Nursallia tethysensis sp. nov., a new pycnodont fish (Neopterygii: †Halecostomi) from the Cenomanian of Lebanon

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Abstract

A new species of Pycnodont, Nursallia tethysensis, is described from the Cenomanian of En Nammoura and Hgula (Lebanon). It is a rarely encountered member of the ichthyofauna in these two localities and represents the smallest-sized species ever described in the genus. The frontal is broad, rounded, with an almost vertical profile. The hypertrophied dermosupraoccipital bears small spines on its median line. The parietal does not contact the frontal. The dermopterotic and the frontal join by only a thin osseous bridge under the dermosupraoccipital and above the orbit. The ventral profile has a characteristic "V"-shape notch at the junction between the head and the abdomen. There are 31 to 33 vertebrae. Nursallia tethysensis shows a closer relationship with N. gutturosum from the Cenomanian of Morocco and Italy than with the other species of the genus. The particularly good state of preservation permits examination of the ultrastructure of the teeth, demonstrating the presence of dentinal canaliculii only in the radicular area of these teeth. The chemical composition of both the eyes (characterized by high sulphur content, presumably derived from the original proteins of this region) and the bones (constituted of hydroxy-apatite almost identical to the bone component of modern fishes) are proof of the complete conservation of the organic remains fossilized in the Lebanese Cenomanian limestones.

Keywords: *Nursallia tethysensis* sp. nov., Pycnodontiformes, Lebanon, Cenomanian, protein conservation.

Résumé

Les auteurs décrivent une nouvelle espèce de pycnodonte, Nursallia tethysensis du Cénomanien d'En Nammoura et de Hgula (Liban). Elle est un membre rare de l'ichthyofaune de ces deux localités et représente la plus petite espèce jamais décrite dans le genre. Le frontal est large, arrondi, avec un profil presque

vertical. Le dermosupraoccipital hypertrophié porte de petites épines sur sa ligne médiane. Le pariétal ne touche pas le frontal. Le dermoptérotique et le frontal sont joints par un étroit pont osseux sous le dermosupraoccipital et au-dessus de l'orbite. Le profil ventral montre une échancrure caractéristique en « V » à la jonction de la tête et de l'abdomen. Il y a 31 à 33 vertèbres. N. tethysensis montre de plus proches relations avec N. gutturosum du Cénomanien du Maroc et d'Italie qu'avec les autres espèces du genre. L'excellent état de conservation a permis l'examen de l'ultrastructure des dents et a montré que la présence de canalicules dentinaires était limitée à la région radiculaire de ces dents. La composition chimique des yeux (caractérisée par une haute teneur en sulfure, provenant probablement des protéines originelles de cette région) et les os (constitués d'hydroxy-apatite presqu'identique au composant osseux des poissons récents) sont une preuve de la conservation complète des restes organiques fossilisés dans les calcaires cénomaniens du Liban.

Mots-clefs: *Nursallia tethysensis* sp. nov., Pycnodontiformes, Liban, Cénomanien, conservation des protéines.

Riassunto

Gli autori descrivono una nuova specie di pycnodonti, Nursallia tethysensis, proveniente dal calcare cenomaniano di En Nammoura e di Hgula, nel Libano centrale. La nuova specie è un componente raro dell'ittiofauna delle due citate località e rappresenta la specie più piccola fra quelle appartenenti al suo genere. Il frontale è espanso, arrotondato, con un profile quasi verticale. Il dermosopraoccipitale è ipertrofico e doato di piccole spine sul suo margine mediano. Il parietale non entra in contatto con il frontale. Il dermopterotico si connette con il frontale solo mediante un piccolo ponte osseo al disotto del dermosopraoccipitale ed al disotto dell'orbita. Il profilo ventrale del pesce presentauna caratteristica incisura a « V » a livello della giunzione fra la testa e l'addome. Sono presenti 32 vertebre. All'interno del genere, N. tethysensis mostra le più strette relazioni con N. gutturosum del Cenomaniano del Marocco e dell'Italia centrale e meridionale. Lo stato di conservazione particolarmente buono ha permesso l'osservazione ultrastrutturale dei denti, dimostrando la presenza di canalicoli della dentina soltante nella regione radicolare. La composizione chimica elementare sia dei bulbi oculari (caratterizzati da un elevato contenuto di zolfo, verosimilmente derivato dalle proteine originali tipiche di questa regione anatomica), sia delle ossa (costituite

da idrossiapatite pressoché identica a quella delle ossa dei pesci moderni) sono la dimostrazione della perfetta conservazione dei resti organici fossilizzati nei calcari cenomaniani del Libano.

Parole chiave: *Nursallia tethysensis* sp. nov., Pycnodontiformes, Libano, Cenomaniano, conservazione dalle proteine.

Introduction

The Pycnodontiformes are a marine halecostome fossil fish order, with an age range from the Late Trias to the Middle Eocene and an almost worldwide distribution (Nursall, 1996a; Kriwet, 2001). They are generally deep-bodied, laterally compressed and durophagous fishes, with a characteristic frontal flexure of the skull in lateral view. They comprise about forty genera of which about ten are only known by dental remains (Nursall, 1996b; Poyato-Ariza & Wenz, 2002; etc.).

The aim of this work is to describe a new pycnodont species from En Nammoura and Hgula, two famous fossil fish localities in Lebanon. This new pycnodont, belonging to the genus Nursallia Blot, 1987, is a rarity in the general assemblage of fossil fishes from the two quoted localities. Although the Pycnodontiformes represent a relatively common finding from the famous quarry of Hagel, this type of extinct fish is relatively rare both in the Hgula quarries and in the En Nammoura limestone. The new species is known by only a few specimens, two of which are in the Natural History Museum of London. They were very superficially described as *Nursallia* sp. ind. by FOREY et al., 2003. We collected nine additional specimens, predominantly from the En Nammoura limestone, through the activities of one of us (P.A.S.) and of Dr. Flavio Bacchia, who selected many of the rare specimens coming from these two Lebanese localities during the past ten years. Despite our examination of thousands of fossil fishes from the famous quarry of Hagel (through the continuous exploration of that quarry by one of us (P.A.S.), and by our friend M. Roy Nohra), no samples of *Nursallia* have been found in this third very important Lebanese fossil locality in the past ten years.

Nursallia is a Late Cretaceous member of the family Pycnodontinae. It is known from Italy (Leonardi, 1966; Sorbini, 1976; Blot, 1987; Capasso, 2007), Morocco (Arambourg, 1954), Lebanon (Heckel, 1854; Davis, 1887; Gayet et al., 2003; Forey et al., 2003), Colorado, U. S. A. (Kriwet, 2005; Shimada et al., 2006), Mexico (Blanco et al., 2001; Blanco-Pinon et al., 2002; Ifrim et al., 2005) and

Brazil (COPE, 1886). The genus includes today four species: *N. goedeli* (HECKEL, 1854) (= *Palaeobalistum ventralis* DAVIS, 1887), *N. flavellatum* (COPE, 1886), *N. gutturosum* (ARAMBOURG, 1954) and *N. veronae* BLOT, 1987, the type species. POYATO-ARIZA & WENZ (2002) range *Nursallia* with two other genera, *Palaeobalistum* BLAINVILLE, 1818 and *Abdobalistum* POYATO-ARIZA & WENZ, 2002, in a subfamily Nursalliinae but KRIWET (2005) contested that point of view.

Localities, conditions, and age of the deposits of En Nammura and Hgula

The specimens of the new species *Nursallia tethysensis* come from two famous Lebanese localities: En Nammoura and Hgula, both in central Lebanon.

