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RESEARCH PAPER

Is Onychodontida (Osteichthyes, Sarcopterygii) monophyletic? Assessing discordant phylogenies with quantitative comparative cladistics

¿Es Onychodontida (Osteichthyes, Sarcopterygii) monofilético? Evaluando filogenias contradictorias con cladística comparativa cuantitativa

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Abstract: Onychodontida (Osteichthyes, Sarcopterygii) was an extinct group of Devonian predatory marine fishes, representing an early branch in sarcopterygian evolution, and currently considered closely related to coelacanths (Actinistia). Due to their limited fossil record, the relationships of onychodonts within sarcopterygians, and whether all taxa traditionally considered as onychodonts form a clade, are still unclear. Here we review the most recent phylogenetic analyses by comparing their data matrices using recent tools and methodology in quantitative comparative cladistics in order to evaluate the source of discrepancies in the different datasets and provide possible practical solutions to test the monophyly of Onychodontida. These discrepancies range from the ambiguous formulation of character statements and character states to the poor preservation of certain fossils, which make interpretation of character states difficult. Understudied but highly complete fossil specimens are also a source of missing data that have an impact in discording tree topologies. In-depth analysis and description of these specimens is needed to improve the resolution of future phylogenetic analyses. Finally, we propose a formal stem-based phylogenetic definition for Onychodontida.

Resumen: Los onicodóntidos (Osteichthyes, Sarcopterygii) fueron un grupo extinto de peces marinos depredadores del Devónico. Se diversificaron al comienzo de la historia evolutiva de los sarcopterigios y se consideran estrechamente emparentados con los celacantos (Actinistia). Debido a su limitado registro fósil, su posición filogenética dentro de los sarcopterigios y las relaciones de parentesco entre taxones tradicionalmente clasificados como onicodóntidos aún no están claras. En este trabajo se evaluaron los análisis filogenéticos más recientes, comparando las matrices de datos mediante nuevas herramientas y metodología en cladística comparativa cuantitativa. Esto ha permitido determinar el origen de las discrepancias en las codificaciones de los estados de carácter para las distintas matrices y proporcionar posibles soluciones prácticas para contrastar la monofilia de Onychodontida. Estas discrepancias tienen origen en la formulación ambigua de enunciados y estados de carácter, la mala preservación de ciertos fósiles y ejemplares poco estudiados que dificultan la interpretación de los estados de carácter. Es necesario un análisis y descripción en profundidad de estos ejemplares para mejorar la resolución de los futuros análisis. Por último, se propone una definición filogenética de tipo troncal para el clado Onychodontida.

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INTRODUCTION

Sarcopterygians (lobe-finned fishes) are a successful group of bony fishes (osteichthyans) with a long evolutionary history, from the middle Palaeozoic to the present day (Jarvik, 1980; Janvier, 1996; Long, 2001). The Sarcopterygii likely originated at the end of the Silurian (Zhu *et al.*, 1999; Lu *et al.*, 2017; Zhao *et al.*, 2021) but diversified during the Devonian (Ahlberg, 1991; Cloutier & Ahlberg, 1995, 1996), giving rise to various groups from which extant coelacanths, lungfish and tetrapods evolved (Janvier, 1996; Forey, 1998; Clack, 2012) (Fig. 1). However, numerous gaps in the fossil record from the early evolutionary history of non-tetrapod sarcopterygians makes the study of their origin and evolution challenging.

One of the most ancient and enigmatic groups of extinct sarcopterygians are the onychodonts (Onychodontida or Onychodontiformes) (Jessen, 1967; Andrews, 1973; Andrews *et al.*, 2006; Lu & Zhu, 2010; Lu *et al.*, 2016; Mondéjar-Fernández, 2020), an exclusively Devonian group of predatory marine fishes with “intermediate”

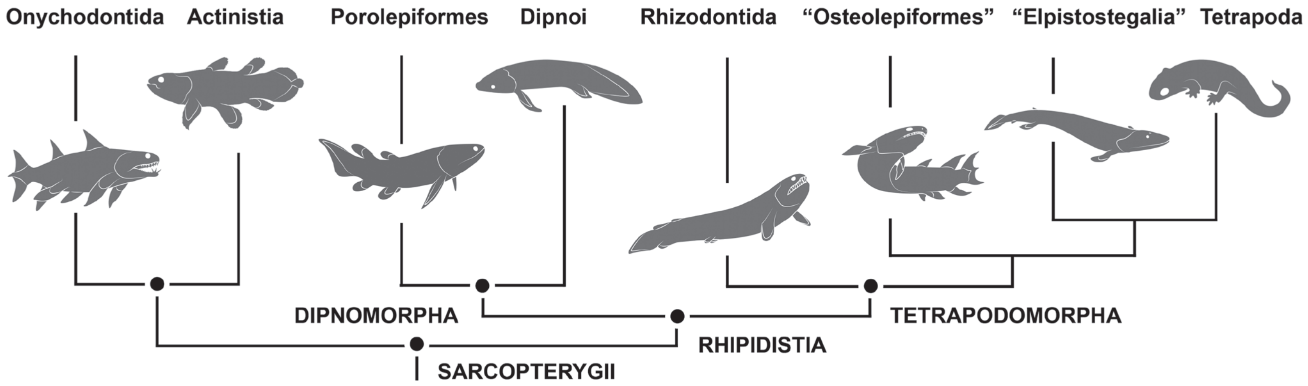

Figure 1. Sarcopterygian phylogeny. Simplified phylogenetic relationships of sarcopterygians after Lu *et al.* (2016).

characteristics between early osteichthyans and coelacanths (*e.g.*, Long, 2001; Botella *et al.*, 2007; Clement *et al.*, 2018; Lu & Zhu, 2010; Lu *et al.*, 2016; Lu *et al.*, 2017; Zhu *et al.*, 1999, 2001, 2006, 2009; Johanson *et al.*, 2007; Mondéjar-Fernández, 2020). Currently, seven genera have been classified as Onychodontida: *Onychodus* Newberry, 1857; *Strunius* Jessen, 1966; *Grossius* Schultze, 1973; *Luckeus* Young & Schultze, 2005; *Bukkanodus* Johanson, Long, Talent, Janvier & Warren, 2007; *Qingmenodus* Lu & Zhu, 2010; and *Selenodus* Mondéjar-Fernández, 2020 (Fig. 2). The majority of these genera are monospecific, with the exception of *Onychodus* (Andrews *et al.*, 2006; Mann *et al.*, 2017) and *Strunius* (Jessen, 1966), and are known by a relatively fragmentary and understudied fossil record (Young & Schultze, 2005; Lu *et al.*, 2016; Mondéjar-Fernández, 2020).

Onychodonts are characterized by their complex and specialized cranial morphology, exemplified by the presence of hypertrophied sigmoid parasymphyseal teeth inserted onto paired whorls articulated on the symphysis of the dentaries with large palatal internasal pits in the floor of the ethmosphenoid complex to accommodate them (Andrews *et al.*, 2006; Lu *et al.*, 2016) (Fig. 2A, 2D). In addition, they have a highly kinetical intracranial joint, which gives a certain capacity for movement to the dermal bones of the skull (Long, 2001; Andrews *et al.*, 2006). All currently described onychodonts lack cosmine on their dermal bones and scales, a remarkable histological feature that was basally present on the dermal skeleton of many other Palaeozoic sarcopterygians (Mondéjar-Fernández, 2020). However, putative onychodont remains from the Lower and Middle Devonian of China are suspected to be covered with cosmine (Lu & Zhu, 2010; Zhu & Yu, 2004; Zhu & Zhao, 2005).

