

NEW DATA ON THE FOSSIL FISH *TERGESTINIA SORBINII* (PYCNODONTIFORMES) FROM THE LATE CRETACEOUS OF TREBECIANO, TRIESTE (ITALY)

LOUIS TAVERNE ⁽¹⁾, LUIGI CAPASSO ⁽²⁾ & DEBORAH ARBULLA ⁽³⁾

(1) Institut Royal des Sciences Naturelles de Belgique, Directoire Terre et Histoire de la Vie, rue Vautier 29, B-1000 Bruxelles, Belgique.
E-mail: louis.taverne@skynet.be

(2) Museo Universitario dell'Università « G. D'Annunzio di Chieti-Pescara, Piazza Trente e Trieste 1, I-66100 Chieti, Italia.
E-mail: lcapasso@unich.it

(3) Museo Civico di Storia Naturale di Trieste, Conservatore Paleontologia, Via dei Tomazin 4 ; I-34139 Trieste TS, Italia.
E-mail: deborah.arbulla@comune.trieste.it

Abstract – The skeleton of *Tergestia sorbinii*, a pycnodont fish from the Late Cretaceous of Trebeciano (Trieste, northern Italy), is described in details and its systematic position is discussed. *Tergestia* belongs to the family Pycnodontidae, as shown by the presence of a brush-like process on the parietal. The posterior region of the endocranium is visible. The exposed region of the hyomandibula is a little deeper than the preopercle. A bifid cloacal scale is present. Some hypochordals are broadened. Most dorsal ridge scutes are scutellum-like. These characters clearly refer *Tergestia* to the subfamily Pycnodontinae. Within the phylogeny of this subfamily, *Tergestia* appears more specialized than *Libanopycnodus*, *Pseudopycnodus* and *Polazzodus* but less advanced than *Sylvienodus*, *Signapycnodus*, *Pycnodus* and *Oropycnodus*. The systematic position of *Tergestia* is thus intermediate between these two groups.

Key words: Pycnodontidae, *Tergestia sorbinii*, osteology, systematic position, Late Cretaceous, Trebeciano, Trieste, Italy.

Riassunto – Gli autori riesaminano i caratteri salienti dello scheletro di *Tergestia sorbinii*, un pesce picnodonte del tardo Cretaceo di Trebeciano (Trieste), alla luce di alcuni nuovi esemplari appartenenti alle collezioni di paleontologia del Museo Civico di Storia Naturale di Trieste. I dettagli dell'anatomia scheletrica emersi dall'esame dei nuovi esemplari consentono, tra l'altro, di ridiscutere e precisare la posizione sistemica del genere *Tergestia*. La presenza delle frange ossificate post-parietali non lascia dubbi sull'appartenenza di *Tergestia* alla famiglia Pycnodontidae. La parte posteriore dell'endocranio è esposta. La regione esposta dell'iomandibolare è situata un po' più alto rispetto al pre-opercolo. È presente una scaglia cloacale bifida. La maggior parte degli scudi dorsali sono scutelliformi. Tutti questi caratteri indicano chiaramente che *Tergestia* appartiene alla sottofamiglia Pycnodontinae. Nell'ambito della filogenesi di questa sottofamiglia, il genere *Tergestia* appare più specializzato di *Libanopycnodus*, *Pseudopycnodus* e *Polazzodus*, ma meno avanzata di *Sylvienodus*, *Signapycnodus*, *Pycnodus* e *Oropycnodus*. La posizione sistemica di *Tergestia* è quindi intermedia tra questi due gruppi.

Parole chiave: Pycnodontidae, *Tergestia sorbinii*, osteologia, posizione sistemica, Cretaceo superiore, Trebeciano, Trieste, Italia.