Hgula is a little village to the East of Byblos. The centre of the village is surrounded by many quarries opened in Cretaceous limestone on the north side of the hill at Hgula, specifically for the purpose of collecting fossils (Fig. 1a, b). This locality was discovered much later than the well-known locality for fossil fishes, Lebanon Mount. In fact, the first such classic locality, Sahel Alma (today completely closed, covered by olive trees and included in the park of a private church), was discovered at the time of the first Crusade, and fossil fishes were first described by medieval scientists. The locality of Hagel was discovered immediately afterwards, and the scientific literature at the end of the XVIII century describes and illustrates several fossil fish from this locality. The locality of Hgula was discovered later, and the first indication of the presence of fossil fishes near the village of Hgula is probably that of Lewin in 1878, who described several fossil fishes coming from Hazhüla, a locality that "s'étend un peu au Sud de Haqel, à une distance d'environ deux heures et demie" (GAYET et al., 2003). The age of the Hgula gisement is determined as Upper Cenomanian by several authors (D'ERASMO, 1946; Arambourg, 1954; Gayet, 1988; Forey et al., 2003). The limestone sedimentation including fossils is not flat: in fact, bending and fractures, with frequent shifting, are common events within very small areas at the Hgula quarries. This non-homogeneous limestone configuration does not permit the recovery of large slabs of limestone. On the other hand, the Hgula limestone is characterized by an impressive richness: dozen of fossil fishes almost completely cover each limestone surface, with frequent overlapping of individual specimens. The most frequent fossils are undoubtedly fishes, but shrimps are also very common.

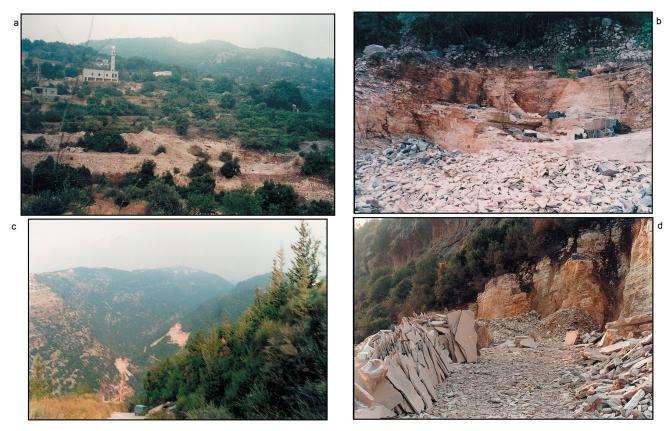


Fig. 1 – The quarries and limestone extraction localities at Hgula (a, b) and En Nammoura (c, d).

These animals are characteristic of the Hgula deposit. Small shrimps were also discovered at Haqel and at En Nammoura by one of us (P.A.S.) but they are less frequent than in Hgula. Remains of reptiles, birds, and many types of invertebrates and plants are also found at this locality. All of these fossils were collected by three generations of non-professional paleontologists of the famous Abi Saad family, who retained official permission for excavations at the quarry at Hgula and became professional collectors working for many years in cooperation with paleontologists and geologists.

En Nammoura is a small village on the south side of the valley of the Adonis River (Fig. 1c, d). Near the village, just beyond the monastery of *Mar ed Inda*, some quarries for extraction of limestone slabs were opened in the fossiliferous limestone. The present workings were opened in the 1950s by the Dakkach family, but – as reported by FOREY *et al.* (2003) – a fossil fish coming from this locality was acquired by the British Museum (London) in the 1920s or earlier. The presence of fossil fish from this locality was officially reported for the first time by GAYET (1988), who described a new genus and species (*Gharbouria libanica*) from the limestone of a locality called Aïn-el-Gharbour, close to the little village of En Nammoura. GAYET (1988) clearly indicated the Cenomanian age

of the En Nammoura limestone. Soon afterwards, DAL SASSO & RENESTO (1999) described a fossil reptile from En Nammoura, BANNIKOV & BACCHIA (2000) published a new fossil fish from the same locality, and KRASSILOV & BACCHIA (2000) described the fossil plants coming from this relatively new fossil locality. More recently, DALLA VECCHIA et al. (2002) reported the results of a geological excavation, completely supported by the Italian company Stoneage (Trieste), devoted to the micropaleontological examination of the limestone stratigraphy of the En Nammoura quarries. In this study, the authors report that the age of the En Nammoura limestone is Middle Cenomanian. In addition, FOREY et al. (2003) described a rich fossil fish fauna from En Nammoura, and reported the latest determination of the exact age of the lithographic limestone of this locality, i.e., the middle portion of the Middle Cenomanian. Finally, BANNIKOV & BACCHIA (2005) published four additional species of fossil fishes (two of which are new) from the same En Nammoura locality.

In past years we visited continuously the En Nammoura quarries, having frequent contact with the families that work in extracting the lithographic limestone for building construction. For this reason, we have been long familiar with the quarries and their fossils. At En Nammoura, the fossils in general are uncommon or, even, very rare. We are convinced that the only reason why we are able to collect numerous fossils in the En Nammoura quarries is that very large quantities of limestone slabs are regularly extracted from the quarries for use in the building industry. In fact, the discovery of a fossil specimen is relatively infrequent, notwithstanding the fact that it is possible to obtain very large slabs of limestone with perfectly flat surfaces. We calculate, more or less, that for each discovery of a fossil, we examined c. 60 square meters of absolutely sterile limestone surfaces. In addition, we have no information about the existence of multiple fishes within slabs, and this situation underlines the rarity of fossil fishes from this locality. Fortunately, the enormous quantity of quarried limestone and the continuous activity in the quarries constantly increases the number of examinable limestone surfaces. Moreover, the people who extract the limestone are familiar with fossils, and in particular with the fossil fishes. They observe closely the extracted limestone surfaces in order to discover saleable fossil specimens, which have a very high commercial value.

Systematic Paleontology

Class Osteichthyes HUXLEY, 1880
Subclass Actinopterygii COPE, 1887
Division Halecostomi REGAN, 1923
sensu PATTERSON, 1973
Order Pycnodontiformes BERG, 1937
Suborder Pycnodontoidei NURSALL, 1996
Family Pycnodontidae AGASSIZ, 1833
sensu NURSALL, 1996
Subfamily Nursalliinae BLOT, 1987
sensu POYATO-ARATIA & WENZ, 2002
Genus Nursallia BLOT, 1987

Type-Species: Nursallia veronae BLOT, 1987

Nursallia tethysensis, sp. nov. Figs 2 - 15

Diagnosis

Small species of *Nursallia*, the maximum total length not exceeding 90 mm. Frontal very broad. Frontal profile rounded and almost vertical. Dermosupraoccipital highly hypertrophied, with five to seven small triangular spines on its median line, constituting a saw-toothed post-frontal ridge. Parietal not contacting frontal. Dermopterotic and frontal in contact by a thin osseous

bridge under the dermosupraoccipital and above the orbit. Two sclerotic bones, the posterior-superior one with a rounded appendix protruding towards the centre of the orbit, and covering the superior part of the ocular globe in the living animal. Parasphenoid bone with sub-triangular profile, with superior margin slightly rounded only in its anterior part. Premaxilla with filiform ascendant process, not extending beyond the inferior part of the orbit, with only one large, welldeveloped, clearly incisor-shaped prehensile tooth. Teeth series of both vomer and prearticular (splenial) very short, with only 5 teeth on the vomer and 6 teeth on the prearticular. Dental bone triangular, with two incisor-shaped teeth. Vomerine and prearticular teeth round and with occlusal surfaces slightly concave and serrated margins. Inferior border of prearticular and angular joining the anterior margin of the cleithrum at an almost right angle, imparting a large "V"-shaped notch in the ventral profile between the head and the abdomen. Vertebral column with 32 vertebrae. of which 16 are caudal. Cleithrum vertical, thin and very high, without spines. Pectoral fins with 5-6 proximal pterygiophores and 17-19 principal rays. Ratio prepelvic distance/standard length 52.7%. Pelvic fins with 7-8 rays. Dorsal and anal fins of A2 strip-like type. Dorsal with 58-60 dorsal pterygiophores. Anal with 52-54 anal pterygiophores. Caudal fin well developed in vertical direction with 38-44 principal rays. The 5 to 6 neural spines of the caudal pedicle short and not supporting the upper procurrent caudal rays. 2-4 last neural spines (epichordal elements) longer and supporting the upper procurrent caudal rays. Three large hypurals with a fanshaped arrangement. Dorsal ridge with 8 scales, each one with one or three spines on the dorsal margin and articulated with two or three couples of very elongated bar scales of the body squamation. Ventral keel with 3-5 scales in the pre-cloacal region, and 2 in post-anal region with a serrated margin. Body squamation of typical peltate type extending to the ventral region and to the caudal area.

