

A phylogeny of extant and fossil buckler dory fishes, family Zeidae (Zeiformes, Acanthomorpha)

by

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ABSTRACT. - A data set of 45 putatively informative morphological characters (mostly osteological, and a few external features) is analyzed for 12 extant and fossil species belonging to the buckler dory fish genera *Zeus* and *Zenopsis*, which together constitute the family Zeidae (Zeiformes, Acanthomorpha), and for two outgroup taxa. *Zeus* consists of two extant and three fossil species, whereas *Zenopsis* consists of four extant and three fossil species. Both genera date back to at least the Oligocene (36 Mya). The phylogenetic analysis of the full data set (extant + fossil) provides strong support for the monophyly of the Zeidae but only weak support for the monophyly of *Zenopsis*, and it calls into question the existence of a clade formed by the extant and fossil taxa assigned to *Zeus*. Additional phylogenetic analyses were performed: (1) the most incomplete fossil taxon, *Zeus robustus*, was excluded; (2) all fossil taxa were excluded; and (3) the new extant species of *Zenopsis* was excluded. All of these analyses confirm a strongly supported clade formed by *Zeus* + *Zenopsis* and of a much less strongly supported clade formed by the extant and fossil species of *Zenopsis*. The analyses do not provide support for a clade formed by extant and fossil species previously assigned to the genus *Zeus*, even though when the fossil species are excluded from the analysis, the two extant species of *Zeus* appear as each other's sister groups in one of three equally parsimonious cladograms.

RÉSUMÉ. - Une hypothèse phylogénétique pour les Zeidae actuels et fossiles (Zeiformes, Acanthomorpha).

Une matrice des 45 caractères morphologiques (principalement ostéologiques) a été constituée pour 12 espèces actuelles et fossiles des deux genres de Zeidae, *Zeus* et *Zenopsis* et pour deux extra-groupes. Le genre *Zeus* comprend deux espèces actuelles et trois fossiles, et le genre *Zenopsis* en comprend quatre et trois respectivement. Les deux genres datent de l'Oligocène moyen (36 millions d'années). L'analyse phylogénétique du jeu des données de toutes les espèces supporte bien la monophylie des Zeidae, mais très peu celle de *Zenopsis*; le clade formé par les espèces actuelles et fossiles du genre *Zeus* n'est toutefois pas soutenu. Des analyses complémentaires ont été effectuées, après avoir éliminé soit *Zeus robustus*, le fossile le moins connu, soit tous les fossiles, soit la nouvelle espèce de *Zenopsis*. Toutes ces analyses soutiennent l'existence d'un clade des Zeidae et d'un clade *Zenopsis*. Il n'y a pas de support pour un clade *Zeus*.

Key words. - Zeiformes - Zeidae - Fossils - Osteology - Phylogeny.

Zeidae (buckler dories, including the John dory or St. Peter's fish) are moderate- to deep-bodied acanthomorph fishes. The family is composed of 12 species (six extant and six extinct) that are presently classified in two genera. The genus *Zeus* Linnaeus, 1758, includes the extant species *Zeus faber* Linnaeus, 1758 and *Zeus capensis* Valenciennes, 1835, and the extinct species *Zeus robustus* Gorjanović-Kramberger, 1891 (Oligocene of Slovenia), *Zeus jermanskae* Baciú *et al.*, 2005 (Oligocene of Poland) and *Zeus primaevus* Scarabelli, 1859 (Miocene of Italy and Algeria). The genus *Zenopsis* Gill, 1863, includes the extant species *Zenopsis nebulosus* (Schlegel, 1847), *Zenopsis conchifer* (Lowe, 1852), *Zenopsis oblongus* Parin, 1989, and *Zenopsis* sp. (to be described by U. Yamada, T. Nakabo and D. Bray – D.

Bray, pers. comm.), and the extinct species *Zenopsis hoernei* Gorjanović-Kramberger, 1891 (Oligocene of Slovenia), *Zenopsis clarus* Daniltshenko, 1960 [Oligocene of the Carpathians (Poland, Romania) and northwestern Caucasus (Russia)] and *Zenopsis tyleri* Baciú & Bannikov, 2001 (Oligocene of Romania).

The first comprehensive phylogenetic hypothesis for the order Zeiformes (dories) (Tyler *et al.*, 2003) showed that the extant Zeiformes form a strongly supported monophyletic group composed of six clades of familial status: the Cyttidae, Oreosomatidae, Parazenidae, Zeniontidae, Grammicolepididae, and Zeidae, with this last family appearing in the terminal, most-derived clade of dories, as the sister group to the Grammicolepididae. However, none of the extinct taxa

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Table I. - List of specimens of extant species examined for this work. For fossil materials, see Baciu *et al.* (2005). [*Liste des spécimens d'espèces actuelles examinés dans cet article. Pour les matériels fossiles, voir Baciu et al. (2005)*].