1. - Introduction

The construction of the so called “RA-13” motorway junction between Sistiano and Trieste began in 1987. A small lens of grey marly limestone, finely stratified and richly fossiliferous, was found, in 1989, during the works in the region of Trebeciano. A large amount of fossils was collected on that occasion. Today, that fossil material is principally preserved in the collections of the Civic Natural History Museum of Trieste. The fossil assemblage includes land plants, decapod crustaceans (GARASSINO, FERRARI, 1992; GARASSINO, BRAVI, 2003), articulated skeletal remains of fishes (SORBINI, BANNIKOV, 1996; BANNIKOV, SORBINI, 2000; CAPASSO, 2000; CARNEVALE, JOHNSON, 2015) and rare remains of reptiles.

The geological age of this limestone is rather controversial. In the first published studies, it was interpreted as Early Paleocene, an interpretation only based on the po-

sition of the fossiliferous layers in the stratigraphic series (SORBINI, BANNIKOV, 1996; BANNIKOV, SORBINI, 2000; CAPASSO, 2000). More recently, VENTURINI *et al.* (2008) reported the presence of the benthic foraminifer *Murciella* in the fossiliferous deposits, suggesting a Late Cretaceous age. The same year, DALLA VECCHIA (2008) proposed a Late Campanian-Early Maastrichtian age on the basis of regional correlations. In the geological map of the area, this fossiliferous organic-rich laminated limestone is reported to the so called “Liburnica Formation”, considered as Cretaceous-Paleocene (JURKOVSEK *et al.*, 1996). This formation is a heterogenous stratigraphic unit, vastly exposed in all the Karst area and in western Slovenia (STACHE, 1889; JURKOVSEK *et al.*, 1996).

On the paleoenvironmental point of view, the organic-rich limestone of Trebiciano was sedimented in paralic and shallow water paleobiotopes.

The fossil fish assemblage of Trebiciano contains some new Holostei and many new species and genera of Teleostei (SORBINI, BANNIKOV, 1996) but only a few of them are presently described: the pycnodont *Tergestia sorbinii* Capasso, 2000, the paracanthopterygian *Trebiciania roseni* Sorbini & Bannikov, 1996 and the ophidiiform *Pastorius methenyi* Carnevale & Johnson, 2015 (SORBINI, BANNIKOV, 1996; CAPASSO, 2000; CARNEVALE, JOHNSON, 2015).

The aim of the present paper is to briefly re-study the pycnodont *Tergestia sorbinii*, partly on the basis of a specimen (T. 208-T. 209) not taken in account in CAPASSO (2000), in order to complete the original description. Indeed, this sample allows a better understanding of the skull than previously, the cranial region being rather well preserved. Some erroneous interpretations are now corrected. We also comment on the systematic position of *T. sorbinii* within Pycnodontiformes.

2. – Systematic Paleontology

Subclass Actinopterygii Klein, 1885

Series Neopterygii Regan, 1923

Division Halecostomi Regan, 1923 *sensu* Patterson, 1973

Superorder Pycnodontomorpha Nursall, 2010

Order Pycnodontiformes Berg, 1937 *sensu* Nursall, 2010

Family Pycnodontidae Agassiz, 1833 *sensu* Nursall, 1996

Subfamily Pycnodontinae Poyato-Ariza & Wenz, 2002

Genus *Tergestia* Capasso, 2000

Emended diagnosis

The same as the species (monospecific genus).

