

5. The Pesciara-Monte Postale Fossil-Lagerstätte: 2. Fishes and other vertebrates

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INTRODUCTION

Fossil fishes are by far the most celebrated and well studied component of the Bolca biota. The fish fauna of Bolca is certainly one of the most important and best known ichthyofaunistic fossil assemblages. The fish material is outstanding in terms of preservation quality and number of specimens, making this extraordinary assemblage the most diverse of all the Cenozoic marine ichthyofaunas. Because of the beauty and scientific relevance of these fossils, one of the most spectacular species from Bolca, *Ceratoichthys pinnatiformis*, has been used for many years as the symbol of the Società Paleontologica Italiana (Fig. 1).

Because of their exquisite preservation and attractive appearance, the fossil fishes from Bolca have been coveted for more than four centuries by aristocrats and noblemen to enrich and enhance their collections of natural history objects.

The existence of excellently preserved “petrified” fishes in the limestone of Bolca was reported for the first time in 1550 by the famous botanist and physician Pietro Andrea Mattioli in the third edition of the translation of his “Dioscorides De Materia Medicinale”. Mattioli examined some fossil fishes from Bolca belonging to the collection of Diego Hurtado de Mendoza, the ambassador of Emperor Charles V to the Venezia Republic from 1539 to 1547, and was impressed by their superb preservation, with the complete transformation into stone of all of their anatomical details.

By 1571 Francesco Calceolari, a renowned apothecary from Verona, had amassed a vast collection of natural history objects, including several fishes from Bolca, in the so-called “Musaeum Calceolarium”. In the 1584 catalogue of the contents of the Calceolari museum by the physician Giovan Battista Olivi, the fossils, including those from Bolca, were regarded as *lusus naturae*. In 1622 the physicians Benedetto Ceruti and Andrea Chiocco from Verona figured for the first time a fish from Bolca in the descriptive catalogue “Musaeum Francisci Calceolari Iunioris Veronensis”, which was gracefully embellished with illustrations, representing a philosophical excursus occasioned by the objects of

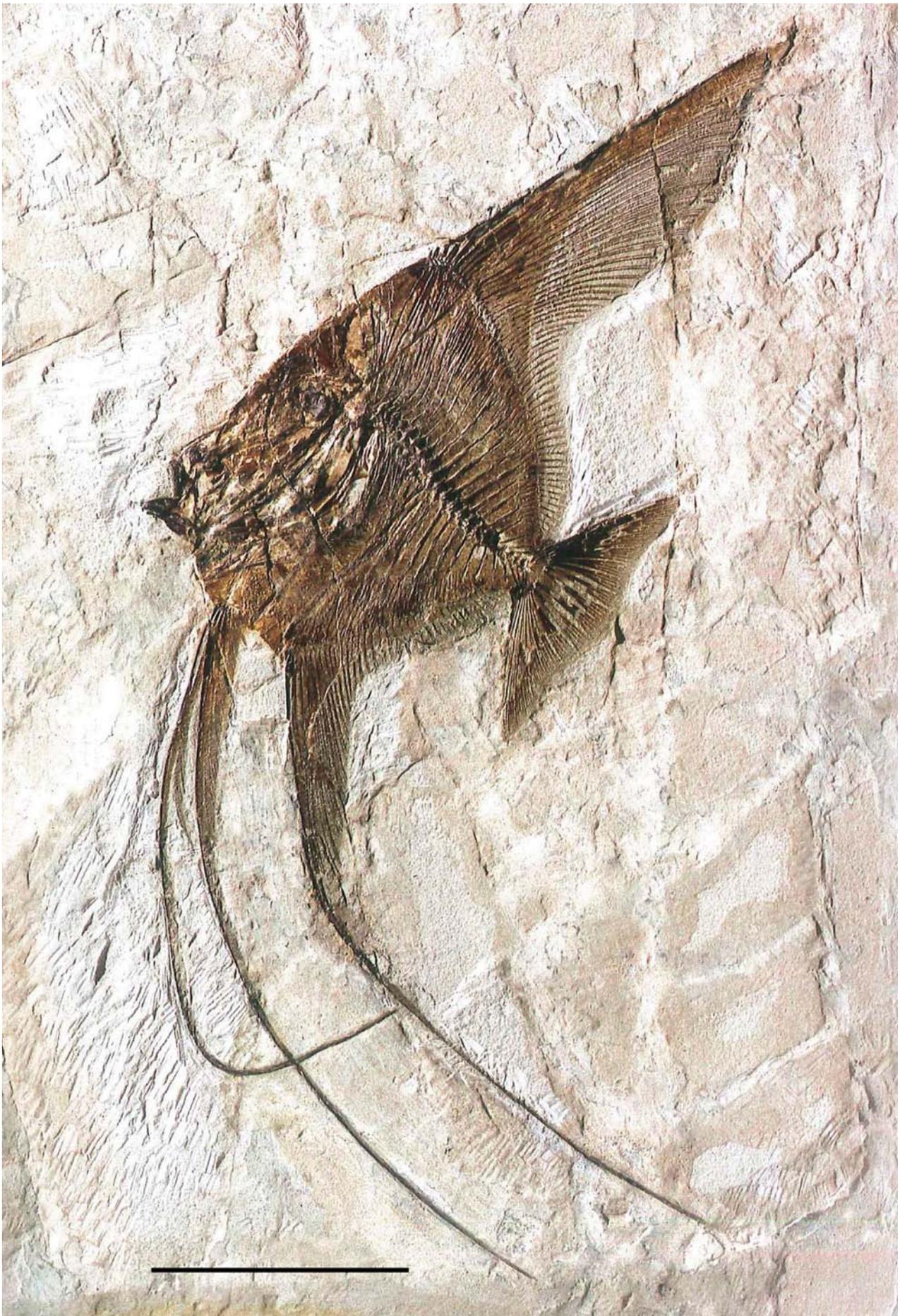


FIG. 1 - *Ceratoichthys pinnatiformis* (Blainville 1818), MCSNV T.950, left lateral view; scale bar 100 mm.

the museum in which the authors provided an elevated status to the museum and its owners (Findlen, 1994). Meanwhile, the bishop and canon lawyer Simone Majoli in his encyclopaedic “*Dies Caniculares*” (1597) considered the fishes from Bolca as remains of marine organisms which had been carried to the mountains through the activity of ancient volcanoes. On the other hand, the naturalist Ulisse Aldrovandi (1648) interpreted the fish skeletons from Bolca as Islebian fish-stones, following the theory elaborated one century earlier by Georgius Agricola. In 1656, the Count Lodovico Moscardo figured some fossil fishes from Bolca in his “*Note, overo, Memorie del Museo di Lodovico Moscardo*”, including what he interpreted as a gilthead seabream (*Orada*) and an eel (*Anguilla*).

The fishes of Bolca and their origins were extensively discussed during the 18th century by several prominent naturalists, including Johann Jakob Scheuchzer, Antonio Vallisneri, Ferdinando Marsili, Anton Lazzaro Moro, Scipione Maffei, Déodat de Dolomieu, and Giovanni Arduino (Sorbini, 1972). Towards the end of the century (1793-1795), a cogent debate about the origin and significance of these fossils involved three abbots, Domenico Testa, Alberto Fortis, and Giovanni Serafino Volta (Gaudant, 1999). During the first half of the 18th century, several large collections of Bolca fishes were assembled in Verona by noblemen such as Vincenzo Bozza, Alessandro Buri, Ottavio Canossa, Giulio Moreni, Ignazio Ronconi, Sebastiano Rotari, and Giovanni Battista Gazola. Most of these collections were purchased by count Gazola and eventually flowed into his own museum, which, at the end of 1791, contained more than a thousand well-preserved fossil fishes from Bolca. One of the abbots involved in the controversy, Giovanni Serafino Volta, who was the brother of the well-known physicist Alessandro Volta, published a short first catalogue of Bolca fishes, based on the large collection of Vincenzo Bozza (Volta, 1789); Volta (1789) assigned most of the fossil fishes to extant species, many of which are distributed in tropical seas. However, in order to properly document the extent of these collections, in 1789 Volta started preparing a beautifully illustrated comprehensive catalogue of the fossil fishes from Bolca, this being the famous “*Ittiolitologia Veronese del Museo Bozziano ora annesso a quello del conte Giovambattista Gazola e di altri gabinetti fossili Veronesi*”, published between 1796 and 1809, and produced by the printing house of the count Bartolomeo Giuliani. The “*Ittiolitologia Veronese*” constitutes the earliest treatise on paleoichthyology and included the description of more than 120 species.

In May 1797, about 600 specimens of the Gazola collection of fossils from Bolca were confiscated by the revolutionary armies of Napoleon that occupied Verona, transported to Paris, and deposited in the *Muséum National d’Histoire Naturelle* (e.g., Eastman, 1904; Frigo & Sorbini 1997; Gaudant, 2011). Henry Ducrotay De Blainville (1818) used this collection for his account of fossil fishes which appeared in the “*Nouveau dictionnaire d’histoire naturelle*”. However, the first critical analysis of the collection was that of the Swiss naturalist Louis Agassiz, a founder of comparative zoology, who reviewed (Agassiz, 1835) the identifications presented by Volta (1796-1809) in the “*Ittiolitologia Veronese*”, and later (Agassiz, 1844) described the fossils in great detail in his monumental “*Recherches sur les Poissons Fossiles*” (1833-1844).

In the years following the confiscation of part of his collection, Giovanni Battista Gazola purchased the collection of Ignazio Ronconi and, together with the naturalist Tommaso Antonio Catullo, organized new excavations in the productive sites of Bolca in order to amass a new collection of fossil fishes, which is now part of the vast collection housed in the *Museo Civico di Storia Naturale*, Verona.

Modern paleoichthyology began with the publication of the “*Recherches sur les Poissons Fossiles*” (Agassiz, 1833-1844), of which Bolca fishes composed a considerable part. After the publication of this transformative work, numerous authors have contributed

to expand our knowledge about the diversity of the Bolca fish assemblage, including Johann Jakob Heckel, Rudolf Kner, Abramo Massalongo, Wladislaw Szajnocha, Paolo Lioy, Dragutin Gorjanović-Kramberger, Otto Jaekel, Achille de Zigno, Franz Steindachner, Arthur Smith Woodward, Francesco Bassani, Charles R. Eastman, Geremia D'Erasmus, and, more recently, Jacques Blot at the Paris museum and Lorenzo Sorbini at the Verona museum, as well as the authors of this chapter.