Material and method

The material, comprising eleven specimens in various states of conservation and completeness, is stored in the following public and private collections: the Museo Civico di Storia Naturale di Milano (MCSNM), the Natural History Museum of London (BMNH), the Institut royal des Sciences naturelles de Belgique (IRSNB), the Capasso collection, legally registered at the State Soprintendenza of Salerno (CLC), and the ABI SAAD Museum collection at the "Mémoire du temps" building in Byblos (CAS).

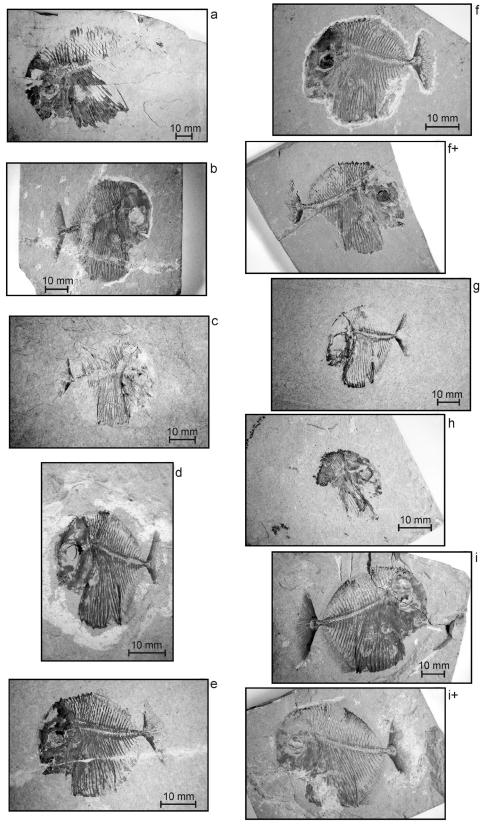


Fig. 2 – *Nursallia tethysensis* sp. nov. (a): specimen MCSNM V 6426 (holotype): TL = 88 mm, from En Nammoura; (b): specimen CLC S.131: TL = 43 mm, from Hgula; (c): specimen CAS 3450: TL = 38 mm, from En Nammoura; (d): specimen CLC S.580: TL = 27 mm, from Hgula; (e): specimen CLC S.136: TL = 43 mm, from En Nammoura; (f): specimen CLC S.363: TL = 37 mm, in conterpart, from En Nammoura, f+: conterpart; (g): specimen CLC S.458: TL = 39 mm, from En Nammoura; (h): specimen CAS 9455: TL = -- (uncomplete fish), from Hgula; (i): specimen CAS 9468-9963: TL = 59 mm, in counterpart (i and i+), from Hgula.

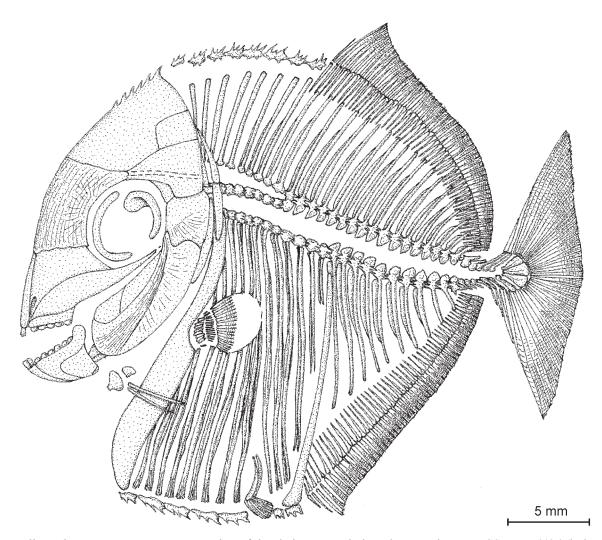


Fig. 3 – *Nursallia tethysensis* sp. nov. Reconstruction of the skeleton mostly based on specimens MCSNM V6426 (holotype) and CLC S.363 to which the scale refers. The body bar scales are omitted.

Holotype:

Specimen MCSNM V 6426 (gift of the ABI SAAD Frères, Mémoire du temps): Total Length (TL) = 88 mm, with most of the caudal region missing; it represents the biggest individual, from En Nammoura (Fig. 2a).

Paratypes:

Specimen IRSNB P 8453: 37 mm, from En Nammoura, counterpart of specimen CLC S. 363 (Fig. 2f+).

Specimen CLC S.131: TL = 43 mm, from Hgula (Fig. 2b).

Specimen CAS 3450: TL = 38 mm, from En Nammoura (Fig. 2c).

Specimen CLC S.580: TL = 27 mm, from Hgula (Fig. 2d)

Specimen CLC S.136: TL = 43 mm, from En Nammoura (Fig. 2e).

Specimen CLC S.363: TL = 37 mm, from En Nammoura (Fig. 2f).

Specimen CLC S.458: TL = 39 mm, from En Nammoura (Fig. 2g).

Specimen CAS 9455: TL = -- (incomplete fish), from Hgula (Fig. 2h).

Specimen CAS 9468, 9963: TL=59 mm, in counterpart, from Hgula (Fig. 2i, i+).

Specimen BMNH P.63244: TL = 48 mm, in counterpart, from En Nammoura.

Specimen BMNH P.63245: TL = 34 mm, in counterpart, from En Nammoura.

We examined all the specimens (except the two samples in the Natural History Museum of London) with stereo-microscopy at the Laboratory of the Museum of the State University of Chieti and at the University of Brussels, and with Scanning Electron Microscopy (SEM) at the Engineering Faculty of the State University of l'Aquila (Italy). Drawings were made with a camera lucida.

Formations and localities

Middle Cenomanian of En Nammoura and Upper Cenomanian of Hgula, Lebanon.

Derivatio nominis

The name of the new species alludes to the Tethys Ocean that occupied the area of the modern Mediterranean Sea, including Lebanon, during the Cretaceous.

Description

General features (Figs 2, 3; Tables 1, 2).

Nursallia tethysensis is a fish of small size, with a laterally compressed, disc-shaped body and a particularly well-developed abdominal region. The frontal region is anteriorly prominent. The inferior margin of the prearticular and angular joins the anterior margin of the cleithrum at almost a right angle, imparting a markedly characteristic profile with a "V"-shaped notch at the junction between the head and the abdomen. The maximum body depth (TD) is located near the dorsal-fin origin and is less than the total length (TL), with a mean of the ratio TL/TD of 1/1.27 = 0.79.

Sample	TL (a)	TD (b)	Ratio (a*100/b)
MCSNM V 6426	88	60	147
CLC S.131	43	42	102 (^)
CAS 3450	38	35	109 (^)
CLC S.580	27	30	90 (^)
CLC S.136	43	34	126
CLC S.363	37	30	123
CLC S.458	39	34	115
CAS 9455		18	
CAS 9468-9963	59	46	128
BMNH P 63244	45 (+)	34 (+)	132
BMNH P 63245	33 (+)	28 (+)	118
Mean			127

^(^) Samples excluded from the calculation of the mean because the bodies were very compressed antero-posteriorly by the process of fossilization.