Species *Tergestia sorbinii* Capasso, 2000

Emended diagnosis

Small-sized pycnodontid fish. Body moderately deep. Upper point of the dorsal border located just behind the head. Large skull, with a long preorbital and a short postorbital region. Mouth gape obliquely oriented. Short brush-like process on the parietal, with only five branches. Long and narrow temporal (= dermocranial) fenestra. Small extrascapular lying against the dermopterotic. Large dermosphenotic sutured to the ventral margin of the skull roof. Basisoccipital and exoccipital exposed behind the rear of the skull. Ventral borders of dermopterotic and dermosphenotic located at the level of the mid-height of the orbit. Prefrontal very narrow. Premaxilla with one large incisiform tooth. Vomer with five rows of teeth. Prearticular with three rows of teeth, those of the two ventral rows being sigmoid. Notochord completely surrounded by vertebral arches in abdominal region and free in the caudal region. Neural and haemal spines with an anterior wing-like component. 29-31 neural spines before epichordal series. First neural spines attached to the neural arches. 14-15 haemal spines before hypochordal series. Neural and haemal arches linked by means of one pre- and one postzygapophysis. 11-12 pairs of ribs. Postcoelomic bone reaching the axial skeleton. Dorsal and anal fins strip-like. Origin of the dorsal fin located behind the highest point of the dorsal border of the body. Dorsal fin supported by 47-50 axonosts. Origin of the anal fin located behind the lowest point of the ventral border of the body. Anal fin supported by 37-39 axonosts. Caudal peduncle short. 4-5 epichordals. 10-11 hypochordals, some moderately broadened. 1 urodermal. Caudal fin double emarginated, with 19-21 principal rays. Bar-scales in the abdominal region. Bifid cloacal scale present. Dorsal ridge with 8-9 scutes, some being scutellum-like. Ventral keel with 11 scutes, 9 prepelvic and 2 postcloacal with spines.

Holotype

T. 203-T. 204, a complete specimen, part and counterpart (CAPASSO, 2000: fig. 1A, B). Total length: 43.3 mm.

Paratypes

T.11, specimen without caudal fin (ibid., 2000: fig. 2C). Total length: 33.6 mm.

T. 17, part of the body and tail (ibid., 2000: fig. 2D). Total length: 27 mm.

T. 19, imprint of a complete specimen (ibid., 2000: fig. 2E). Total length: 43.3 mm.

T. 66, almost complete specimen [a part of the skull is missing] (ibid., 2000: fig. 2F). Total length: 38.5 mm.

T. 201-T. 202, part and counterpart of a complete specimen (ibid., 2000: fig. 2A, B), Total length: 37.8 mm.

T. 206-T.207, caudal region and tail, part and counterpart (ibid., 2000: fig. 2G, H). Total length: 23.4 mm.

T. 211-T. 212, complete specimen, part and counterpart (ibid., 2000: fig. 2I, J). Total length: 38.5 mm.

Other material

T. 208-T. 209, specimen devoid of tail, part and counterpart (Fig. 1). Total length: 30 mm.



Fig. 1 – *Tergestia sorbinii* Capasso, 2000. Specimen T. 208.

Osteology

The skull (Fig. 2)

The skull is as long as deep and rather large when compared to the body size. The preorbital part of the braincase is longer than the postorbital region. The orbit is wide. The dermal bones of the skull are ornamented with small and generally weakly developed tubercles. The mouth gape is ventrally inclined.

The mesethmoid is the largest bone of the braincase. Its upper margin is covered by a narrow but strongly ornamented prefrontal. The vomer is a long bone, with a thin anterior extremity and a broad posterior region. There are five rows of vomerian teeth, those of the median row being the largest. The number of teeth in each row can not be determined.

The frontal is rather short and overhangs the orbital region. The dermosupraoccipital has a short acuminate posterior extremity that is slightly depressed in comparison with the upper margin of the bone. The parietal bears a short brush-like process

(= peniculus) containing five posterior branches (CAPASSO, 2000: fig. 7A, B). The supratemporal sensory canal is visible on the parietal of the holotype (ibid., 2000: figs 6, 7A). A long and narrow temporal (= dermocranial) fenestra is opened between the frontal, the dermosupraoccipital and the parietal. This fenestra is clearly visible on the holotype (ibid., 2000: fig. 6) and on specimen T. 208-T.209. In the original study,