Overall, the excellent preservation of the fully articulated fish skeletal remains of Bolca has traditionally favoured detailed morphological comparisons with extant taxa. As a consequence, these fossils contributed significantly to the development of modern fish systematics, especially to that of teleosts. Therefore, the fossil fishes from Bolca have exerted a considerable influence in the fields of paleo- and neoichthyology.

THE BOLCA FISH ASSEMBLAGE: TAXONOMIC DIVERSITY

Blot (1969) estimated that about 100,000 fish specimens have been extracted from the Pesciara and Monte Postale sites at Bolca during approximately four centuries of extensive exploitation. Considering the reduced volume of available fossiliferous deposits, it is evident that these two productive sites are extremely rich in terms of numbers of specimens. Such a huge number of specimens available for study, now disseminated in many museums, research institutions, and private collections around the world, has allowed for the description of an impressive number of taxa, making Bolca the most diverse fossil marine fish assemblage known to date.

As mentioned above, the first list of Bolca fishes was provided by Volta (1789), who recognized slightly less than 100 species within the material of the collection of Vincenzo Bozza. A few years later, based on investigations on the large collection of the Count Giovanni Battista Gazola, he (Volta, 1796) recognized 123 species, most of which were illustrated in 76 magnificent plates. In his magnum opus “Recherches sur les Poissons Fossiles”, Agassiz (1833-1844) recognized 127 species of fishes belonging to 55 genera. Subsequently, updated catalogues of Bolca fishes were provided by de Zigno (1874) and D'Erasmus (1922). A resurgence of studies of Bolca fishes started in the 1960s, mostly due to the efforts of Jacques Blot, and culminated with the publication of a new catalogue (Blot, 1980), in which he listed 208 nominal species belonging to 117 genera included in not less than 72 families. Since the publication of Blot's (1980) catalogue, many new taxa have been described and the taxonomic status of many others has been corrected. When Lorenzo Sorbini, a former doctoral student of Blot in Paris, became the director of the Verona museum, he encouraged and expedited the study of the Verona collection of Bolca fishes by a broad array of international scientists. Subsequent directors of the Verona museum, Alessandra Aspes and, presently, Giuseppe Minciotti, have wisely continued that fine tradition.

In order to properly define the full extent of the known ichthyofaunal diversity, Bannikov (in press) recently assembled a new catalogue of Bolca actinopterygians, listing 219 species in 191 genera. The list presented herein in Tab. 1 comprises 238 taxa and represents a modified version of that by Bannikov (in press), with the inclusion of cartilaginous fishes plus a few insertions and deletions within the teleostean fishes.

The compositional differences between the fish assemblages of the Pesciara and Monte Postale are difficult to define. However, the overall structure of the two assemblages appears to be rather similar (Sorbini, 1972) even if the Monte Postale site may have a somewhat larger component of off-shore and pelagic taxa (Bannikov & Tyler, 1999; Bannikov & Zorzin, 2004).

Order	Family	Taxon
Carcharhiniformes	Carcharhinidae	<i>Eogaleus bolcensis</i> Cappetta, 1975 <i>Physogaleus cuvieri</i> (Agassiz, 1835) <i>Alopiopsis plejodon</i> Lioy, 1865
Orectolobiiformes	Hemiscylliidae	<i>Mesiteia emiliae</i> Kramberger, 1885
Rajiformes	Rhinobatidae	<i>Rhinobatus dezinnoi</i> Heckel, 1853 <i>Rhinobatus primaevus</i> de Zigno, 1874
Torpediniformes	Narcinidae	<i>Titanonarke molini</i> (Jaekel, 1894) n. gen. et n. sp.
Myliobatiformes	Dasyatidae	" <i>Dasyatis</i> " <i>muricata</i> (Volta, 1796) "Dasyatis" <i>dezinnoi</i> Molin, 1861
	Myliobatidae	<i>Promyliobatis gazolae</i> de Zigno, 1885
	Urolophidae	" <i>Urolophus</i> " <i>crassicaudatus</i> (Blainville, 1818) "Urolophus" sp.
	Plathyrrhinidae	<i>Platyrrhina bolcensis</i> Heckel, 1851 <i>Platyrrhina gigantea</i> (Blainville, 1818) <i>Platyrrhina egertoni</i> de Zigno, 1878
Pycnodontiformes	Pycnodontidae	<i>Pycnodus apodus</i> (Volta, 1796) <i>Nursallia veronae</i> Blot, 1987 <i>Abdopalistum thyrus</i> Poyato-Ariza & Wenz, 2002 <i>Palaeopalistum orbiculatum</i> Blainville, 1818
Crossognathiformes	Pachyrhizodontidae	<i>Platinx macropterus</i> (Blainville, 1818)
Osteoglossiformes	Foreyichthyidae	<i>Foreyichthys bolcensis</i> Taverne, 1979
	Arapaimidae	<i>Thrissopterus catullii</i> Heckel, 1856
	Osteoglossiformes incertae sedis	<i>Monopteros gigas</i> Volta, 1796
Anguilliformes	Anguilloididae	<i>Anguilloides branchiostegalis</i> (Eastman, 1905) <i>Veronanguilla ruffoi</i> Blot, 1978
	Milananguillidae	<i>Milananguilla lehmani</i> Blot, 1978
	Anguillidae	<i>Eoanguilla leptoptera</i> (Agassiz, 1835)
	Paranguillidae	<i>Paranguilla tigrina</i> (Agassiz, 1839) <i>Dalpiaziella brevicauda</i> Cadrobbi, 1962
	Congridae	<i>Voltaconger latispinus</i> (Agassiz, 1839) <i>Bolcyrus formosissimus</i> (Eastman, 1905) <i>Bolcyrus bajai</i> Blot, 1978 <i>Paracongruides heckeli</i> Blot, 1978
	Chlopsidae	<i>Whitapodus breviculus</i> (Agassiz, 1835)
	Proteomyridae	<i>Proteomyrus ventralis</i> (Agassiz, 1839)
	Ophichthyidae	<i>Goslinophis acuticaudus</i> (Agassiz, 1835)
	Patavichthyidae	<i>Patavichthys bolcensis</i> (Bassani, 1897)
	Anguilliformes incertae sedis	<i>Bolcanguilla brachycephala</i> Blot, 1980 <i>Gazolapodus homopterus</i> Blot, 1980
Clupeiformes	Clupeidae	<i>Bolcaichthys catopygopterus</i> (Woodward, 1901) <i>Trollichthys bolcensis</i> Marramà & Carnevale, 2014
	Engraulidae	n. gen. et n. sp.
Anotophysi	Anotophysi incertae sedis	<i>Coelogaster leptostea</i> (Eastman, 1905) "Chanos" <i>forcipatus</i> (Heckel, 1854)
Otophysi	Chanoididae	<i>Chanoides macropoma</i> (Agassiz, 1844)
Aulopiformes	Paralepididae	<i>Holosteus esocinus</i> Agassiz, 1839
Lampridiformes	Veliferidae	<i>Velifer</i> n. sp. <i>Veronavelifer sorbinii</i> Bannikov, 1990

TAB. 1 - A synoptic list of the Eocene fishes of Bolca.

	Bajaichthyidae	<i>Bajaichthys elegans</i> Sorbini, 1983
	Lampridiformes incertae sedis	" <i>Pegasus</i> " <i>volans</i> Volta, 1796
Ophidiiformes	Ophidiidae	" <i>Ophidium</i> " <i>voltianum</i> Massalongo, 1859
Lophiiformes	Lophiidae	<i>Caruso brachysomus</i> (Agassiz, 1839) <i>Sharfia mirabilis</i> Pietsch & Carnevale, 2011
	Brachionichthyidae	<i>Histionotophorus bassanii</i> (de Zigno, 1887) <i>Orrichthys longimanus</i> Carnevale & Pietsch, 2010
	Antennariidae	<i>Eophryne barbutii</i> Carnevale & Pietsch, 2009
	Ogcocephalidae	<i>Tarkus squirei</i> Carnevale & Pietsch, 2011
Atheriniformes	Atherinidae	<i>Atherina</i> (?) <i>macrocephala</i> Woodward, 1901
	Rhamphognathidae	<i>Rhamphognathus paralepoides</i> Agassiz, 1844
	Mesogasteridae	<i>Latellagnathus teruzzii</i> Bannikov, 2008 <i>Mesogaster sphyraenoides</i> Agassiz, 1844
Beloniformes	Exocoetidae	<i>Rhamphexocoetus volans</i> Bannikov, Parin & Pinna, 1985 " <i>Engraulis</i> " <i>evolans</i> (Blainville, 1818)
	Hemiramphidae	<i>Hemiramphus edwardsi</i> Bassani, 1876
Beryciformes	Holocentridae	<i>Berybolcensis leptacanthus</i> (Agassiz, 1838) <i>Eoholocentrum macrocephalum</i> (Blainville, 1818) <i>Tenuicentrum lanceolatum</i> (Bassani, 1876)
Syngnathiformes	Rhamphosidae	<i>Ramphosus rastrum</i> (Volta, 1796) <i>Ramphosus biserratus</i> Bassani, 1876
	Urosphenidae	<i>Urosphen dubius</i> (Blainville, 1818)
	Aulostomidae	<i>Eoaulostomus bolcensis</i> (Blainville, 1818) <i>Eoaulostomus gracilis</i> Blot, 1980 <i>Synhypuralis jurgenseni</i> Blot, 1980 <i>Synhypuralis banisteri</i> Blot, 1980 <i>Jurgensenichthys elongatus</i> Blot, 1980 <i>Macroaulostomus veronensis</i> Blot, 1980 <i>Tyleria necopinata</i> N.N. Parin, 1993
	Parasynarcualidae	<i>Parasynarcualis longirostris</i> (Blainville, 1818)
	Fistularioididae	<i>Fistularioides veronensis</i> Blot, 1980 <i>Fistularioides phyllolepis</i> Blot, 1980 <i>Pseudosyngnathus opisthopterus</i> (Agassiz, 1833)
	Aulostomoidea incertae sedis	<i>Aulostomoides tyleri</i> Blot, 1980
	Aulorhamphidae	<i>Aulorhamphus bolcensis</i> (Steindachner, 1863) <i>Aulorhamphus capellinii</i> de Zigno, 1887 <i>Aulorhamphus chiarasorbinae</i> Bannikov & Tyler, 2011 <i>Veronarhamphus canossae</i> (Heckel, 1856) <i>Pesciarhamphus carnevalei</i> Bannikov & Tyler, 2011
	Paraeoliscidae	<i>Paraeoliscus robinetae</i> Blot, 1980
	Centriscidae	<i>Aeoliscoides longirostris</i> (Blainville, 1818) <i>Paramphisile weileri</i> Blot, 1980
	Syngnathidae	" <i>Syngnathus</i> " <i>heckeli</i> de Zigno, 1874 " <i>Syngnathus</i> " <i>bolcensis</i> de Zigno, 1887 <i>Prosolenostomus lessinii</i> Blot, 1980
	Solenostomidae (?)	<i>Solenorhynchus elegans</i> Heckel, 1854
	Syngnathoidei incertae sedis	<i>Calamostoma breviculum</i> (Blainville, 1818)
Dactylopteriformes	Pterygocephalidae	<i>Pterygocephalus paradoxus</i> Agassiz, 1839
Perciformes	Latidae	<i>Eolates gracilis</i> (Agassiz, 1833)
	Percichthyidae	<i>Cyclopoma gigas</i> Agassiz, 1833
	Acropomatidae	<i>Acropoma lepidotum</i> (Agassiz, 1836)

