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Review of *Vallecillichthys multivertebratum* (Teleostei: Ichthyodectiformes), a Late Cretaceous (early Turonian) "Bulldog fish" from northeastern Mexico

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ABSTRACT

A complete description of Vallecillichthys multivertebratum Blanco and Cavin, 2003, is provided. This ichthyodectiform fish was collected in the Vallecillo Member of the Agua Nueva Formation (Upper Cretaceous: lower Turonian) at Vallecillo, Nuevo León State, northeastern Mexico. On the basis of a comparative study, this monospecific genus is recognized as member of the suborder Ichthyodectoidei and placed with Ichthyodectes and Xiphactinus into the family Ichthyodectidae. This work provides data on Vallecillichthys for a future comprehensive phylogenetic analysis including all ichthyodectiform species.

Key words: Vallecillichthys, Ichthyodectiformes, Turonian, Agua Nueva Formation, Vallecillo, Mexico.

RESUMEN

Se proporciona una descripción completa de Vallecillichthys multivertebratum Blanco y Cavin, 2003. Este pez ictiodectiforme fue colectado en los sedimentos del Cretácico Superior (Turoniano temprano) de Vallecillo pertenecientes al Miembro Vallecillo, Formación Agua Nueva, expuestos en el Estado de Nuevo León, México. Un análisis comparativo demuestra que este género monoespecifico es miembro del suborden Ichthyodectoidei y es colocado junto con Ichthyodectes y Xiphactinus dentro de la familia Ichthyodectidae. El objetivo de este trabajo es ofrecer información sobre Vallecillichthys para su futura integración en un amplio análisis filogenético que incluya a todas las especies ictiodectiformes.

Palabras clave: Vallecillichthys, Ichthyodectiformes, Turoniano, Formación Agua Nueva, Vallecillo, México.

INTRODUCTION

During the 1980s, a large array of well-preserved vertebrate and invertebrate fossils from Vallecillo quarries started to be discovered by inhabitants of the Vallecillo village, Nuevo León, northeastern Mexico (Figure1). Later, in the 1990s, Vallecillo started to be recognized as the most important Late Cretaceous (Turonian) fossil fish locality in this country (Blanco-Piñón, 1998, 2003; Blanco *et al.*, 2001; Alvarado-Ortega *et al.*, 2006c). The fish assemblage from Vallecillo includes ichthyodectiformes that were described as *Vallecillichthys multivertebratum* Blanco and Cavin, 2003 (Figures 2-5). However, that descriptive work just included the diagnostic characters and a short discussion. The aim of present work is to provide a complete description of this Mexican fossil fish as well as to discuss the possible interrelationships of this species with other ichthyodectiforms.

Ichthyodectiformes, commonly called "bulldog fish" due to the flat form of his head and the fierce aspect of his jaws, are an extinct order of basal teleosts erected by Bardack and Sprinkle (1969). Approximately 19 to 23 nominal genera (including about 42 species) are included in this order. These genera are: *Saurocephalus* Harlan, 1824; *Saurodon* Hays, 1830; *Thrissops* Agassiz, 1833; *Cladocyclus* Agassiz, 1841; *Chirocentrites* Hekel, 1849; *Ichthyodectes* Cope, 1870; *Xiphactinus* Leidy, 1870; *Prymnetes* Cope, 1871; *Chiromystus* Cope, 1885; *Gillicus* Hay, 1898; *Eubiodectes* Hay, 1903; *Proportheus* Jaekel, 1909; *Allothrissops* Nybelin, 1964; *Occithrissops* Schaeffer and Patterson, 1984; *Cooyoo* Lees and Bartholomai, 1987; *Prosaurodon* Stewart, 1999; *Faugichthys* Taverne and Chanet, 2000; *Vallecillichthys* Blanco and Cavin, 2003; *Antarctithrissops* Arratia *et al.*, 2004; and *Unamichthys* Alvarado-Ortega, 2004. The validity of *Itaparica* Silva-Santos, 1986, erected on the basis of *Chiromystus woodwardi* Silva-Santos, 1949, is under investigation by M.E.C. Leal (personal communication, 2006).

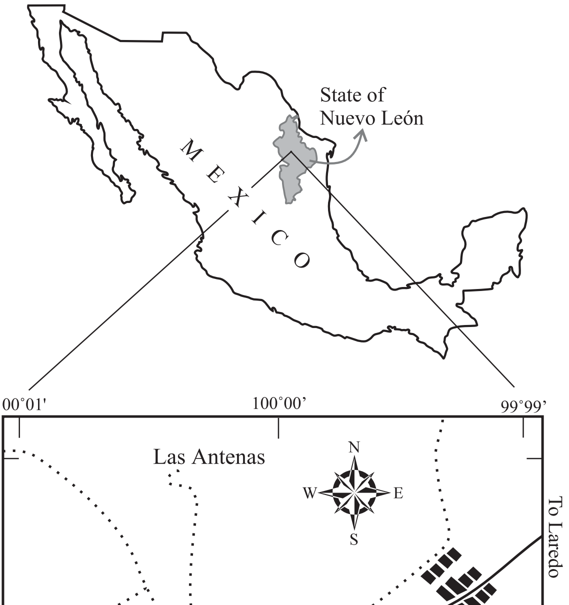


Figure 1. Location map of the Vallecillo quarries, near Vallecillo Village, Nuevo León, Mexico.

Ichthyodectiforms are known from the Middle Jurassic to the Late Cretaceous in both marine and estuarine sediments of North America, South America, Antarctica, Africa, Middle East, Australia, and Europe (Bardack, 1965; Patterson and Rosen, 1977; Taverne, 1986; Forey *et al.,* 2003; Arratia *et al.*, 2004; among others). *Mesoclupea*, Ping and Yen, 1933, and *Chuhsiungihthys* Lew, 1974, probably represent this group in the eastern part of Asia; however, their inclusion has been questioned (see Ping and Yen, 1933; Yabumoto, 1994; Bardack, 1965; Cavin and Forey, in press). An isolated and fragmentary skull from the lower Eocene of New Zealand was erected as *Portheus dunedinensis* Chapman, 1934 [today *Portheus* is synonymous with *Xiphactinus* (Bardack, 1965)]; however, this specimen does not exhibit the diagnostic characters neither for the genus *Xiphactinus* nor for the order Ichthyodectiformes.

The relationships among ichthyodectiforms had been hypothesized in some pre-Henningnian (Saint Seine, 1949; Bardack 1965) and cladistic studies (Patterson and Rosen, 1977; Taverne, 1986; Maisey, 1991; Stewart, 1999; Taverne and Chanet, 2000; Alvarado-Ortega, 1998, 2004, 2005). Nevertheless, a desirable comprehensive phylogenetic analysis requires the inclusion of poorly studied taxa (*i.e.*, *Proportheus*, *Eubiodectes,* and *Chirocentrites*), as well as some bad preserved and scarcely represented (*i.e.*, *Prymnetes, Chiromystus,* and *Cooyoo*), in order to understand in detail the interrelationships of Ichthyodectiformes. In addition, ongoing works include the description of new taxa from Jordan (Mustafa *et al.*, 2003), Mexico (Alvarado-Ortega, 2005, Ovalles-Damián *et al.*, 2006), Italy (Signore *et al.*, 2005), and Brazil (Alvarado-Ortega and Brito, personal observation, 2006).

The Mexican ichthyodectiform record known in the last century is so poorly understood that these fishes were excluded from the first phylogenetic studies (Alvarado-Ortega, 1998, 2004, 2005). This record now includes Cretaceous specimens belonging to *Vallecillichthys multivertebratum* redescribed here; *Prymnetes longiventer* Cope, 1871, from an unknown locality in Chiapas; *Unamichthys espinosai* Alvarado-Ortega, 2004, and at least other three species from Tlayúa, Puebla (Applegate, 1996), *Saurodon* sp. from Múzquiz, Coahuila (Alvarado-Ortega *et al.*, 2006a; Blanco-Piñón and Alvarado-Ortega, 2005a); and still not described specimens from the Muhi quarry, Hidalgo, from Mexcala Formation Guerrero (Alvarado-Ortega *et al.*, 2006b), from