These osteological and histological features have been traditionally used to broadly characterize onychodonts (*e.g.*, Jessen, 1967; Andrews, 1973; Ahlberg, 1991; Andrews *et al.*, 2006; Johanson *et al.*, 2007; Lu & Zhu, 2010). Nevertheless, their status as synapomorphies of the group is dubious, as many of these features (*e.g.*, parasymphyseal tooth whorls, internasal cavities, kinetic intranial joint) have been found to be plesiomorphic for osteichthyans (Zhu *et al.*, 1999, 2009; Zhu & Yu, 2004; Qiao & Zhu, 2010; Lu *et al.*, 2017). Due to this, in recent phylogenetic analyses many taxa traditionally considered as onychodonts have not been recovered as a clade (Mondéjar-Fernández, 2020) or, if a monophyletic Onychodontida is recovered (Lu & Zhu, 2010; Lu *et al.*, 2016; Mann *et al.*, 2017), the relationships between the different genera differ notably (*e.g.*, Mondéjar-Fernández, 2020 *contra* Lu *et al.*, 2016). This discrepancy may be due either to (1) the fragmentary nature of some fossil specimens, (2) insufficient knowledge of the anatomy of complete but difficult to interpret specimens, or (3) discordant character scoring. Identifying the origin of these systematic discrepancies is key to efficiently resolve them.

Here, we review the most recent phylogenetic analyses of onychodonts comparing the data matrices. Recent phylogenetic datasets were analyzed using the latest tools and methodology in comparative cladistics (recently implemented in phylogenetic analysis software), to evaluate the source of discrepancies in the different phylogenetic hypotheses, and propose possible practical solutions to test the monophyly and synapomorphies of Onychodontida.

MATERIALS AND METHODS

A revision of Onychodontida has been carried out, analyzing most recent data matrices for cladistic analysis (Lu & Zhu, 2010; Lu *et al.*, 2016; Mann *et al.*, 2017; Mondéjar-Fernández, 2020). The four analyzed matrices came originally from the two matrices presented by Lu and Zhu (2010) and Lu *et al.* (2016). The former was modified by Mann *et al.* (2017), adding two taxa, *Onychodus sigmoides* and *Onychodus eriensis,* and two new characters. The second one was modified by Mondéjar-Fernández (2020) adding a new taxon, *Selenodus,* and changing some of the character scorings. Once revised, the characters were reformulated to adapt them to the same logical proposition that would allow them to be discussed

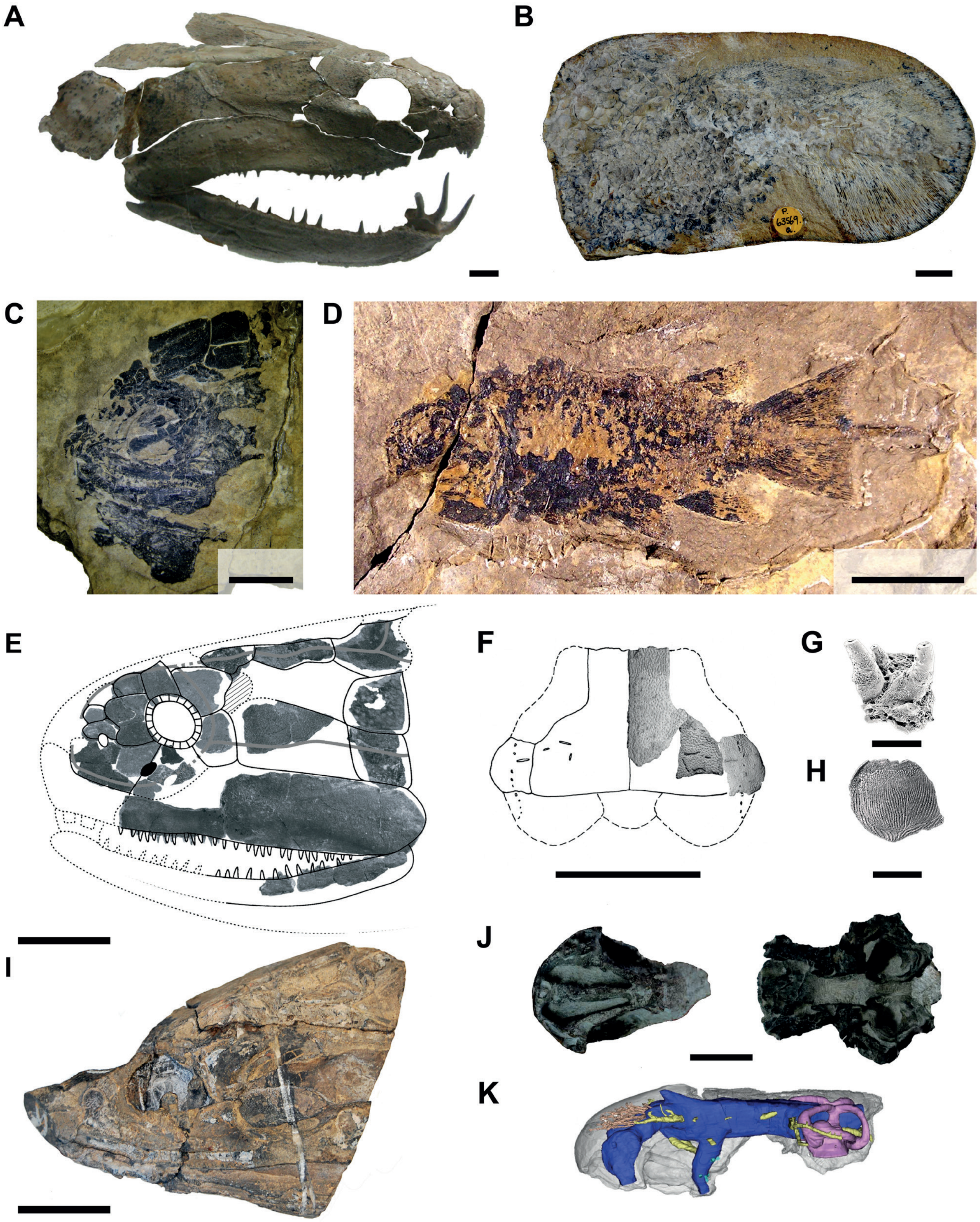

Figure 2. Onychodont fossil record. Representative fossils of the most complete taxa of Onychodontida. **A,** skull of *Onychodus jandemarrai* (BMNH P63576); scale bar = 1 cm; **B,** Caudal fin of *Onychodus jandemarrai* (BMNH P63569); scale bar = 1 cm*;* **C,** skull from *Strunius walteri* (BMNH P4977-71); scale bar = 50 mm; **D,** complete specimen of *Strunius walteri* (MB.f. 5224); scale bar = 1 cm; **E,** *Selenodus aquesbiae* (assemblage of dermal skull bones, several specimen numbers) (Mondéjar-Fernández, 2020); scale bar = 5 cm; **F,** reconstruction of the parietal shield of the skull roof of *Bukkanodus jesseni* (NMV P218314, P218315, P218316; Johanson *et al.*, 2007); scale bar = 5 mm; **G,** Parasymphyseal tooth row of *Bukkanodus jesseni* (NMV P218338); scale bar = 1 mm; **H,** scale from *Bukkanodus jesseni* (NMV P218348); scale bar = 1 mm; **I,** skull of *Grossius aragonensis* (Gö-709-1); scale bar = 5 cm; **J,** anterior and posterior cranial portions of *Qingmenodus yui* (IVPP V16003.5, V16003.6); scale bar = 5 mm*;* **K,** reconstruction of the neurocranium of *Q. yui*.

later. The reformulation was carried out from the logical structure proposed by Sereno (2008).