Taxons	Museum number	Number of specimens in lot	SL (mm)
<i>Zenion hololepis</i>	CAS 38409	1	90
	CAS 76856	2	70-73
	USNM 187864	3	50-73
	USNM 307305	2	45-48
<i>Xenolepidichthys</i>	AMNH 29455	4	70-75
	CAS 38403	1	70
	CAS 38406	1	75
	USNM 320013	1	64
	USNM 320015	3	59-77
	USNM 320016	2	59-64
<i>Zenopsis conchifer</i>	CAS 47401	1	54
	FMNH 67090	3	44-58
	USNM 117280	2	51-81
	AMNH 4451	1	126, D
	AMNH 56447	1	368, D
	AMNH 56833	1	405, D
<i>Zenopsis nebulosus</i>	AMNH 92291	1	325, D
	AMNH 95024	1	335, D
	AMNH 95028	1	340, D
<i>Zenopsis oblongus</i> *	USNM 285048 (paratype)	1	272 R
	USNM 353898	1	347 (CS, in poor condition)
	Uncatalogued specimen from Shirshov Institute of Oceanology	1	255 R
<i>Zenopsis</i> sp.	AMS.I 22825-019	1	R
	AMS.I 22826-004 (paratypes)	2	R
	FAKU 64803 (holotype)	1	R
	FAKU 64804 (paratype)	1	R
<i>Zeus capensis</i>	USNM 330849	8	173-193, R (1 CS, in poor condition)
<i>Zeus faber</i>	USNM 307842	2	48-67
	USNM 320014	2	59-89
	USNM 320063	1	80
	AMNH 22707	1	300, D
	AMNH 91448	1	230, D
	AMNH 95055	1	270, D
	USNM 176975	1	215, D
	USNM 328597	1	223, R

*This species is unique among Zeidae in having the third interneural space vacant (rather than the fourth) and only three dorsal-fin pterygiophores anterior to the neural spine of the fourth abdominal vertebra (rather than four pterygiophores).

and only three of the six known extant species of zeid fishes (*Zeus faber*, *Zenopsis conchifer*, and *Zenopsis nebulosus*) were included in that (mostly osteological) analysis because of the lack of sufficient material. Baciu *et al.* (2005) have since published a revision of the fossil record of the Zeidae, including the description of new species and detailed redescription of the osteology of several others. The availability of these new data for the fossil zeids, in addition to the fact that osteological material for the least known extant zeid

taxa has become available for the first time, makes it possible to produce the first phylogenetic hypothesis for the Zeidae that includes all of the species currently assigned to this family.

MATERIALS AND METHODS

Fourteen taxa are included in this analysis, including 12 zeids and two outgroups. In addition to the zeid taxa and the two outgroups already analyzed in Tyler *et al.* (2003), three additional extant zeid species (*Zeus capensis*, *Zenopsis oblongus*, *Zenopsis* sp.) are included. The six extinct taxa of Zeidae included in this analysis were described with reconstructions in Baciu *et al.* (2005); the reader is referred to that paper for the descriptions and measurements of those species. Minor differences from the data in that paper are based upon our re-interpretation of the number of vertebral segments or anal pterygiophores in a few specimens. Table I lists all examined species, and for extant species it includes museum number, number of specimens in each lot, and standard length (SL) when available. Museum abbreviations follow Leviton *et al.* (1985).

Phylogenetic analysis

External morphological and osteological characters were obtained from direct observation of the specimens listed in table I; the character list is reported in appendix I. The characters were analyzed following the principles of phylogenetic systematics (Kitching *et al.*, 2000). A matrix for all the specimens examined was first constructed using WINCLADA (Nixon, 2002). This matrix was subsequently analyzed using NONA (Goloboff, 1999) and is shown in table II. Following Tyler *et al.* (2003) one species of Zeniontidae and one of Grammicolepididae were used as outgroups. The zeniontid *Zenion* was selected as the first outgroup, following the protocol suggested by Nixon and Carpenter (1993). All characters were assigned equal weight (1), and all multistate characters were analyzed as unordered. Heuristic searches, with random addition of taxa, the TBR + TBR branch swapping option of NONA, and 10,000 replications were performed. Tree length (L), consistency index (CI), and retention index

Table II. - Data set of 45 morphological characters for the 14 species in this analysis (12 Zeidae plus two outgroups). Numbers in parentheses at the right side of the table indicate the number of characters that could be determined, when some characters are unknown for a taxon. [Jeu de données de 45 caractères morphologiques pour les 14 espèces utilisées dans cette analyse. Les nombres entre parenthèses à droite du tableau indiquent le nombre de caractères qui ont pu être déterminés dans les cas où quelques-uns d'entre eux restent inconnus pour un taxon.]

Taxon	Character number and state									
	5	10	15	20	25	30	35	40	45	
<i>Zenion</i>	00000	00000	00000	00000	00000	00000	000--	00000	00000	
<i>Xenolepidichthys</i>	00011	00022	10100	00000	00000	00000	020--	03021	01010	
<i>Zeus faber</i>	11110	11111	01101	11111	11120	11101	11101	112p1	22211	
<i>Zeus capensis</i>	11110	11111	00101	11110	11120	11101	11101	11201	22210	
<i>Zeus robustus</i>	?????	?????	???0?	?1?10	1112?	?1???	?????	?p11?	112??	(15)
<i>Zeus jermanskae</i>	?0???	?1???	1??01	???	11112	11?0?	11101	11301	122??	(29)
<i>Zeus primaevus</i>	?1?1?	??1?1	???	?1?11	11111	11?0?	11101	11311	122??	(30)
<i>Zenopsis conchifer</i>	1p122	11112	01111	11011	11110	11111	13310	122p1	p2122	
<i>Zenopsis nebulosus</i>	1p122	11112	01111	11111	11111	11111	13310	12311	12122	
<i>Zenopsis oblongus</i>	10?22	11111	11111	11111	10110	11?11	13310	12201	1p122	
<i>Zenopsis sp.</i>	11?2?	?1???	?1?1?	?1110	11110	?1?1?	1?310	?1211	0212?	(30)
<i>Zenopsis clarus</i>	?1?2?	?11?1	10?11	?1?11	11112	11?1?	13210	12301	p21?2	(34)
<i>Zenopsis tyleri</i>	?1???	?11?1	1??11	?1?11	11112	11?1?	13210	12301	221?2	(32)
<i>Zenopsis hoernesii</i>	?????	?????	?????	?1???	011??	?1???	132?0	122??	11???	(15)