TAB. 1 - Continuation.

Priacanthidae	<i>Pristigenys substriatus</i> (Blainville, 1818)
Apogonidae	<i>Eosphaeramia pygopterus</i> (Agassiz, 1836) <i>Eoapogon fraseri</i> Bannikov, 2005 <i>Bolcapogon johnsoni</i> Bannikov, 2005 <i>Apogoniscus pauciradiatus</i> Bannikov, 2005 Apogonidae gen. et sp. indet.
Pomatomidae	<i>Carangopsis brevis</i> (Blainville, 1818) <i>Carangopsis dorsalis</i> Agassiz, 1844
Ductoridae	<i>Ductor vestenae</i> (Volta, 1796)
Carangidae	<i>Seriola prisca</i> (Agassiz, 1834) <i>Vomeropsis triurus</i> (Volta, 1796) <i>Ceratoichthys pinnatifomis</i> (Blainville, 1818) <i>Eastmanalepes primaevus</i> (Eastman, 1904) <i>Lichia veronensis</i> Bannikov & Sorbini in Bannikov, 1990 <i>Paratrachinotus tenuiceps</i> (Agassiz, 1834) <i>Trachicarax pleuronectiformis</i> (Blot, 1969)
Menidae	<i>Mene rhombea</i> (Volta, 1796) <i>Mene oblonga</i> (Agassiz, 1833)
Leiognathidae	<i>Eoleiognathus dorsalis</i> (Agassiz, 1838)
Exelliidae	<i>Exellia velifer</i> (Volta, 1796)
Lutjanidae	<i>Ottaviana mariae</i> Sorbini, 1983 <i>Ottaviana leptacanthus</i> (Agassiz, 1839) <i>Veranichthys ventralis</i> (Agassiz, 1839) <i>Goujetia crassispina</i> (Agassiz, 1839) <i>Lessinia horrenda</i> Bannikov & Zorzin, 2014 <i>Lessinia</i> sp.
Gerreidae (?)	<i>Aspesiperca ruffoi</i> Bannikov, 2008
Sparidae	<i>Sparnodus elongatus</i> Agassiz, 1839 <i>Sparnodus vulgaris</i> (Blainville, 1818) <i>Pseudosparnodus microstomus</i> (Agassiz, 1839) <i>Ellaserrata monksi</i> Day, 2003 <i>Abromasta microdon</i> (Agassiz, 1839) "Dentex" <i>microdon</i> Agassiz, 1839 "Dentex" <i>ventralis</i> Agassiz, 1839
Quasimullidae	<i>Quasimullus sorbinii</i> Bannikov, 1999
Monodactylidae	<i>Psettopsis subarcuatus</i> (Blainville, 1818) <i>Psettopsis latellai</i> Bannikov, 2005
Ephippidae	<i>Archaephippus asper</i> (Volta, 1796) <i>Eoplatax papilio</i> (Volta, 1796)
Scatophagidae	<i>Eoscatophagus frontalis</i> (Agassiz, 1839)
Pomacentridae	<i>Palaeopomacentrus orphae</i> Bellwood & Sorbini, 1996 <i>Lorenzichthys olihan</i> Bellwood, 1999 <i>Sorbinichromis francescoi</i> Bannikov & Bellwood, 2014
Carangodidae	<i>Carangodes bicornis</i> (Volta, 1796)
Eocottidae	<i>Eocottus veronensis</i> (Volta, 1796) <i>Bassanichthys pesciaraensis</i> (Bannikov, 2004)
Robertanniidae	<i>Robertannia sorbiniorum</i> Bannikov, 2011 <i>Hendrixella grandei</i> Bannikov & Carnevale, 2009
Percoidei incertae sedis	<i>Veronabrax schizurus</i> (Agassiz, 1836) <i>Voltamulloidis ceratorum</i> Bannikov, 2008 <i>Parapelates quindecimalis</i> (Agassiz, 1836)

TAB. 1 - Continuation.

	<i>Jimtylerius temnopterus</i> (Agassiz, 1836)
	<i>Pavarottia lonardonii</i> Bannikov & Zorzin, 2011
	<i>Montepostalia annamariae</i> Bannikov & Zorzin, 2004
	<i>Blotichthys coleanus</i> (Agassiz, 1838)
	<i>Pygaeus bolcanus</i> (Volta, 1796)
	<i>Pygaeus nobilis</i> Agassiz, 1838
	<i>Pygaeus nuchalis</i> Agassiz, 1838
	<i>Malacopygaeus oblongus</i> (Agassiz, 1838)
	<i>Gillidia antiqua</i> (Agassiz, 1835)
	<i>Bradyurus szainochae</i> (de Zigno, 1887)
	<i>Frigoichthys margaritae</i> Bannikov, 2004
	<i>Frippia labroiformis</i> Bannikov & Carnevale, 2012
	<i>Squamibolcoides minciottii</i> Bannikov & Zorzin, 2013
Sphyraenidae	<i>Sphyraena bolcensis</i> Agassiz, 1844
Tortonesidae	<i>Tortonesia esilis</i> Sorbini, 1983
Labridae	<i>Eocoris bloti</i> Bannikov & Sorbini, 1990
	<i>Phyllopharyngodon longipinnis</i> Bellwood, 1990
	<i>Bellwoodilabrus landinii</i> Bannikov & Carnevale, 2010
Labroidei incertae sedis	" <i>Labrus</i> " <i>valenciennesi</i> Agassiz, 1839
	<i>Sorbinia caudopunctata</i> Bellwood, 1995
Callipterygidae	<i>Callipteryx recticaudus</i> Agassiz, 1838
	<i>Callipteryx speciosus</i> Agassiz, 1838
Gobioidei incertae sedis	" <i>Gobius</i> " <i>microcephalus</i> Agassiz, 1839
Caproidae	<i>Eoantigonia veronensis</i> (Sorbini, 1983)
Sorbinipercidae	<i>Sorbiniperca scheuchzeri</i> Tyler, 1999
	<i>Sorbinicapros sorbiniorum</i> Bannikov & Tyler, 1999
Zorzinichthyidae	<i>Zorzinichthys annae</i> Tyler & Bannikov, 2002
Acanthonemidae	<i>Acanthonemus subaureus</i> (Blainville, 1818)
Siganidae	<i>Ruffoichthys spinosus</i> Sorbini, 1983
	<i>Ruffoichthys bannikovi</i> Tyler & Sorbini, 1990
	<i>Aspesiganus margaritae</i> Bannikov & Tyler, 2002
	<i>Acanthopygaeus agassizi</i> (Eastman, 1904)
Acanthuridae	<i>Proacanthurus tenuis</i> (Agassiz, 1838)
	<i>Proacanthurus bonatoi</i> Blot & Tyler, 1990
	<i>Proacanthurus ovalis</i> (Agassiz, 1838)
	<i>Proacanthurus elongatus</i> Blot & Tyler, 1990
	<i>Metacanthurus veronensis</i> Blot & Tyler, 1990
	<i>Eorandallius rectifrons</i> (Agassiz, 1838)
	<i>Eorandallius elegans</i> Blot & Tyler, 1990
	<i>Acanthuroides massalongoi</i> Blot & Tyler, 1990
	<i>Lehmanichthys lessiniensis</i> Blot & Tyler, 1990
	<i>Metaspisurus emmanueli</i> Blot & Tyler, 1990
	<i>Pesciarichthys punctatus</i> Blot & Tyler, 1990
	<i>Frigosorbinia baldwinae</i> (Sorbini & Tyler, 1998)
	<i>Tylerichthys nuchalis</i> (Agassiz, 1838)
	<i>Tylerichthys milani</i> Blot & Tyler, 1990
	<i>Protozebrasoma bloti</i> Sorbini & Tyler, 1998
	<i>Sorbinithurus sorbinii</i> Tyler, 1999
	<i>Tauichthys padremenini</i> Tyler, 1999
	<i>Tauichthys aspesae</i> Tyler & Bannikov, 2000
	<i>Gazolaichthys vestenanovae</i> Blot & Tyler, 1990

TAB. 1 - Continuation.