Table 1 – Body proportions of *Nursallia tethysensis* sp. nov.

Skull (Figs 4, 5, 6)

The frontal is broad, with the anterior-superior margin markedly rounded and expanded, so that the orbit appears to be placed in a particularly posterior and low position. The suture between the frontal

Sample	SL	PPD	Ratio (%)
MCSNM V 6426	80	41	51.3
CLC S.131	38	21	55.3 (^)
CAS 3450	35		
CLC S.580	24	14	58.3 (^)
CLC S.136	37	21	56.7
CLC S.363	33	19	57.6
CLC S.458	34	16	47.1
CAS 9455		9	
CAS 9468-9963	52	30	57.7
BMNH P 63244	41 (+)	20 (+)	48.8
BMNH P 63245	28 (+)	14 (+)	50.0
Mean			52.7

^(^) Samples excluded from the calculation of the mean because the bodies were very compressed antero-posteriorly by the process of fossilization.

Table 2 – Ratio of pre-pelvic distance/standard length in *Nursallia tethysensis* sp. nov.

and the dermosupraoccipital is situated at the level immediately above the orbit. The dermosupraoccipital is extremely large. It has five to seven well-developed spines with triangular outlines at the superior-posterior margin, constituting a saw-toothed post-frontal ridge. These spines are particularly well preserved in specimens MCSNM V 6426 (holotype) and CLC S.363 (Fig. 4). The parietal is well developed and inserted in a broad recess of the ventral border of the dermosupraoccipital. The parietal does not contact the frontal. A large dermopterotic is present at the inferior margin of the parietal. A thin posterior branch of the frontal joins a thin anterior branch of the dermopterotic below the dermosupraoccipital and above the orbit. The otic sensory canal runs through the dermopterotic from beginning to end. The sphenotic fits in a notch of the ventral margin of the dermopterotic. A temporal fenestra is missing. Specimen CLC S.363 has a small basiocciptal and a part of the exoccipital is evident just behind the dermopterotic.

Two sclerotic bones are present. The anterior bone is semi-lunar shaped, thin and curved, with the same outline as the anterior margin of the orbit, while the posterior bone is situated in the posterior-superior corner of the orbit. This last bone is well preserved in specimens CLC S.131, S.363 and CAS 9455. It has a rounded appendix protruding towards the centre of

⁽⁺⁾ Metric data taken from the photographs printed by FOREY *et al.* (2003).

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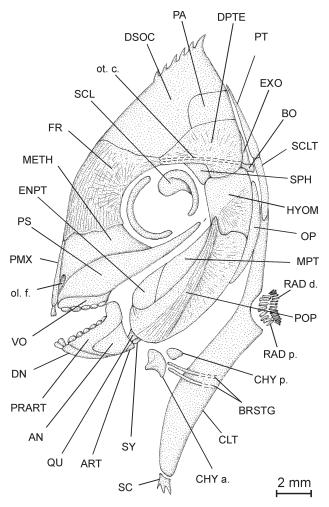


Fig. 4 – *Nursallia tethysensis* sp. nov. Reconstruction of the skull in left lateral view, based on all the specimens. The scale refers to specimen CLC S.363.

the orbit, presumably covering the superior part of the ocular globe in the living animal. No infraorbital is visible.

The parasphenoid bone has almost a triangular outline, anteriorly deeper and posteriorly acuminate. The anterior part of the superior margin is slightly rounded. The posterior part of this superior margin forms the lower border of the orbit and reaches the hyomandibula, as seen in specimen CLC S.136. The anterior and superior margins of the parasphenoid have extensive contact with the mesethmoid, which is rhomboid-shaped. Its posterior border represents the antero-inferior margin of the orbit, as seen on specimens CLC S.136 and S.458. On the mesethmoid of specimen CLC S.458 also shows the olfactory fossa is very small, narrow, and low, and the line of connection with the frontal is relatively regular, with few undulations.

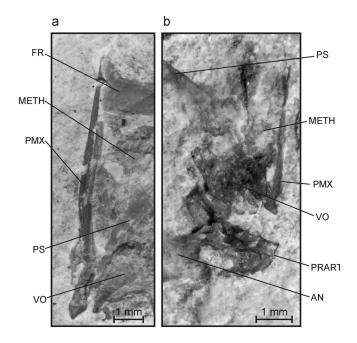


Fig. 5 – *Nursallia tethysensis* sp. nov. Premaxillary bone supporting prehensile superior teeth in holotype MCSNM V 6426 (a), and in specimen CAS 9455 juvenile (b).

The vomer is well preserved on specimen CLC S.458. It is a thick bone, with a generally rectangular shape and a concave superior margin (Figs 5a, b). The vomerine teeth are round, arranged apparently in five series. In the lateral series we can count only five teeth, regardless of the size of the fish. This matches the same observation made by FOREY et al., 2003, on the two samples in the Natural History Museum of London, and confirms also that the small number of teeth in each series is not a juvenile character but a characteristic of this species. The occlusal surfaces of the vomerine teeth are concave. This profile is more evident in the posterior teeth and less visible in the anterior ones (Fig. 6). The SEM analysis reveals that the tooth surfaces are unequal. In the crown region the surface is perfectly smooth, but in the roof area the surface appears impressed by small foveae. In the fractured teeth it is evident that these foveae represent the end of the dentinal canaliculi, about 10 µm in diameter (Fig. 7). This picture seems to be consistent with the hypothesis that the canalicular openings exist only in the radicular region, i.e., in the parts of the teeth covered by soft tissues in the living animals.

The premaxilla is very thin, with a filiform ascending process extending up to the level of the inferior part of the orbit, but not beyond. Each premaxilla bears

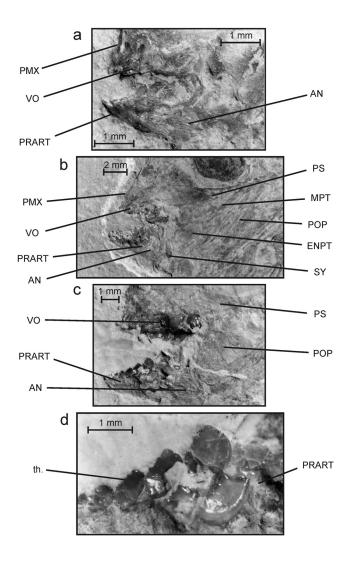


Fig. 6 – *Nursallia tethysensis* sp. nov. Bony structures of the mouth region, and teeth in specimen CLC S.458 (a), in specimen CLC S.363 (b), and in specimen CLC S.136 (c and d).

only one big, well-developed, clearly incisor-shaped prehensile tooth as seen in specimen MCSNM V 6426 (holotype). Specimen CLC S.363 shows that the free margin of the incisors bears a few small serrations. The maxilla is unknown, and perhaps is absent.

The dentary is small, triangular, with two little incisor prehensile teeth with rounded free margins as seen on specimen CLC S.363. The prearticular (splenial) is well developed, triangular shaped, with a large coronoid process and three series of six teeth with the same morphology as the vomerine teeth, i. e. with concave occlusal surfaces, and serrated margins as shown by specimens CLC S.136 and S. 363 (Fig. 6). The angular externally covers the ventral part of the prearticular. A small articular is also present,

forming the posterior-ventral corner of the lower jaw. The quadrate, partly hidden by the preopercle, is visible in some specimens. There is a small symplectic below the quadrate and before the ventral border of the preopercle. In specimen CLC S.363, the symplectic is entirely visible. It has an ovoid anterior articular head and a thin acuminate posterior extension. Both the quadrate and the symplectic articulate with the lower jaw.

The preopercle is a broad bony lamina, elongated in the supero-inferior dimension, longer and much larger than the opercle. Its external surface bears a large median crest. This preopercle extends from the posterior corner of the lower jaw to the level of the lower part of the orbit. The opercle is a thin bony lamina wedged between the preopercle and the hyomandibula on the one hand and the cleithrum on the other hand. At least two long branchiostegal rays are articulated with the posterior border of the anterior ceratohyal.