Zeus faber : 39(0,1)

Zeus robustus : 37(0,1)

Zenopsis conchifer : 2(0,1); 39(0,1); 41(1,2)

Zenopsis nebulosus : 2(0,1)

Zenopsis oblongus : 42(1,2)

Zenopsis clarus : 41(1,2)

(RI) are provided for each analysis (Kluge and Farris, 1969; Farris, 1989). When more than one most-parsimonious tree was obtained, a strict consensus tree was calculated. Character evolution (appendix II) was studied using the delayed transformation (DELTRAN) option of WINCLADA, because most characters were scored as unknown (“?”) for at least some taxa, and the use of the accelerated transformation (ACCTRAN) option would have necessitated hypothesizing the presence of certain character states within lineages, for which there is no evidence that these states have ever been present. The decay index (Bremer, 1988, 1994) was calculated using NONA (Goloboff, 1999). Cladograms for publication were produced using TREEVIEW (Page, 1996). Unknown character states in the fossil taxa are indicated with a question mark “?”. Inapplicable characters are indicated with a horizontal dash “-”. It should be remembered that although tree-building programs treat dashes and question marks in the same way, they are conceptually different.

RESULTS

Analysis of the full data set produces two equally parsimonious trees (EPTs hereafter) (Fig. 1). The topology of the resultant strict consensus tree strongly supports the mono-

phyly of the Zeidae, with a high decay index of nine, and illustrates the existence of a clade formed by the extant and extinct species of *Zenopsis*, whereas *Zeus* appears to be paraphyletic. Furthermore, the two extant species of *Zeus*, *Z. faber* and *Z. capensis*, never appear to form a monophyletic group, and *Z. capensis* appears to be a more basal taxon than *Z. faber*. The relationships of the Oligocene *Zeus robustus*, whose fossil record is based upon highly incomplete materials, appear to be problematic because its placement is significantly variable among the cladograms in figure 1. The relationships for the species of *Zenopsis* are stable despite the weak decay index for all groups within the *Zenopsis* clade. This low support might be a reflection of the presence of fossil taxa, which have many unknown character states (see also Santini and Tyler, 2004). In the *Zenopsis* clade, the yet-to-be-described species *Zenopsis sp.* appears as the most basal lineage. Subsequently, two subclades can be identified: one formed by the extant *Zenopsis conchifer* and *Zenopsis nebulosus*; and one formed by *Zenopsis oblongus* plus the three extinct species. Within this last clade, *Zenopsis oblongus* is the sister lineage to *Zenopsis hoernesii* + (*Zenopsis clarus*, *Zenopsis tyleri*).

Exclusion of the highly incomplete *Zeus robustus* from the data set does not help to resolve the relationships among the various species assigned to *Zeus*. On the contrary, it