		<i>Padovathurus gaudryi</i> (de Zigno, 1887)
	Zanclidae	<i>Eozanclus brevirostris</i> (Agassiz, 1835)
	Massalongiidae	<i>Massalongius gazolai</i> (Massalongo, 1859)
	Euzaphlegidae	<i>Veronaphleges brunae</i> Bannikov, 2008
	Scombridae	<i>Auxides propterygius</i> (Agassiz, 1835)
		<i>Pseudaxides speciosus</i> (Agassiz, 1835)
		<i>Thunnoscomberoides bolcensis</i> (Agassiz, 1835)
		<i>Godsilia lanceolata</i> (Agassiz, 1835)
	Blochiidae	<i>Blochius longirostris</i> Volta, 1796
		<i>Blochius macropterus</i> de Zigno, 1887
	Palaeorhynchidae	<i>Palaeorhynchus zorzini</i> Fierstine, Bannikov & Monsch, 2008
	Centrolophidae	<i>Zorzinia postalensis</i> Bannikov, 2000
	Perciformes incertae sedis	<i>Quasicichla mucistonaver</i> Bannikov, 2004
		<i>Parapygaeus polyacanthus</i> Pellégrin, 1907
Pleuronectiformes	Amphistiidae	<i>Amphistium paradoxum</i> Agassiz, 1844
		<i>Heteronectes chaneli</i> Friedman, 2008
	Pleuronectiformes incertae sedis	<i>Eobothus minimus</i> (Agassiz, 1839)
Tetraodontiformes	Triacanthidae	<i>Protacanthodes ombonii</i> (de Zigno, 1887)
		<i>Protacanthodes nimesensis</i> Tyler & Santini, 2001
	Protobalistidae	<i>Spinacanthus cuneiformis</i> (Blainville, 1818)
		<i>Protobalistum imperiale</i> (Massalongo, 1857)
	Bolcabalistidae	<i>Bolcabalistes varii</i> Tyler & Sorbini, 1998
	Aracnidae	<i>Proaracana dubia</i> (Blainville, 1818)
	Ostraciidae	<i>Eolactoria sorbinii</i> Tyler, 1975
	Eoplectidae	<i>Eoplectus bloti</i> Tyler, 1975
	Zignoichthyidae	<i>Zignoichthys oblongus</i> (de Zigno, 1874)
	Tetraodontidae	<i>Eotetraodon pygmaeus</i> (de Zigno, 1887)
		<i>Eotetraodon tavernei</i> Tyler & Bannikov, 2013
	Diodontidae	<i>Prodiodon tenuispinus</i> (Agassiz, 1844)
		<i>Prodiodon erinaceus</i> (Agassiz, 1844)
		<i>Heptadiodon echinus</i> (Heckel, 1854)
		<i>Zignodon fornasieroae</i> Tyler & Santini, 2002
Acanthomorpha incertae sedis		<i>Pietschellus aenigmaticus</i> Bannikov & Carnevale, 2011
		<i>Xiphopterus falcatus</i> (Volta, 1796)
		<i>Oncolepis isseli</i> Bassani, 1897
		<i>Protoaulopsis bolcensis</i> Woodward, 1901

TAB. 1 - Continuation.

The fossil fishes of Bolca are usually represented by complete or partially complete articulated skeletons, in many cases in part and counterpart, often characterized by preservation of the complete scale covering and occasionally by the original pigmentation pattern (e.g., Fig. 2d). Incomplete or disarticulated skeletal remains and isolated scales are also present.

Overall, the fish assemblage consists of sharks, batoids, remnants of Mesozoic neopterygians (pycnodontiforms) and teleosts, representing the earliest record of an acanthomorph dominated fish assemblage with an overall diversity foreshadowing that of today (Patterson, 1993a). The size of specimens is extremely variable, ranging from a few millimetres to more than one meter.

Cartilaginous fishes are relatively uncommon and scarcely diversified compared to bony fishes (16 vs 222 taxa; see Tab. 1). The only comprehensive account of the Bolca

cartilaginous fishes was provided by Jaekel (1894). According to Blot (1980), sharks are represented by members of the families Carcharhinidae (Fig. 2a) and Orectolobidae. The Carcharhinidae were partially reviewed by Cappetta (1975), who assigned some of the best preserved specimens formerly referred to *Galeus* (= *Alopiopsis*, *Protogaleus*, *Carcharias*, *Notidanus*) *cuvieri* to the triakid genus *Galeorhinus*; a recent close examination of the dentition, however, demonstrated that this material must be assigned to the extinct carcharhinid genus *Physogaleus* (see Adnet & Cappetta, 2008). Blot (1980) tentatively referred to the family Orectolobidae the material assigned to *Mesiteia emiliae*, even though the genus *Mesiteia* is currently regarded as a member of the family Hemiscylliidae; this material is badly in need of revision. Batoids are relatively diverse and include rhinobatids (Blot, 1980), narcinids (Carvalho, 2010), platyrhinids (Blot, 1980; Carvalho, 2004), dasyatids (Fig. 2b; Carvalho et al. 2004), myliobatids (de Zigno, 1885; Carvalho et al., 2004), and urolophids (Carvalho et al., 2004).

The Bolca bony fish assemblage includes the youngest occurrence of the extinct Mesozoic clade Pycnodontiformes (Fig. 2c), represented by four taxa (see Poyato-Ariza & Wenz, 2002), being the last members of a group that was very common in shallow-water marine habitats up to the end of the Cretaceous.

Non-acanthomorph teleosts are represented by only 27 taxa of anguilliforms, aulopiforms, clupeiforms, crossognathiforms, ostariophysans, and osteoglossiforms.

Another relict among the bony fishes of Bolca is the pachyrhizodontid *Platinx macropterus*, which possibly represents the youngest record of the order Crossognathiformes, a clade of Late Jurassic-Cretaceous primarily marine basal teleosts (Taverne, 1980; Arratia, 2008).

Members of the order Osteoglossiformes are relatively uncommon in the Bolca assemblage, represented by three taxa, the small *Foreyichthys bolcensis*, *Monopterus gigas*, and the arapaimid *Thrissopterus catullii* (see Taverne, 1998; Bonde, 2008). These fossils document the last part of the marine history of this heterogeneous group which today is restricted to freshwaters with a Gondwana distribution.

Eels of the order Anguilliformes are relatively common, with 16 taxa belonging to both extant (Anguillidae, Chlopsidae, Congridae, Ophichthyidae) and extinct [Anguilloididae, Milananguillidae, Paranguillidae (Fig. 2d), Patavichthyidae, Proteomyridae] families, plus several taxa (*Bolcanguilla brachycephala*, *Gazolapodus homopterus*) of difficult phylogenetic interpretation. The diversity of the anguilliforms of Bolca has been the subject of monographic studies by Cadrobbi (1962) and Blot (1978, 1980, 1984a).

Of the ostariophysans, only the otophysan *Chanoidea macropoma* has been investigated in detail (Patterson, 1984). The relatively rare anotoophysans *Coelogaster leptostea* and “*Chanos*” *forcipatus* need revisionary study.

Herrings of the order Clupeiformes are by far the most common elements of the Bolca fish assemblage. However, despite their abundance, these fossils have been scarcely investigated. A recent revision of the collections of the main Italian museums with Bolca materials led to the recognition of two taxa, the extremely abundant sardine *Bolcaichthys*

FIG. 2 - a) *Eogaleus bolcensis* Cappetta 1975, MGP-PD 8870C, left lateral view; scale bar 100 mm. b) “*Dasyatis*” *muricata* (Volta 1796), MCSNV 1021, dorsal view; scale bar 50 mm. c) *Pycnodus apodus* (Volta 1796), MCSNV T999, left lateral view; scale bar 10 mm. d) *Paranguilla tigrina* (Agassiz 1839), MGP-PD 26288, left lateral view; scale bar 20 mm. e) *Bolcaichthys catopygopterus* (Woodward 1901), NHMUK P.3829, holotype, left lateral view; scale bar 10 mm. f) *Veronavelifer sorbinii* Bannikov 1990, MCSNV I.G. 37576, holotype, left lateral view; scale bar 10 mm. g) *Bajaichthys elegans* Sorbini 1983, MCSNV T923, holotype, right lateral view; scale bar 10 mm.