Comparative cladistics

A simple method to compare patterns of regional character inclusion amongst phylogenetic analyses is the use of character distribution maps (**CDMs**) (Whitlock & Wilson, 2012). We applied CDMs to the four matrices mentioned before (Lu *et al*., 2016; Lu & Zhu, 2010; Mann *et al*., 2017; Mondéjar-Fernández, 2020). Characters were divided firstly into cranial (dermocranium, splanchnocranium and neurocranium), postcranial, and histology-related features. Then, in a spreadsheet, we counted the number of characters belonging to each anatomical region and obtained the percentages in relation to the total number of characters in order to know which anatomical regions were over or under-represented in each of the matrices. This method is therefore useful in identifying under-studied body regions and examining patterns of morphological evolution (Whitlock & Wilson, 2012). However, it only provides an overall comparison that does not reveal were the specific differences causing discordant tree topologies lie.

Goloboff and Sereno (2021) have recently proposed a new methodology that provides tools to identify, compile, and evaluate differences in taxa, characters and character states between two datasets that yield different trees and degrees of node support. This method not only showcases where two datasets differ in taxa, characters or character scoring, but also which of these differences favor the results of each dataset.

Mesquite (Maddison & Maddison, 2007) and TNT (Goloboff & Catalano, 2016) were used for analysis. Matrices were compared by pairs: (1) Lu *et al*. (2016) and Mondéjar-Fernández (2020), and (2) Lu and Zhu (2010) and Mann *et al.* (2017) since they have the same character statements and character state names, and outgroup taxa. They all used the cladistic analysis program PAUP 4.0b10 (Swofford, 2003) and also considered all the characters as unordered, and weighted equally. Here, each dataset was loaded into TNT (Goloboff & Catalano, 2016) and a heuristic search was applied using a parsimony analysis with 1000 replicates and 10 rearrangements using the TBR (tree bisection-reconnection) algorithm, for each of those 1000 replicates. From the resulting most parsimonious trees, a strict consensus was obtained. The results of these analyses were saved into separate TNT files for later comparison as described in Goloboff and Sereno (2021).

The data from both analyses were then imported using the "pairwise comparison/combination" option in the File > Merge/Import data menu and following the steps proposed by Goloboff and Sereno (2021). In the pop-up window, the "complete trees with taxa" and "record decisions in file" boxes were checked. The results of this analysis consist of (1) two strict consensus trees with highlighted synapomorphies that may differ between datasets (marked in blue for the oldest dataset and red for the newest), (2) a matrix comparison file highlighting differences with the same color coding, and (3) a text file with the decisions made by the program (Supplementary Information).

Discrepancies in scoring with an impact in discordant tree topologies were evaluated to assess whether they are (1) a product of a fragmentary specimen/s causing dubious interpretation of a character state by different researchers, (2) ambiguous character states that can make scoring subjective, or (3) typological errors.

RESULTS

The phylogenetic results of previous analyses (Lu & Zhu, 2010; Lu *et al*., 2016; Mann *et al*., 2017; Mondéjar-Fernández, 2020) differ significantly in topology and in the number of steps and trees obtained (Fig. 3). In the case of Lu and Zhu (2010), the analysis found a single most parsimonious tree (**MPT**) of 46 steps. Onychodontida is recovered as a well-resolved clade, sister group of Actinistia (Fig. 3B) (Lu & Zhu, 2010). On the other hand, the matrix of Mann *et al.* (2017), derived from the previous one, presents a different scenario. It was analyzed following the same parameters as Lu and Zhu (2010) using the exhaustive search option and the DELTRAN option in PAUP. The phylogenetic analysis recovered three MPTs of 48 steps. A monophyletic Onychodontida and *Diplocercides* (representative of Actinistia) as sister group were recovered, however, the genus *Onychodus* was recovered as paraphyletic, with the unresolved position of the type species *Onychodus sigmoides* relative to *Grossius* and the other *Onychodus* species (Fig. 3D).

The analysis by Lu *et al.* (2016), carried out from a new, more comprehensive matrix, obtained a strict consensus of 845 MPTs using heuristic algorithm and the DELTRAN option to obtain the synapomorphies (Lu *et al.,* 2016). The result recovered *Bukkanodus* as a sister group to a clade that includes Actinistia and a clade containing all the other remaining onychodonts. However, the relationships within the clade Onychodontida are not well resolved, with *Strunius*, *Qingmenodus*, *Grossius* and *Onychodus* forming a polytomy in the strict consensus (Fig. 3A) (Lu *et al*., 2016).

Finally, the most recent analysis (Mondéjar-Fernández, 2020) added a new taxon, *Selenodus*, to the Lu *et al.* (2016) matrix and recoded some of the original characters. The matrix was subjected to a maximum parsimony analysis in PAUP using the heuristic algorithm. Here, *Bukkanodus* was recovered in a less inclusive clade, but within a large polytomy formed by Actinistia, *Selenodus*, and the taxa traditionally classified as onychodonts (Fig. 3C).