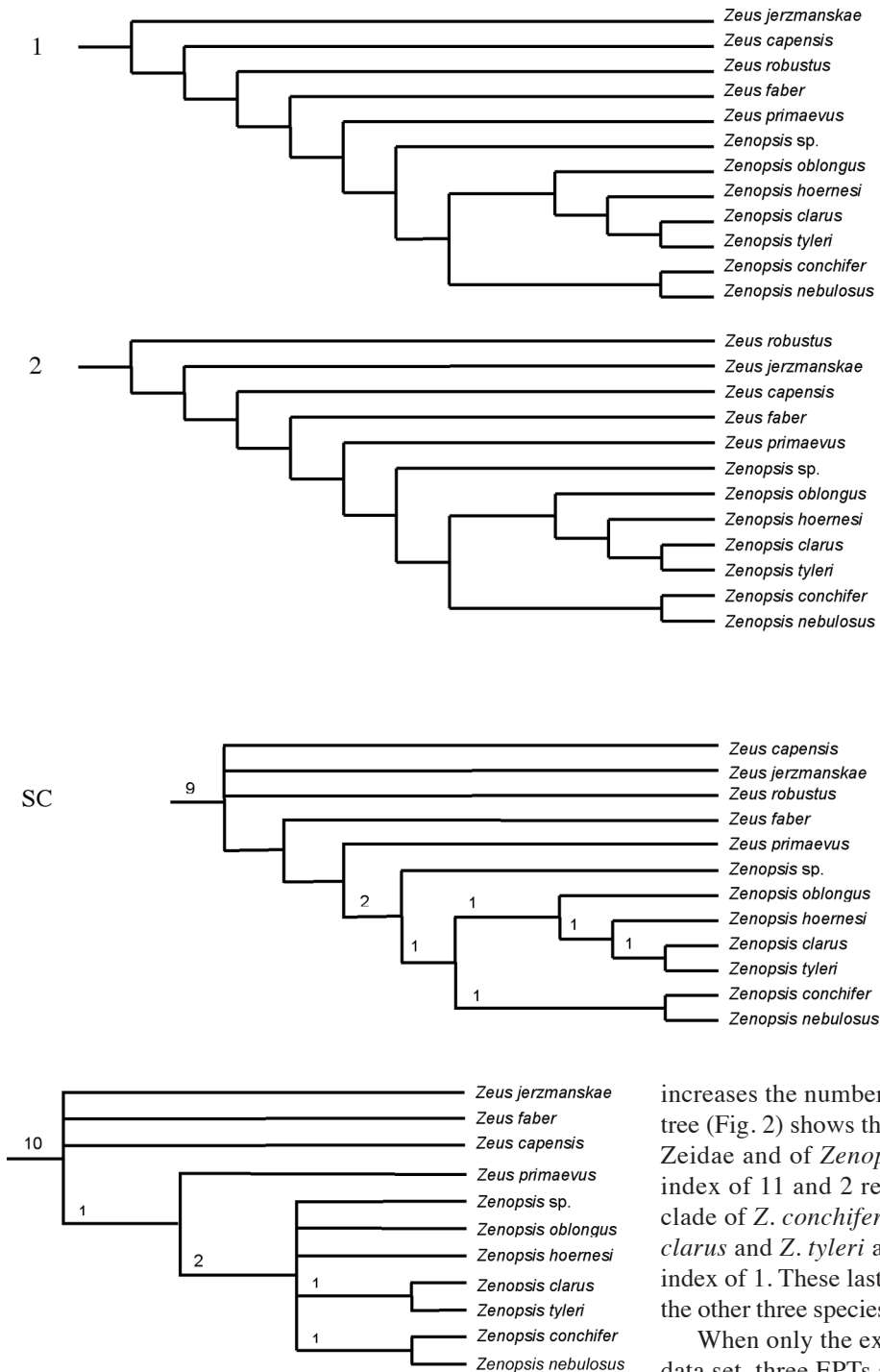


Figure 1. - Equally parsimonious trees (EPTs) 1 and 2 ($L = 85$, $CI = 0.76$, $RI = 0.80$), and strict consensus (SC) tree produced by the analysis of the full data set of 12 extant and extinct species of Zeidae plus two outgroups. Decay index is indicated above the tree branches of the SC tree. Cladogram #2 was selected for character optimization in figure 5. [EPTs 1 et 2 ($L = 85$, $CI = 0,7,6$ $RI = 0,80$), et arbre de consensus strict (SC) produits par l'analyse de toutes les informations pour 12 espèces de Zeidae vivants et fossiles, et deux extra-groupes. L'indice de Bremer est indiqué sur les branches de l'arbre SC. Le deuxième cladogramme a été utilisé pour l'optimisation des caractères dans la figure 5.]

Figure 2. - Strict consensus tree of the five EPTs ($L = 0.83$, $CI = 0.78$, $RI = 0.82$) produced by the analysis of the data set of extant and extinct species of Zeidae plus two outgroups when *Zeus robustus* is not included. Decay index is indicated above the tree branches. [Arbre de consensus strict des 5 EPTs ($L = 0,83$, $CI = 0,78$, $RI = 0,82$) produit par l'analyse du jeu de données contenant les espèces actuelles et fossiles de Zeidae et deux extra-groupes, à l'exclusion de *Zeus robustus*. L'indice de Bremer est indiqué sur les branches de l'arbre.]

increases the number of EPTs to five. The strict consensus tree (Fig. 2) shows that although both the monophyly of the Zeidae and of *Zenopsis* are still supported, with a decay index of 11 and 2 respectively, within *Zenopsis* only the clade of *Z. conchifer* and *Z. nebulosus* and the clade of *Z. clarus* and *Z. tyleri* are recovered, albeit with a low decay index of 1. These last two clades appear in a polytomy with the other three species of *Zenopsis*.

When only the extant taxa are included in the analyzed data set, three EPTs are recovered (Fig. 3). The consensus tree supports the monophyly of *Zenopsis*, even though the relationships among the various taxa are less well resolved than in the analysis with the fossils, whereas *Zeus* still appears as paraphyletic. Within *Zenopsis*, *Z. sp.* and *Z. oblongus* appear in a polytomy with the *Z. nebulosus* + *Z. conchifer* clade. The support for the monophyly of the Zeidae is very high (decay index of 19), whereas that of the monophyly of