A small entopterygoid and a long metapterygoid are visible between the parasphenoid and the anterior margin of the preopercle. Those two pterygoid bones are toothless.

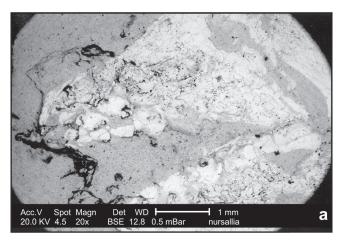
A well-developed hyomandibula is articulated with the dermopterotic and the sphenotic, forming the orbit's posterior margin. Its lower part is covered by the preopercle. This covering is more extensive in some specimens (f.i. sample CLC S.131) than in others (f.i. sample CLC S.363).

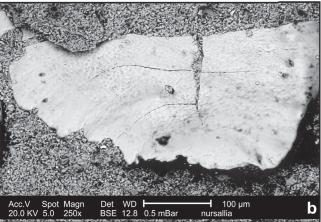
The anterior ceratohyal is short, with a very thin anterior part and a broad posterior region with a rounded border. Both the dorsal and ventral margins are concave. A very small posterior ceratohyal is preserved in some specimens. No hypohyal is visible.

Pectoral girdle (Figs 4, 8)

The cleithrum is high and thin, with a long ventral limb, larger than the dorsal one. The position of the cleithrum is almost vertical, but the ventral limb is slightly inclined forward, as seen in specimen CLC S.458. The anterior margin of this ventral limb represents the anterior profile of the fish under the mandibular region. The ventral extremity of the cleithrum is rounded and connects with the first scale of the ventral ridge, as shown by specimen CAS 9464-9963. No spines are present at the surface of the cleithrum. The long and very thin posttemporal and supracleithrum are visible above the cleithrum and just behind the skull in a few specimens.

The pectoral fins are relatively expanded, with 5 to 8 proximal pterygiophores supporting 17 to 19 very thin but elongated osseous distal pterygiophores





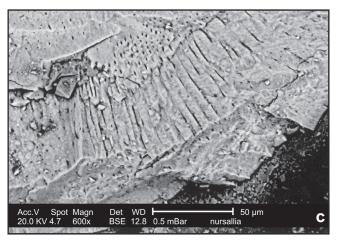


Fig. 7 – *Nursallia tethysensis* sp. nov. Scanning Electron Microscopy observation of bony structure of the mouth region and teeth in specimen CLC S.363. (a): mouth region; (b): each tooth shows an inferior (radicular) part in which the external openings of the dentinal canaliculi are clearly visible (this part of the tooth was covered by soft tissues, i.e., gingival tissue, in the living animals), and the free part of the tooth (i.e., the sole functional masticatory part, the dental crown) without openings of the dentinal canaliculi; (c): naturally broken tooth showing the canalicular ends, and the sections of dentinal canaliculi both transversal and longitudinal.

(Fig. 10e) as seen by SEM observations. Each distal pterygiophore supports one pectoral ray. These rays show a very particular morphology, since each principal ray appears to be conic-shaped (Fig. 10c, d).

Pelvic girdle (Figs 3, 10)

The small pelvic fins are situated on the anterior wall of the cloaca. The ratio of pre-pelvic distance/standard length has a mean value of 52.7% in our sample of specimens. This value corresponds to character 64(0) of POYATO-ARIZA & WENZ (2002). Between 7 and 8 principal pelvic rays are present on each side, as seen on specimen CAS 9468-9963 (Fig. 8c). The support of the pelvic fins is often unclear because the region is covered by the ventral keel scales. However, some specimens (e. g. CLC S.363) have a pair of well-developed vertical pelvic bones located between two pairs of ribs.

Axial skeleton (Figs 3, 9, 10)

Starting from the caudal pedicle, the vertebral axis elevates slightly in the posterior median region in comparison with the general axis of the body. In the anterior part of the body the vertebral column elevates more rapidly and reaches the level of the superior margin of the orbit. There are 31 to 33 vertebrae, of which 15-16 abdominal and 16-18 caudal.

Neural and haemal arches (basidorsals and basiventrals) almost completely surround the notochord. However, some samples, e.g. specimens CLC S.580 and S.458, were subject of an anterior-posterior compression during fossilization that has resulted in a post mortem separation of those arches. The bases of the neural and haemal arches and spines interlock with their successive neighbours through complex interdigitating sutures. These digitations are numerous (three to five) in the anterior part of the column, but the number of digitations declines to two on both sides of the arches in the posterior region. The digitations disappear in the caudal pedicle. The first five or six neural spines are nearly vertical in relation to the body axis. However, after the sixth or seventh vertebra, the neural spines are directed posteriorly. The first seven neural spines are autogenous, i.e., not connected to the corresponding arches, and are quite robust and almost cylindrical. All of the following neural spines are fused with the arches. These following neural spines are also well developed, but more gracile than the autogenous ones, and they all have a sagittal flange, like an osseous lamina, developed on their anterior margins. In the caudal region the distal tips of the neural spines are

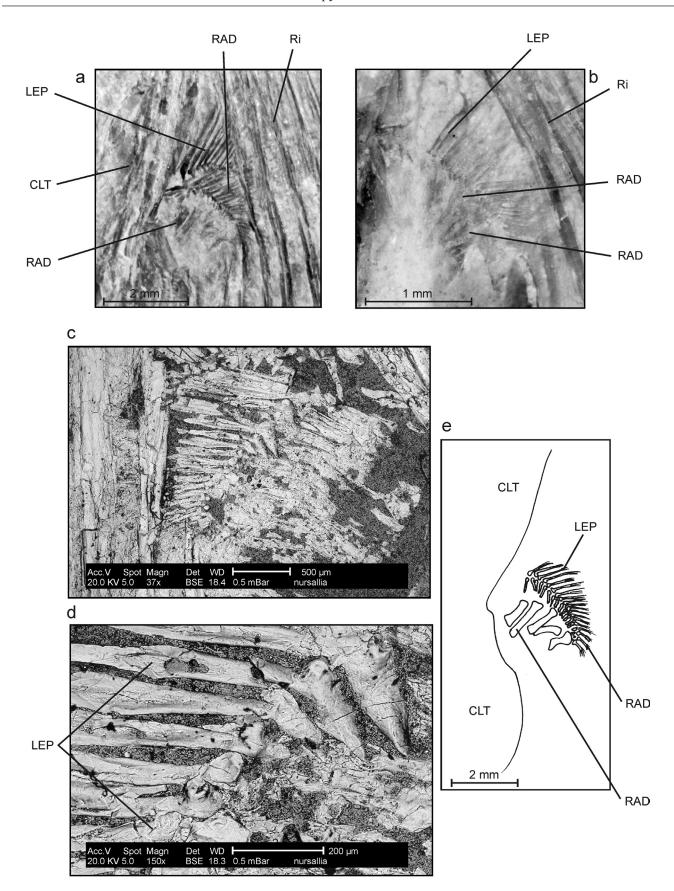


Fig. 8 – *Nursallia tethysensis* sp. nov. Pectoral fin. (a): in specimen CLC S.136, showing both sides of the fins; (b): in specimen CLC S.580; (c and d) in specimen CLC S.363, to showing the conic-shaped principal rays; (e): camera lucida scheme of the structure of the pectoral fin in specimen CLC S.136.