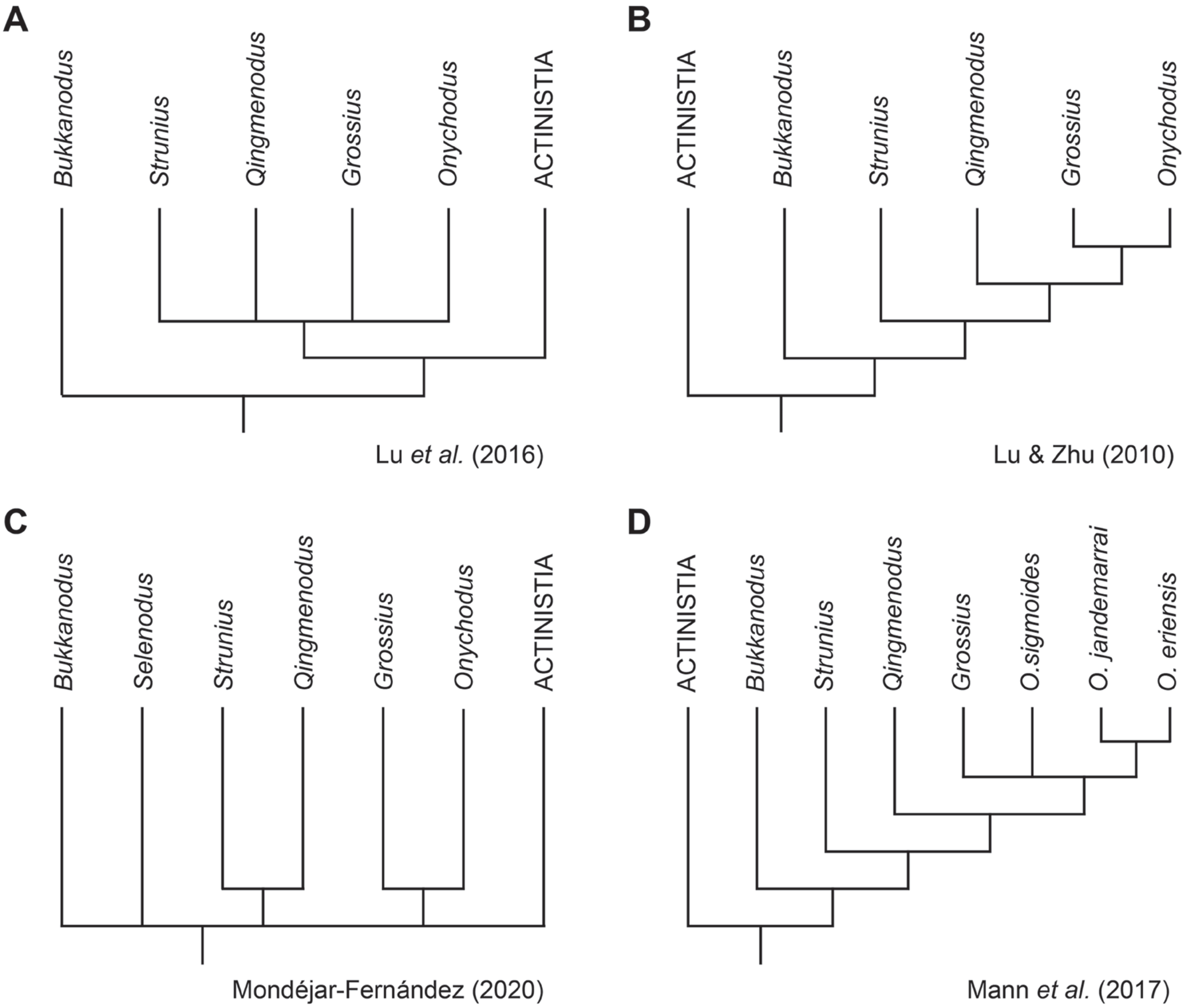

Figure 3. Onychodontida phylogenetic analyses. Results of recent cladistic analyses of the matrices from **A,** Lu *et al.* (2016); **B,** Lu & Zhu (2010); **C,** Mondéjar-Fernández (2020); **D,** Mann *et al.* (2017).

Character distribution maps

The matrix of Mann *et al.* (2017) has 10 taxa (two more than Lu & Zhu, 2010) and 41 characters (two more than Lu & Zhu, 2010), while that of Mondéjar-Fernández (2020) has 38 taxa (one more than Lu *et al.*, 2016) and 242 characters. The dermocranium accounts for 50% of the total of scored characters in the Mondéjar-Fernández (2020) dataset, the mandibles and gulars being the most represented (15%) (Fig. 4A), while in Mann *et al.* (2017), the dermocranium represented 70% of the total with the skull roof being the most represented (26%) (Fig. 4B).

The splanchnocranium accounted for only 12% of the total number of characters in the case of Mondéjar-Fernández (2020) (Fig. 4A) and only 3% in the case of Mann *et al.* (2017) (Fig. 4B), being the dermal palatal elements the most represented in both cases (8% *vs* 3%) (Fig. 4).

The neurocranium represents 19% of the Mondéjar-Fernández (2020) data matrix, the ethmosphenoid region being the most represented neurocranial region with 9% (Fig. 4). In Mann *et al.* (2017) the neurocranium represents 11% of all characters, with the otic-occipital region being the best represented with 8% (Fig. 4).

As for post-cranial characters, they are very poorly represented in both datasets, 15% in Mondéjar-Fernández (2020) (Fig. 4A) and 19% in Mann *et al.* (2017) (Fig. 4B). The pectoral girdle (5%) is the best represented in the former data set (Fig. 4A), while scales (8%) gather the higher number of characters in the latter (Fig. 4B).

Finally, histological characters are only represented in Mondéjar-Fernández (2020), accounting for 4% of the total (Fig. 4A).