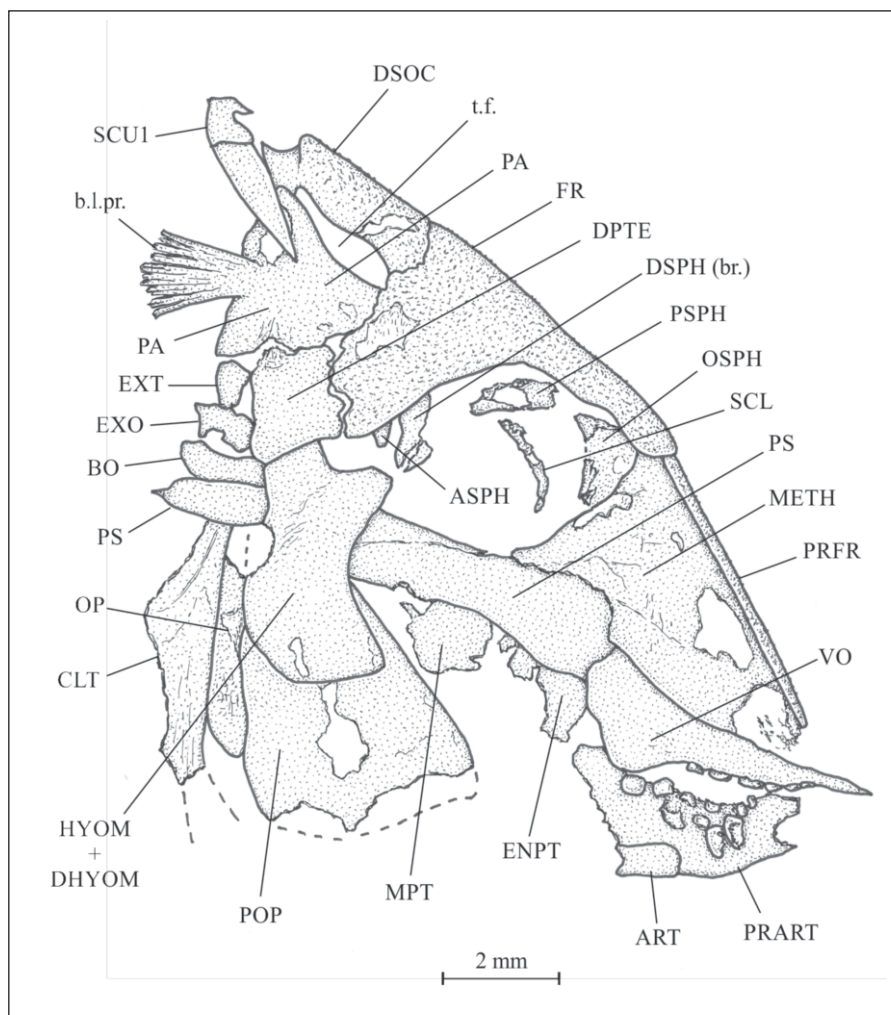


Fig. 2 – *Tergestia sorbinii* Capasso, 2000. Skull of specimen T. 208. ART: articular; ASPH: autosphenotic; BO: basioccipital; CLT: cleithrum; DHYOM: dermohyomandibula; DPTE: dermopterotic; DSOC: dermosupraoccipital; DSPH: dermosphenotic; ENPT: entopterygoid; EXO: exoccipital; EXT: extrascapular; FR: frontal; HYOM: hyomandibula; METH: mesethmoid; MPT: metapterygoid; OP: opercle; OSPH: orbitosphenoid; PA: parietal; POP: preopercle; PRART: prearticular; PRFR: prefrontal; PS: parasphenoid; PSPH: pleurosphenoid; SCU 1: first dorsal scute; SCL: sclerotic bone; VO: vomer; b. l. pr.: brush-like process (= peniculus) of the parietal; br.: broken; t. f.: temporal (= cranial) fenestra.

T. sorbinii is erroneously described as devoid of temporal fenestra (ibid., 2000: 265, 276). The dermopterotic is as long as deep. A small autosphenotic, appended to the frontal, is visible on specimen T. 208-T.209, the dermosphenotic being crushed and slightly displaced due to the fossilisation. In the holotype, the dermosphenotic completely covers the autosphenotic and is sutured with the dermopterotic and the frontal (ibid., 2000: fig. 3, where the dermosphenotic is called dermopterotic). The ventral margin of the dermopterotic and of the dermosphenotic is located at the level of the mid-height of the orbit.