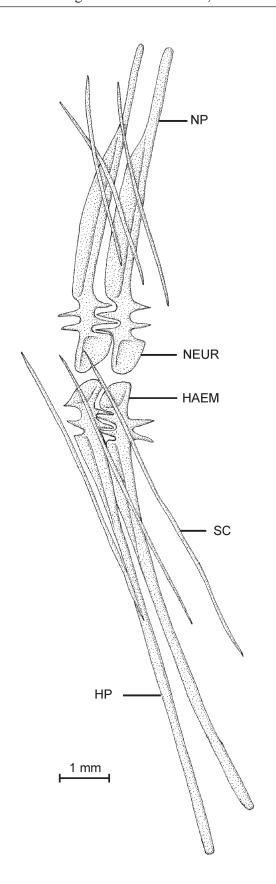


Fig. 9 – *Nursallia tethysensis* sp. nov. Two successive vertebrae in the beginning of the caudal region in specimen CLC S.363.

connected to several of the axonosts of the dorsal fin. The haemal spines are similar to the neural ones, and all have well-developed sagittal flanges, with the tips contacting several axonosts of the anal fin.

The ribs are thin, elongated, anteriorly curved, and bear narrow sagittal flanges on both the anterior and posterior margins. The ventral tips of each rib are frayed.

The post-coelomic bone is thin, sinuous, and connected below with the second post-anal scale of the ventral keel, as visible on specimen CLC S.363. This bone is thicker than a rib, and is connected with the anterior margin of the first haemal spines and with the tips of the first reduced anal pterygiophores. Dorsally, it does not reach the axial skeleton but comes near to it (Fig. 8a, b).

Dorsal and anal fins (Figs 3, 12)

The dorsal fin originates at the level of the 13th vertebra. There are 58-60 dorsal pterygiophores, as seen on specimen CAS 9468-9963. This sample also shows that the general shape of the dorsal fin corresponds to the A2 strip-like type [character 68(0)] of the classification by POYATO-ARIZA & WENZ (2002). Three to four pterygiophores are inserted in the space between two subsequent neural spines, and each pterygiophore generally is articulated with only one dorsal fin ray, but in sample CLC S.363 we documented the possible articulation of one pterygiophore with two distinct dorsal-fin rays. This joint was well documented by SEM observation. The upper ends of the pterygiophores are flattened and enlarged, but the lower ends of the dorsal rays are pointed, almost triangular in shape.

The anal fin originates at the level of the 15th or 16th vertebrae. There are 52-54 anal pterygiophores, and three or four pterygiophores are inserted in the space between two subsequent haemal spines. The general morphology of the anal fin also corresponds to the A2 strip-like type of POYATO-ARIZA & WENZ (2002), because the length of the first five anal rays increases rapidly, and from the sixth ray slowly decreases in length posteriorly, as shown in specimen CAS 9468-9963.

Caudal skeleton and fin (Figs 11, 12)

The caudal pedicle is well developed and elongated. The three to five neural spines not connected to the procurrent caudal rays are shorter and notably thinner than the preceding ones. This situation indicates the vestigial condition [character 57(3)] of POYATO-ARIZA & WENZ (2002). The epichordal elements (neural

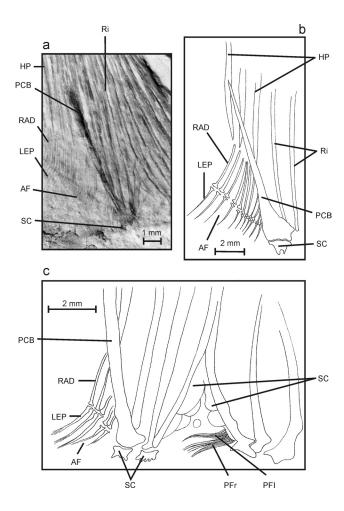


Fig. 10 – *Nursallia tethysensis* sp. nov.. (a): post-coelomic bone in specimen CLC S.580 with corresponding post-anal scales; (b): camera lucida scheme of the post-coelomic bone in specimen CLC S.131; (c): camera lucida scheme of the anal region in specimen CAS 9468.

spines sustaining procurrent caudal rays) are longer than the immediately preceding neural spines but seem to be scarce, with only two to four elements, corresponding to character 58(3) of POYATO-ARIZA & WENZ (2002). There are eight to nine hypochordal elements (haemal spines connected with the procurrent caudal rays). The last three of these hypochordal pieces are considerably enlarged, forming broad, subtriangular hypurals. All three show a well marked longitudinal crest and they exhibit a fan-shaped arrangement. Such a situation corresponds to the hypertrophied condition [character 59(2)] of POYATO-ARIZA & WENZ (2002). Urodermals seem absent.

The caudal fin is well developed in the vertical direction, with two distinct lobes and a convex posterior

margin, corresponding to the type F [vertical type, character 73(6)] of POYATO-ARIZA & WENZ (2002). The number of the principal caudal fin rays ranges from 37 to 44, and they are supported by an urophore complex derived from the transformation of at least five caudal vertebrae. There are a few procurrent rays, frequently two in the upper lobe and four in the lower lobe.

Dermal scales (Figs 13, 14)

Seven to eight scales (scutes) comprise the dorsal ridge between the head and the origin of the dorsal fin. The size of these dorsal ridge scales increases from anterior to posterior, and the largest scale is the penultimate, the last scale being less developed. In some specimens (i.e., specimen CLC S.363) each scale is surmounted by three spines: the anterior one is directed anteriorly, while the second and third are directed posteriorly (Figs 10a, 11a), as is well documented by SEM observation. In other specimens (i.e., specimen CLC S.580) the scales of the dorsal ridge are surmounted by only one

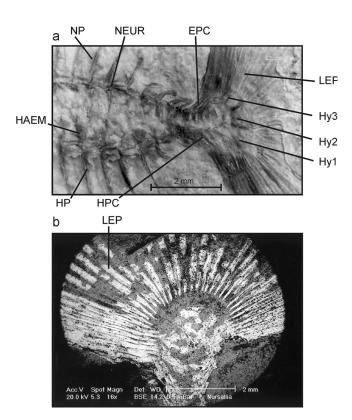


Fig. 11 – *Nursallia tethysensis* sp. nov. Caudal pedicle and bone structures supporting the caudal fin. (a): stereomicroscopic observation in sample CLC S.580 (6x); (b): S.E.M. observation in sample CLC S.363 (16x).

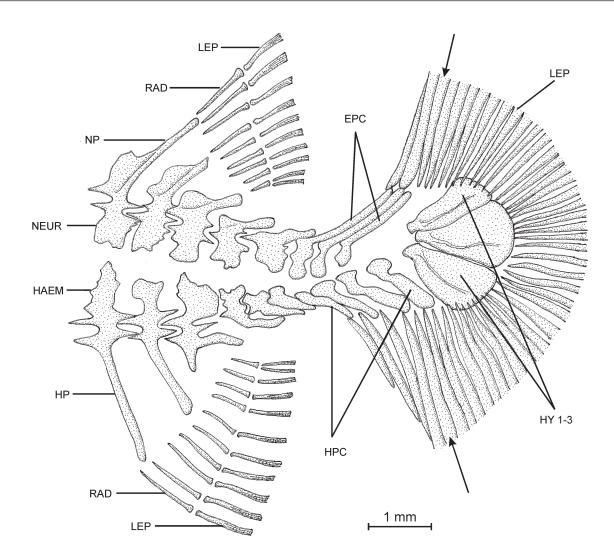


Fig. 12 – *Nursallia tethysensis* sp. nov. Reconstruction of the caudal skeleton based on specimens CLC S.136 and CLC S.363. The scale refers to specimen CLC S.363.

spine, with a rounded tip (Figs 13b, 14b). It is possible that these differences in the ornamentation of the free margin of the scales of the dorsal ridge are related to sexual dimorphism.

There are three to five ventral keel scales (scutes) in the pre-cloacal region, and two in the post-anal region. The pre-cloacal ventral keel scales are in close contact with each other, with a large spine on the free margin, directed posteriorly, as seen in specimen CLC S.458 (Fig. 13c, d). The first scale of the pre-anal series is barely connected with the inferior margin of the cleithrum (Fig. 13e). The succeeding scales of this pre-anal series decrease in size from front to back (Fig. 13d). The two post-cloacal scales present a denticulated free margin. The first post-cloacal scale free margin is really serrated, but the free margin of the second post-cloacal scale presents only three or four denticles, as well documented by SEM analysis (Fig.