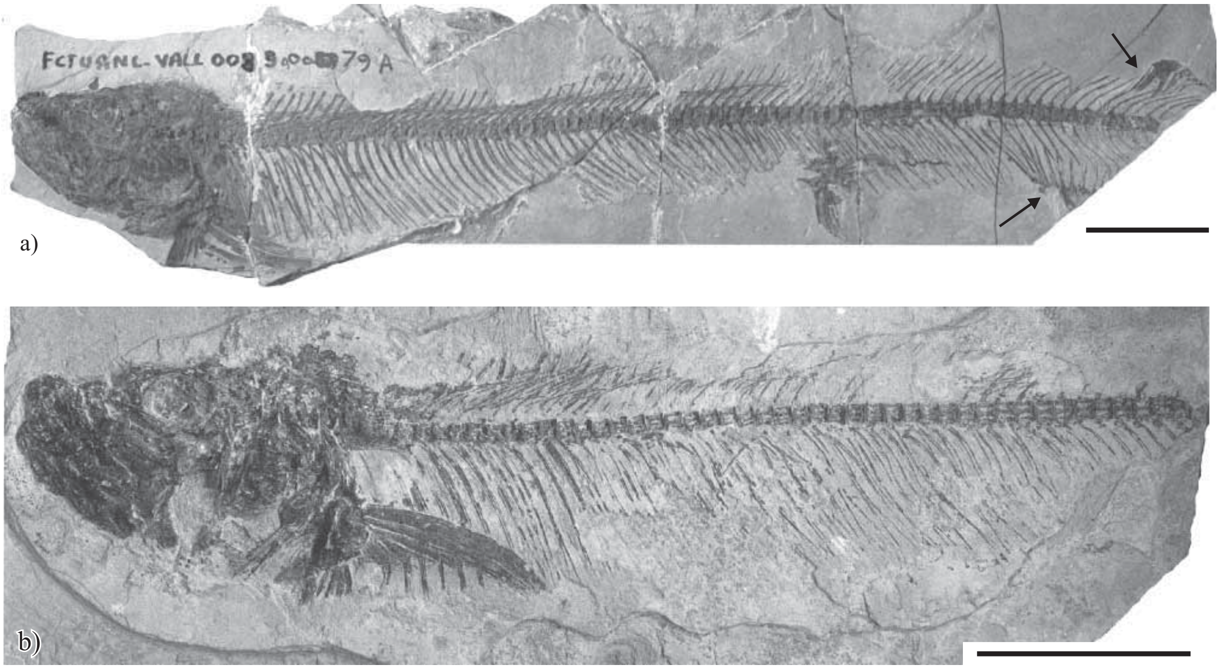


Figure 2. *Vallecillichthys multivertebratum* Blanco and Cavin, 2003. a: FCT 079, holotype and most complete specimen known, arrows show the origin of anal and dorsal fins; b: FCT 331, a referred specimen. Scale bars equal 10 cm.

Xilitla, San Luis Potosí [previously this specimens were described as *Xiphactinus* and *Ichthyodectes* by Maldonado-Koerdell (1956); however, they do not show diagnostic characters (Alvarado-Ortega, 2005)], and from El Chango quarry, Chiapas (Ovalles-Damián *et al.*, 2006); as well by a specimen possibly belonging to *Thrissops* from the Jurassic deposits of Mazapil, Zacatecas (Villaseñor *et al.*, 2006).

Geological setting of the Vallecillo quarries

The fossil bearing strata at Vallecillo are known as the Vallecillo Member of the Agua Nueva Formation. It consists of a homogeneous sequence about 4 m thick of finely laminated pink marlstone and 6–3 cm thick red-brown shale interlayed (Blanco, 2003; Blanco *et al.*, 2001; Blanco-Piñón *et al.*, 2002). According to Blanco-Piñón *et al*. (2005, 2007) and Ifrim (2006), an early Turonian age can be assigned to the fossiliferous beds of Vallecillo by the presence of the ammonite *Watinoceras coloradoense*. Fossil fishes are the most abundant group found in Vallecillo, however, also invertebrates (ammonites, bivalves) and reptiles (Blanco-Piñón, 1998, 2003; Blanco-Piñón *et al.*, 2002) have been reported. Fishes are represented mainly by sharks and osteichthyans. Sharks are represented by the trunk of a *Scyllyorhinus*-like specimen (Blanco *et al.*, 2001), teeth of *Ptychodus mortoni* (Blanco *et al.*, 2001; Blanco-Piñón, *et al.*, 2007) and centra of indeterminated lamniforms (Blanco-Piñón *et al.*, 2005). Osteichthyan from Vallecillo are *Tselfatia* sp., *Nursallia* sp., *Araripichthys* sp., *Goulmimichthys roberti* Blanco and Cavin, 2003, *Robertichthys riograndensis* Blanco-Piñón and Alvarado-Ortega, 2005b, and *Rhynchodercetis regio* Blanco and Alvarado-Ortega, 2006.

Millimeter-scale lamination, micritic matrix bearing rare to abundant bioclasts (planktic forams and calcispheres), the lack of bioturbation, and the occurrence goethite indicate that in Vallecillo the fossil fish strata were deposited under stagnation and deficient oxygen conditions, probably as a consequence of the Oceanic Anoxic Event (OAE) II occurred during the early Turonian (Blanco, 2003; Blanco *et al.*, 2006; Blanco-Piñón *et al.*, 2007).

MATERIAL AND METHODS

Anatomical abbreviations

The abbreviations follow Patterson and Rosen (1977) and Alvarado-Ortega (2004): alb: alveolar border; ang: angular; ao: antorbital; bpp: basipterygoid process on parasphenoid; boc: basioccipital; br: branchiostegal rays; bsc: basal sclerotic; c: ceratobranchial; cl: cleithrum; cor: coracoid; crp: coronoid process; d: dentary; dsp: dermosphenotic; e: epibranchial; epi: epioccipital; epn: epineural; etpa: ethmopalatine; fr: frontal; hym: hyomandibula; ic: intercalar; io: infraorbital; le: lateral ethmoid; mx: maxilla; n: nasal; na: neural arch or spine of preural centra; op:

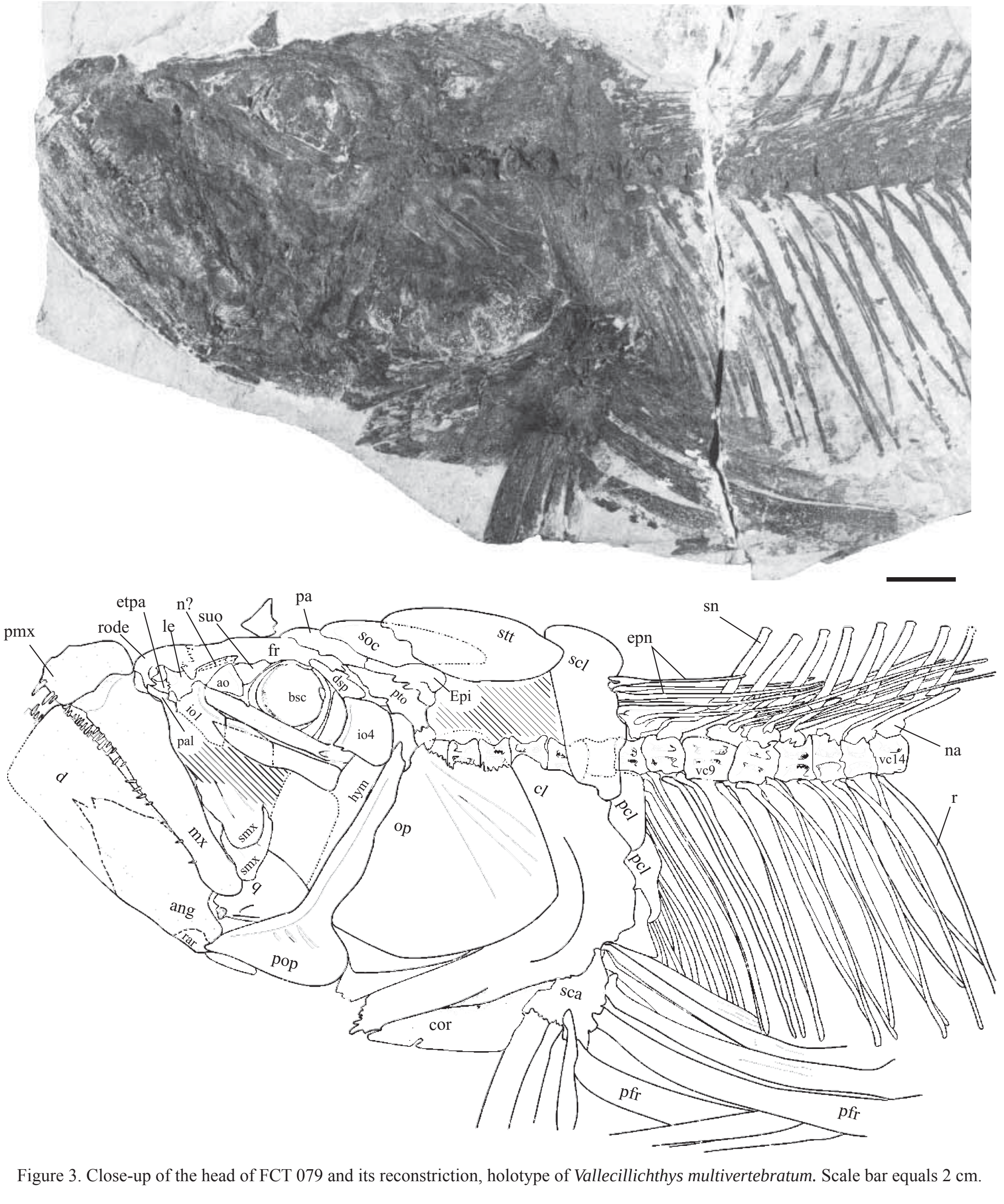


Figure 3. Close-up of the head of FCT 079 and its reconstriction, holotype of *Vallecillichthys multivertebratum.* Scale bar equals 2 cm.

opercle; pa: parietal; pal: palatine; pcl: postcleithrum; pfr: pectoral fin rays; pmx: premaxilla; pop: preopercle; psp: parasphenoid; pto: pterotic; q: quadrate; r: ribs; rad: radials; rar: retroarticular; rode: rostrodermethmoid; s: symphysis of dentary; sbo: suborbital; sca: scapula; sc: sclerotic; scl: supracleithrum; smx: supramaxilla; sn: supraneural; soc: supraoccipital; stt: supratemporal; suo: supraorbital; tf: tooth foramen; vc: vertebral centra (numbered in anterior-posterior direction).

