	0	1	0	0	1	?	1	0	1	0	1	0	0	1	1	1	1	2	1	0	0	0	0	0	0	0	0	0	0
Atolvorator longipectoralis	0	0	0	0	0	?	?	0	?	?	?	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	2	0	1	1	0	0	0	1	0	?	0	1	0	0	1	0	0	0	0	0	1	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	?	?	0	0	1	0	0	0
Benthesikyme spp.	2	?	1	0	?	0	0	?	?	0	1	?	0	0	0	0	?	0	1	0	1	?	0	?	?	1	?	?	1	1	?	?	0	1	0	0	0	1	1	3	0	?	?	1	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	0	0	?	?	?	?	0	?	0	1	?	1	3	?	0
Brazilodercetis longirostris	?	1	1	2	?	0	0	?	0	0	1	0	0	0	0	0	0	0	0	0	1	?	1	?	?	1	3	0	0	0	1	0	1	1	0	0	0	1	1	2	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	1	3	2	?
Candelarhynchus padillai	?	1	1	0	?	?	?	0	1	?	1	?	?	1	?	0	0	0	0	0	0	1	0	0	0	?	-	1	?	?	0	0	1	1	1	0	0	1	1	0	0	1	0	0	1	?	?	0	2	0	1	0	0	1	0	2	0	0	1	0	0	0	0	?	0	?	?	?	1	0	1	0	?	?	0	2	1	0	?	?	?	?	?	1	0	0	0
Caudadercetis bannikovi	2	1	1	0	?	0	0	?	?	0	0	?	?	?	0	0	0	1	?	?	1	?	1	?	?	?	?	1	?	0	1	0	0	?	0	0	?	?	?	2	?	0	2	1	0	0	0	0	2	0	0	0	0	0	?	1	0	?	0	0	0	0	?	?	0	?	0	0	1	1	1	1	?	0	0	0	1	?	0	1	1	1	1	1	0	0	0
Cimolichthys spp.	0	0	0	2	1	0	0	?	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	?	1	1	1	0	1	0	0	1	0	0	0	0	0	1	0	2	0	0	0	1	0	2	1	0	0	0	1	?	1	0	0	0	1	0	1	1	?	?	0	0	0	?	0	0	1	0	?	1	?	1	0	?	0	?	1	0	1	2	2	0
Cyranichthys ornatissimus	1	1	1	2	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0	0	1	?	0	?	?	1	?	?	?	?	?	?	0	1	0	0	?	0	1	0	0	?	?	1	0	0	?	?	?	?	?	?	?	?	?	1	0	0	1	0	0	0	?	0	?	?	?	?	?	0	1	?	?	?	?	?	1	1	?	?	?	?	?	1	1	2	0
Dercetoides venator	2	1	1	1	?	?	?	?	1	0	0	0	?	1	0	1	0	1	0	0	1	0	1	?	?	1	?	0	0	0	1	0	0	1	0	0	?	1	1	3	0	0	1	0	1	0	1	0	2	1	0	0	0	0	?	3	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	3	1	0
Enchodus spp.	0	0	0	3	?	2	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0	?	?	?	?	?	?	1	1	?	1	0	?	?	?	?	?	0	0	0	1	0	0	1	0	?	1	1	1	0	?	0	1	0	?	1	1	0	0	1	0	1	1	0	0	0	1	1	1	?	0	1	0	0	1	2	1	?	?	1	0	0	?	1	0	0	1
Eurypholis spp.	0	0	0	1	1	2	1	?	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	2	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0	2	0	0	0	0	0	0	1	0	1	1	?	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Halec spp.	0	0	0	1	0	0	0	?	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	?	?	0	?	1	1	1	1	1	0	0	1	0	0	1	0	2	1	0	1	1	0	0	1	0	0	1	0	0	0	?	?	1	1	0	0	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Hastichthys gracilis	2	1	1	0	?	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	?	0	0	?	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	2	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	?	0	0	0	1	1	1	1	0	0	?	0	1	0	0	1	0	1	1	1	3	1	0
Hastichthys totonacus	2	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	?	0	0	0	1	1	1	1	?	?	0	1	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	?	1	0	0	1	0	0	0	0	?	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	3	1	?