The orbitosphenoid is present just behind the posterior margin of the mesethmoid. The pleurosphenoid is visible in the orbit. The parasphenoid is long, broad and toothless, with the trabecular region obliquely inclined. The posterior part of the parasphenoid largely outpaces the level of the skull rear. The basioccipital and the exoccipital are completely exposed behind the dermopterotic. A small extrascapular is located behind the dermopterotic and between the exoccipital and the parietal.

The metapterygoid and the entopterygoid are large bones. Both the quadrate and the symplectic are articulated with the lower jaw.

The long and narrow premaxilla bears only one large incisiform tooth (ibid., 2000: fig. 10). A few fragments of the maxilla are visible on paratype T. 11 but the shape of the bone is not determinable. No specimen has a complete dentary. Only parts of the bone are preserved. The articular is massive. The triangle-shaped prearticular bears three rows of teeth, those of the lower row being the largest (ibid., 2000: fig. 11). The teeth of the two ventral rows generally are sigmoid, with the ventral extremity more or less acuminate. The teeth of the upper row are smaller, the first ones rounded and the posterior ones more ovoid. The surface of the teeth is smooth, with a central region slightly concave. In the holotype, there are 7 teeth in the upper and the middle rows. The lower row is incomplete.

A few tubular infraorbitals are preserved on face T. 204 of the holotype. As already written, the dermosphenotic is a wide bone sutured to the ventral margin of the skull roof. A bony sclerotic ring is present.

The hyomandibula-dermohyomandibula and the preopercle are sutured together. The exposed part of the hyomandibula-dermohyomandibula is deeper but narrower than the preopercle. The anterior dorsal corner of the preopercle bears a long ascending process that is pressed against the hyomandibula. The opercle is a long and narrow bone wedged between the cleithrum and the preopercle. In the original description, the broken upper part of the preopercle is erroneously considered as the opercle (ibid., 2000: fig. 9). The hyoid bar is massive.

The girdles

The cleithrum is rather similar to the one of *Pycnodus apodus* (Volta, 1809) (NURSALL, 1996: fig. 11E). The pectoral fin is very short and contains numerous rays supported by seven pterygiophores (= radials) (CAPASSO, 2000: fig. 15A, B, C).

The pelvic bones and the ventral fins are not preserved.

The axial skeleton

The axial skeleton progressively elevates from the caudal region and reaches anteriorly the orbit level. The vertebrae are formed by separated dorsal and ventral arcocentra. The notochord is completely surrounded by those bony elements in the abdominal region but not in the caudal one where the notochord is partially free (CA-PASSO, 2000: figs 12-14). There are 29 to 31 neural spines before the epichordal series and 14 to 15 haemal spines before the hypochordal series. These neural and haemal spines bear anterior bony sagittal wings (*ibid.*, 2000: Figs 12-14). In the caudal region, each neural and haemal arches are linked with the following one by means of one pre- and one postzygapophysis. The first neural spines are not autogenous but attached to the corresponding arches. There are 11 or 12 pairs of long ribs, with a broadened upper region. The postcoelomic bone is long, narrow and almost rectilinear. It contacts the axial skeleton.

The dorsal and anal fins

The dorsal and anal fins are strip-like (type A2 of POYATO-ARIZA, WENZ, 2002: fig. 34). The rays of the dorsal and anal fins are missing on several specimens and no one as a complete series of rays. The dorsal fin is supported by 47 to 50 pterygiophores (= radials, axonosts) and the anal fin by 37 to 39 pterygiophores. The origins of the dorsal and anal fins are respectively located behind the highest point of the dorsal border of the body and behind the lowest point of its ventral border.

The caudal skeleton and fin

The caudal peduncle is very short, the dorsal fin ending near the tail. The caudal endoskeleton is composed of 4 or 5 epichordals, 10 or 11 hypochordals and 1 urodermal. Four posterior hypochordals are broadened but there is no real hypertrophy (CA-PASSO, 2000: fig. 21).