13g). The second post-anal scale is clearly connected with the lower margin of the post-coelomic bone.

The body squamation is of the peltate type (NURSALL, 1996). In the lower part of the abdominal region, in the area between the posterior margin of the cleithrum and the cloaca, we can observe a series of complete scales, longitudinally arranged (bar-scales), in close contact with each other, as clearly seen in specimen CAS 9468-9963. In the dorsal region the scales are filiform. They extend also in the caudal region, and some filiform bar-scales are present also immediately before the caudal pedicle. Between the head and the dorsal fin, these dorsal body scales are in relationship with the dorsal keel scales, and two or three pairs of bar-scales originated from the inferior margin of each dorsal ridge scale (Fig. 13b, f). In the anterior part of the body these dorsal scales, originated from the dorsal ridge, regularly cross the vertebral column,

extending also into the abdominal region. In the caudal area these bar-scales originated more inferiorly relative to the dorsal ridge, in the area of contact between the neural spines and the dorsal axonosts, as shown by specimen CAS 9468-9963.

Non osseous remains (Fig. 15) In specimens MCSNM V 6426 (holotype) and CLC S. 363 examined from En Nammoura, we observed some black remains in correspondence of the ocular ball (Fig. 15a). These remains are almost perfectly circular in general shape and occupy exactly the centre of the orbit, and their margins are partially covered by two sclerotic bones.

We examined these remains with a SEM to demonstrate the structure and chemical composition

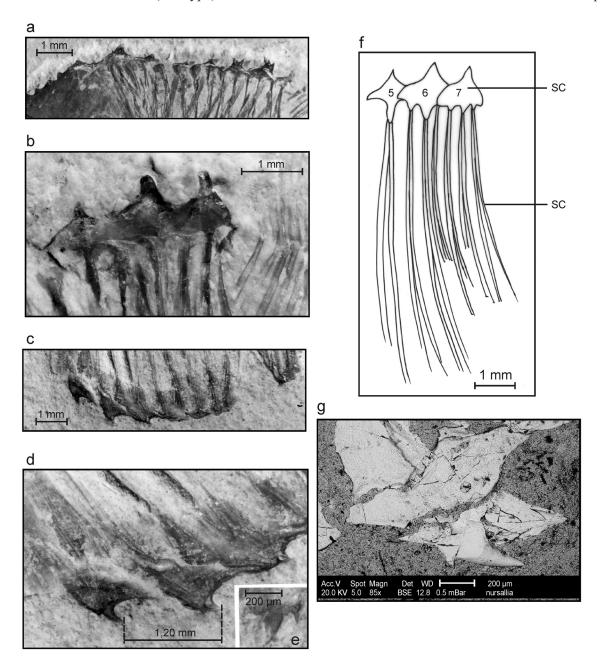


Fig. 13 – *Nursallia tethysensis* sp. nov.: dermal scales and squamation; (a): dorsal ridge scales (specimen CLC S.363); (b): connection between the dorsal ridge's last three scales and the bar scales (specimen CLC S.580; (c and d): pre-anal scales of the ventral keel (specimen CLC S.458); (e): first scale of the ventral keel connected with the lower margin of the cleithrum (specimen CAS 9455); (f): camera lucida scheme of the last scales (5 to 7) of the dorsal ridge showing the joints with the bar scales (specimen CLC S.580); (g): S.E.M. observation of the pre-anal scale structure, morphology and connections in specimen CLC S.363.

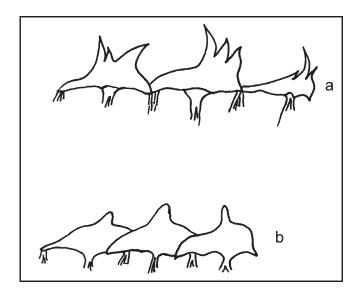


Fig. 14 – *Nursallia tethysensis* sp. nov. Possible sexual dimorphism in the scales of the dorsal keel. In some samples these scales have three pointed spines (i.e. specimen CLC S.363) (a); on the contrary, in other samples these scales exhibit only one spine with rounded tip (i.e. specimen CLC S.580) (b).

of this black material. Using this microscope, no structural details are visible in the region covered by black remains (Fig. 15b). To study the chemical composition of this black material, we determined the micro-chemical composition in three different areas in specimen CLC S.363: (i) limestone matrix, (ii) dense bone in the vomerine region, and (iii) the centre of the orbit, with abundant black remains on the limestone surface (Fig. 15c, d, e).

The chemical micro-analysis of the limestone (Fig. 15c) demonstrates the presence of Calcium, Oxygen, Carbon, Silicium, Aluminium, and minor components, in relative proportions consistent with a mixture of limestone (calcium carbonate) and alumino-silicates. This picture is exactly consistent with the chemical composition reported by HÜCKEL (1970) in the Haqel flints (75% of CaCo₂ and 20% of SiO₂).

The chemical micro-analysis of the bone of the fossil fish (Fig. 15d) revealed a very different pattern of elemental composition, in which we can observe the prevalence of Calcium, Oxygen, and Carbon, but also a relatively high proportion of Phosphorus (absent in the matrix). The relationship between these various elements seems to mirror the stechiometric relationship typical of hydroxy-apathite, a normal component of bone in living vertebrates, including fishes. These

data represent the first information about the chemical composition of the fossil bones from the Lebanese Upper Cretaceous localities.

The chemical micro-analysis of the black material in the orbit region (Fig. 15e) revealed a composition similar to that of the matrix, with only one significant difference: the relevant quantity of Sulphur. This element is abundantly present in the eye liquid in living fishes. The internal surface of the sclera (the so-called "argents"), the lens (which in extant fishes is very big and thick), and the great mass of the vitreous humour (also rich in proteins), all seem to be possible sources of the high organic content of the orbital region. In particular, the sclera in all the extant fishes consists of partially ossified cartilage, a tissue almost completely composed of collagen, a protein characterized by a very high content of Sulphur.

The conservation of chemical characteristics of both bone and some soft tissues, in our case, only the eyes, reveals new, unexpected, and intriguing perspectives on the possible paleontological analysis of fossil fishes from these Lebanese localities in which the preservation of organic materials seem to be extraordinary.

Discussion

All of the specimens described here present the following combination of characters that are considered absolutely typical of the genus Nursallia (BLOT, 1987; NURSALL, 1996, 1999; POYATO-ARIZA & WENZ, 2002; FOREY et al., 2003): (1) body discoid with abdominal region well developed; (2) head short; (3) frontal bones very broad, curved and imparting a markedly round profile to the anterior-dorsal surface of the head; (4) orbits perfectly round; (5) mouth horizontal; (6) temporal fossa absent; (7) vomerine teeth with a subcircular contour; (8) neural and haemal arches almost completely surrounding the notochord; (9) inter-vertebral sutures extremely complicated, with many indentations in the abdominal region, and two long digitations in the caudal region; (10) caudal peduncle extremely narrow; (11) pelvic fins present and situated in the cloacal vestibule; (12) dorsal and anal fins nastriform, with well-developed pterygiophores; (13) last three hypochordal elements enlarged as subtriangular hypurals which exhibit a fanshaped arrangement [the two ventral hypurals are fused in one very broad plate in some specimens of Nursallia (POYATO-ARIZA & WENZ, 2002: fig. 26A, C); that is not a specific character and both states can exist within the same species; e. g. N. goedeli has two (POYATO-ARIZA