Hemisaurida hakelensis	0	0	0	0	0	0	0	?	1	?	1	0	?	1	0	?	?	?	?	0	0	0	?	?	?	1	?	0	1	1	1	1	0	0	0	0	0	1	0	3	1	0	1	1	1	0	0	0	2	0	0	0	0	1	?	2	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	2	1	0	0	0	0	0	0	1	0	0	0
Ichthyotringa spp.	1	1	1	0	0	0	0	1	?	0	?	0	0	0	1	0	?	0	0	0	0	?	0	0	0	?	?	1	1	1	?	0	0	1	0	0	0	1	0	0	?	0	2	0	0	0	1	0	?	0	1	0	0	1	?	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Nardodercetis vanderwallei	2	1	1	0	0	0	0	?	?	0	0	?	0	0	0	1	0	1	?	0	0	?	?	?	?	1	?	0	0	0	?	0	1	1	0	0	?	1	0	0	0	1	0	0	1	0	0	0	2	0	0	0	0	0	0	?	?	?	1	?	0	0	?	0	0	0	0	0	1	1	1	1	0	0	1	1	0	?	?	0	0	0	1	1	3	1	0
Nardorex zorzini	?	0	0	2	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	1	0	?	0	1	?	1	3	1	1	?	?	?	0	0	0	0	1	0	1	3	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	?	1	0	0	0	0	0	1	0	0	0	0	1	?	?	?	1	0	0	0
Ophidercetis italiensis	2	1	1	0	?	2	1	?	0	0	1	0	0	0	0	0	0	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	0	0	1	1	1	2	0	0	2	1	0	0	1	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	0	0	0	2	0	1	0	1	0	?	?	1	1	2	0
Pelargorhynchus dercetiformis	1	1	1	3	?	?	?	?	?	0	0	0	0	0	0	1	0	1	1	0	1	?	1	?	?	1	?	1	1	?	?	?	0	0	1	0	0	1	1	0	0	0	2	0	1	0	0	0	?	1	?	0	0	?	?	1	?	0	0	0	?	0	1	0	?	?	0	?	?	0	1	1	?	?	1	?	1	1	?	0	?	?	?	0	2	2	0
Palaeolycus dreginensis	1	0	0	2	?	2	1	?	1	?	?	0	?	1	0	?	?	1	?	?	1	?	1	?	?	?	?	1	1	0	?	?	0	0	0	1	0	0	1	0	?	0	0	1	0	0	1	0	1	1	1	0	1	0	?	?	1	0	0	1	0	1	1	0	?	0	0	0	1	?	0	1	0	0	1	2	0	0	0	1	0	?	?	1	0	0	1
Parenchodus longipterygius	0	0	0	3	?	2	?	1	?	0	1	0	1	1	0	1	1	1	0	0	1	0	1	0	?	1	?	0	1	1	?	1	0	0	1	0	1	0	0	3	0	0	2	1	0	0	1	1	2	1	1	0	1	0	1	1	1	0	0	1	0	1	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	1	0	1	0	1	0	1	0	0	1
Rharbichthys ferox	0	0	0	2	?	2	1	?	0	0	1	0	?	0	0	0	?	1	1	0	0	?	0	?	?	?	?	1	?	1	1	0	0	1	0	0	1	1	0	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	?	0	0	0	0	1	2	1	0	0	0	1	0	0	1	4	1	0
Rhynchodercetis spp.	2	1	1	0	0	0	0	?	0	0	0	1	0	0	1	1	0	1	0	0	1	?	1	?	?	1	?	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?	0	0	0	2	1	1	0	0	0	1	1	1	3	1	0
Saurorhamphus judeaensis	1	1	1	1	?	0	0	?	1	0	1	0	0	0	0	1	1	1	0	0	1	?	0	1	1	1	2	1	1	?	1	0	0	0	1	1	?	0	1	3	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	2	0	0	0	1	0	0	0	0	1	1	1
Serrilepis spp.	0	0	0	3	0	0	0	0	?	0	1	0	1	0	0	1	0	0	0	0	1	?	1	1	1	0	0	1	1	1	?	0	0	1	1	0	?	1	0	3	1	0	1	0	1	0	1	0	?	1	1	0	1	0	1	1	1	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0