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA. DNPM: Departamento Nacional de Produção Mineral, Brazil. FCT: Facultad de Ciencias de la Tierra, Universidad Autónoma de Nuevo León, campus Linares, Mexico. IGM: Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México. UERJ-PMB: Universidade do Estado do Rio de Janeiro. USNM: United States National Museum, Smithsonian Institute, USA.

Comparative material

The following specimens were reviewed for comparative proposes.

Cladocyclus gardneri Agassiz, 1841: AMNH 1841, AMNH 11877, AMNH 11992, UERJ-PMB 510, UERJ-PMB 520, and UERJ-PMB 531; Early Cretaceous (Aptian-Albian), Romualdo Member, Santana Formation, Ceará, Brazil.

Gillicus Hay, 1898*: G. arcuatus* (Cope, 1875), AMNH 8571; Late Cretaceous, Niobrara Formation, Kansas, USA.

Ichthyodectes ctenodon Cope, 1870: AMNH 2005, AMNH 2005; Late Cretaceous, Niobrara Formation, Kansas, USA.

Proportheus kameruni Jaekel, 1909: AMNH 8394; AMNH 6302, Early Cretaceous [Aptian or Albian (L. Taverne, pers. comm., 2007)], Bituminous shale of Rio San Benito, Spanish Guinea.

Prymnetes longiventer Cope, 1871, USNM 4090 (silicone peel deposited in IGM), Chiapas, Mexico, from unknown locality and age.

Saurocephalus Harlan, 1824: DNPN 1269-P (*Saurocephalus* sp.), fragment of jaw, Late Cretaceous (Maastrichtian), Gramame Formation, Pernambuco, Brazil.

Saurodon Hays, 1830: IGM 6762 (*Saurodon* sp.), Late Cretaceous (Turonian), Eagle Ford Formation, La Mula Quarry, Coahuila, Mexico. AMNH 9907 (*S. leanus*), Late Cretaceous (Campanian), Niobrara Chalk, Montana, USA.

Unamichthys espinosai Alvarado-Ortega, 2004: IGM 8373 and IGM 8374, Early Cretaceous (Albian), Tlayúa Quarry, Middle Member of Tlayúa Formation, Puebla, Mexico.

Xiphactinus audax Leidy, 1870: AMNH 8547, AMNH 8574, and AMNH 1639; Late Cretaceous Niobrara Formation, Kansas, USA.

SYSTEMATIC PALEONTOLOGY

Subdivision Teleostei Müller, 1845
Order Ichthyodectiformes Bardack and Sprinkle, 1969
Suborder Ichthyodectoidei Romer, 1966
Family Ichthyodectidae Crook, 1892

Vallecillichthys multivertebratum Blanco and Cavin, 2003

Holotype. FCT 079, holotype; articulated specimen lacking the posterior part of the body behind the dorsal fin (Figures 2a and 3).

Referred specimens. FCT 331; articulated specimen preserving the head and anterior abdominal area (Figure 2b). FCT 127, head and pectoral part of the trunk disarticulated (Figure 4). FCT 332, head and anterior part of the body (Figure 5a). FCT 196, articulated cranium (Figure 5b-d).

Occurrence. Early Turonian Marlstones of Agua Nueva Formation at Vallecillo quarries, near Vallecillo Village, Nuevo León, Mexico.

Preservation. All *Vallecillichthys multivertebratum* specimen have bones largely replaced by calcite crystals. Several boundaries between bones are obscured and their surfaces, including ornaments and sensory canal pores, are often total or partially destroyed. However, the following features are preserved.

Description.

General features. *Vallecillichthys multivertebratum* is a large and fusiform fish. Currently, because the lack of complete specimens, the total and standard lengths of this species remain unknown. However, other measurements are known from FCT 079 (Figure 2a), which represents the holotype and most complete specimen known for this species. The predorsal length is about 91 cm, the preanal and prepelvic length are 84 and 65 cm respectively, the head length including the opercle is 16 cm, and the maximum body depth is 13 cm. A maximum total length of 122 cm was estimated by Blanco and Cavin (2003). An objective estimation of this measurement is based on three observations: 1) The length of the head and all the abdominal vertebrae is 77 cm in FCT 079; 2) in the same specimen, the length known of the 15 most anterior caudal centra preserved is 14.7 cm (the mean centrum length is 0.98 cm); 3) in other ichthyodectiforms there are 20–32 caudal centra (Table 1). It is possible to calculate for this fish a probable length of the caudal section of vertebral column, which could range from 19 to 30 cm. This length of caudal region, added to the length of anterior part of the body shows that the standard length (SL) of this fish could range between 96 and 107 cm and its total length probably was 120–130 cm.

Skull. The supraoccipital is large and it bears a well high triangular crest, which is extended on the skull roof along all the postorbital area and overhangs the occiput. The maximum depth of the supraoccipital crest is contained two times in the neurocranium depth. The frontal is an elongated bone that covers the skull roof from the ethmoid area to back of the orbit. The parietals are located on the skull roof just behind the postorbital level, probably they are fused forming a mesoparietal and they have a small ascending section forming the anterior part of the supraoccipital crest. In lateral view the mesoparietal is extended laterally, reaching the epioccipital near to the middle part of the supraoccipital crest length (Figures 3 and 4).

The epioccipital form a massive, short, and rounded crest (Figure 4). This bone joints the pterotic ventrally and the intercalar posteroventrally. The pterotic is a large bone

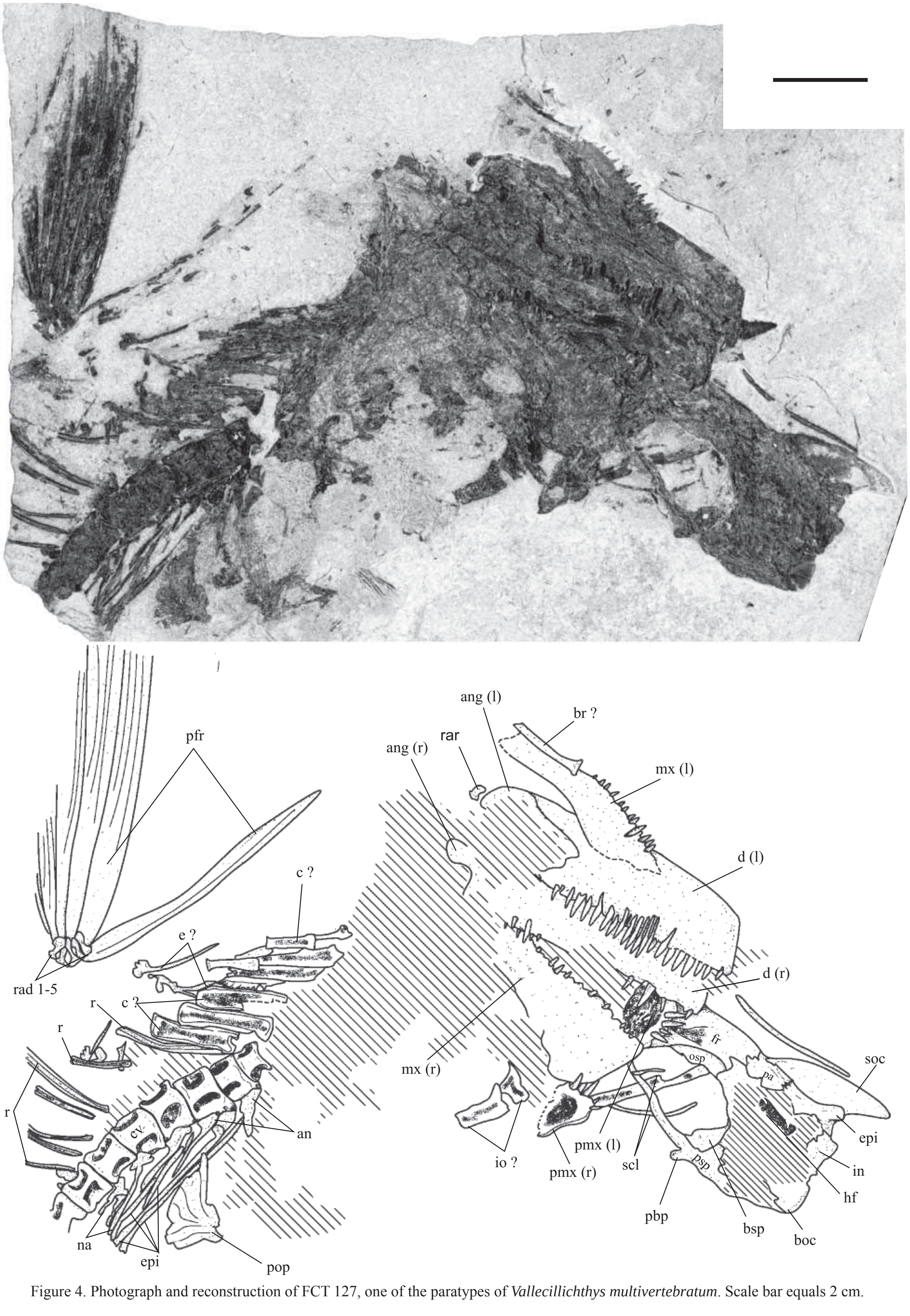


Figure 4. Photograph and reconstruction of FCT 127, one of the paratypes of *Vallecillichthys multivertebratum*. Scale bar equals 2 cm.