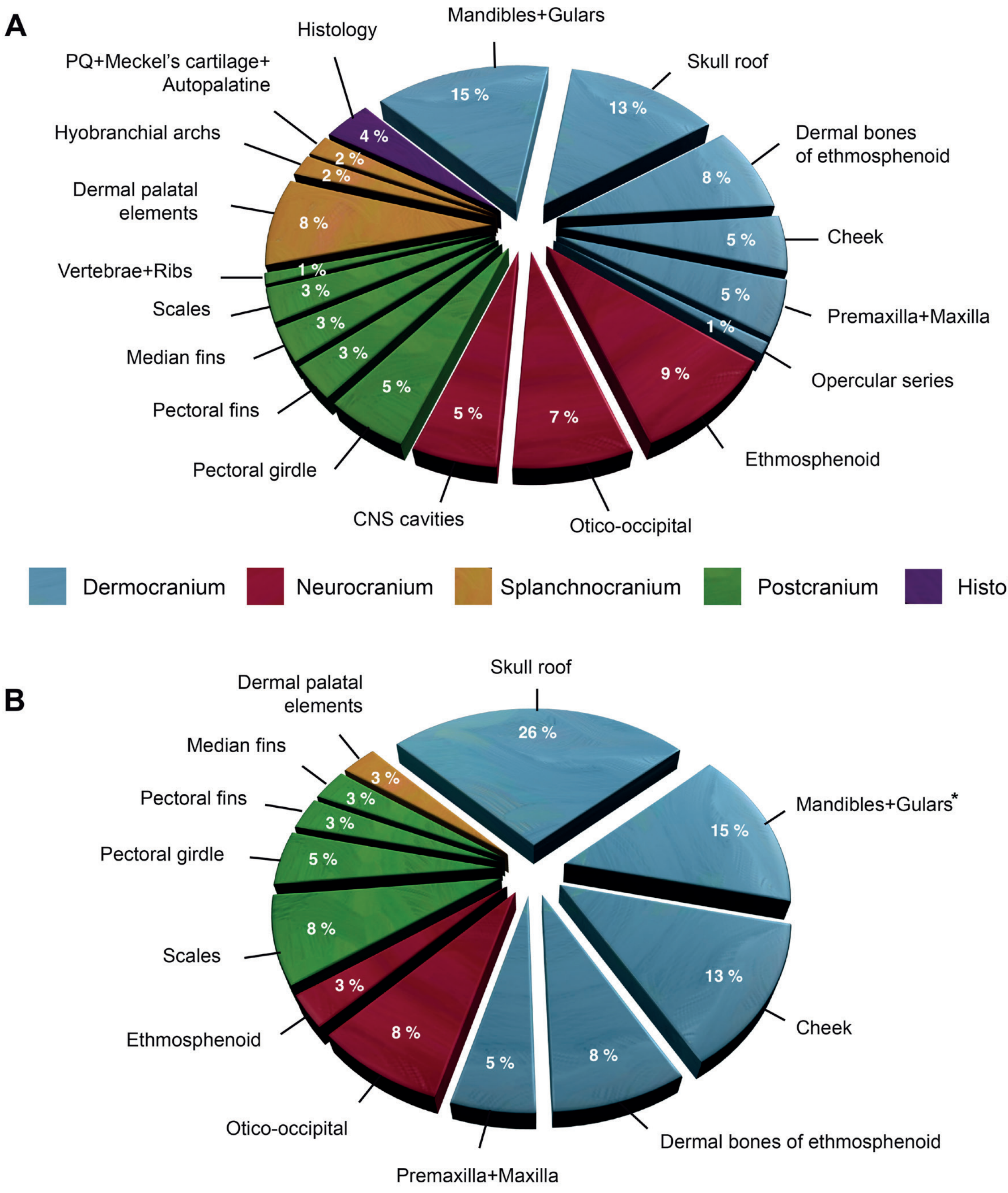

Figure 4. Character distribution maps. **A**, Lu *et al.* (2016) and Mondéjar-Fernández (2020); **B,** Lu & Zhu (2010) and Mann *et al.* (2017). *character percentages after Mann *et al.* (2017) which added two additional characters to the Mandibles & Gulars category.

Comparative cladistics

In the first pair of matrices compared (Lu & Zhu, 2010 and Mann *et al.*, 2017), the only differences between both datasets come from the new characters related to the mandibles, and the new taxa (*Onychodus eriensis* and *Onychodus sigmoides*) added by Mann *et al.* (2017). There are two characters (course of the mandibular canal (C.31) and mandibular sensory canal through the lowermost part of the infradentary series with many tubes (C.32)) whose scorings for *Onychodus eriensis* favor the result of Mann *et al.* (2017) over that of Lu and Zhu (2010).

The comparison of Lu *et al.* (2016) *vs* Mondéjar-Fernández (2020) datasets seems much more complex, since the matrices greatly increase both in character and taxa numbers compared to the previous datasets. Comparing the matrices (Tab. 1) allows to identify both the differences in the scoring of each taxon, and the specific changes in scoring that have an impact on the discordant topologies of the trees (Tabs. 1, 2).

Bukkanodus presents a total of 5 changes from the matrix of Lu *et al.* (2016) to that of Mondéjar-Fernández (2020), 3 of them having an impact on discordant topologies. In the case of *Qingmenodus* there are

Table 1. Number of discordant characters between the datasets of Lu *et al*. (2016) and Mondéjar-Fernández (2020), showing the total number of discordant characters and the number of characters that have an impact on differences in tree topology between both analyses.

TAXA	TOTAL	WITH IMPACT
Bukkanodus	5	3
Qingmenodus	2	0
Strunius	13	4
Onychodus	3	2
Grossius	32	1

no differences from one matrix to the other, nor any characters affecting the different tree topologies. In *Strunius* there are 13 characters with changes, only 4 of them affecting the tree topologies. Regarding *Onychodus,* it presents 3 characters that differ from one matrix to the other and only 2 of them have weight in favoring one result over the other. *Grossius* presents a total of 32 characters modified from one matrix to the other, but only 1 has impact in favoring one consensus tree over the other. Finally, *Selenodus* was newly scored in the Mondéjar-Fernández matrix, with 6 characters favoring his phylogenetic hypothesis.

DISCUSSION

Variation in tree topology and character discussion

Variations in tree topologies can be caused by differences in character scoring. These may be due to: (1) ambiguous character statements or character states too prone to interpretation (*e.g.*, “Element, size: small (0) or big (1)”); (2) poor or insufficient preservation of the fossil specimens making interpretation of the morphology difficult; (3) mistakes in the scoring (*e.g.*, typographic). In order to assess the possible causes of the scoring differences, we evaluate the characters with different scorings between datasets, identifying which ones favor one phylogenetic result over another, and discuss them for each taxon of Onychodontida (Tab. 2). Character numbers correspond to the Mondéjar-Fernández (2020) dataset, unless specified otherwise.

Bukkanodus. The genus is represented by a single species, *B. jesseni,* and it is one of the most unstable taxa (Fig. 3). It is not always recovered within the Onychodontida clade. Three characters, all of them related to the scales, have influenced discording tree topologies.

The first character “scales” (referring to their morphology) (C217) has three states: rhombic (0), intermediate between rhombic and round (1), and round (2). The second character state (“intermediate”) is ambiguous and subject to interpretation. Moreover, only four scales have been referred to *Bukkanodus*, all of them incomplete (Johanson *et al*., 2007). Only in one of them the character state was interpreted as rounded, although it has some broken edges (Johanson *et al.*, 2007, fig. 5.9–5.12) (Fig. 2H). Thus, the character is interpreted in an unambiguous way.

The next character is “scales with interlocking pegs and sockets” (C218) and its character states are: absence (0) or presence (1). This character is only measurable in one scale (NMV P.218348) and was coded as absent, but this is problematic because of the poor preservation of the dorsal margin of the scale, as well as the small scale sample for this taxon.

The last character is “anterodorsal peg-like process on scale” (C220) and it is neomorphic as the previous one. Since the scales do not present any pegs, they can be interpreted as absent (0). Again, only one scale (NMV P.218348) is useful to interpret the character, since the rest of the scales show very damaged edges.

Table 2. Changes in character scoring for those characters that have an impact on differences in tree topology between both analyses. Asterisks (*) indicate which tree topology was favored by that scoring.

TAXA	Lu ***et al.*** (2016)	Mondéjar-Fernández (2020)
Bukkanodus	C217 (Scales): (?) C218 (Scales with interlocking pegs and sockets): (?) C220 (Anterodorsal peg-like process on scale): (?)	C217: (2)* C218: (0)* C220: (0)*
Qingmenodus	-	-
Strunius	C9 (Number of supraorbitals): (?) C43 (Spiracle): (0)* C173 (Middle pit line): (?)* C212 (Caudal fin): (1)	C9: (1)* C43: (2) C173: (0) C212: (2)*
Onychodus	C212 (Caudal fin): (?) C230 (Plicidentine): (?)	C212: (2)* C230: (1)*
Grossius	C43 (Spiracle): (?)*	C43: (0)
Selenodus	-	C9 (Number of supraorbitals): (0) C27 (Postparietal narrowing posteriorly): (0) C 217 (Scales): (2) C218 (Scales with interlocking pegs and sockets): (0) C220 (Anterodorsal peg-like process on scale): (0) C230 (Plicidentine): (1)

Strunius. The genus *Strunius* is also a somewhat unstable taxon within Onychodontida, although it is usually retrieved within the clade. Despite being known from several specimens of *S. walteri* and *S. rolandi* that range from fragmentary to nearly complete (Jessen, 1966, 1967), the flattened nature of its preservation makes it especially difficult to interpret. In this case we have four characters impacting the discording phylogenetic tree topologies (Tab. 2).