Phylactocephalus microlepis	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	0	0	1	1	?	?	?	?	1	1	?	0	1	0	0	1	0	0	1	0	2	1	0	1	1	1	0	0	0	2	1	0	0	0	0	?	1	1	0	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Unicachichthys multidentata	0	0	0	3	1	0	0	?	?	?	?	?	0	?	?	?	1	?	1	?	0	?	?	?	?	1	?	1	1	?	?	?	0	0	1	?	1	0	1	2	1	0	0	1	0	0	1	1	2	1	?	0	1	0	?	1	1	1	0	1	0	1	1	?	?	0	1	1	1	?	0	0	0	0	1	2	1	0	0	0	0	1	0	1	0	0	1
Vegrandichthys coitecus	0	1	1	1	?	0	1	?	?	0	?	0	0	0	0	1	0	1	?	?	?	1	?	?	?	?	?	0	?	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	?	1	1	0	0	1	?	1	1	?	?	0	?	?	?	?	0	?	?	?	0	2	0	0	?	?	?	?	?	1	1	1	1
Veridagon avendanoi	0	0	0	2	?	0	?	?	0	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	0	0	?	1	0	0	1	3	1	0	2	1	0	0	0	1	0	1	1	0	1	0	?	1	1	0	0	1	?	1	1	?	?	0	1	0	1	?	0	0	1	0	1	2	0	0	0	1	0	1	0	1	2	1	1
Yarbrudichthys striatus	0	0	1	1	0	1	0	1	?	?	?	0	0	0	0	?	?	?	?	0	1	0	1	0	?	?	?	0	0	0	?	1	0	1	0	0	?	1	?	0	0	0	0	0	0	0	0	0	?	1	1	0	1	0	?	1	1	1	1	?	0	0	1	1	0	0	1	0	0	?	0	1	0	0	1	2	1	1	1	0	0	1	0	1	0	0	0
Spinascutichthys pankowskiae	1	1	1	0	0	1	?	1	1	?	2	1	0	0	?	1	0	1	1	0	0	1	0	1	1	1	0	1	1	0	1	0	1	1	0	0	0	0	1	3	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	2	0	1	1	1	1	0	1	?	1	?	1	0	?	0	?	?	?	?	0	0	0	0	1	1	0	1	?	1	?	1	1
Dercetis elongatus	2	1	1	3	0	0	0	?	?	1	1	0	0	0	0	1	0	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	1	0	1	1	1	2	0	0	1	1	1	0	1	0	2	1	1	0	0	1	?	1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	1	1	0	0	0	0	1	?	0	?	?	?	?	1	3	2	0
Dercetis triqueter	2	1	1	1	0	0	0	?	?	1	1	0	0	0	0	?	0	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	0	0	1	1	1	2	0	0	1	1	1	1	1	0	2	0	1	0	0	1	?	1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	1	0	1	3	2	0
Dercetis magnificus sp. nov.	?	1	1	3	0	0	0	?	?	1	1	0	0	0	0	1	0	0	0	0	1	?	0	1	1	1	2	1	1	0	1	0	0	1	1	0	1	1	1	2	0	0	1	1	1	1	1	0	1	1	0	0	0	0	?	0	0	0	?	?	?	0	0	?	?	?	0	?	?	0	1	1	0	0	1	0	?	?	?	?	?	?	?	1	3	2	0
Stratodus apicalis SDSM81334	2	?	?	?	?	0	0	?	?	?	?	0	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	?	0	1	?	?	0	?	?	1	1	?	?	?	1	?	1	3	2	0

B.4 The modified character matrix with six modified characters with changes on the character states of some taxa (see 3.3.4 Changes to character coding).