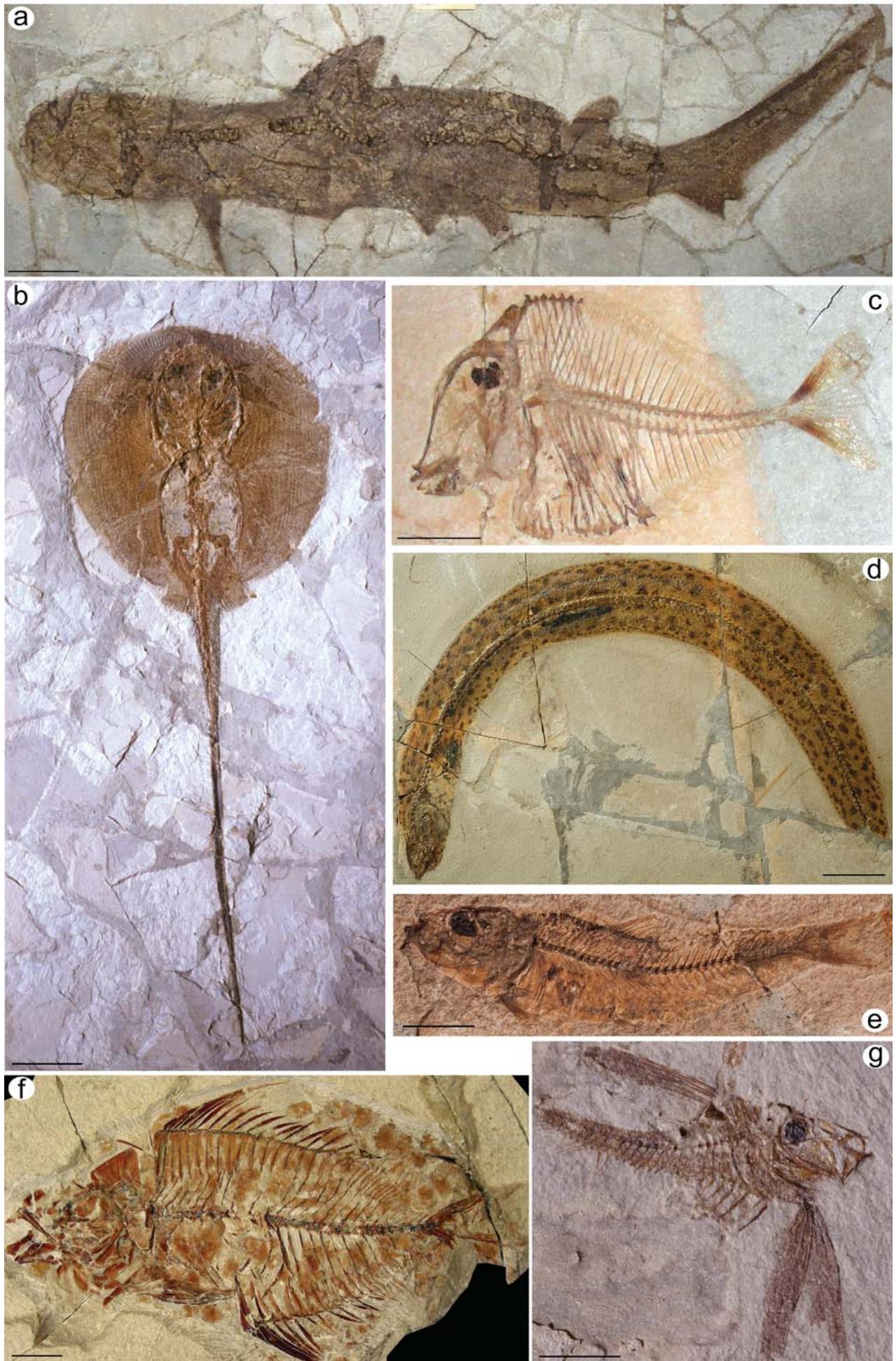


FIG. 2

catopygopterus (Fig. 2e) and the round herring *Trollichthys bolcensis* (Marramà & Carnevale, in press). A single specimen of a new anchovy genus and species has recently been found in the collection of the Museo Civico di Storia Naturale, Verona, representing the earliest evidence of the family Engraulidae in the fossil record.

The relatively large shallow water barracudina *Holosteus esocinus* is the only aulopiform taxon present in the Bolca fish assemblage.

The large majority of the Bolca fish assemblage consists of acanthomorph taxa, represented by almost 200 known taxa. In terms of taxonomic diversity, acanthomorphs are more than seven times more abundant than non-acanthomorphs. However, such an asymmetric ratio is balanced in terms of individuals/biomass by the extremely abundant sardine *Bolcaichthys catopygopterus* (Fig. 2e). Recent excavations carried out between 1999 and 2011 by the Museo Civico di Storia Naturale, Verona demonstrated that about half of the collected fossil fishes are sardines, followed by members of the extant perciform families Apogonidae, Latidae, Menidae, and Sparidae. The perciforms (sensu Johnson & Patterson, 1993) are conspicuously diverse, with about 120 taxa, followed by syngnathiforms and tetraodontiforms. Other acanthomorph groups (atheriniforms, beloniforms, beryciforms, dactylopteriforms, lampridiforms, lophiiforms, ophidiiforms, and pleuronectiforms) are represented by six or less taxa each; a few acanthomorph taxa of problematic phylogenetic interpretation are also present (e.g., Bannikov & Carnevale, 2011). Overall, this remarkable number of taxa exhibits a vast morphological diversity, providing a robust documentation of the early Cenozoic diversification of the perciforms, with the proliferation of new anatomical body plans and the exploitation of new ecological strategies (Friedman, 2010).

The basal acanthomorph order Lampridiformes is presently represented by six specimens representing four taxa. There are two taxa of the family Veliferidae (Fig. 2f; Bannikov, 1990), one of which is currently under study by two of us (G.C. and A.F.B.). The bizarre *Bajaichthys elegans* is currently regarded as a lampridiform of uncertain affinities (Fig. 2g; Sorbini & Bottura, 1988; Olney et al., 1993). Finally, the enigmatic “*Pegasus*” *volans* is tentatively interpreted herein as a taeniosomous lampridiform; this taxon is greatly in need of revision.

Cusk-eels (Ophidiiformes) are extremely rare in the Bolca fish assemblage and are unquestionably in need of revision.

Lophiiformes are represented by taxa of the families Antennariidae, Ogcocephalidae (Fig. 3c), Brachionichthyidae (Fig. 3b), and Lophiidae (Fig. 3a); the lophiiform material from Bolca constitutes the earliest known skeletal record for all four of these families. The Lophiidae includes two taxa (Pietsch & Carnevale, 2011; Carnevale & Pietsch, 2012), one of which, *Sharfia mirabilis*, is characterized by a peculiar set of characters and is currently regarded as a stem-lophiid, being the sister taxon of all the other genera of the family. A single frogfish (Antennariidae) taxon has been described to date (Carnevale & Pietsch, 2009) but additional undescribed specimens have been recognized in the collections of the Museo Civico di Storia Naturale, Verona and of the Museo dei Fossili di Bolca. Handfishes of the family Brachionichthyidae are represented by two taxa (Carnevale & Pietsch, 2010); this family is today restricted in distribution to the shallow temperate and subtropical waters of Tasmania and southern and eastern Australia. Finally, the Bolca assemblage includes six individuals of the batfish *Tarkus squirei* (family Ogcocephalidae) (Carnevale & Pietsch, 2011).

According to Bannikov (2008), the Bolca fish assemblage includes four atheriniform taxa, the small atherinid *Atherina* (?) *macrocephala* and the streamlined predatory species of the extinct families Mesogasteridae and Rhamphognathidae.

Flying fishes (Fig. 3d) and halfbeaks (Beloniformes) are a rare component of the Bolca fish assemblage (see Bannikov et al., 1985).

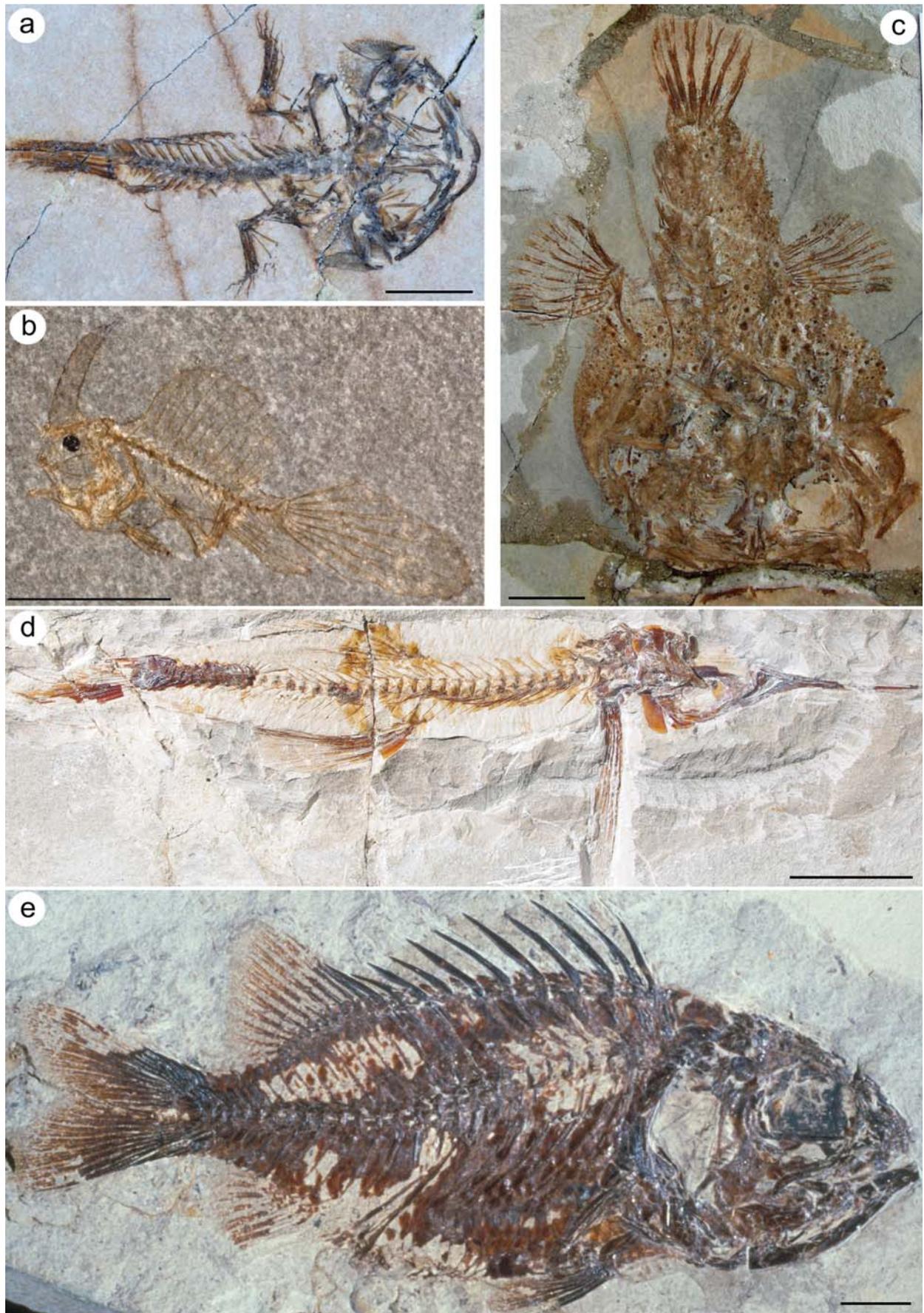


FIG. 3 - a) *Sharfia mirabilis* Pietsch & Carnevale 2011, MNHN Bol 38, holotype, dorsal view; scale bar 10 mm. b) *Histionotophorus bassani* (de Zigno 1887), NHMUK 19060, left lateral view; scale bar 10 mm. c) *Tarkus squirei* Carnevale & Pietsch 2011, MCSNV T159, holotype, dorsal view; scale bar 20 mm. d) *Rhamphoexoetetus volans* Bannikov, Parin & Pinna 1985, MCSNM V294, holotype, right lateral view; scale bar 20 mm. e) *Eoholocentrum macrocephalum* (Blainville 1818), MCSNV T969, right lateral view; scale bar 10 mm.

Squirreelfishes of the order Beryciformes are relatively common, represented by three taxa (Fig. 3e); the morphology and affinities of these taxa have been extensively discussed (Sorbini, 1975, 1984; Sorbini & Tirapelle, 1975).