The caudal fin is double emarginated (POYATO-ARIZA, WENZ, 2002: fig. 36 E). There are 19-21 principal caudal rays, 4 dorsal and 5 ventral procurrent rays. The most dorsal and the most ventral principal rays are segmented and pointed. The other principal rays are segmented and branched.

Squamation (Fig. 3)

The squamation is only present in the abdominal region of the fish, not in the caudal one.

The flank scales are bar-like. Dorsally, there is a series of paired bar-scales linked to the dorsal ridge scutes from the second to the last one. Near the ventral margin, there is a series of slightly broadened bar-scales but there are however no complete scales. No flank scales are visible between the dorsal and the ventral series.

There are 8 or 9 dorsal ridge scutes. The first dorsal ridge scute lies against the posterior margin of the dermosupraoccipital and is the largest of the series. It bears a hook-like tip associated with a slightly enlarged ventral scale. The more posterior scutes are scutellum-like (CAPASSO, 2000: figs 8, 22). Their upper margin is ornamented with microspines.

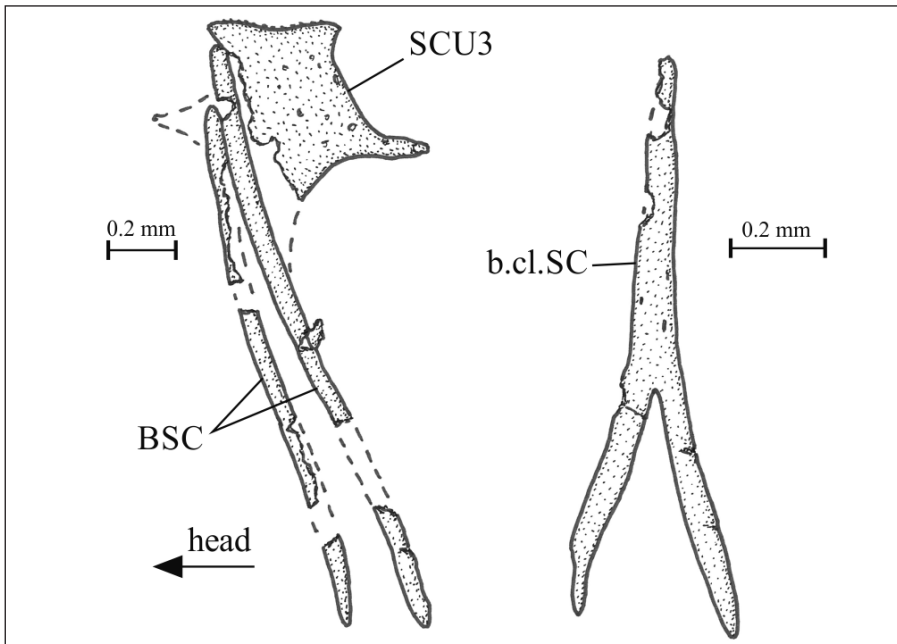


Fig. 3 – *Tergestia sorbinii* Capasso, 2000. Left: third dorsal scute of paratype T. 202. Right: bifid cloacal scale of paratype T. 207. BSC: bar scales; SCU 3: third dorsal scute; b. cl. SC: bifid cloacal scale.

There are 11 ventral keel scutes, 9 before and 2 behind the cloaca. The precloacal ones are badly preserved. The second postcloacal scute is the larger of the series and it bears two or three large spines (ibid., 2000: fig. 19A, B, C).

A bifid scale is present in the cloacal region as seen on paratypes T. 66 and T. 206 (ibid., 2000: figs 19B, 20A, B).