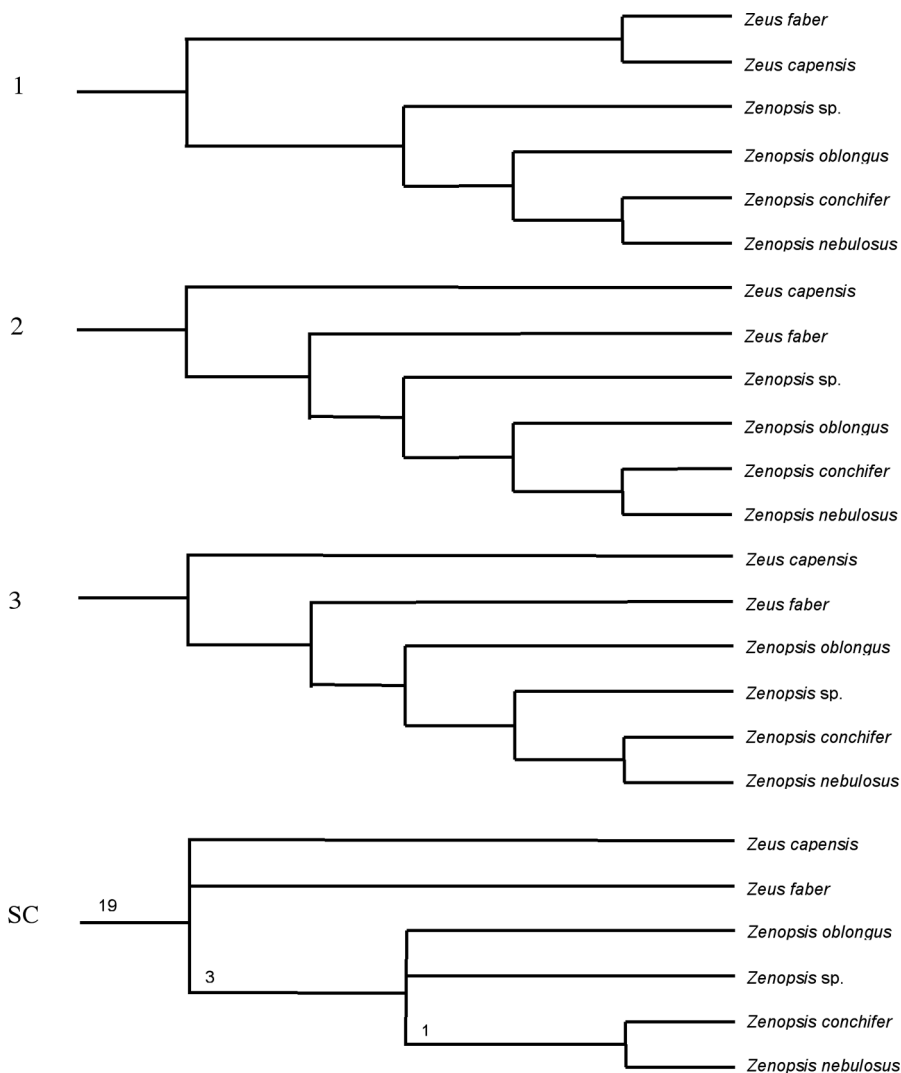


Figure 3. - EPTs 1 through 3 ($L = 0.70$, $CI = 0.92$, $RI = 0.95$) and the strict consensus tree (SC) produced by the analysis of the data set of six extant species of Zeidae plus two outgroups only. Decay index is indicated above the tree branches of the SC tree. [EPTs 1-3 ($L = 0.70$, $CI = 0.92$, $RI = 0.95$) et arbre de consensus strict (SC) produits par l'analyse du jeu de données de six espèces actuelles de Zeidae et seulement deux extra-groupes. L'indice de Bremer est indiqué sur les branches de l'arbre SC.]

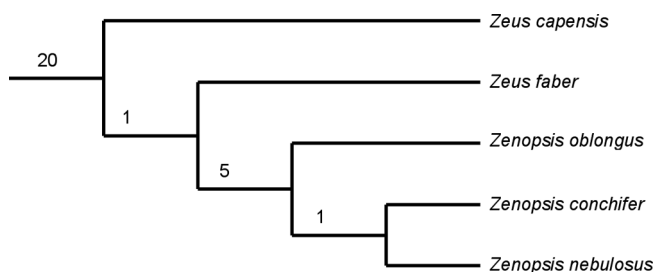


Figure 4. - Most parsimonious tree ($L = 0.67$, $CI = 0.97$, $RI = 0.98$), produced after analysis of the data set of extant species of Zeidae plus two outgroups, when *Zenopsis* sp. is not included. Decay index is indicated above the tree branches. [Arbre le plus parcimonieux ($L = 0.67$, $CI = 0.97$, $RI = 0.98$) produit de l'analyse du jeu de données des espèces actuelles de Zeidae avec deux extragroupes, à l'exclusion de *Zenopsis* sp. L'indice de Bremer est indiqué sur les branches de l'arbre.]

Zenopsis is relatively good (decay index of 3, which corresponds to slightly more than 4% of the tree length).

Exclusion from the analysis of *Zenopsis* sp., with many unknown internal characters, recovers one EPTs (Fig. 4). In this case, the monophyly of the extant *Zeus* is again not recovered because *Zeus capensis* appears as the most basal zeid, whereas *Zeus faber* is the sister group to *Zenopsis*.

DISCUSSION

Phylogenetic analysis

One result of this work is that the inclusion of even very incomplete fossil materials does not prevent the inference of a phylogeny when a phylogenetic signal is present in the data set (a conclusion already supported by Santini and Tyler, 2003, 2004; Tyler and Santini, 2005). The monophyly of the Zeidae and of *Zenopsis* are recovered in all analyses with and without the inclusion of the fossils. Also, the relationships among the extant species of *Zenopsis* do not change

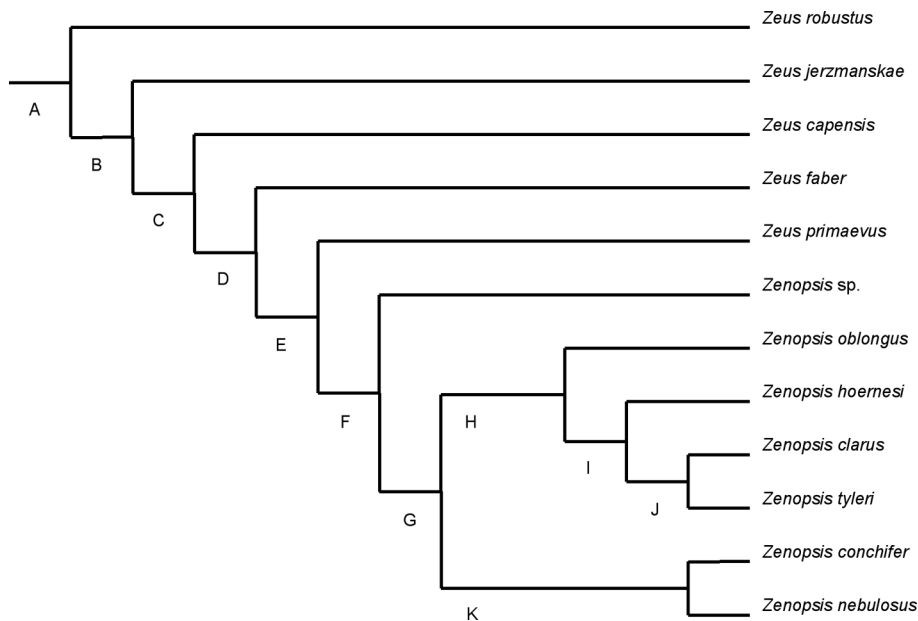


Figure 5. - EPT 2 from figure 1 selected for the study of character evolution. Letters below branches correspond to letters in the character evolution section in appendix II. [EPT 2 de la figure 1 utilisé pour l'étude de l'évolution des caractères. Les lettres au-dessous des branches correspondent aux lettres dans la partie de l'appendice II qui traite de l'évolution des caractères.]

when the fossils are included in the analysis. The situation is different for *Zeus*, in which the monophyly of the group is not recovered in the analyses when the fossils are included. When only the extant species of *Zeus* are analyzed, the monophyly of the group is supported, but with a weak decay index (see following section on classification for further comments).