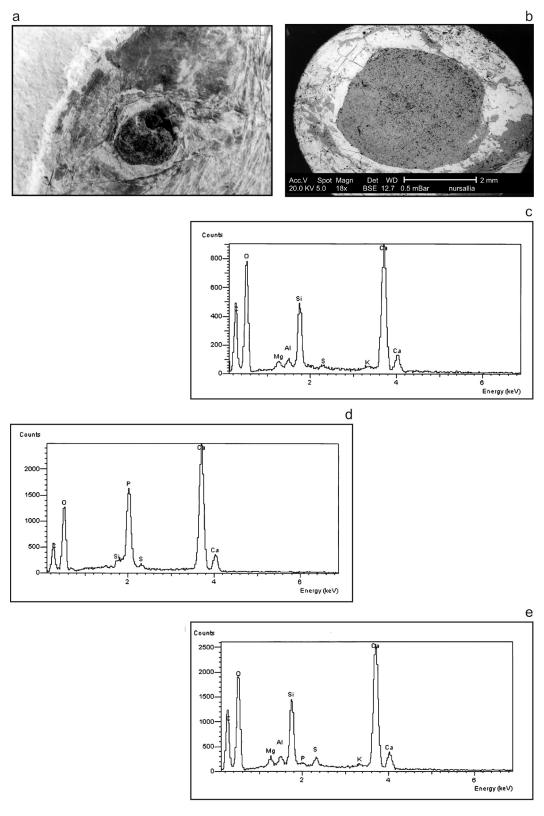


Fig. 15 – *Nursallia tethysensis* sp. nov. Remains of the eye soft tissues at the center of the eye orbit (specimen CLC S.363). (a): stereomicroscopic image showing also a well preserved superior sclerotic bone; (b): S.E.M. image in the same sample CLC S.363 (counterpart) demonstrating absence of structural details in this area. The chemical microanalysis (obtained by a microanalytical analyzer annexed with a Scanning Electorn Microscopy) of the limestone (c), of the cranial bones in specimen F (d), and of the black remains in the orbital region in the same specimen F (e): note the high level of Sulphur, presumably linked to the remains of the sulfo-proteins originally contained in the sclera and in the soft tissues of the eyes of the living fish.

& WENZ, 2002: fig. 26A) or three hypurals (HECKEL, 1856: pl. 2, fig. 3; ARRATIA & TINTORI, 1999: fig. 11B; NURSALL, 1999: fig. 10D)]; (14) caudal fin of "vertical type", i.e., extremely short antero-posteriorly relative to depth, with a convex posterior profile to the fin; (15) dorsal and ventral keel scales (scutes) reduced; (16) squamation pattern corresponding to the "peltate" type, but with scales extended also on the caudal region, and on the abdominal area.

The closest relationship of the new species seems to be with Nursallia gutturosum, a species known from the Cenomanian of Jebel Tselfat, Morocco (ARAMBOURG, 1954), of Floresta, Sicily (LEONARDI, 1966), of Cinto Euganeo, Italy (SORBINI, 1976) and of Passo del Furlo, Italy (CAPASSO, 2007). Both species share a rounded and almost vertical frontal profile, a considerably enlarged dermosupraoccipital ornamented with small median spines, a parietal not joining the frontal (ARAMBOURG, 1954: fig. 4; POYATO-ARIZA & WENZ, 2002: fig. 9) and the same number (around 40) of principal caudal rays. But there are also many differences. In N. gutturosum, the dermosupraoccipital is less huge, the pterotic presents a broad contact with the frontal, there are seven teeth in the median vomerine row, the hyomandibula is much larger, a prefrontal and a maxilla are present, the preopercle has a different shape (ARAMBOURG, 1954: figs 4, 7A; POYATO-ARIZA & WENZ, 2002: fig. 9), the dorsal fin is longer (around 70 rays) with an origin above the 10th vertebra, the number of vertebrae is a little higher (around 34-35), the scales of the dorsal ridges have only one spine, and the scales of the ventral keel are not in close contact but seem to be slightly separated.

Nursallia goedeli, including (WOODWARD, 1895: 274-275) also *Palaeobalistum ventralis*, is typical for the two Lebanese Upper Cenomanian localities, Haqel and Hgula. We have had the opportunity to examine four specimens in the Capasso collection (CLC S.11, S.356, S.375, and S.477) for comparison with *N. tethysensis*, and also to refer to HECKEL (1856), DAVIS (1887) and FOREY et al. (2003). A major difference is the size, as all the known samples of N. goedeli correspond to medium size fishes, adults measuring from 15 to 33 cm in total length. In N. goedeli, the frontal outline is less rounded, the angle between the lower margin of the prearticular and the anterior margin of the cleithrum is more obtuse, the vomerine and prearticular teeth do not possess marginal serrations, the vomerine teeth have a convex occlusal surface and there are six to eight teeth in the median row, the abdomen is less protruded, the number of vertebrae is higher (39), the number of dorsal (around 50) and anal (around 45) pterygiophores is lower, the first hypural is longer but more slender, and the caudal comprises 26 to 35 principal rays.

Nursallia flabellatum, from the Aptian-Albian of the Santana Formation, North-East Brazil, is known only by the holotype (COPE, 1886; BLOT, 1987; MAISEY, 1991) which is an incomplete specimen. A great part of the head and the beginning of the dorsal and anal fin are missing. It does, however, have the characteristic shape of the caudal fin as well as interlocking neural and haemal arches (WOODWARD, 1907). In addition the inter-vertebral sutures have a very high number of digitations. Unfortunately the original description by COPE (1886) does not allow a reasonable comparison with *N. tethysensis*.

Nursallia veronae from the Monte Bolca, Italy, the type species of the genus, is also known by only one badly preserved specimen (BLOT, 1987). This Eocene species is much bigger (30 cm in total length) than N. tethysensis. Other differences are the two teeth on each premaxilla, more vomerine median teeth (8), more prearticular upper row teeth (8 to 10), a higher number of vertebrae (34 or 35 with 22 or 23 caudal), a longer dorsal (67 pterygiophores), a longer anal (62 pterygiophores), a lower number of principal caudal rays (35 or 36), no spines on the dorsal and ventral scutes, and the scales covering all the body.

Conclusions

Nursallia tethysensis sp. nov. is a new species of pycnodont fish, with all the typical apomorphies of Nursallia but differing from the other species of the genus. The new species is the smallest representative of Nursallia known today. The species is a characteristic, but quite rare, member of the ichthyofauna of En Nammoura, and – more rarely – of Hgula. In both these fossil biocoenoses, N. tethysensis sp. nov. is the second species of Nursallia in number of specimens, after the bigger species N. goedeli, typical of the Hgula and Haqel quarries. Within the genus, N. tethysensis sp. nov. seems to be more closely related to Nursallia gutturosum.

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List of abbreviations used in the text-figures

AF: anal fin AN: angular ART: articular BO: basioccipital

BRSTG: branchiostegal ray CHY a.: anterior ceratohyal CHY p.: posterior ceratohyal

CLT: cleithrum DN: dentary

DPTE: dermopterotic

DSOC: dermosupraoccipital ENPT: entopterygoid EPC: epicordal elements

EXO: exoccipital FR: frontal

HAEM: haemal arch HP: haemal spine

HPC: hypochordal elements HY 1-3: hypurals 1 to 3 HYOM: hyomandibula

LEP: fin ray

PA: parietal

METH: mesethmoid MPT: metapterygoid NEUR: neural arch NP: neural spine OP: opercle

PCB: postcoelomic bone

PF: pelvic fin PMX: premaxilla POP: preopercle

PRART: prearticular (splenial)

PS: parasphenoid PT: posttemporal QU: quadrate Ri: ribs

RAD: dorsal and anal pterygiophores

SC: scale

SCL: sclerotic bone

SCLT: supracleithrum (hypercleithrum)

SPH: sphenotic SY: symplectic VO: vomer 1.: left

ol. f.: olfactive fossa ot. c.: otic sensory canal

r.: right th.: teeth

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