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86
Protostomias macroccanus	0	0	0	0	0	1	0	0	0	0	0	0	?	0	0	0	0	1	0	1	?	1	?	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	?	0	1	0	0	0	?	0	0	0	0	0	0	0	?	0	1	0	0	0	1	0	0	0
Trachinocephalus myops	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	?	0	0	0	1	0	2	0	0	2	1	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lestidium prolixum	1	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	3	0	0	2	1	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	?	0	0	1	0	0	0
Lestrolepis japonica	1	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	3	1	0	2	1	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
Apateodus spp.	?	0	0	0	0	0	0	?	?	0	1	0	1	0	0	0	0	0	0	1	0	0	0	?	0	?	?	1	1	1	0	0	1	0	0	0	0	1	0	0	0	2	0	0	0	0	0	2	0	0	0	1	0	0	3	0	0	0	1	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Apateopholis spp.	0	0	1	1	?	0	0	?	?	0	?	0	0	0	0	1	?	1	?	0	0	1	1	1	?	?	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	2	0	1	0	0	1	?	1	1	1	0	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	?	0	1	0	0	0
Apuliadercetis spp.	2	1	1	0	1	0	0	?	?	0	0	0	0	1	1	0	0	0	0	1	?	0	?	0	1	3	1	0	0	1	0	0	1	0	0	1	1	1	2	0	0	0	1	0	0	0	0	2	0	0	0	0	0	1	1	0	0	1	0	0	0	0	?	0	0	0	0	1	1	1	1	0	0	1	2	1	0	0	0	0	1	0	1	2	1	0
Aspidopleurus spp.	0	0	0	1	1	0	0	?	?	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	?	?	1	1	0	0	1	0	0	1	?	1	0	1	0	1	0	0	1	1	1	1	2	1	0	0	0	0	0	0	0	0	0	0
Atolvorator longipectoralis	0	0	0	0	0	?	?	0	?	?	?	1	1	0	0	0	1	1	0	1	0	1	0	0	0	2	0	1	1	0	0	0	1	0	?	0	1	1	0	1	0	0	0	0	0	1	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	?	?	0	0	1	0	0	0
Benthesikyme spp.	2	?	1	0	?	0	0	?	?	0	1	?	0	0	0	0	?	0	1	1	?	0	?	?	1	?	?	1	1	?	?	0	1	0	0	0	1	1	3	0	?	?	1	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	0	0	?	?	?	?	0	?	0	1	?	1	2	?	0
Brazilodercetis longirostris	?	1	1	1	?	0	0	?	0	0	1	0	0	0	0	0	0	0	0	1	?	1	?	?	1	3	0	0	0	1	0	1	1	0	0	0	1	1	2	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	1	2	2	?
Candelarhynchus padillai	?	1	1	0	?	?	?	0	1	?	1	?	?	1	?	0	0	0	0	0	1	0	0	0	?	2	1	?	?	0	0	1	1	1	0	0	1	1	0	0	1	0	0	1	?	?	0	2	0	1	0	0	1	0	2	0	0	1	0	0	0	0	?	0	?	?	?	1	0	1	0	?	?	0	2	1	0	?	?	?	?	?	1	0	0	0
Caudadercetis bannikovi	2	1	1	0	?	0	0	?	?	0	0	?	?	?	0	0	0	1	?	1	?	1	?	?	?	?	1	?	0	1	0	0	?	0	0	?	?	?	2	?	0	2	1	0	0	0	0	2	0	0	0	0	0	?	1	0	?	0	0	0	0	?	?	0	?	0	0	1	1	1	1	?	0	0	0	1	?	0	1	1	1	1	1	0	0	0
Cimolichthys spp.	0	0	0	1	1	0	0	?	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	?	1	1	1	0	1	0	0	1	0	0	0	1	0	1	0	2	0	0	0	1	0	2	1	0	0	0	1	?	1	0	0	0	1	0	1	1	?	?	0	0	0	?	0	0	1	0	?	1	?	1	0	?	0	?	1	0	1	3	2	0
Cyranichthys ornatissimus	1	1	1	1	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0	1	?	0	?	?	1	?	?	?	?	?	?	0	1	0	0	?	0	1	0	0	?	0	1	0	0	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	?	0	?	?	?	?	?	0	1	?	?	?	?	?	1	1	?	?	?	?	?	1	2	2	0
Dercetoides venator	2	1	1	1	?	?	?	?	1	0	0	0	?	1	0	1	0	1	0	1	0	1	?	?	1	?	0	0	0	1	0	0	1	0	0	?	1	1	3	0	0	1	0	1	0	1	0	2	1	0	0	0	0	?	3	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	2	1	0
Enchodus spp.	0	0	0	1	0	2	1	?	?	?	?	?	?	?	0	?	?	?	0	0	?	?	?	?	?	?	1	1	?	1	0	0	0	1	1	?	0	1	0	1	0	0	1	0	0	1	1	2	0	?	0	1	0	?	1	1	0	0	1	0	1	1	0	0	0	1	0	1	?	0	1	0	0	1	2	1	?	?	1	0	0	0	1	0	0	1
Eurypholis spp.	0	0	0	1	1	2	1	?	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	1	2	1	1	0	1	1	0	0	1	1	1	1	1	0	0	2	2	0	0	0	1	0	0	1	0	1	1	?	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	3	1	1
Halec spp.	0	0	0	1	0	0	0	?	1	0	1	0	0	0	0	1	0	1	0	0	0	1	?	?	0	?	1	1	1	1	1	0	0	1	0	0	1	1	2	1	0	1	1	0	0	1	0	0	1	0	0	0	?	?	1	1	0	0	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Hastichthys gracilis	2	1	1	0	?	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	?	0	0	?	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	2	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	?	0	0	0	1	1	1	1	0	0	?	0	1	0	0	1	0	1	1	1	2	1	0
Hastichthys totonacus	2	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	?	0	0	0	1	1	1	1	?	?	0	1	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	?	1	0	0	1	0	0	0	0	?	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	2	1	?