The first of these is the number of supraorbitals: one (0), two (1), and more than two (2) (C9). As said before, the issue in this case comes from the preservation of the fossil and the difficulty of its visualization: Mondéjar-Fernández (2020) identified two supraorbitals in *S. walteri* (1) following Jessen (1966), whereas Lu *et al.* (2016) scored the character as indeterminate (?).

The next character is “spiracle: absent-small hole (0), narrow groove (1), and wide notch (2)” (C43). These character states are again ambiguous or badly defined; how big or how small a structure is must be relative to something measurable in order to be scored unequivocally. The spiracle is quite visible in the *S. walteri* holotype (P 4999) being located in the posterior margin of the postorbital (Jessen, 1966). According to the coding of Lu *et al.* (2016) the spiracle would be absent or small (0) while Mondéjar-Fernández (2020) considered it a wide notch (2). As a side note, this character is a “hybrid” type of character that mixes neomorphic character states (absence/presence of spiracle) with transformational ones (those related to the size of the spiracle). We suggest to split this character in two: (1) Spiracle: presence (0), absence (1) (neomorphic); and (2) Spiracle, size: small hole (0), narrow groove (1), and wide notch (2) (transformational) following recommendations of Sereno (2008) and to formulate non ambiguous character states to measure its size.

The character “middle pit line” (C173) is well formulated, its character stages being: on the same lineation as the tabular pit-line (0), and not on the same lineation as the tabular pit-line (1). However, this character is very difficult to observe and interpret in the specimens of *Strunius*. Lu *et al*. (2016), scored it as indeterminate (?), which actually favors their consensus tree (Tab. 2). On the other hand, Mondéjar-Fernández (2020) tentatively interpreted the middle pit-line as on the same lineation as the tabular pit-line (0).

The last character considered is “caudal fin (C212): heterocercal (0), triphycercal (1), and diphycercal (2)”. In this case, the character states allude to two different features: first, the arrangement of the internal structure of the caudal fin (heterocercal, when the axial skeleton turns dorsally and extends into the dorsal lobe *vs* diphycercal when the vertebral column extends horizontally to the end of the caudal fin, dividing the tail into two equal parts, and fin rays are supported dorsally and ventrally). “Triphycercal” is in fact a type of diphycercal tail, most commonly named “modified diphycercal” (see, *e.g.*, Kurik & Botella, 2009). The second feature, is the number of lobes (with diphycercal having two lobes and triphycercal having three lobes). Since these features are independent, we suggest splitting the character into two: (1) Caudal fin, internal configuration of the axial skeleton: dorsally deflected (“heterocercal-epicercal”) (0), horizontal (“diphycercal”) (1); and (2) Caudal fin, number of lobes: two (0), three (1). The preservation of the caudal fin in several specimens of *S. walteri* is very good (Jessen, 1966), and it shows a symmetrical tail with two lobes of rays (one dorsal, one ventral). However, the notochord continues beyond the posteriormost extent of the paired lobes, but does not have a third lobe of rays at the tip of the tail as in most actinistians (Fig. 3E). This is likely the source of the discordant scoring of both matrices, with Lu *et al*. (2016) scoring *Strunius* as having a triphycercal fin (1) and Mondéjar-Fernández (2020) scoring a diphycercal fin (2). In our splitting of the character into two, we suggest the scoring of this fin as horizontal (“diphycercal) (1), since it is a symmetrical tail supporting both lobes, and its number of lobes as two (0).

Onychodus. *Onychodus* is the best-known and diverse onychodontid genus. It also presents the most complete fossil record among Onychodontida, particularly the species *O. jandemarrai* (Andrews *et al*., 2006), which is usually the only species scored for the genus. However, the possibility of it being a “wastebasket” genus cannot be ruled out without a comprehensive taxonomic revision of the genus (Mann *et al*., 2017). Despite this good representation, there are two characters key in favoring one phylogenetic result over the other; the caudal fin (C212), discussed before in *Strunius*, and the plicidentine (C230) (Tab. 2).

As mentioned before, “Caudal fin” (C212) is an ambiguous character that refers to two independent structures. However, in *O. jandemarrai*, there are several specimens with well-preserved caudal fins (Andrews *et al*., 2006). In the Lu *et al.* (2016) analysis the character was scored as indeterminate (?), but in the matrix of Mondéjar-Fernández (2020) it is interpreted to have a diphycercal fin. The latter interpretation is in agreement with a horizontal caudal axial skeleton and the number of lobes present, as described by Andrews *et al.* (2006). As for *Strunius,* we would score the caudal fin as horizontal (“diphycercal”) (1), with two lobes (0).

The character “plicidentine” (C230) was formulated by Lu *et al.* (2016) with the following states: absent (0), simple (1), labyrinthodont (2), dendrodont (3). Simple plications of the dentine at the base of large tusks can be seen in *O. jandemarrai* (Andrews *et al*., 2006) and *O. sigmoides* (Schultze, 1969). In Lu *et al.* (2016) interpretation, plicidentine was absent in *Onychodus* (0), but Mondéjar-Fernández (2020) scored this character as simply folded (1) (simplexodont type). Other types of more complex plicidentine occur in sarcopterygians (*e.g.*, dendrodont in porolepiforms, eusthenodont in certain “osteolepiforms”, polyplocodont in *Powichthys,* *Youngolepis,* and *Panderichthys,* among others) (Schultze, 1970; Chang & Smith, 1992; Mondéjar-Fernández & Janvier, 2021). This terminology completes the "labyrinthodont" type of plicated dentine known in early tetrapods, which is merely a variant of the generalized polyplocodont type (Schultze, 1970). The character "plicidentine" (C230) is a "hybrid" type of character, that is, it presents both neomorphic (present/absent) and transformational character states (Sereno, 2008). Hybrid characters have been shown to have logical and independence issues and their use is not recommended (Sereno, 2008). We therefore suggest to use the "contingent coding" solution of Forey and Kitching (2000) in which we split the character into two: (1) Plicidentine: absent (0); present (1), and (2) Plicidentine, type: simplexodont (0); polyplodocont (1); eusthenodont (2); dendrodont (3).

Grossius. The genus *Grossius*, represented by the single species *G. aragonensis* (Gö-709-1) (Schultze, 1973) is a very enigmatic onychodont which preserves an almost complete skull. Despite a large number of characters scored differently by Mondéjar-Fernández (2020) relative to Lu *et al.* (2016), only one character has an impact in favoring a phylogenetic result over the other: the spiracle (C43). This character was previously discussed for *Strunius* as having ambiguous formulation of character states. Nevertheless, the currently available information on *Grossius* is insufficient to determinate the presence and morphology of the spiracle, and a more thorough study of the remains is required (see discussion below).