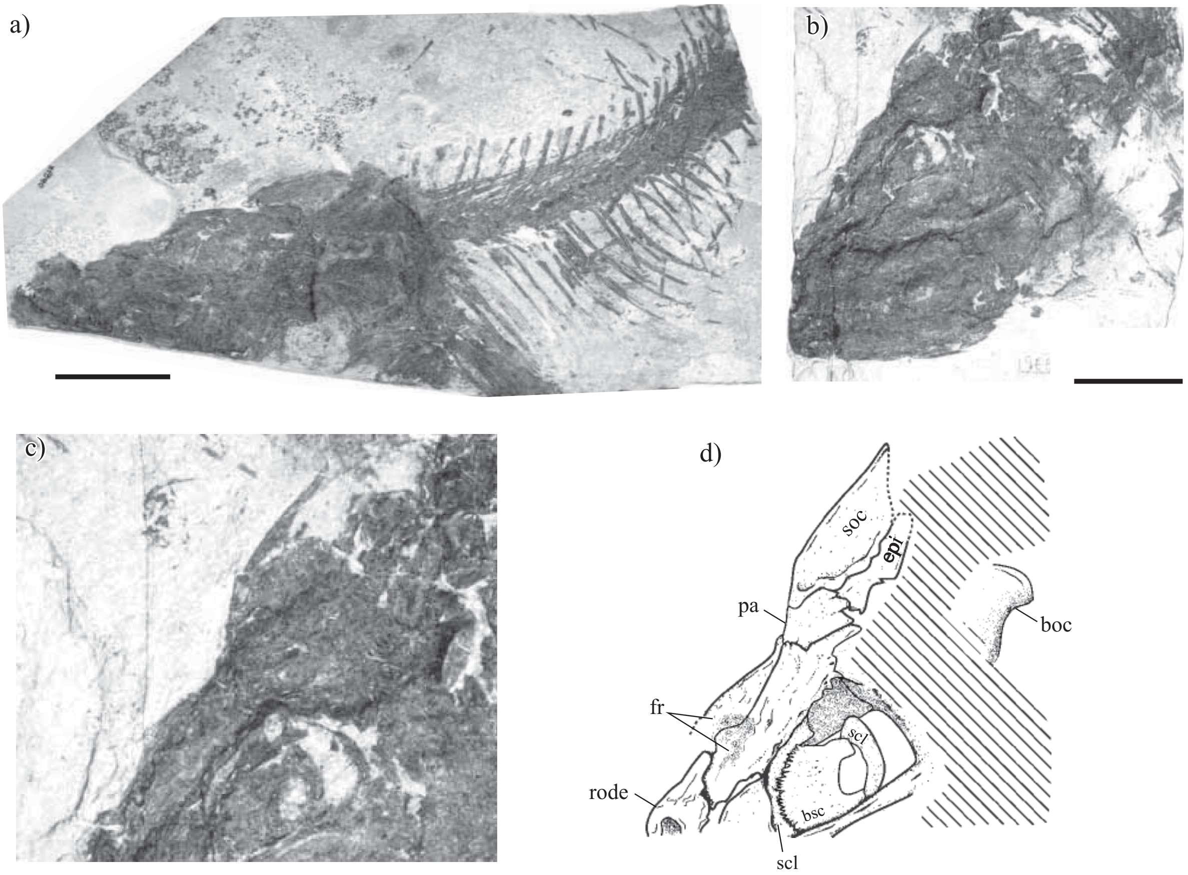


Figure 5. Referred specimens of *Vallecillichthys multivertebratum.* a: general view of FCT 332; b and c: general view and close-up of bones in the skull preserved in FCT 196; d: reconstruction of c. Scale bar equals 2 cm.

that covers approximately the 55% of the otic region of the skull. In FCT-331 it is preserved as a rectangular bone with slightly rounded margins. The pterotic meets the frontal anteriorly, the parietal and the epioccipital dorsally, the prootic ventrally and the sphenotic anteriorly. Laterally, the pterotic bears the caudal part of the hyomandibular facet, which main and longitudinal axis is projected horizontally and parallel to orbital part of parasphenoid. The prootic is known in FCT-332, in which this rectangular bone, about 3 times longer than deep, occupies about the 40% of the lateral wall of the skull.

The orbital section of the parasphenoid is a thin, long, straight bone. In FCT-079 its maximum length is about 6 cm whereas the maximum depth reaches 0.4 cm (Figure 4). The angle between the orbital and otic sections of the parasphenoid is about 150 degrees. At the end of the orbital section of this bone there is a rounded basipterigoid process directed anteroposteriorly.

The rostrodermethmoid is a complex bone having an anterior rounded border and a couple of lateral processes bordering the nasal capsule anteriorly (Figure 3). The joint between the rostrodermethmoid and frontals is not clear. In FCT 079, just behind the nasal capsule this bone seems to have sinuous zig-zag sutures attaching both frontals. In the floor of nasal capsule, sinuous bony outgrowings of the ethmopalatine sutures it with rostrodermethmoid and lateral ethmoid. It seems that fragments of a single nasal bone are preserved in FCT 079.

Circumorbital bones. Thin bones of the circumorbital series are not well preserved in the referred specimens but they probably form a complete and enclosing series around the orbit (Figure 3). An ovoid anterior supraorbital and posterior triangular dermosphenotic bones, which form the ventral part of this series, are almost equal in length. A large part of a nasal capsule ant lateral ethmoid bone is covered by an ovoid-rounded anterorbital. A rectangular infaorbital, slightly longer than deep, forms the posterior margin of the orbit covering large part of the skull base. A couple of well ossified and laminar sclerotic bones unite dorsal and ventrally involving a rounded sclerotic basal bone, which is strongly serrated anteriorly (Figures 3 and 4).

Jaws. The upper jaw includes a premaxilla, a maxilla and a pair of supramaxillae (Figures 3 and 4). The premaxilla is elongated dorsoventrally and irregular in shape, about twice as deep as long. Its straight alveolar border bears a row of at least six stout teeth, which are more or less regular in

Table 1. Composition of the vertebral column among ichthyodectiforms. Two ural centra included within the caudal count. Sources: 1: Nybelin (1964); 2: Arratia *et al*. (2004); 3: Maisey (1991); 4: Lees and Bartholomai (1986); 5: Bardack (1965); 6: Taverne (1986); 7: Schaeffer (1947); 8: Silva-Santos (1949); 9: Cavin (1997); 10: Schaeffer and Patterson (1984, fig. 8); 11: Bardack and Sprinkle (1969); 12: Taverne (1977); 13: Taverne and Bronzi (1999); 14: Forey *et al*. (2003); 15: Alvarado-Ortega (2004, 2005).

Especies	**Vertebrae**			**References**
	Abdominal	**Caudal**	**Total**	
Allothrissops mesogaster	30–33	26–29	58–61	1
Allothrissops regleyi	27–29	25–28	53–54	1
Allothrissops salmonelus	35	27–28	62–63	1
Antarctithrissops antarcticus	33–35	22–23	56–57	2
Cladocyclus gardneri	37	27	64	3
Cooyoo australis	≈ 38	?	More than 65	4
Chirocentrites coroninii	33	28	61–62	5
Chirocentrites neocomiensis	28	32	60?	5
Chirocentrites vexillifer	36	28	64	6
Chiromystus alagoensis	21–23	27	48–50	7
Chiromystus mawsoni	28	22	50	8
Chiromystus woodwardi	19	21	40	8
Eubiodectes libanicus	37–38	27–32	64–70	3, 14
Gillicus arcuatus	42	27	69	5
Ichthyodectes bardacki	?	?	67	13
Ichthyodectes ctenodon	41–44	26–27	68–72	5
Occithrissops willsoni	33	25	58	8
Proportheus kameruni	32	26	63	3
Prymnetes longiventer	50	25	75	10
Saurocephalus lanciformis	?	?	?	11
Saurodon elongatus	88	26–31	114–119	13
Saurodon leanus	?	?	99–101	11
Thrissops cirinensis	28	25	53	12
Thrissops formosus	33–35	26–28	59–61	12
Thrissops subovatus	32–34	28–29	61–63	1, 12
Vallecillichthys multivertebratum	73	More than 17	More than 90	This work
Xiphactinus audax	52–57	29–33	85–90	5
Unamichthys espinosai	45–46	32–34	78–80	15

size. In FCT 079 the crown of the larger of these premaxillar teeth is approximately 0.4 cm long.

The maxilla is triangular, with its anterior border about twice as deep as its posterior border. Its length is about 4 times the depth of its anterior section. A couple of well developed dorsal articular processes are present in the anterior part of this bone. The alveolar border is straight and bears a row of teeth showing regular sizes, in which the heights of crowns are approximately 0.5 cm. A pair of supramaxillae is present above the posterior half of maxilla. The articulation between the maxilla and premaxilla involves their complete heights.

Lower jaw is rectangular, about three times longer than depth. The symphysis and coronoid process are almost equal in depth, its ventral border is slightly convex and its alveolar border is almost straight. The dentary is the largest bone in the lower jaw; it occupies about 80% of its length and bears a single row of teeth in which the crown height varies between 0.02 and 0.43 cm. In this bone, as well as in the maxilla, the alveoli are as deep as the crowns (Figure 4). The dentary, angular, articular, and retroarticular are not fused and the angular and articular participate on the articulation for the quadrate.