3. – Discussion

Tergestia sorbinii within Pycnodontiformes

In the original description of *Tergestia sorbinii*, a peculiar family, the Tergestiiniidae, was erected for this fossil fish (CAPASSO, 2000: 265) and included in the order Pycnodontiformes. Today, however, all the specialists agree that the presence of a brush-like process on the parietal is the main character of the pycnodont species belonging to the family Pycnodontidae (POYATO-ARIZA, WENZ, 2002: node 13, character 14[1]). The process is missing in all other pycnodont fishes. *T. sorbinii* exhibits such a process and thus must be ranged within the Pycnodontidae. That was already the point of view expressed in POYATO-ARIZA (2010: 662) and in TAVERNE, CAPASSO (2012: 42).

POYATO-ARIZA (2010: 662) also presented *T. sorbinii* as a possible member of the subfamily Pycnodontinae but in need of revision before any definitive decision about its systematic position. On the other hand, TAVERNE, CAPASSO (2012: 42, fig. 13) considered that *T. sorbinii* did belong to this subfamily. However, these two authors did not explain in a detailed way the reasons of their choice.

In fact, three osteological features clearly refer the Italian pycnodontid fish to that subfamily.

T. sorbinii has the basioccipital and the exoccipital well visible behind the dermopterotic. The most posterior part of the endocranium posteriorly exposed is typical of the Pycnodontinae (POYATO-ARIZA, WENZ, 2002: node 24, character 19[1]), except for the members of the tribe Nursalliini that are devoid of such a character (TAVERNE *et al.*, 2015: figs 4, 9, 10, 11). This peculiar pattern also exists in two Cenomanian Lebanese Pycnodontidae not pertaining to the subfamily Pycnodontinae, *Rhinopycnodus gabriellae* Taverne & Capasso, 2013 and *Haqelpycnodus picteti* Taverne & Capasso, 2018 (TAVERNE, CAPASSO, 2013: fig. 4, 2018b: fig. 9).

T. sorbinii also exhibits a cloacal bifid scale, with two acuminate ventral branches. Such a special scale is only present in the Pycnodontinae, including the Nursalliini (POYATO-ARIZA, WENZ, 2002: node 23, character 104[1]). A bifid scale in the cloacal region is not known in any other pycnodontid fish.

The broadened hypochordals present in the caudal skeleton of *T. sorbinii* are another specialized character typical of the subfamily.

One peculiar feature is often present in Pycnodontinae. The lower margin of the dermopterotic and of the dermosphenotic is located at the level of the lower border of the orbit, with the *dilatator fossa* well visible between the two bones and above the hyomandibula. In *T. sorbinii*, this evolved character is missing.

***Tergestia sorbinii* within Pycnodontinae**

Today, in addition to *Tergestia*, the subfamily Pycnodontinae contains seven other genera, *Pycnodus* Agassiz, 1833, *Oropycnodus* Poyato-Ariza & Wenz, 2002, *Pseudopycnodus* Taverne, 2003, *Polazzodus* Poyato-Ariza, 2010, *Sylvienodus* Poyato-Ariza, 2013, *Libanopycnodus* Taverne & Capasso, 2018 and *Sigmapycnodus* Taverne & Capasso, 2018, and also the members of the tribe Nursalliini. Until now, the most complete analysis of the phylogeny within the subfamily is the one given by TAVERNE, CAPASSO (2012: fig. 13).

Three characters allow to precise the exact systematic position of *Tergestia sorbinii* within the subfamily.

(1) The exposed part of the hyomandibula-dermohyomandibula is a little deeper than the preopercle in *T. sorbinii*. Within Pycnodontinae, a hyomandibula as deep or deeper than the preopercle is a specialized feature shared by *Pycnodus*, *Oropycnodus*, *Polazzodus*, *Sylvienodus* and *Sigmapycnodus* (TAVERNE, 1997: fig. 4; POYAYO-ARIZA, WENZ, 2002; figs 10, 17; POYAYO-ARIZA, 2010: fig. 4, 2013: fig. 3; TAVERNE, CAPASSO, 2018a: fig. 17). This character is not yet present in *Pseudopycnodus* and *Libanopycnodus*, the two most primitive genera of the subfamily (TAVERNE, CAPASSO, 2012: fig. 7, 2018a: fig. 4), and is also missing in the Nursalliini.