Adequacy of current matrices to evaluate onychodont phylogenetic relationships

Bukkanodus. The vast majority of remains belong to the dermatocranial region of *B. jesseni* (Johanson *et al.*, 2007) (Fig. 2F–2H), which is by far the best represented region in all matrices (between 50 and 70% of total characters) (Fig. 4). Within the dermocranium, *B. jesseni* only preserves the premaxilla, a median rostral and the lateral rostrals of the ethmosphenoid portion of the skull. The skull roof is known from the postparietal and tabular (Fig. 2F). The cheek region is represented by the jugal and postorbital. Finally, the mandibles are known by the dentary, parasymphisial whorls, coronoids, and isolated teeth (Fig. 2G). Turning to the splanchnocranium and associated ossifications, *B. jesseni* preserves the dermopalatines, the ectopterygoids and the parasphenoids, which are all dermal bones of the palate. Regarding postcranial elements, *B. jesseni* only preserves the supracleithrum from the pectoral girdle and isolated scales (Fig. 2H).

Despite the preservation of several bones from most anatomical regions, *Bukkanodus* is scored for a relatively low number of characters in the different matrices. In the case of Lu and Zhu (2010) and Mann *et al.* (2017), in which the number of characters is smaller than in other matrices, this percentage is 38.4 and 36.5% respectively (Tab. 3). However, in the larger matrices of Lu *et al.* (2016) and Mondéjar-Fernández (2020) there are only between 10.7 to 12.8% of scored characters (Tab. 3). This is likely due to the fact that the remains of *B. jesseni* are very fragmentary, despite representing many regions of the dermocranium. A re-study of the remains may enable to score some of the indeterminate character states and formulation of new characters accounting for the variability of some features not represented by current characters may warrant more phylogenetically informative results. However, the search for new and more complete specimens would be the best way to understand the phylogenetic position of *Bukkanodus*.

Qingmenodus. The species *Q. yui* is known by relatively well-preserved remains of the anterior and posterior portions of the skull and other associated elements (Lu & Zhu, 2010; Lu *et al.*, 2016). The dermocranium is mainly represented by the skull roof in which few sutures can be identified in the ethmosphenoid (anterior) portion (Fig. 2J). A referred maxilla is also preserved as well as a dentary and teeth. The splanchnocranium is represented by a fragment of the hyomandibula (hyobranchial arch). Finally, the neurocranium is very well preserved, represented by the anterior part (ethmosphenoid) and the posterior region (otico-occipital). *Q. yui* was studied via computerized axial microtomography (**μ-CT**) techniques, which enabled to model the cavities of the neurocranium for the first time in an onychodont (Lu *et al.*, 2016) (Fig. 2K).

Although *Q. yui* only presents partial skull remains, *Qingmenodus* is represented by 44.6–47.9% of the characters in the Lu *et al.* (2016) and Mondéjar-Fernández (2020) matrices, and by 35.9–34.1% in Lu and Zhu (2010) and Mann *et al.* (2017) respectively (Tab. 3). Therefore, *Qingmenodus* is relatively well represented thanks to the use of new technologies. New fossils, especially from the postcranial skeleton and cheek regions, as well as histological surveys would be necessary to complete the description of *Qingmenodus*.

Strunius. This is a genus known from complete to nearly complete and relatively well-preserved fossil remains (Fig. 2C–2D). However, the percentage of characters scored in the matrices of Lu *et al.* (2016) and Mondéjar-Fernández (2020) is between 39.6–46.7% (Tab. 3), lower than the far less complete *Qingmenodus*. This large amount of missing data is probably due to the preservation of these specimens (see above) (Fig. 2D). A re-study of key specimens through new techniques, such as μ-CT, would be very beneficial to increase the number of characters scored, as has been the case for *Qingmenodus* (Lu *et al.*, 2016). On the other hand, in the matrices of Lu and Zhu (2010) and Mann *et al.* (2017), the percentage of scored characters is much higher (79.4–75.6%) since these are small matrices with fewer characters. Therefore, in the case of *Strunius*, we would encourage a detailed re-study of certain key fossils via the use of computerized microtomography techniques, and a review all the available specimens.

Onychodus. *O. jandemarrai* is the best preserved onychodont (Andrews *et al.*, 2006), as thus the characters represented in all the matrices reflect its anatomy very well. Proof of this is that practically all of the dermocranium, splanchnocranium and neurocranium are known, as well as the histology and part of his postcranial anatomy (Fig. 2A–2B). Accordingly, the percentages of scored characters are high, ranging between 73.9 and 84.3% in the matrices of Lu *et al.* (2016) and Mondéjar-Fernández (2020) respectively, which are the highest values seen of any other onychodont scoring (Tab. 3). In the case of Lu and Zhu (2010) this percentage is even higher (97.4%) (Tab. 3). However, in the matrix of Mann *et al.* (2017) three different *Onychodus* species (*O. sigmoides*, *O. eriensis* and *O. jandemarrai*) were scored, with 14.6, 19.5 and 97.6% of the matrix scored respectively. As mentioned above, a revision of the genus is necessary.

Grossius. The holotype and only known specimen of *G. aragonensis* (Gö-709-1) is a relatively well-preserved single skull that is missing its anteriormost tip and part of the posterior region (Fig. 2I). Preserved in a calcareous nodule (Fig. 1C; Schultze, 1973), most of its dermocranium, neurocranium and splanchnocranium is present. Despite this, only 41 to 39.2% of characters have been successfully scored in the matrices of Lu and Zhu (2010) and Mann *et al.* (2017). In the case of the larger matrices of Lu *et al.* (2016) this percentage is just 5.7% and in Mondéjar-Fernández (2020) this increases to 19.8% (Tab. 3). This significant amount of missing data in a three-dimensionally preserved specimen is likely due to the lack of an updated thorough revision of the taxon. Mondéjar-Fernández (2020) reviewed the anatomy of *G. aragonensis*, and this was reflected in the higher percentage of characters scored compared to Lu *et al.* (2016). However, over the 80% of missing data in a skull this complete (this is more missing data than in the case of the more fragmentary *Selenodus*) is likely due to its preservation, in which the sutures of some bones are difficult to observe. Also, the splanchnocranium and neurocranium are only visible in section through breakages of the fossil (Schultze, 1973). As in the case of *Strunius*, new studies with μ-CT and even stereophotogrammetry (Díez-Díaz *et al.*, 2021) could help improve the resolution of future phylogenetic analyses.

Selenodus. The remains of *S. aquesbiae* are very fragmentary, mainly represented by the dermal skull and scales (Mondéjar-Fernández, 2020) (Fig. 2E). Most of the described bones belong to the dermocranium, specially from the snout, cheek, and skull roof regions. One of the most underrepresented regions in the data matrices is the opercular series but curiously *S. aquesbiae* preserves 3 bones of this series (spiracular, preopercular, and opercular). Only the ceratohyal, a bone belonging to the hyomandibular arches, has been preserved from the splanchnocranium.

These data, in combination with the percentage obtained in the character scoring of 21.4%, one of the lowest among onychodonts, indicate that there is a problem in the adequacy of the characters for *Selenodus* (Tab. 3). The preserved bones, although fragmentary, were extensively described, and this is reflected in the scoring, since it has a higher percentage of characters scored than a more completely preserved taxon such as *Grossius* (21.4 *vs* 19.8%) (Tab. 3). Nevertheless, it is still close to 80% of missing data. As is the case for *Bukkanodus*, unearthing more specimens for study would be key, as well as formulating additional characters.