Hyomandibular series. Bones of the hyomandibular series are partially exposed. The hyomandibular is T-shaped. The head of the hyomandibular bone is a massive rectangular structure with slightly rounded margins. This bone articules the hyomandibular facet of the skull dorsally, the preopercle and the opercle posteriorly, the metapterygoid anteriorly, and with the quadrate ventrally. The vertical part of this bone is approximately 10 times deeper than long. The entopterygoid is a long rectangular bone that lies in contact with the ventral margin of the parasphenoid. It is approximately 10 times longer than deep. The ectopterygoid is attached to the endopterygoid dorsally, ventrally its shows a concave margin, and anteriorly it sutures with the palatine. The metapterygoid is rectangular and joins the endopterygoid dorsally, ectopterygoid anteriorly, quadrate ventrally, and hyomandibular posteriorly. The quadrate is an equilateral triangle with a well developed and rounded ventral condyle articulating with the lower jaw and a straight dorsal border. In general view, the palatine is triangular with a rectangular or malleolus head articulating with the maxilla ventrally and ethmopalatine dorsally.

Gill arch. In FCT 127 part of the gill arch is present showing some ceratobranchials and epibranchials (Figure 4). However the precise composition of the gill is not well observed.

Opercular series. Bones of the opercular series are also partially known. Opercle is D-shaped element, which seems to have entire borders although the dorsal part is not preserved (Figure 3). There are superficial parallel grooves radiating from the articular facet for the hyomandibula. The preopercle is inverted L-shape with vertical section twice larger than the horizontal one. The subopercle has convex ventral margin and is as large as the opercle.

Paired fins and girdle. The cleithrum is a boomerang-shaped bone with vertically and horizontally oriented limbs about equal in size (Figure 3). Its ventral section, directed anteroventrally-dorsoposteriorly meets a large coracoid. The scapula is located in the posterior ventral corner of the girdle. There are two large postcleithra behind the vertical limb of cleithrum. Large supracleithrum and supratemporal bones join the girdle to skull. At least five short and massive proximal pectoral radials are present. The number of pectoral rays is not well known but at least the first eight or nine of them are wide and show the well documented saber-shape of the paired fin rays found in other ichthyodectiforms; however these are branched longitudinally. The articulation between the pectoral fin rays and the scapula involves at least 5 radials, as preserved in FCT 127 (Figure 4).

The pelvic fin is only exposed in FCT-079. It is located below vertebrae 58-61. The distance between pelvic and pectoral fins is three times that one between pelvic and anal fins (Figure 2a). The triangular pelvic bone is directed up and forward. At least 6-8 wide saber-shape rays are preserved in this specimen.

Unpaired fins. Only the anterior part of anal fin and dorsal fin are preserved in FCT 079 (Figure 2a). It includes the anterior 12 pterygiophores and the base of 5 or 6 rays. The base of this fin begins below the vertebra 77, although the first and larger petrygiophore is located between the haemal spine of centrum 74 (which is the most anterior of caudal centra) and ribs on centrum 73.

The dorsal fin is short and its anterior margin lies above vertebrae 86-88. The rays are not preserved but at least 15 pterygiophores are present, the first and larger of them is located between neural spines of centra 82-83.

Vertebral column. The vertebral column forms a straight line from the posterior part of the skull to the anterior part of the dorsal fin (Fig. 1). In FCT-079, 90 vertebrae are preserved, all of them showing a couple of longitudinal pits. There are 73 abdominal centra, 6 of them obscured by the opercle and pectoral girdle. There are 69 pairs of large uniform ribs enclosing the abdominal area articulating to vertebrae trough out small parapophyses. Based on previous accountings of caudal centra on well known ichthyodectiform species (Bardack, 1965, Bardack and Sprinkle, 1969, Taverne, 1986; Silva-Santos, 1986, Maisey, 1991; Alvarado-Ortega, 2004, 2005; among others), in which their range between 22 and 34 centra (including both urals), it is possible estimate that *Vallecillichthys multivetebratum* could have at least 100 vertebrae. In lateral view, centra are square. Neural and haemal arches are autogenus. In the abdominal area there are small haemal arches. In the first three quarters of the abdomen, long epineurals are associated with the neural arches (which probably are fused each other) and at least three free epineurals join the posterior part of the skull. Additionally, all predorsal centra behind the occiput are associated with large free spatula-like supraneurals.

Scales. In *Vallecillichthys multivertebratum* the scales are ovoid, about twice as deep as long. Their external surface is ornamented with anterior punctae and posterior radii, as in the most derived ichthyodectiforms. Some scarce concentric circuli are also preserved near their borders.

DISCUSSION

The relationships of the order Ichthyodectiformes had been recently hypothesized by different authors (Taverne, 1986; Maisey, 1991; Stewart, 1999; Taverne and Chanet, 2000; among others). The actual state of the taxonomy of this teleostean group can by traced back to Romer (1966), who erected the suborder Ichthyodectoidei (into Osteoglossomorpha) to include the fossil forms allied to *Ichthyodectes* [fossil chirocentrids of Woodward (1919), Saint-Seine (1949), and Bardack (1965)] and the family Saurodontidae (*Saurodon* and *Saurocephalus*) erected by Cope (1870). Bardack and Sprinkle (1969) erected the Order Ichthyodectiformes including the Romer´s Ichthyodectoidei as an *incertae sedis* group of basal teleosts, considering all non-saurodontid taxa within the family Ichthyodectidae [firstly named by Crook (1892)]. Patterson and Rosen (1977) erected the suborder Allothrissopoidei to include *Allothrissops*. Recently, Arratia *et al.* (2004) described *Antarctithrissops* as an allothrossopoid fish. Schaeffer and Patterson (1984) described *Occithrissops* but they were unable to resolve its relationships with *Allothrissops* (Allothrissopoidei) and *Thrissops* (Ichthyodectoidei). Taverne and Chanet (2000) suggest the suborder Occithrissopoidei to include *Occithrissops.* Actually the relationships among these three suborders are unresolved (Figure 6). Alvarado-Ortega (2004) reviewed the relationships of basal ichthyodectoids to include *Unamichthys*, based on the previous hypotheses suggested by Taverne (1986), Maisey (1991), Stewart (1999), and Taverne and Chanet (2000). However, today the relationships among derived ichthyodectoids also are unclear (Figure 6).

Vallecillichthys multivertebratum is well established as a member of the order Ichthyodectiformes. It has three of those five diagnostic characters of the order suggested by Patterson and Rosen (1977:115, also see Figure 6): 1) A pair of ethmopalatine bones in the floor of the nasal capsule (Figure 3); 2) anal and dorsal fin opposite and remote in the posterior part of the body (Figure 2); and 3) teeth in a single series in the jaws (Figures 3, 4). Other diagnostic characters are not observed in the available specimens of *Vallecillichthys:* [4) Six or seven uroneurals, the first three or four extending anteroventrally to cover the entire lateral surface of the first, second, or third preural centra; and 5) coracoids enlarged ventrally, meeting each other in a mid-ventral coracoid symphysis].

Vallecillichthys multivertebratum also is member of the Suborder Ichthyodectoidei because it has all the diagnostic characters regarded by Patterson and Rosen (1977:115, also see Figures 3, 4 and 6): 6) Well ossified ethmopalatine, which has membranous outgrowths separating and suturing the rostrodermethmoid and lateral ethmoid; 7) high and triangular supraoccipital crest; 8) basal sclerotic bone with serrate margin; 9) palatine head modified into a malleolus; 10) epioccipital forming a massive rounded crest; 11) relatively elongate parietal and epioccipital bones with their anterior borders located near to the posterior orbital border.

Ichthyodectoid families already recognized are Saurodontidae Cope, 1970, Ichthyodectidae Crook, 1892, Cladocyclidae Maisey, 1991, and Unamichthyidae Alvarado-Ortega, 2004. Stewart (1999) considered that Ichthyodectidae is an unnatural group, as well as Cladocyclidae according to this author and Alvarado-Ortega (1998, 2004). Unamichthyidae, a monogeneric family characterized by the presence of parietals unfused and a deep mandibular symphysis, is the sister group of all other Cretaceous ichthyodectoids, including *Vallecillichthys,* that have fused parietals (character 22, Figure 6). Against this background, only the monophyletic nature of Saurodontidae has not been refuted.

The phylogenetic hypotheses of the Ichthyodectiformes include a great number of characters from caudal skeleton. Unfortunately the caudal skeleton of *Vallecillichthys* is not known; nevertheless, its possible phylogenetic position can be drawn up based on data from its head and body. *Vallecillichthys* presents characters 12, 13, 18, 19, 20, 22, 25-27, 29 (≈ 35), 48 and 49 (Appendix and Figure 6) show-