Hemisaurida hakelensis	0	0	0	0	0	0	0	?	1	?	1	0	?	1	0	?	?	?	?	0	0	?	?	?	1	?	0	1	1	1	1	0	0	0	0	0	1	1	3	1	0	1	1	1	0	0	0	2	0	0	0	0	1	?	2	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	2	1	0	0	0	0	0	0	1	0	0	0
Ichthyotringa spp.	1	1	1	0	0	0	0	1	?	0	?	0	0	0	1	0	?	0	0	0	?	0	0	0	?	?	1	1	1	?	0	0	1	0	0	0	1	1	0	?	0	2	0	0	0	1	0	?	0	1	0	0	1	?	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Nardodercetis vanderwallei	2	1	1	0	0	0	0	?	?	0	0	?	0	0	0	1	0	1	?	0	?	?	?	?	1	?	0	0	0	?	0	1	1	0	0	?	1	1	0	0	1	0	0	1	0	0	0	2	0	0	0	0	0	0	?	?	?	1	?	0	0	?	0	0	0	0	0	1	1	1	1	0	0	1	1	0	?	?	0	0	0	1	1	2	1	0
Nardorex zorzini	?	0	0	1	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	?	0	1	?	1	3	1	1	?	?	?	0	0	0	0	1	0	1	3	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	?	1	0	0	0	0	0	1	0	0	0	0	1	?	?	?	1	0	0	0
Ophidercetis italiensis	2	1	1	0	?	2	1	?	0	0	1	0	0	0	0	0	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	0	0	1	1	1	2	0	0	2	1	0	0	1	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	0	0	0	2	0	1	0	1	0	?	?	1	1	2	0
Pelargorhynchus dercetiformis	1	1	1	1	?	?	?	?	?	0	0	0	0	0	0	1	0	1	1	1	?	1	?	?	1	?	1	1	?	?	?	0	0	1	0	0	1	1	0	0	0	2	0	1	0	0	0	?	1	?	0	0	?	?	1	?	0	0	0	?	0	1	0	?	?	0	?	?	0	1	1	?	?	1	?	1	1	?	0	?	?	?	0	1	2	0
Palaeolycus dreginensis	1	0	0	1	?	2	1	?	1	?	?	0	?	1	0	?	?	1	?	1	?	1	?	?	?	?	1	1	0	?	?	0	0	0	1	0	0	1	0	?	0	0	1	0	0	1	0	1	1	1	0	1	0	?	?	1	0	0	1	0	1	1	0	?	0	1	0	0	1	2	0	0	0	1	0	?	?	1	0	0	1					
Parenchodus longipterygius	0	0	0	1	?	2	?	1	?	0	1	0	1	1	0	1	1	1	0	1	0	1	0	?	1	?	0	1	1	?	1	0	0	1	0	1	0	1	3	0	0	2	1	0	0	1	1	2	1	1	0	1	0	1	1	1	0	0	1	0	1	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	1	0	1	0	1	0	1	0	0	1
Rharbichthys ferox	0	0	0	1	?	2	1	?	0	0	1	0	?	0	0	0	?	1	1	0	?	0	?	?	?	?	1	?	1	1	0	0	1	0	0	1	1	1	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	?	0	0	0	0	1	2	1	0	0	0	1	0	0	1	3	1	0
Rhynchodercetis spp.	2	1	1	0	0	0	0	?	0	0	0	1	0	0	1	1	0	1	0	1	?	1	?	?	1	?	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?	0	0	0	2	1	1	0	0	0	1	1	1	2	1	0
Saurorhamphus judeaensis	1	1	1	1	?	0	0	?	1	0	1	0	0	0	0	1	1	1	0	1	?	0	1	1	1	2	1	1	?	1	0	0	0	1	1	?	0	1	3	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	2	0	0	0	1	0	0	0	0	3	1	1