Syngnathiforms are relatively common and highly diverse. At least ten families [Aulorhamphidae, Aulostomidae, Centriscidae (Fig. 4a), Fistularioididae, Paraeoliscidae, Parasynarcualidae, Rhamphosidae (Fig. 4b), Solenostomidae, Syngnathidae, Urosphenidae] plus two incertae sedis taxa (*Aulostomoides tyleri*, *Calamostoma breviculum*) are known. Except for the extinct family Aulorhamphidae, which has been recently investigated in great detail (e.g., Tyler, 2004), the other syngnathiforms were cursorily and inadequately described by Blot (1980) and are in need of a comprehensive revision.

The phylogenetic affinities of the enigmatic *Pterygocephalus paradoxus* have been discussed by several authors (e.g., Hubbs, 1952; Blot, 1980, 1984b; Springer, 1993); we follow the opinion of Blot (1984) and tentatively consider this fish as in some way related to the dactylopteriforms.

As discussed above, the perciforms (Figs 4c-j, 5-7c) are represented by a remarkably large number of species, representing at least 37 families, both extinct [Acanthonemidae, Blochiidae (Fig. 6a), Callipterygidae, Carangodidae, Ductoridae, Eocottidae (Fig. 7b), Euzaphlegidae, Exelliidae (Fig. 4g), Massalongiidae (Fig. 7c), Palaeorhynchidae, Quasimullidae, Robertanniidae, Sorbinipercidae, Tortonesidae, Zorzinichthyidae] and extant [Acanthuridae (Figs 6b, 7a), Acropomatidae, Apogonidae (Fig. 4c), Caproidae, Carangidae (Figs 1, 4d), Centrolophidae, Ephippidae (Figs 4f, 5), Gerreidae, Labridae, Leiognathidae, Latidae, Lutjanidae, Menidae (Fig. 6a), Monodactylidae, Percichthyidae, Pomacentridae, Pomatomidae, Priacanthidae, Scatophagidae (Fig. 4h), Scombridae, Siganidae (Fig. 4j), Sparidae (Fig. 4e), Sphyaenidae, Zanclidae]; a number of species are of difficult phylogenetic interpretation and are currently considered as *incertae sedis* within the Perciformes or within one of the perciform suborders (Gobioidei, Labroidei, Percoidei; see Tab. 1). The family Acanthuridae is by far the most diverse of the perciform families with 20 species (Figs 6b, 7a; e.g., Blot & Tyler, 1990; Tyler, 1999a).

FIG. 4 - a) *Paramphisile weileri* Blot 1980, MCSNV T22, right lateral view; scale bar 10 mm. b) *Rhamphosus rastrum* (Volta 1796), MCSNV I.G. 24560, left lateral view; scale bar 10 mm. c) *Eosphaeramia pygopterus* (Agassiz 1836), MCSNV I.G. 23172, right lateral view; scale bar 10 mm. d) *Vomeropsis triurus* (Volta 1796), MCSNV T1022, right lateral view; scale bar 20 mm. e) *Sparnodus vulgaris* (Blainville 1818), MCSNV I.G. 24546, right lateral view; scale bar 20 mm. f) *Archaehippus asper* (Volta 1796), MCSNV VIII D.98, left lateral view; scale bar 20 mm. g) *Exellia velifer* (Volta 1796), MCSNV VIII D.87, right lateral view; scale bar 10 mm. h) *Eoscatophagus frontalis* (Agassiz 1839), MCSNV VII C.68, left lateral view; scale bar 50 mm. j) *Ruffoichthys bannikovi* Tyler & Sorbini 1990, MCSNV I.G. 132596, holotype, left lateral view; scale bar 10 mm.

FIG. 5 - *Eoplatax papilio* (Volta 1796), MGP-PD 26285, right lateral view; scale bar 50 mm.

FIG. 6 - a) *Mene rhombea* (Volta 1796) and *Blochius longirostris* Volta 1796, MCSNV T1133; scale bar 100 mm. b) *Eorandallius rectifrons* (Agassiz 1838), MCSNV T986, right lateral view; scale bar 50 mm.

FIG. 7 - a) *Gazolaichthys vestenanovae* Blot & Tyler 1990, MCSNV B65.14, holotype, left lateral view; scale bar 10 mm. b) *Bassanichthys pesciaraensis* (Bannikov 2004), MCSNV T.111, holotype, right lateral view; scale bar 10 mm. c) *Massalongius gazolai* (Massalongo 1859), MCSNV VIII D.200, holotype, left lateral view; scale bar 10 mm. d) *Eobothus minimus* (Agassiz 1839), MCSNV T968, right lateral view; scale bar 10 mm. e) *Amphistium paradoxum* Agassiz 1844, MCSNV V D91, right lateral view, scale bar 20 mm. f) *Eolactoria sorbinii* Tyler 1975, MCSNV T6, holotype, right lateral view; scale bar 10 mm.