A second result is that according to the topology of the trees recovered, the radiation of the Zeidae is likely much older than previously thought. The fact that the three Oligocene species of *Zenopsis* appear to be very derived taxa within the *Zenopsis* clade indicates that the radiation of the various lineages in this group had already occurred by 35 Mya.

Classification

The two extant species of *Zeus* appear to form a monophyletic group in only one of the trees produced by the analyses of extant species alone (Fig. 3). A similar result is produced when the fossils are included in the analyses. The present results do not allow us to recover a monophyletic *Zeus*, a genus that was first created in 1758 by Linnaeus and has been recognized as valid ever since. Because in one of the analyses the two extant species appear to be each other's sister groups, and because the decay index for the relationships among most species of *Zeus* is always very weak, we prefer to retain the current generic classification. We thus continue to recognize the generic name *Zeus* as a valid taxon pending further work, which either may reveal support for the existence of a clade formed by all fossil and extant *Zeus* or may find increased support for the paraphyly of this group and, hence, the recognition of additional generic categories.

Paleobiogeography of the Zeidae

The only putative Eocene zeid was originally described from the Tertiary of Georgia as *Platax* (?) *colchicus* by Simonovich *et al.* (1875); however, Bogatshov (1933) concluded that this fish instead belongs to *Zeus* and he noted that the marls in Georgia in which this species was found are of Eocene age. The two type specimens cannot be located. Danilchenko (1960) mentioned the opinion of Bogatshov and hypothesized that the Georgian fish is in fact a *Zenopsis*. Baciú *et al.* (2005) considered this taxon to be a *Zenopsis nomen dubium*; however, on the basis of the phylogeny presented herein and on the other known fossil zeids, we think it is likely that the zeids first appeared in the Eocene. Five of the six additional fossil zeid species are in fact distributed in the Oligocene of the Central Paratethys (Slovenia, Poland, Romania) and Eastern Paratethys (Caucasus), with several of these species from the Rupelian, the oldest part of the Oligocene (approximately 30-36 Mya). *Zeus primaevus*, the single species from the late Miocene (5-11 Mya), is distributed only in the Mediterranean basin (Algeria, Italy, Spain). The extant zeid species occur in the Atlantic, Indian, and Pacific Oceans and are mostly distributed throughout the coastal waters of the continents, with only *Zeus faber* occurring in the Mediterranean and Black Seas.

Most of the Oligocene zeids are geographically distributed in a single location, probably corresponding to isolated basins. For example, *Zeus robustus* is known only from Slovenia; *Zeus jermanskae* from Poland; *Zenopsis hoernesii* from Slovenia; and *Zenopsis tyleri* from Romania. The only exception is *Zenopsis clarus*, which is widely distributed throughout the Paratethys, with fossil specimens known from Russia, Romania, and Poland. The Upper Miocene

Zeus primaevus is known from deposits in Italy, Oran (Algeria), and Spain (Baciu *et al.*, 2005), and its more expansive distribution might indicate that the ichthyofauna had by then been homogenized across the Mediterranean region. The recent species *Zeus faber* was described by Bassani (1905) from the Pleistocene deposits of Taranto (southern Italy). We have not examined materials from Taranto, but it is possible that these Pleistocene specimens are referable to the extant *Zeus faber*, which likely belongs to a phylogenetically very ancient lineage. No fossils are known for any of the other extant species of Zeidae.

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Appendix I

Character list

The character list is modified and reduced from Tyler *et al.* (2003) to compensate for the different taxonomic sampling. Two new characters, numbers 34 and 35 in our list, and some additional character states have been added. Characters are arranged according to body region.

Cranial

1. Basisphenoid: present (0); absent (1).
2. Frontal, supraocular serrations: present (0); absent (1).
3. Otolith, shape: moderate to large size, rounded or slightly to deeply indented on one or both sides, or oblong with humps (0); tiny, trilobed (bow-tie shaped) (1).
4. Lachrymal, size/depth: large, deep, height about one to four times in the length (0); moderate, height about five to seven times in the length (1); slender (2).
5. Infraorbitals, number of (well-developed elements exclusive of the lachrymal, dermosphenotic, and of variable rudiments): five to eight (0); four or less (1); nine or more (2).
6. Dermosphenotic: a distinctly separate ossification from the sphenotic, sometimes relatively free from the skull (0); fused or highly consolidated with the sphenotic (1).
7. Premaxilla, alveolar process: ventrally rounded or moderately indented to form a pair of blunt lobes (0); deeply bifurcated ventrally (1).
8. Symplectic, ventral flange: present (0); absent (1).
9. Dentary, cartilages (on lateral surface of dentary): two cartilages of moderate size, lying sequentially one behind the other, of about the same size or the first only slightly shorter than the second (0); two cartilages of moderate size, each attached anteriorly to the dentary and lying sequentially one behind the other, the first shorter than the second (1); absent or unconsolidated (2).
10. Dentary, serrations on the lower border of: multiple serrations behind the symphysis (0); a single barb near the symphysis (1); none (2).
11. Ceratohyal, notches on the lower border of: prominent notches for the heads of some of the branchiostegal rays in the anterior group (0); no prominent notches (1).
12. Ceratohyal-epihyal articulation: exclusively through cartilage (0); with bony interdigitated articulations, at least in specimens of large size (1).
13. Epihyal, depth of the anterior end of: equal, or about equal, to the depth of the adjacent part of the ceratohyal (0); distinctly less deep than the adjacent part of the ceratohyal (1).