Serrilepis spp.	0	0	0	1	0	0	0	0	?	0	1	0	1	0	0	1	0	0	0	1	?	1	1	1	0	0	1	1	1	?	0	0	1	1	0	?	1	1	3	1	0	1	0	1	0	1	0	?	1	1	0	1	0	1	1	1	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0
Phylactocephalus microlepis	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	0	1	1	?	?	?	?	1	1	?	0	1	0	0	1	0	0	1	1	2	1	0	1	1	1	0	0	0	2	1	0	0	0	0	?	1	1	0	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Unicachichthys multidentata	0	0	0	1	1	0	0	?	?	?	?	?	0	?	?	?	1	?	1	0	?	?	?	?	1	?	1	1	?	?	?	0	0	1	?	1	0	1	2	1	0	0	1	0	0	1	1	2	1	?	0	1	0	?	1	1	1	0	1	0	1	1	?	?	0	1	1	1	?	0	0	0	0	1	2	1	0	0	0	0	1	0	1	0	0	1
Vegrandichthys coitecus	0	0	1	1	?	0	1	?	?	0	?	0	0	0	0	1	0	1	?	?	1	?	?	?	?	?	0	?	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	?	1	1	0	0	1	?	1	1	?	?	0	?	?	?	?	0	?	?	?	0	2	0	0	?	?	?	?	?	1	3	1	1
Veridagon avendanoi	0	0	0	1	?	0	?	?	0	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	0	0	?	1	0	0	1	3	1	0	2	1	0	0	0	1	0	1	1	0	1	0	?	1	1	0	0	1	?	1	1	?	?	0	1	0	1	?	0	0	1	0	1	2	0	0	0	1	0	1	0	1	1	1	1
Yarbrudichthys striatus	0	0	1	1	0	1	0	1	?	?	?	0	0	0	0	?	?	?	?	1	0	1	0	?	?	?	0	0	0	?	1	0	1	0	0	?	1	1	0	0	0	0	0	0	0	0	0	?	1	1	0	1	0	?	1	1	1	1	?	0	0	1	1	0	0	1	0	0	?	0	1	0	0	1	2	1	1	1	0	0	1	0	1	0	0	0
Spinascutichthys pankowskiae	1	1	1	0	0	1	?	1	1	?	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	1	0	1	1	0	0	0	0	1	3	0	2	1	0	0	0	0	1	0	0	1	0	0	1	0	2	0	1	1	1	1	0	1	?	?	?	1	0	?	0	?	?	?	?	0	0	0	0	1	1	0	1	?	1	?	1	1
Dercetis elongatus	2	1	1	1	0	0	0	?	?	1	1	0	0	0	0	1	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	1	0	1	1	1	2	0	0	1	1	1	0	1	0	2	1	1	0	0	1	?	1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	1	1	0	0	0	0	1	?	0	?	?	?	?	1	2	2	0
Dercetis triqueter	2	1	1	1	0	0	0	?	?	1	1	0	0	0	0	?	0	0	0	1	?	0	?	?	1	2	1	1	1	?	0	0	1	0	0	1	1	1	2	0	0	1	1	1	1	1	0	2	0	1	0	0	1	?	1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	1	0	1	2	2	0
Dercetis magnificus sp. nov.	?	1	1	1	0	0	0	?	?	1	1	0	0	0	0	1	0	0	0	1	?	0	1	1	1	2	1	1	0	1	0	0	1	1	0	1	1	1	2	0	0	1	1	1	1	1	0	1	1	0	0	0	0	?	0	0	0	?	?	?	0	0	?	?	?	0	?	?	0	1	1	0	0	1	0	?	?	?	?	?	?	?	1	2	2	0
Stratodus apicalis SDSM81334	2	?	?	?	?	0	0	?	?	?	?	0	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	?	0	1	?	?	0	?	?	1	1	?	?	?	1	?	1	2	2	0