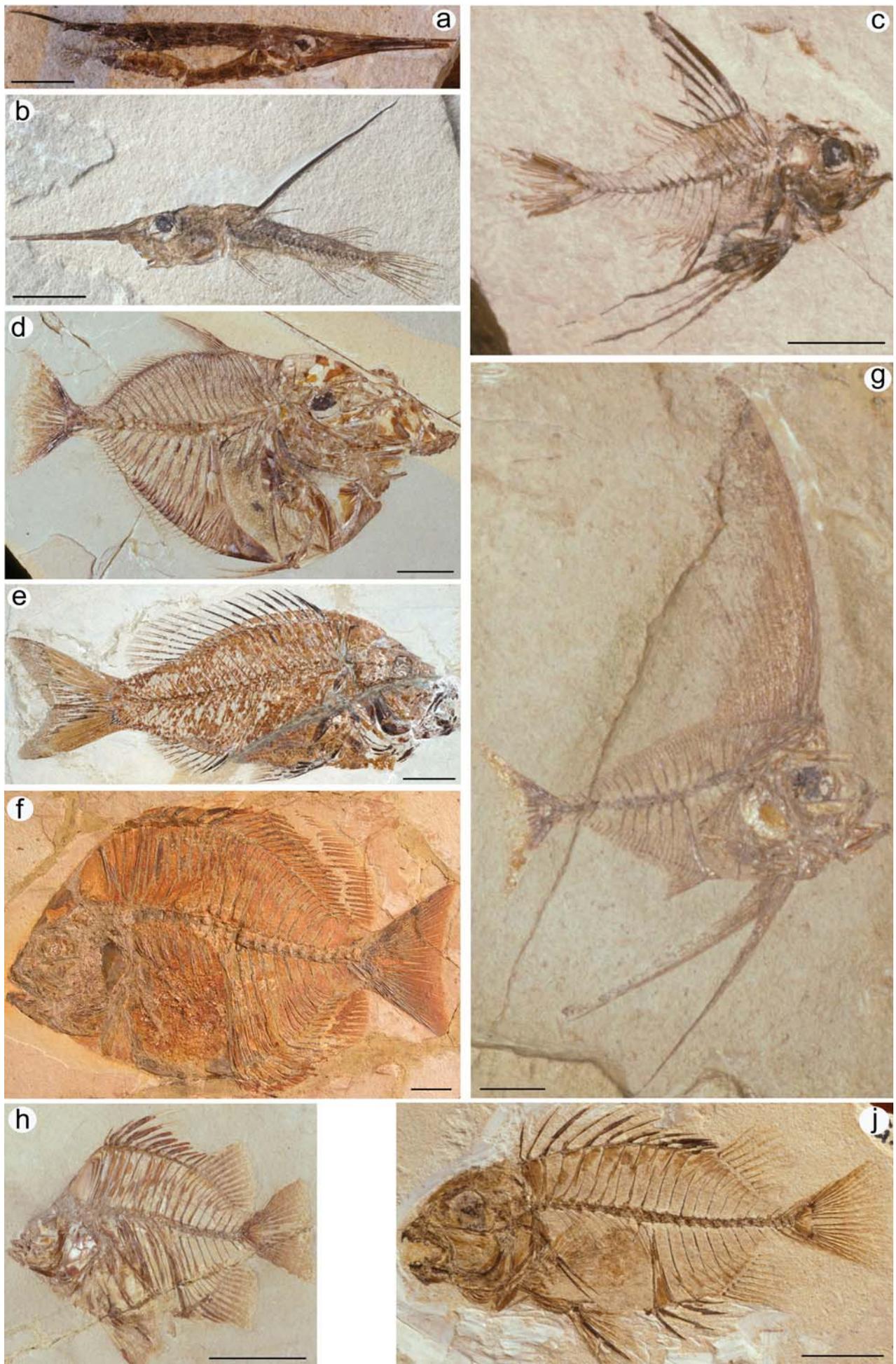


FIG. 4



FIG. 5

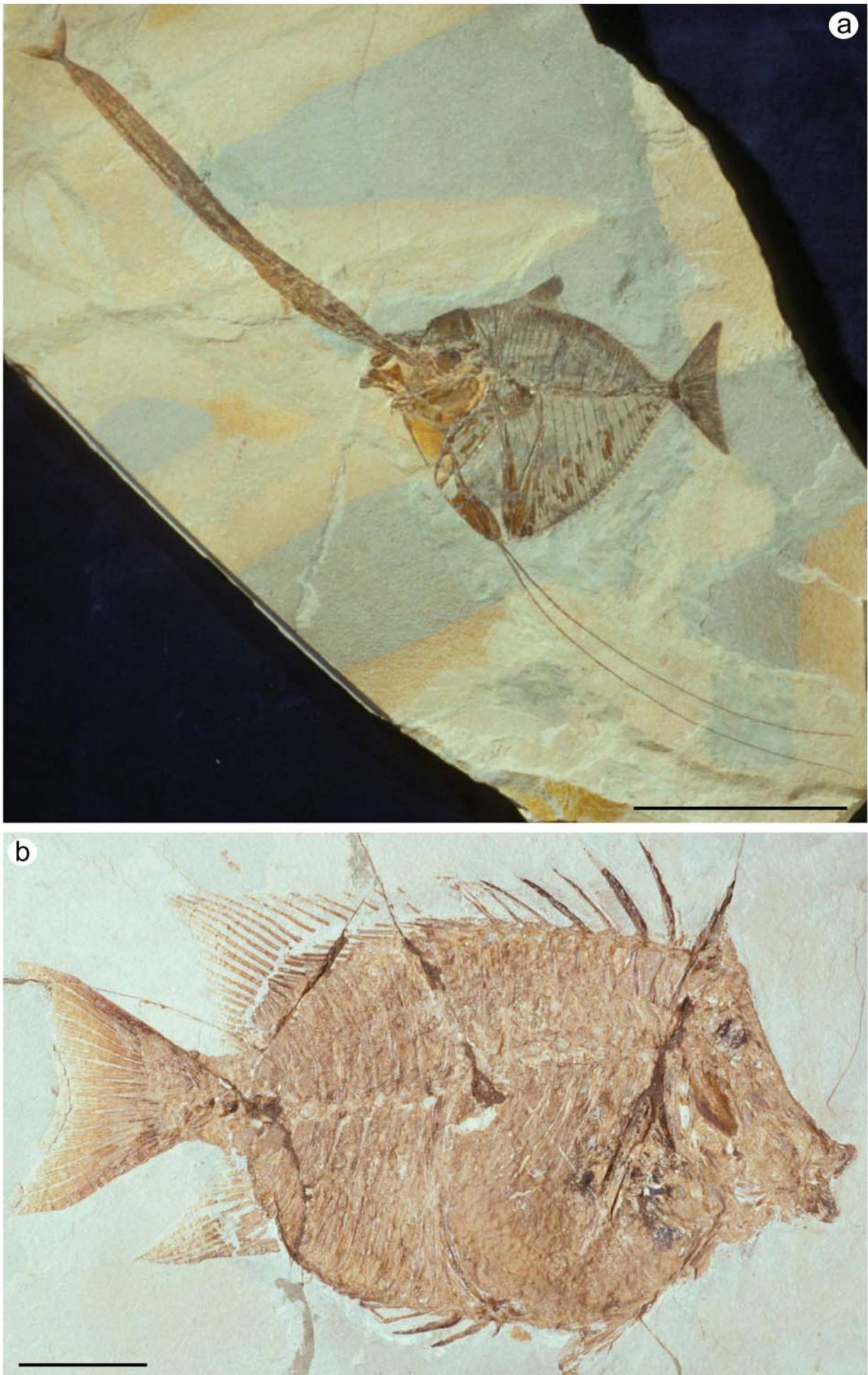


FIG. 6

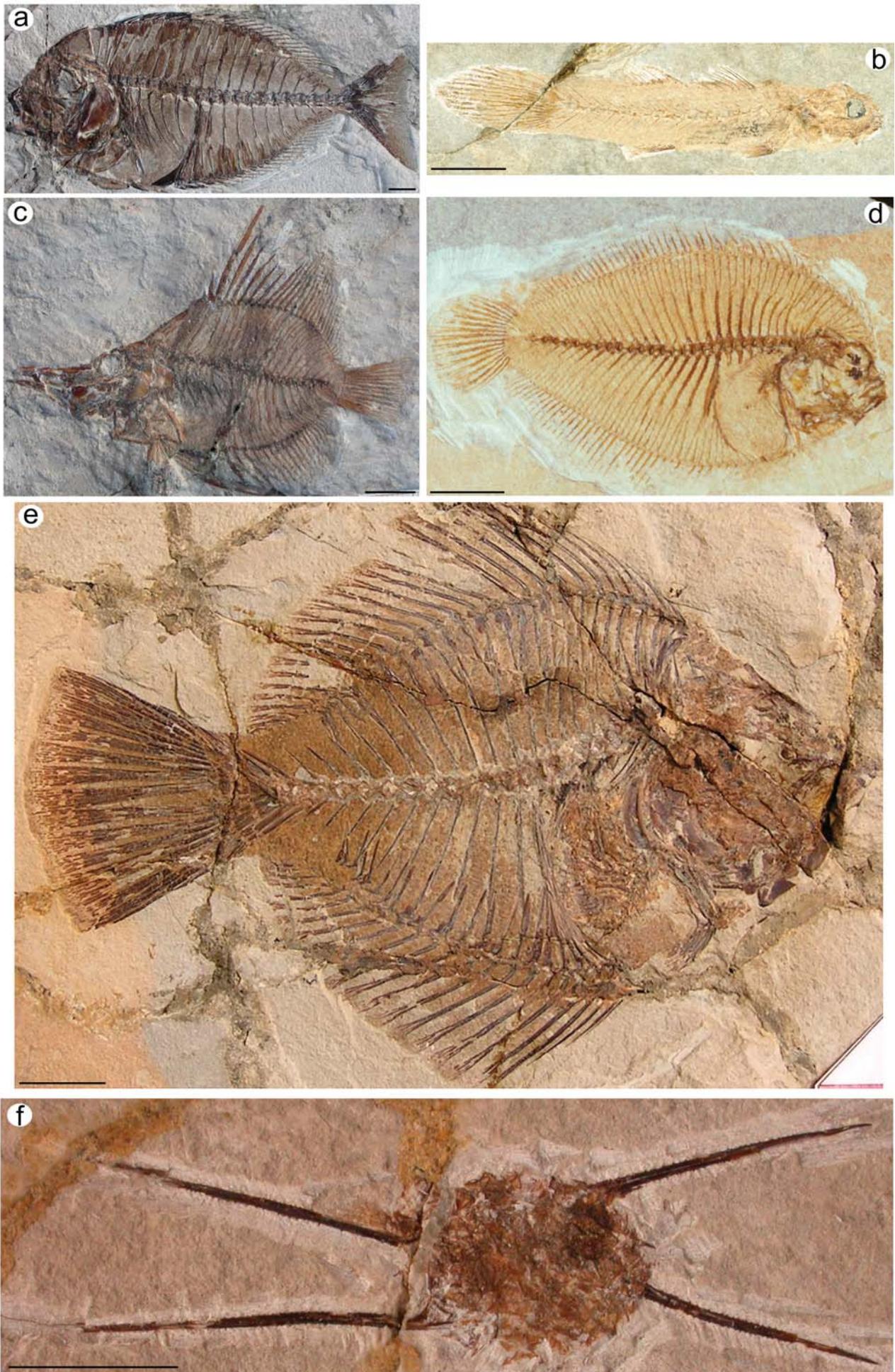


FIG. 7

The amazing diversity of this family is clearly exemplified by the 14 genera known from Bolca, several times the number of those (six) living today; see Tyler & Micklich (2011) for a classification of the fossil (mostly Bolca) and extant genera of acanthurids and their immediate outgroups. Other families exhibiting a considerable diversity are the Apogonidae, Carangidae, Lutjanidae, and Sparidae. Our knowledge of the morphology and taxonomic status of the perciform taxa of the Bolca fish assemblage is in general satisfactory, and many groups have been investigated in great detail (e.g., Blot, 1969; Tyler & Bannikov, 1997, 2005; Tyler, 1999b; Fierstine & Monsch, 2002; Day, 2003; Bannikov, 2004, 2005, 2006; Monsch, 2006; Bannikov & Carnevale, 2010). For many perciform families, Bolca constitutes their earliest evidence in the fossil record (Patterson, 1993b). It is interesting to note that despite the extraordinarily high diversification rates characteristic of perciform fishes (see Alfaro et al., 2009), a few taxa of the Bolca assemblage belong to morphologically conservative genera (*Acropoma*, *Lichia*, *Mene*, *Pristigenys*, *Seriola*, *Sphyræna*) that are still living today; therefore, the evolutionary history of these genera extends back at least to the Early Eocene, about 50 Mya.

Flatfishes are moderately abundant, being represented by the “bothoid” *Eobothus minimus* (Fig. 7d; see Chanet, 1999) and two stem-pleuronectiforms, *Amphistium paradoxum* and *Heteronectes chaneti* (Fig. 7e; see Friedman, 2008, 2012). Despite their low diversity, the Bolca flatfishes are of remarkable evolutionary significance. The two stem-pleuronectiforms can be considered as transitory forms providing anatomical evidence of the gradual evolution of the marked cranial asymmetry of flatfishes (Friedman, 2008), whereas *Eobothus minimus* appears to be the oldest known crown pleuronectiform (Chanet, 1999).

In the Bolca fish assemblage, the tetraodontiforms comprise 15 taxa belonging to nine families. Because of their broad taxonomic diversity, the tetraodontiform fishes of Bolca constitute an unparalleled source of information about the earliest stages in the evolutionary history of the extant lineages of this clade [Aracanidae, Diodontidae, Ostraciidae (Fig. 7f), Tetraodontidae, Triacanthidae]. The extinct groups comprise taxa characterized by a very peculiar morphology (*Eoplectus bloti*, *Proaracana dubia*, *Protobalistum imperiale*, *Spinacanthus cuneiformis*, *Bolcabalistes varii*; Tyler, 1975a, b; Tyler & Santini, 2002) that clearly indicate that the anatomical diversity of tetraodontiforms was remarkably high at least since the earliest part of the Eocene.

PALEOECOLOGICAL IMPLICATIONS

Despite the considerable efforts devoted to the definition of the taxonomic composition and phylogenetic significance of the Bolca fish assemblage, its paleoecological and biogeographical features have received only limited attention.

During the Eocene, the Bolca area was part of the northern margin of the West Tethys region, a region characterized by remarkably high α -diversity, and very abundant coral reefs and mangrove systems. This biodiversity hotspot constitutes a precursor and a sort of Eocene analogue of the modern Indo-Australian Archipelago hotspot, the center of current maximum marine diversity (e.g., Renema et al., 2008).

Because of its high taxonomic diversity and evident tropical shallow-water nature, the Bolca fish assemblage has been traditionally interpreted as closely linked to a coral reef system (e.g., Blot, 1969, 1980; Sorbini, 1972, 1999). This hypothesis appears to be supported (at least in part) by the presence of remains of hermatypic corals in Lower Eocene sediments exposed in the surroundings of Bolca and possibly approximately coeval with the fish-bearing strata (Malaroda, 1954; Blot, 1969).