Vertebral column and median fins

14. First vertebra in the caudal peduncle with a modified neural or haemal spine: third preural centrum, PU3 (0); second preural centrum, PU2 (1).
15. First vertebra, dorsal extension of the neural spine when the neural arch and spine are plastered to the skull: the neural spine with a long dorsal portion free from the skull beyond the curvature of the supraoccipital and the exoccipitals (0); the neural spine extending only slightly, or not at all, dorsally above its attachment to the skull (1).
16. Baudelot's ligament, placement of the proximal attachment of: to the first vertebra (0); to the exoccipital (1).
17. Ossified ribs: present only on the last few abdominal vertebrae (0); present on most of the abdominal vertebrae behind the fourth (1).

18. Ossified epineurals: present on most of the abdominal vertebrae or their ribs (0); present on only a few of the anterior abdominal vertebrae (1).
19. Epurals, number: two (0); one (1).
20. PU2, extra-caudal ossicle in the haemal spine of: absent (0); present, in at least some specimens (1).
21. Vacant interneural spaces, number of groups of (when two or more spaces are vacant): two (0); three or four (1).
22. Dorsal-fin pterygiophores, number of anterior to the neural spine of the fourth abdominal vertebra: two or three (0); four (1).
23. Supraneurals, number of: one (0); none (1).
24. Second anal-fin spine, length of: very short, much less than one-half the length of the first spine (0); moderate to long, more than one-half the length of the first spine to almost as long (1); longer than first spine (2).
25. Anal-fin pterygiophores, number of anterior to the haemal spine of the third caudal vertebra: five or six (0); seven (1); eight or nine (2).

Paired-fin girdles

26. Supracleithrum, ventral end of: simple (0); deeply bifurcate (1).
27. Cleithrum, posterior edge: without a posterodorsal prong above the articulation with the postcleithrum (0); cleithral process present as a prong above the articulation with the postcleithrum (1).
28. Extrascapulars: one long bone, sometimes forming an open tube, more or less closely held to the skull (0); two tubular bones, not closely held to the skull, except at large specimen sizes (1).
29. Pelvic-fin spines: present (0); absent (1).
30. Pelvic-fin rays, anterolateral processes of the medial (lower) surfaces of: absent (0); present as prongs from the medial surfaces of the ray bases (1).
31. Pelvis, posterior process of behind pelvic-fin base: short to moderate in length, and in shape a moderate to broad plate or flattened shaft (0); long and rod-like, moderately separated from its opposite member along the midline (1).

Scales

32. Scales, on most of the body: moderate to small, spiny "ctenoid" (spinoid) (0); moderate to small, cycloid (1); greatly elongate vertically (2); absent (excluding enlarged buckler-like scales), or only in the lateral line (3).
33. Scales, buckler-like (greatly enlarged midline scales): absent (0); present midabdominally and from the far rear end of the spinous dorsal fin (from no further forward than the last dorsal spine) to the end of the soft dorsal-fin base (1); present midabdominally and from the posterior region of the spinous dorsal fin (from under the last two or three dorsal spines) to the end of the soft dorsal-fin base (2); present midabdominally and from the front to middle regions of the spinous dorsal fin to the end of the soft dorsal-fin base (3).
34. Buckler-like scales, in addition to major spiny process, accessory spiny process: present (0); absent (1); not applicable, when buckler-like scales absent (-).
35. Buckler-like scales, radiating striations: present (0); absent (1); not applicable, when buckler-like scales absent (-).
36. Scales, along the bases of the dorsal- and anal-fin rays: absent along the bases of the rays, but spiny processes present on the scales alongside the lateral expansions of the distal ends of the dorsal- and anal-fin pterygiophores (0); absent from along

the bases of the rays, and the scales nearby without spiny projections and not extending beyond the lateral expansions of the distal ends of the dorsal- and anal-fin pterygiophores (1).

Meristic data

37. Vertebrae, total number of: 27 or 28 (0); 29 to 32 (1); 33 to 36 (2); 37 or 38 (3).
38. Abdominal vertebrae, number of: ten or 11 (0); 13 (1); 14 (2); 15 (3).
39. Vertebrae, number of in the caudal peduncle (posterior to the last vertebra whose neural or haemal spine supports a pterygiophore): five (0); three or four (1); eight (2).
40. Procurrent caudal-fin rays, number of (including the number in both the dorsal and ventral sides, if different): two or three (0); one (1).
41. Dorsal-fin spines, number of: six or seven (0); eight or nine (1); ten or more (2).
42. Vacant interneural spaces, total number of below the spiny and anterior part of the soft dorsal-fin base, posterior to the first dorsal-fin pterygiophore: two (0); four (1); five (2).
43. Anal-fin spines, number of: two (0); three (1); four (2).
44. Pectoral-fin rays, number of: 15 or 16 (0); 13 or 14 (1); 11 or 12 (2).
45. Pelvic-fin elements, total number of: seven (0); eight (1); six (2).

Appendix II

Character evolution

The difficulties produced by the use of consensus trees in the study of character evolution are well known (e.g., see Maddison, 1989). In order to investigate the evolution of the various characters, we selected one of the two EPTs obtained from the analysis of the full data set. We selected EPT number 2 (Fig. 1) because in this cladogram *Zeus robustus*, one of the oldest fossil zeids, is represented as being a stem zeid, and we judge this interpretation of the data to be more reliable, on the basis of the stratigraphic criterion, than any of the others.