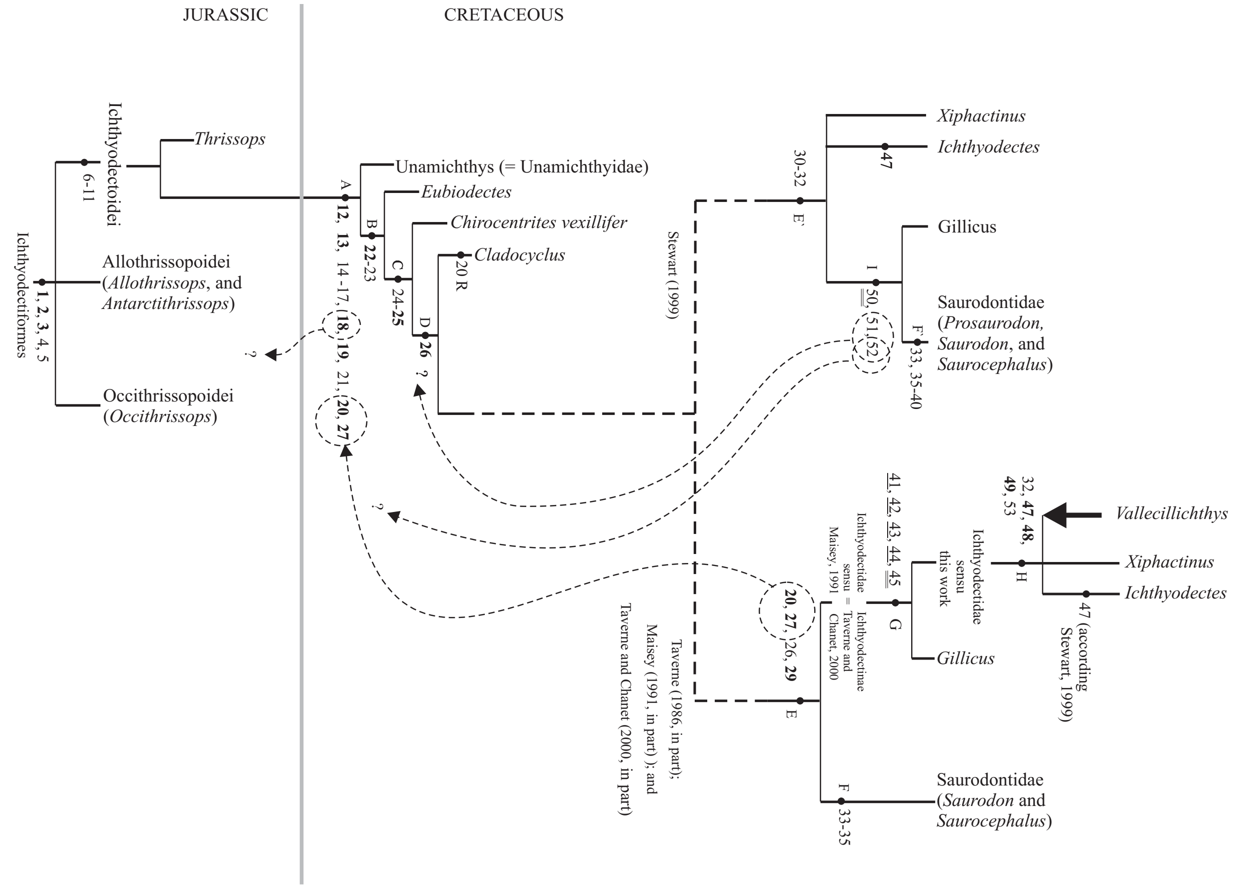


Figure 6. Interrelationships of Ichthyodectiformes (modified from Taverne, 1986; Maisey, 1991; Stewart, 1999; Taverne and Chanet, 2000; and Alvarado-Ortega, 2004). Observations reported in this paper suggest new positions (pointed by the arrows) of characters marked into circles. Bold characters were observed in *Vallecillichthys*. Simple underlined characters are invalid (see Stewart, 1999). Double underlined characters require revision (see present work). The characters are listed in the Appendix and those present in *Valllecillichthys* are discussed in the text of discussion section.

ing that it is close related to *Xiphactinus* and *Ichthyodectes*. Some aspects of these characters are discussed next.

Vallecillichthys and the rest of Cretaceous ichthyodectoids have a relatively deep dentary symphysis (character 12 in Figure 6, Figure 7). This character altogether with the presence of a relatively reduced slightly elevated coronoid process causes a lower jaw with a rectangular aspect, where alveolar and ventral borders are almost parallel. In contrast, in Jurassic ichthyodectiforms the lower jaw is triangular because in these fishes the dentary has a relatively less deep symphysis and a wider and deeper coronoid process (Figure 7). A poorly understood character is the "angled coronoid process", that was suggested by Taverne (1986) and repeated by Maisey (1991) to separate basal ichthyodectoids from Ichthyodectidae plus Saurodontidae (character 27, Appendix and Figure 6). This Taverne´s character is indicating the reduction of the coronoid process described above and it must be located within node A of Figure 6.

Vallecillichthyys as other Cretaceous ichthyodectoids, has a deep maxilla-premaxilla attachment (character 13, Appendix and Figure 6), in where the maxilla depth is uniform and the articular regions of both bones have the same depth. In contrast, in Jurassic ichthyodectiforms the articular region of the maxilla is reduced and its articulation with the premaxilla is weak.

Taverne and Chanet (2000) suggested the occurrence of rays wide or with saber shape in first positions of pectoral and pelvic fin as a distinctive character of Cretaceous ichthyodectiforms (character 18, Appendix and Figure 6). However, *Thrissops* and *Occithrissops*, as well as in *Unamichthys* also have this characteristic wide, strong, and saber rays (see Nybelin, 1964; Schaeffer and Patterson, 1984, fig. 23A; Tischlinger, 1998; and Alvarado-Ortega, 2004). Therefore, it seems that this character has a wider distribution among ichthyodectiforms but it must be analyzed in other Jurassic forms.

In *Vallecillichthys* as in other Cretaceous ichthyodectiforms where the mandibular facet for quadrate is known, the angular participates in this (character 19, Appendix, Figure 6). The exclusion of the angular from this facet is only documented in *Allothrissops*, which facet involves the articular and retroarticular (Patterson and Rosen, 1977:101). Considering the condition found in *Allothrissops*, it is possible to suggest the exclusion of the retroarticular as a derived character (20, Appendix, Figure 6). Unfortunately, the composition of this facet is documented neither in other Jurassic ichthyodectiforms nor in most of the Cretaceous forms. In *Unamichthys*, the retroarticular is excluded from such facet as it was documented for *Ichthyodectes*, *Gillicus*, *Xiphactinus*, *Saurodon* and *Prosaurodon* (Bardack, 1965; Stewart, 1999; among others). In this scenario, the participation of the retroarticular in the lower jaw articulation of *Cladocyclus* must be considered as an apomorphic condition acquired after the inclusion of the angular in this facet as seen in *Unamichthys* (Alvarado-Ortega, 2004).

Unamichthys, *Thrissops*, *Allothrissops*, and

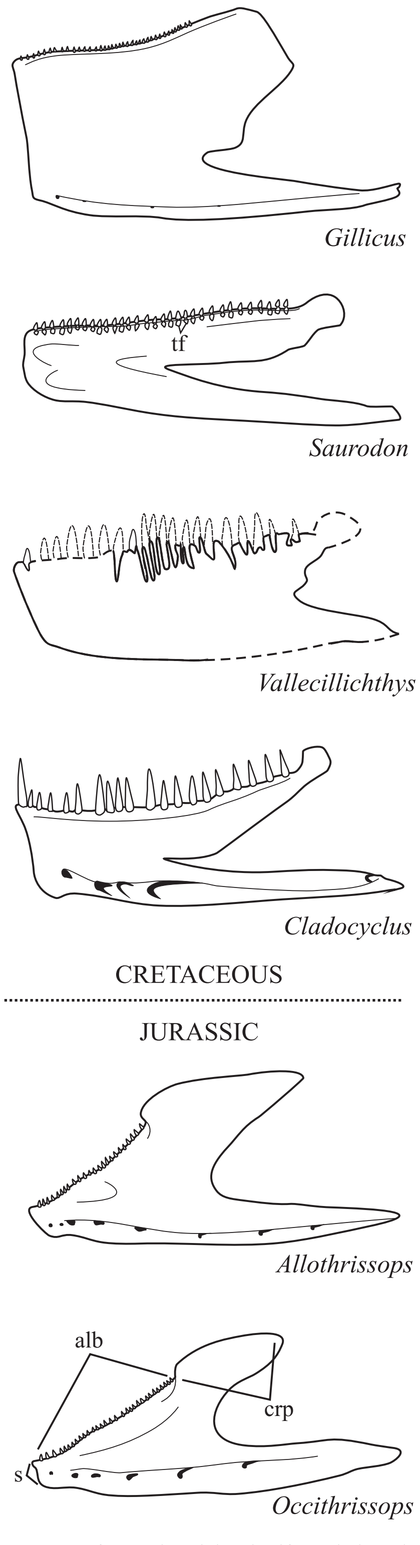


Figure 7. Dentary of some the Ichthyodectiforms in lateral external view but *Saurodon*. *Gillicus*, based on AMNH 8571; *Saurodon* in lateral lingual view, after Bardack and Sprinkle (1969, figs. 5, 6); *Vallecillichthys*, based on FCT 127 (Figure 4); *Cladocyclus*, after Patterson and Rosen (1977, figs. 2 and 28C); *Allothrissops*, after Patterson and Rosen (1977, fig. 9); *Occithrissops*, after Schaeffer and Patterson, (1984, fig. 28).

Occithrissops and probably *Antarctithrissops* have parietals unfused. A monophyletic group is suggested by the fusion of the parietals, a condition considered as derived that is well documented in *Eubiodectes, Chirocentrites vexillifer, Cladocyclus, Prosaurodon, Saurodon, Saurocephalus, Gillicus, Ichthyodectes,* and *Xiphactinus*, as well *Vallecillichthys* (character 22, Appendix, node B in Figure 6).

After the analysis of the position of the pelvic fin among ichthyodectiforms, Alvarado-Ortega (2004) concluded that Cladocyclidae [which includes *Cladocyclus*, *Chirocentrites*, *Chiromystus*, and *Proportheus* as synonymous with *Cladocyclus*] is an unnatural group. According to the first author, all Jurassic ichthyodectiforms plus *Unamichthys* and *Eubiodectes*, as well the poorly known *Chiromystus* and *Proportheus,* have pelvic fins located just in the middle of the standard length. A derived condition is present in *Cladocyclus*, *Chirocentrites vexillifer*, *Ichthyodectes, Gillicus,* and *Xiphactinus, Saurodon* (documented in *S. elongatus* by Taverne and Brozni, 1999), as well as *Cooyoo* and *Vallecillichthys* (Figure 2), in which the pelvic fin is located behind the middle SL, closer to the anal fin base (character 25, Appendix, Figure 6).