(2) Most dorsal ridge scutes of *T. sorbinii* are scutellum-like, with a series of microspines on the upper margin. This highly evolved character is also present in *Pycnodus*, *Oropycnodus* and *Sylvienodus* (HECKEL, 1856: pl. 11, figs 1, 2, 12, 13; BLOT, VORUZ, 1987: fig. 29A, B; NURSALL, 1999: fig. 12; POYATO-ARIZA, 2013: fig. 6A). This apomorphy does not exist in *Pseudopycnodus*, *Polazzodus* and *Libanopycnodus* (POYATO-ARIZA, 2010: fig. 8; TAVERNE, CAPASSO, 2012: fig. 12, 2018b: fig. 10). The situation is unknown in *Sigmapycnodus*, the dorsal ridge scutes of this fish being not preserved.

(3) The Nursalliini have the neural and haemal arcocentra in hypercomplex contact by means of numerous pre- and postzygapophyses (POYATO-ARIZA, WENZ, 2002: node 25, character 54[3]; BLOT, 1987: fig. 63; NURSALL, 2010: fig. 4). A complex contact between the vertebral arches already exist in three not-nursalliinid Pycnodontinae (POYATO-ARIZA, WENZ, 2002: node 24, character 54[2]), the genera *Pycnodus*, *Oropycnodus* and *Sigmapycnodus* (HECKEL, 1856, pl. 11, fig. 10; BLOT, VORUZ, 1987: figs 17, 18; TAVERNE, CAPASSO, 2018a: fig. 30). This specialized feature is not yet present in the other members of the subfamily, including *T. sorbinii*.

The characters discussed in points (1), (2) and (3) show that *Tergestia* is more specialized than *Pseudopycnodus*, *Polazzodus* and *Libanopycnodus* but less advanced than *Pycnodus*, *Oropycnodus* and *Sigmapycnodus*. The systematic position of *Tergestia* is thus intermediate between these two groups, as is *Sylvienodus*.

These two last genera share some peculiar features. For instance, their parietal pectinulus is short, with only a few branches, and their premaxilla bears only one tooth. However, *Sylvienodus* already exhibits a scutellum-like first dorsal ridge scute forming a notch with the second one (POYATO-ARIZA, 2013: fig. 6A), while the first dorsal ridge scute of *Tergestia* is not yet scutellum-like. Thus, *Sylvienodus* appears a little more specialized than *Tergestia*.

T. sorbinii also exhibits a temporal fenestra. Within Pycnodontinae, this evolved character is shared by two genera, *Pycnodus* and *Oropycnodus* (BLOT, VORUZ, 1987: fig. 6; TAVERNE, 1997: fig. 4; POYATO-ARIZA, WENZ, 2002: fig. 11B). However, we think that this feature is not necessary an indication of close relationships. The presence of a temporal fenestra seems to be a homoplasious character that occurs at different levels within the family Pycnodontidae, even in species that do not belong to the subfamily Pycnodontinae, for instance “*Coelodus*” *costae* Heckel, 1856, *Tepe-xichthys aranguthyrorum* Applegate, 1992, *Akromystax tilmachiton* Poyato-Ariza & Wenz, 2005 and *Haqelpycnodus picteti* Taverne & Capasso, 2018 (APPLEGATE, 1992: fig. 9; POYATO-ARIZA, WENZ, 2005: fig. 3 A, B; TAVERNE, CAPASSO, 2018a: fig. 9; TAVERNE *et al.*, 2019: fig. 7). The occurrence of a temporal fenestra is probably a manner for alleviating the heavily ossified skull of some Pycnodontidae and this advanced feature is homoplasious within the family.

Lavoro consegnato il 28/05/2019

ACKNOWLEDGMENTS

We greatly thank M. Adriano VANDERSYPEN, from the Royal Institute of Natural Sciences of Belgium, and M. Luciano LULLO, from the University of Chieti-Pescara, for their technical help. We are also indebted to the anonymous reviewers who have read and commented our text.

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