The selected tree is shown in figure 5. All internodes have been labeled with letters in order to more easily list the character states that support the various clades. The character optimization was performed using DELTRAN.

A: 4(0→1) lachrymal moderate, height about five to seven times in the length, convergent in *Xenolepidichthys*; 13(0→1) anterior end of epihyal distinctly less deep than adjacent part of ceratohyal, convergent in *Xenolepidichthys*; 17(0→1) ossified ribs present on most abdominal vertebrae behind fourth; 19(0→1) one epural; 21(0→1) three or four groups of vacant interneural spaces; 22(0→1) four dorsal-fin pterygiophores anterior to neural spine of fourth abdominal vertebra; 23(0→1) no supraneural; 24(0→2) second anal-fin spine longer than first spine; 27(0→1) cleithral process present as prong above articulation with postcleithrum; 40(0→1) one procurrent caudal-fin ray, convergent in *Xenolepidichthys*; 41(0→1) eight or nine dorsal-fin spines; 42(0→1) four vacant interneural spaces, convergent in *Xenolepidichthys* and in *Zenopsis hoernesii*; 43(0→2) four anal-fin spines; 44(0→1) 13 or 14 pectoral-fin rays, convergent in *Xenolepidichthys*.

B: 7(0→1) alveolar process of premaxilla deeply bifurcated ventrally; 10(0→1), serration on lower border of dentary consists of a single barb near the symphysis; 15(0→1) first neural spine extends only slightly, or not at all, dorsally above its attachment to skull; 26(0→1) ventral end of supracleithrum deeply bifurcate;

31(0→1) posterior process of pelvis behind pelvic-fin base long and rod-like, moderately separated from its opposite member along midline; 32(0→1) moderate to small cycloid scales; 33(0→1) buckler-like scales present midabdominally and from far rear end of spinous dorsal fin to end of soft dorsal-fin base; 36(0→1) scales absent from along bases of rays, and scales nearby without spiny projections and not extending beyond lateral expansions of distal ends of dorsal- and anal-fin pterygiophores; 37(0→1) 29 to 32 vertebrae; 42(1→2) five vacant interneural spaces.

C: 1(0→1) basisphenoid absent; 2(0→1) supraocular serrations of frontal absent; 3(0→1) tiny, trilobed otolith; 6(0→1) dermosphenotic fused or highly consolidated with the sphenotic; 8(0→1) ventral flange of symplectic absent; 9(0→1) two cartilages of moderate size, each attached anteriorly to dentary and lying sequentially one behind the other, the first shorter than second; 16(0→1) Baudelot's ligament attached to exoccipital; 18(0→1) ossified epineurals present on only a few of anterior abdominal vertebrae; 28(0→1) extrascapulars two tubular bones, not closely held to skull, except at large specimen sizes; 30(0→1) anterolateral processes of medial surfaces of pelvic-fin rays present as prongs; 38(0→2) 14 abdominal vertebrae.

D: 12(0→1) ceratohyal-epihyal articulation with bony interdigitated articulations, at least in specimens of large size; 20(0→1) extra-caudal ossicle in haemal spine of PU2 present.

E: 14(0→1) PU2 is first vertebra in caudal peduncle with a modified neural or haemal spine; 24(2→1) second anal-fin spine moderate to long, more than one-half length of first spine to almost as long, convergent in *Zeus jermanskiae*; 39(0→1) three or four vertebrae in caudal peduncle, convergent in *Zeus robustus*.

F: 4(1→2) lachrymal slender; 29(0→1) pelvic-fin spines absent; 33(1→3) buckler-like scales present midabdominally and from front to middle regions of spinous dorsal fin to end of soft dorsal-fin base; 34(0→1) accessory spiny process of buckler-like scales absent; 35(1→0) radiating striations of buckler-like scales present; 43(2→1) three anal-fin spines; 44(1→2) 11 or 12 pectoral-fin rays.

G: 5(0→2) nine or more infraorbitals; 32(1→3) scales (excluding enlarged buckler-like scales) absent from most of body, or only lateral line scales present; 37(1→2) 33 to 36 vertebrae; 45(0→2) six pelvic-fin elements.

H: 11(0→1) no prominent notches on lower border of ceratohyal, convergent in *Xenolepidichthys* and *Zeus jermanskiae*; 39(1→0) five vertebrae in caudal peduncle.

I: 33(3→2) buckler-like scales present midabdominally and from posterior region of spinous dorsal fin to end of soft dorsal-fin base.

J: 25(0→2) eight or nine anal-fin pterygiophores anterior to haemal spine of third caudal vertebra, convergent in *Zeus jermanskiae*; 38(2→3) 15 abdominal vertebrae, convergent in *Zeus jermanskiae*, *Zeus primaevus*, and *Zenopsis nebulosus*.

K: 10(1→2) no serrations on lower border of dentary, convergent in *Xenolepidichthys*.

Autoapomorphic features are not informative with regard to the phylogenetic relationships of the species analyzed, but we include them here for diagnostic purposes: for *Zeus robustus* 38(0→1), 39(0→1); for *Zeus jermanskiae* 11(0→1), 24(2→1), 25(0→2), 38(0→3); for *Zeus capensis* 41(1→2); for *Zeus faber* 41(1→2), 45(0→1); for *Zeus primaevus* 25(0→1), 38(2→3); for *Zenopsis* sp. 20(1→0), 41(1→0); for *Zenopsis oblongus* 2(1→0), 22(1→0); for *Zenopsis hoernesii* 21(1→0), 42(2→1); for *Zenopsis tyleri*, 41(1→2); for *Zenopsis conchifer* 18(1→0); for *Zenopsis nebulosus* 25(0→1), 38(2→3).