Bellwood (1996) emphasized the role of Bolca fishes in understanding the evolution of modern reef fish communities and considered these fossils as the earliest clearly defined evidence of a coral reef fish assemblage. The Bolca fish assemblage seems to mark the starting point of the documented evolution of many fish families associated with coral reefs (Bellwood & Wainwright, 2002), providing substantial evidence of a general stability of the morphological characteristics of tropical shallow marine fish faunas throughout the Cenozoic. In many cases, the morphology of the Bolca taxa belonging to reef fish families is very similar to that of extant representatives. Most structural characters and functional (and possibly ecological) features of these Eocene taxa are in some ways comparable to those of modern reef fishes. The Bolca fish assemblage, however, also includes numerous taxa belonging to extinct lineages of uncertain ecological interpretation and, at the same time, representatives of some of the fish groups commonly associated with Recent coral reefs (blenniids, chaetodontids, mullids, parrotfishes, serranids) have not been found at Bolca. Moreover, the relative abundance of representatives of reef fish families in the Bolca assemblage is significantly different than that observed on Recent coral reefs (Bellwood, 1996). Despite the compositional differences between the Bolca fish assemblage and those characteristic of modern reefs, a general affinity is evident and the presence of a reefal signature in the Bolca assemblage is undeniable. Indeed, recent investigations on the evolutionary dynamics of modern reef fishes have revealed that one of the main waves of invasion of reef habitats occurred in the Paleocene and that by approximately 50 Mya reef lineages saturated the ecomorphological niches available on reefs with the origination of many functional groups within reef-dwelling acanthomorphs (Price et al., 2014).

Overall, sedimentological and paleontological evidence concur to indicate that the fossiliferous deposits of Bolca originated in a tropical coastal region in close proximity to coral reefs and emerged areas (e.g., Massari & Sorbini, 1975). Based on the ecological requirements of the fish taxa, Landini & Sorbini (1996) proposed a paleoenvironmental scenario in which the general physiographic context is a heterogeneous coastal area characterized by fluvial systems, coastal lagoons and open expanses of *Halochloris* sand and seagrass beds surrounding reef zones and influenced by the open sea. In such context, Landini & Sorbini (1996) placed the fish taxa into three main ecological assemblages, the sand/seagrass bed assemblage characterized by taxa (e.g., batoids, anguilliforms, lophiids, syngnathiforms, ehippids, eocottids, callipterygids, labrids, siganids, pleuronectiforms, some tetraodontiforms) closely associated with the sediment, the true coral assemblage (anguilliforms, lophiiforms, holocentrids, syngnathiforms, apogonids, sparids, carangids, monodactylids, ehippids, pomacentrids, labrids, acanthurids, siganids, tetraodontiforms), and the perireefal and pelagic assemblage (sharks, clupeids, beloniforms, atheriniforms, veliferids and other lampridiforms, latids, ductorids, carangids, menids, exelliids, sphyraenids, euzaphlegids, scombrids, blochiids, palaeorhynchids).

The excellent preservation of fish skeletons and their remarkable similarity to extant tropical shallow water fishes allow for the interpretation of the trophic significance of the various taxa and to hypothesize the main trophic relationships that characterized the Bolca paleobiotopes (Landini & Sorbini, 1996). The highly diverse fish assemblage includes taxa of a variety of trophic guilds, such as planktivores (clupeiforms, holocentrids,

FIG. 8 - a) Detail of *Archaeophis proavus* Massalongo 1859 [excerpt from Massalongo (1859, Plate II)]. b) Detail of *Anomalophis bolcensis* (Massalongo 1859) [excerpt from Massalongo (1859, Plate III)]. c) Fossil feather from Bolca illustrated by Faujas de Saint-Fond (1804).

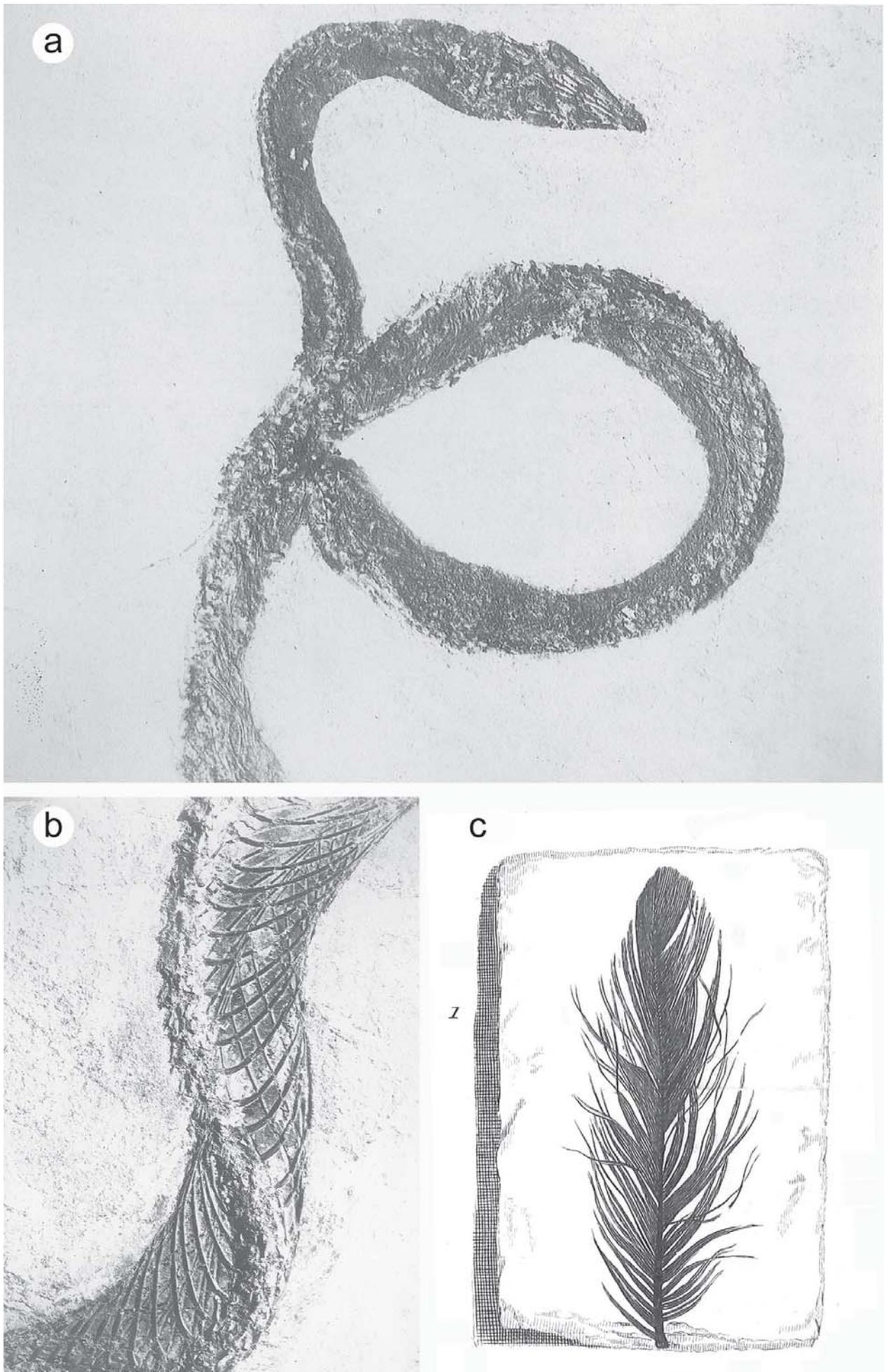


FIG. 8

menids, monodactylids, exelliids, pomacentrids), invertebrate feeders (batoids, veliferids, holocentrids, syngnathiforms, latids, percichthyids, caproids, priacanthids, carangids, menids, sparids, ehippids, pomacentrids, labrids, tetraodontiforms), piscivores (sharks, batoids, anguilliforms, lophiiforms, larger atheriniforms, latids, percichthyids, acropomatids, apogonids, carangids, sparids, sphyraenids, euzaphlegids, scombrids, blochiids, palaeorhynchids, pleuronectiforms), and herbivores (acanthurids, siganids, labrids, pomacentrids). The Bolca assemblage documents the origin of new feeding modes in fishes: herbivory, nocturnal feeding, and high-precision benthic feeding (Bellwood, 2003; Goatley et al., 2010). Nocturnal feeders are relatively abundant in the assemblage, represented by squirrelfishes (Holocentridae) and cardinalfishes (Apogonidae), whereas herbivores are primarily represented by surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae). The acanthurids from Bolca are characterized by remarkable functional and ecological similarities to their extant counterparts, with grazers, browsers, and long-snouted crevice-feeding forms that possibly have played a significant role as herbivores during the origin of modern coral reef systems (Bellwood et al., 2014). The analysis of the Bolca trophic system reveals a strongly asymmetric herbivore/predator relationship in terms of biomass and overall diversity; the dominance of predators and the abundance of nocturnal feeders and clupeids seem to indicate that the original paleobiotopes of Bolca were not characterized by typical coral reef trophic systems, but, rather, these can be confidently interpreted as perireefal trophic systems largely influenced by both the open sea and the coastal environments (Landini & Sorbini, 1996).

OTHER VERTEBRATES

Remains of other vertebrates have been occasionally found at the Pesciara site. Reptiles are represented by two specimens of boid-like snakes assigned to *Anomalophis bolcensis* and *Archaeophis proavus* (see Massalongo, 1859; Janensch, 1904, 1906; Auffenberg, 1959; Figs 8a-b, 9) and by a single carapace of a terrestrial turtle (Sorbini, 1999). Impressions of bird feathers, known since 1777 (Faujas de Saint-Fond, 1804; Fig. 8c), are relatively common at Bolca and have been traditionally referred to the genus *Ornitholites* (e.g., Omboni, 1885). According to Massimo Cerato, his great-grandfather Massimiliano found also a fragment of a single wing and an isolated beak (Cerato, 2011; pp. 166-167).

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FIG. 9 - *Archaeophis proavus* Massalongo 1859, MBR 3554, holotype; scale bar 50 mm. Photo by Carola Radke (2012) © Museum für Naturkunde, Berlin.

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