According to Alvarado-Ortega (2004), Cladocyclus, as well as genera before considered as ichthyodectids and saurodontids, has anterior radii and posterior fine pitting covering the external surface of scales (see Bardack, 1965), similar to those found in *Vallecillichthys* (character 26, Appendix, Figure 6). In contrast, a pattern of numerous concentric circuli on the scales is present in other ichthyodectiforms.

Taverne (1986), Maisey, 1991, and Taverne and

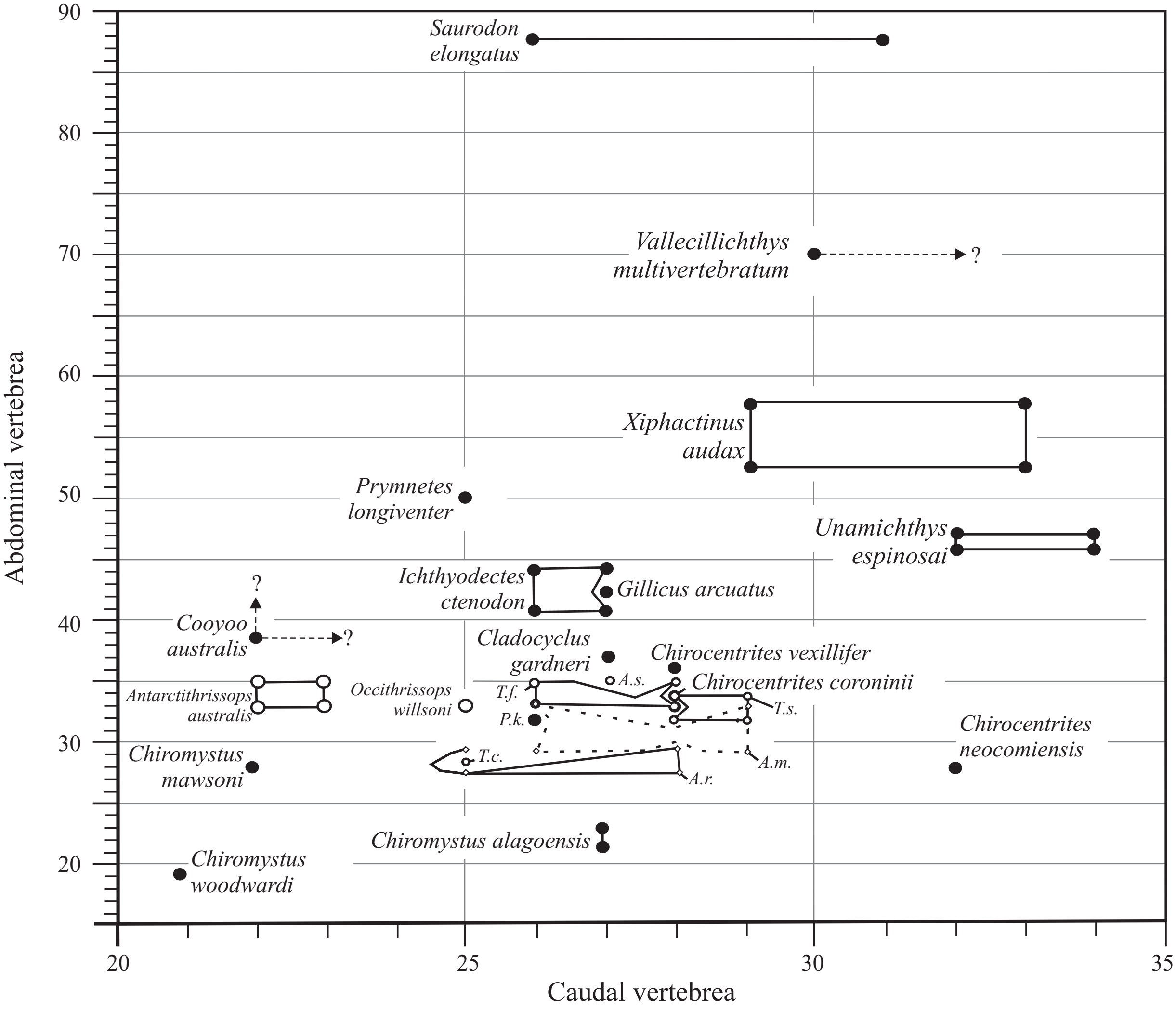
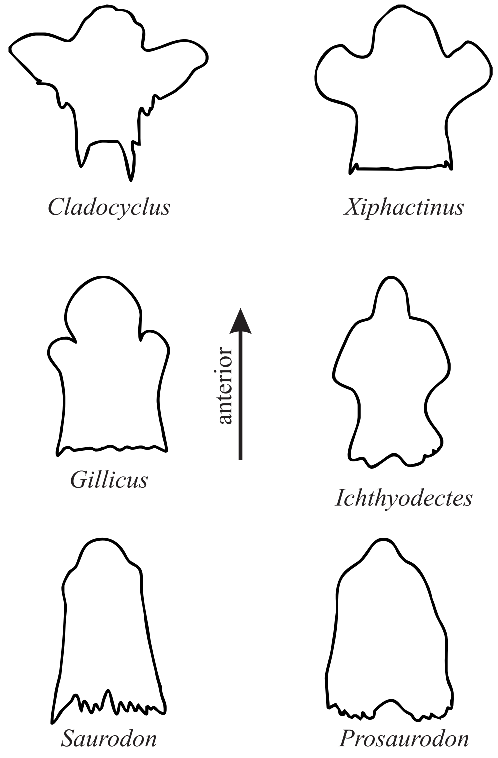


Figure 8. Distribution of abdominal and caudal vertebrae in ichthyodectiforms (based on Table 1). White dots: Jurassic taxa; black dots: Cretaceous taxa; *A.m.: Allothrissops mesogaster; A.r.: A. regleyi; A.s.: A. salmonelus; P. k.: Proportheus kameruni; T.c.: Thrissops cirinensis; T. f.: T. formosus; T.s.: T. subovatus.*

Chanet (2000) recognized in the number of vertebrae a diagnostic character of some ichthyodectiform groups. According to these authors, the number of vertebrae increases along the evolution of ichthyodectiforms from less than 63 toward about 70 and more than 100 (characters 29 and 35, Appendix, Figure 6) (see also Taverne, 1997). After the analysis of the number of abdominal and caudal vertebrae present in the ichthyodectiforms (Table 1 and Figure 8), it is possible to see that such tendency is not clear, because a basal form as *Unamichthys* (with 78-80 total vertebrae) shows higher amount than more derived forms such as *Cladocyclus*, *Ichthyodectes* and *Gillicus* (with 64, 68-72, and 69 total vertebrae respectively). However, it is clear that number of caudal, abdominal, and total vertebrae can be used as diagnostic characters in the large part of the ichthyodectiform genera including *Vallecillichthys* that is well characterized by its 73 abdominal centra, the second highest account among all ichthyodectiforms as far known (Figure 8).

The angle formed between the orbital and otic sections of the parasphenoid ranges between 149° and 160° in *Xiphactinus* and *Ichthyodectes* (Bardack, 1965; Taverne, 1986; Maisey, 1991), as well as in *Cooyoo* and *Faugichthys* (Lees and Bartholomai, 1987; Taverne and Chanet, 2000). The parasphenoid of *Vallecillichthys* is also broad and it is about 150° (character 48, Appendix, Figures 4, 6, 9). In contrast, other ichthyodectiforms where this angle is documented, it is about 130° (Figure 9).



Cladocyclus *Xiphactinus*

Gillicus *Ichthyodectes*

Saurodon *Prosaurodon*

Figure 9. Shapes of the rostrodermethmoid of ichthyodectiforms in dorsal view. *Cladocyclus* after Patterson and Rosen (1977, fig4); *Xiphactinus*, *Gillicus*, and *Ichthyodectes* after Bardack (1965, figs. 5, 18, and 15 respectively); *Saurodon* after Bardack and Sprinkle (1969, fig. 2); *Prosaurodon* after Stewart (1999, fig. 7).

Xiphactinus, *Ichthyodectes*, and *Vallecillichthys* share the presence of a hyomandibular facet parallel to the orbital part of the parasphenoid (character 49, Appendix, Figures 4, 6, 9). In contrast, the longitudinal axis of this facet is projected downward crossing with the ethmoid area of the skull (Figure 9) in *Allothrissops, Occithrissops, Antarctithrissops, Thrissops, Cladocyclus, Chiromystus*, *Chirocentrites vexillifer, Saurodon, Gillicus, Unamichthys, Cooyoo,* and *Faugichthys* (see descriptions and illustrations in Silva-Santos, 1949; Lees and Bartholomai, 1987; Taverne, 1977; Schaeffer and Patterson, 1984; Taverne and Chanet, 2000; Arratia *et al.*, 2004; Alvarado-Ortega, 2004; among others).