Luckeus. This taxon is usually not scored in any of the matrices due to the scarcity of its remains. The holotype of *L. abudda* (ANV V2969) is composed of a dentary and referred incomplete teeth (Young & Schultze, 2005). As in all cases, recovering new remains is essential, especially in for *Luckeus*. The character scoring of this taxon cannot be calculated as no author has used this taxon in their matrices due to its extremely fragmentary nature.

Phylogenetic definition of Onychodontida

The first comprehensive phylogenetic analysis including a large number of taxa traditionally classified as onychodonts, as well as members of all the major clades of Sarcopterygii, is that of Lu *et al.* (2016). In

Table 3. Percentage of characters scored for each of the taxa traditionally classified as onychodonts in the matrices of Lu and Zhu (2010), Mann *et al.* (2017), Lu *et al.* (2016) and Mondéjar-Fernández (2020).

	Lu and Zhu (2010)	Mann *et al.* (2017)	Lu *et al.* (2016)	Mondéjar-Fernández (2020)
Bukkanodus	38.46	36.58	10.70	12.80
Qingmenodus	35.90	34.14	44.60	47.90
Strunius	79.49	75.60	39.60	46.70
Selenodus	-	-	-	21.48
Onychodus	97.44	97.56	73.96	84.30
Grossius	41.03	39.02	5.78	19.83

this analysis, *Bukkanodus* was excluded from the clade that included the majority of onychodonts, nested basal to coelacanths and onychodonts (Fig. 3). This made Onychodontida, as originally conceived (*i.e.*, including all taxa classified *a priori* as onychodonts) paraphyletic, although the authors used Onychodontida to refer to the clade including *Strunius*, *Qingmenodus, Grossius* and *Onychodus*, but excluding *Bukkanodus* (Lu *et al.*, 2016). With the incorporation of *Selenodus* by Mondéjar-Fernández (2020), several different clades were recovered (*Strunius* + *Qingmenodus* and *Onychodus* + *Grossius*), but without well resolved relationships among them (Fig. 3). All this has led to an uncertainty regarding the monophyly of Onychodontida and, if monophyletic, which taxa actually belong to the clade.

The absence of an explicit phylogenetic definition of Onychodontida makes impossible to determine which taxa should and should not be classified as onychodonts. Taxa traditionally classified as onychodonts were based on comparative anatomy alone (Jessen, 1966; Schultze, 1973; Johanson *et al.*, 2007; Young & Schultze, 2005), thus without phylogenetic analyses, the use of symplesiomorphies for grouping them, cannot be ruled out. The Phylocode recommends that *"Establishment of clade names should be done with careful consideration of possible nomenclatural consequences if the phylogenetic hypothesis turns out to be incorrect. It may frequently be advisable to use only informal names for poorly supported clades"* (Cantino & De Queiroz, 2020).

Using a stem-based definition (also known as "branch-based"); "all organisms more closely related to a designated taxon than to a second such taxon" *sensu* De Queiroz and Gauthier (1992) of onychodonts, as recommended for phylogenetic systematics (Martin *et al.*, 2010) would be a valuable tool to assess which taxa can be included and which excluded from the group, instead of shoehorning a selection of taxa based on *a priori* assumptions. Stem-based definition specifies the membership of a taxon by ''the most inclusive clade that contains at least one internal specifier'' (Sereno, 2005).

Here we erect the rank-free, stem-based taxon Onychodontida, defined as the clade comprising all taxa more closely related to *Onychodus jandemarrai* than to *Latimeria chalumnae, Protopterus aethiopicus* or *Tiktaalik roseae*. However, in all reviewed phylogenetic hypotheses only *Grossius* is always nested with *Onychodus* (Fig. 2) with the rest of the taxa sometimes retrieved as onychodonts with the exception of *Bukkanodus* (Lu *et al.,* 2016) or forming an unresolved polytomy with Actinistia and *Grossius*+*Onychodus* (Mondéjar-Fernández, 2020). The remaining challenge consists of determining which taxa traditionally classified as onychodonts are actually more related to *Onychodus* than to coelacanths within the onychodont+actinistian clade thus falling within the newly defined Onychontida clade.

CONCLUSION

Recent quantitative comparative cladistic methodology has allowed to identify the precise discordant character scorings that cause current phylogenetic hypotheses for Onychodontida to differ. These differences in character scorings are both due to ambiguous character formulation and poor preservation of fossils that difficult scoring the characters. Practices that may help solve this issue include having more explicit formulation of character states, to ensure they are really mutually exclusive, and keep collecting fossils to obtain better preserved specimens to reduce uncertainty in interpreting morphology.

Comparing character distribution maps of current phylogenetic data matrices reveals that taxa with similar degrees of completeness can have extreme differences in percentage of total characters scored, as is the case for *Strunius* and *Grossius*. Both these taxa preserve rather complete skulls but are scored for lower percentages of characters than less complete taxa such as *Qingmenodus*. Restudying these taxa by applying new techniques such as tomographic scanning is critical to increase the amount of scorable characters.

While the monophyly of Onychodontida could be secured using a stem-based definition for the clade, based on current phylogenetic evidence only *Onychodus* and *Grossius* are recovered as a clade in all the analyses. *Qingmenodus* and *Strunius* are nested as onychodonts in most analyses while *Bukkanodus* and *Selenodus* are the more unstable taxa.

Further studies on these genera, application of tomographic techniques, and formulating new phylogenetic characters will help in obtaining better resolved phylogenies.

This work has employed comparative cladistic methodologies for the first time in a group of sarcopterygian fishes, showcasing its usefulness in this field of palaeontology. Character mapping and the recent quantitative comparative cladistics methodology have proven extremely useful tools to quickly evaluate large datasets without the need of manual inspection and promise to revolutionize the field of quantitative systematics.

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Supplementary information. Supplementary material of this manuscript is available at the Spanish Journal of Palaeontology web-site (https://sepaleontologia.es/spanish-journal-palaeontology/) linked to the corresponding contribution. LuxMann file contains the comparison between the matrices of Lu_&_Zhu (2010, Lu_et_Zhu_2010atest.tnt) and Mann *et al.* (2017, Mann_etal_2017a.tnt), which includes the consensus tree with synapomorphies of the groups found in Lu_&_Zhu but not in Mann et al. (Lu_et_Zhu_2010atest-not-Mann_etal_2017a.svg), the consensus tree with synapomorphies of the groups found in Mann et al. but not in Lu_&_Zhu (Mann_etal_2017a-not Lu_et_Zhu_2010atest.svg) and the comparative data matrix highlighting differences between both datasets (matrix_differences.svg). Lu16xMonde file contains the comparison between the matrices of Lu *et al.* (2016, Lu_2016_comp.tnt) and Mondéjar-Fernández (2020, monde_2020_comp.tnt), which includes the consensus tree with synapomorphies of the groups found in Lu *et al.* but not in Mondéjar-Fernández (Lu_2016_comp-not-monde_2020_comp.svg), the consensus tree with synapomorphies of the groups found in Mondéjar-Fernández but not in Lu *et al.* (monde_2020_comp-not-Lu_2016_comp.svg) and the comparative data matrix highlighting differences between both datasets (matrix_differences.svg).

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