On the basis of the characters discussed in two prior paragraphs, it is clear that *Vallecillichthys* forms a monophyletic group with *Xiphactinus* and *Ichthyodectes*. This group represents a new sense of the family Ichthyodectidae (Figure 6). These characters were excluded from the analysis performed by Stewart (1999), who only argued on the inexistence of those characters that support the inclusion of *Gillicus*, *Ichthyodectes*, and *Xiphactinus* into the family Ichthyodectidae *sensu* Maisey (1991, characters 41-43, Appendix, Figure 6), disabling therefore the recognition of the monoplyletic group including the latter two genera. Taverne and Chanet (2000) named this same group as Ichthyodectinae suggesting that it is supported additionally by the presence of a very deep dentary symphysis and a preopercle with a wide dorsal section bearing a broad notch (characters 44 and 45 respectively, Appendix, Figure 6). The lower jaw shape of *Xiphactinus* and *Ichthyodectes* is similar to that one of *Cladocyclus* and *Unamichthys* (see Bardack, 1965; Patterson and Rosen, 1977; and Alvarado-Ortega, 2004). This leaves the dentary symphysis hypertrophed as an exclusive character of *Gillicus* (Figure 7). The other Tavernes´s character (45) is not well documented and a comparative study of the preopercle on ichthyodectiformes is required to confirm this suggested diagnostic difference.

Notes about the possible relationships of *Gillicus*

Some things are remarkable in relation to those characters that support the inclusion of *Gillicus* and saurodontids within an unnamed group suggested by Stewart (1999) (see characters, 50-52, node I, Figure 6, and Appendix). This author suggested that the quadrate head lies ahead of the orbit in these fishes (character 50); this could be true for saurodontids but, following the illustration of Bardack (1965, pl.2, fig. A), it is not for *Gillicus*. Also, this author noted that in dorsal view the rostrodermethmoid shows a slight constriction behind of its anterior expansion in both, *Gillicus* and saurodontids (character 51); whereas in other ichthyodectiforms this constriction is conspicuous. The review of the rostrodermethmoid shape in dorsal view shows that in *Gillicus* it is similar to that star-shape found in *Cladocyclus*, *Xiphactinus* and *Ichthyodectes*, which is different to the triangular shape seen in *Saurodon* and *Prosaurodon* (Figure 9). This result suggest that the star-shape of the rostrodermethmoid (in dorsal view) probably is present in basal ichthyodectoids and that the triangular shape does not represent a synapomorphy of *Gillicus* + Saurodontidae (see characters 51, Figure 6, Appendix).

Additionally, Stewart (1999:357-358, fig. 10) found that the quadrate condyle shows a simple articular surface in *Gillicus, Prosaurodon, Saurodon,* and *Saurocephalus* (character 52, Appendix, Figure 6); whereas in *Ichthyodectes* and *Xiphactinus* this surface is complex because it shows an anterior lateral projection. Unfortunately, Stewart (1999) did not recognized the derived condition between these two shapes, suggesting that one present in *Gillicus* and his saurodontids could be a synapomorphy. Acid-prepared *Cladocyclus* specimens study by Leal (2003) show the presence of a simple articular surface of the quadrate condyle showing that it is the plesiomorphic condition and the complex articular surface is the derived one (53, Appendix, Figure 6). The character is unknown in *Vallecillichthys* but it could show a complex a articular surface of the quadrate condyle providing additional support to the monophyly of our Ichthyodectidae family.

Considering the actual scenario, the position of *Gillicus* as sister group of Saurodontidae *sensu* Stewart (1999) or as possible basal form of the Ichthyodectidae (*sensu* Maisey, 1991) is not supported (Figure 6). The phylogenetic position of this fish could be resolved after the analysis of at least one bad documented character: the length of the anal fin (character 43). Stewart (1999:351) reported a short anal fin in *Xiphactinus*, *Ichthyodectes*, *Gillicus*, and *Saurodon*; however the same year, Taverne and Bronzi (1999) described an undoubted *Saurodon* specimen as *S. elongatus* which has a very large anal fin including at least 30 rays (also see Taverne, 1997), which is comparable to those found in *Occithrissops*, *Thrissops*, as well as in *Unamichthys, Cladocyclus, Eubiodectes,* and other basal ichthyodectioids. Such discovery suggests that the condition of anal fin among saurodontids had been badly interpreted or not enough documented and probably all of them have large anal fins. If the occurrence of a short anal fin in *Gillicus* is confirmed it could be placed again among the ichthyodectids. In the meanwhile *Gillicus* must be considered as an *incertae sedis* derived ichthyodectoid.

CONCLUSIONS

The present description of *Vallecillichthys multivertebratum*, a Mexican ichthyodectiform fish erected by Blanco and Cavin (2003), provides data for its comparative study into the suborder Ichthyodectoidei. A comprehensive phylogenetic study of this order is desirable; however, today there are a large number of ichthyodectiform species that require a re-description [*i.e.*, *Chiromystus* species, *Chirocentrites* species, *Proporteus kameruni*, among others] and ongoing studies deal with recently discovered forms that represent new species [*i.e.*, one basal ichthyodectoid from Brazil (Alvarado-Ortega and Brito, submitted); new Mexican ichthyodectiforms found in Cretaceous sedimentary outcroups in the states of Puebla, Hidalgo, Chiapas, Coahuila, and San Luis Potosí (Alvarado-Ortega, 2004, 2005; Alvarado-Ortega *et al.*, 2006c; Ovalles-Damián *et al.*, 2006)].

Contrary to Blanco and Cavin (2003), *Vallecillichthys* is placed with *Ichthyodectes* and *Xiphactinus* into the family Ichthyodectidae. The emended diagnosis of this family includes the participation of parietals (fused forming a mesoparietal) in the supraoccipital crest (not well documented in *Vallecillichthys*); quadrate condyle with an articular surface having a lateral anterior projection (illustrated by Stewart, 1999, fig. 10 E-F; unknown in *Vallecillichthys*); broad parasphenoid angle (ranging between 149-160°); and hyomandibular facet parallel to orbital part of parasphenoid.

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APPENDIX

The following characters had been used on the phylogenetic hypotheses of Ichthyodectiformes by Taverne (1986), Maisey (1991), Taverne and Chanet (2000), Stewart (1999), and Alvarado-Ortega (1998, 2004, 2005). In the present work they are represented in Figure 6 and are cited along the discussion section.

1. A pair of ethmopalatine bones in the floor of the nasal capsule.
2. Anal and dorsal fin opposite and remote in the posterior part of the body.
3. Teeth in a single series in the jaws.
4. Six or seven uroneurals, the first three or four extending anteroventrally to cover the entire lateral surface of the first, second, or third preural centra.
5. Coracoids enlarged ventrally, meeting each other in a midventral coracoid symphysis.
6. Well ossified ethmopalatine, which has membranous outgrowths separating and suturing the rostrodermethmoid and lateral ethmoid.

7. High and triangular supraoccipital crest.
8. asal sclerotic bone with serrate margin.
9. alatine head modified into a malleolus.
10. Epioccipital forming a massive rounded crest.
11. Relatively elongate parietal and epioccipital bones with their anterior borders located near to the posterior orbital border.
12. Deep dentary symphysis.
13. Deep premaxilla-maxilla attachment.
14. Five uroneurals.
15. First uroneurals relatively short, reaching preural centra 2 or 3.
16. Absence of urodermals.
17. Sensitive pit openings in parietals are lacking or reduced.
18. Wide first pectoral and pelvic fin rays showing saber shape.
19. Angular participates in the mandibular facet for quadrate.
20. Retroarticular excluded of the mandibular facet for quadrate (the condition: reoarticular included in the mandibular facet for quadrate (noted as 20R in Figure 6), which present in *Cladocyclus* and *Allothrissops,* could be interpreted as a regressive condition due this bone is excluded from that articulation in an intermediate form, *Unamichthys*).
21. Presence of a notch on the upper posterior border of preopercle (the Taverne´s notch) (also see character 45).
22. Parietals fused each other.
23. Two epurals.
24. One epural.
25. Pelvic fin located behind the middle part of the body (the distance pectoral-pelvic fins is higher than two times the distance pelvic-anal fins).
26. External surface of scales having anterior radii and posterior fine pitting.
27. Angled coronoid process.
28. Ball-and-Socket attachment between hypurals 1 and 2 and ural 1.
29. High vertebral number [approximately 70-100 or more (see Taverne and Bronzi, 1999)].
30. Lateral margin of frontals with an anterior-directed notch (which may receive the nasal).
31. Anterior ceratohyal with narrow fenestra.
32. Parietals participates in the supraoccipital crest.
33. Predentary bone.
34. Internal surface of maxilla, premaxilla and dentary bones with a foramen on (or notch) at the base of each tooth.
35. Near to 100 total vertebrae.
36. Sigmoid dorsal margin of quadrate.
37. Teeth with carinae.
38. Long dentary bone.
39. Deep maxilla without a notch at rear of the palatine facet.
40. Upward indentation in ventral margin of occipital condyle.
41. Anteriorly extended epioccipitals.
42. Subdivided nasal bone.
43. Short remote anal fin.
44. Very deep dentary symphysis.
45. The widened dorsal end of preopercle with a broad notch.
46. Epioccipials and suparoccipital of equal forward extent.
47. Broad parasphenoid angle.
48. Hyomandibular facet parallel to orbital part of parasphenoid.
49. Enlarged premaxillar fangs.
50. The quadrate head lies ahead of orbit.
51. Rostrodermethmoid with slight constriction behind of its anterior expansion (visible in dorsal view) (Figure 9).
52. Quadrate condyle with an articular surface simple (see Stewart, 1999: 357-358, fig. 10 A-D).
53. Quadrate condyle with an articular surface having a lateral anterior projection (see Stewart, 1999: 357-358, fig. 10 E-F).

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