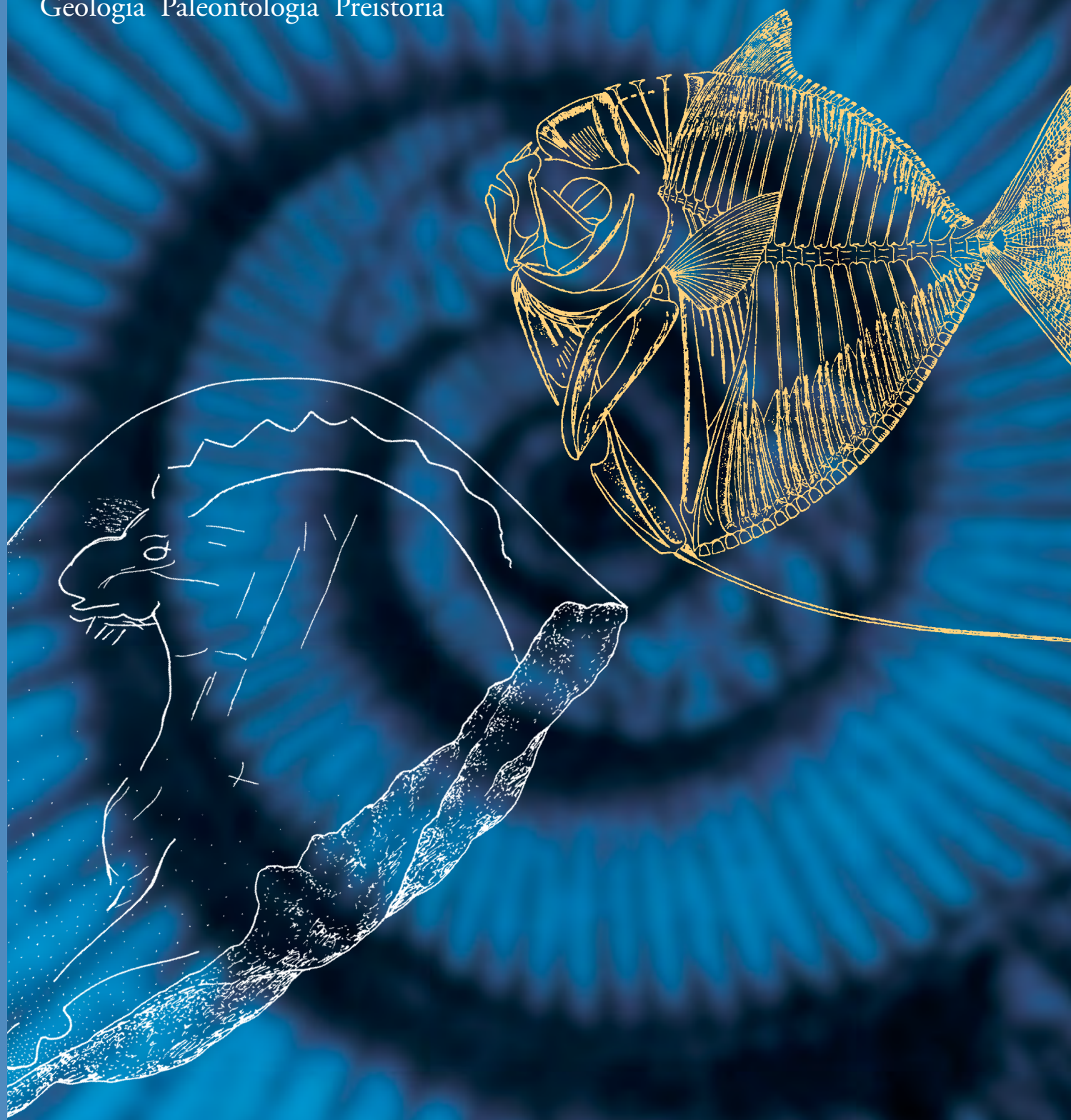


Museo Civico di Storia Naturale di Verona

Geologia Paleontologia Preistoria

anno 2022
volume 46





Bollettino del Museo Civico di Storia Naturale
Redazione: Lungadige Porta Vittoria 9, I-37129 Verona
E-mail: leonardo.latella@comune.verona.it

Il "Bollettino del Museo Civico di Storia Naturale di Verona" è la rivista del Museo, nata nel 1948 come "Memorie del Museo Civico di Storia Naturale di Verona" e divenuta nel 1974 "Bollettino". Dal 2000 esce annualmente in due distinte sezioni: 1. Botanica e Zoologia; 2. Geologia, Paleontologia e Preistoria, e pubblica sia estesi contributi sia brevi note riguardanti gli aspetti naturalistici di tali discipline.

The "Bollettino del Museo Civico di Storia Naturale di Verona" is the Museum's journal. Founded in 1948 as "Memorie del Museo Civico di Storia Naturale", it became "Bollettino" in 1974. Since 2000 it is issued annually in two distinct parts: 1. Botany and Zoology; 2. Geology, Paleontology and Prehistory; both extended contributions and brief notes regarding the naturalistic aspects of these disciplines are published.

FOUNDING EDITOR: Sandro Ruffo †

EDITOR IN CHIEF: Leonardo Latella

EDITORS: Sebastiano Andreatta, Alessandra Aspes, Angelo Brugnoli, Roberto Zorzin

EDITORIAL BOARD

BOTANICA: C. Blasi (Roma), Giovanni Cristofolini (Bologna), David L. Hawksworth (London), Guido Moggi (Firenze), Pier Luigi Nimis (Trieste), Franco Pedrotti (Camerino), Sandro Pignatti (Roma), Livio Poldini (Trieste), Filippo Prosser (Rovereto), Harald Riedl (Wien), Giovanni Sburlino (Venezia)

ZOOLOGIA: Roberto Argano (Roma), Paolo Audisio (Roma), Francesco Ballarin (Tokyo), Sebastiano Barbagallo (Catania), Denise Bellan-Santini (Marseille), Marco Bologna (Roma), Dan Danielopol (Mondsee), Louis Deharveng (Toulouse), Folco Giusti (Siena), Franz Krapp (Bonn), Alessandro Minelli (Padova), Giuseppe Osella (L'Aquila), Bruno Sabelli (Bologna), Valerio Sbordoni (Roma), Wim Vader (Tromsø), Aldo Zullini (Milano)

GEOLOGIA E PALEONTOLOGIA: Alexandre Bannikov (Moskva), Alberto Castellarin (Bologna), Maria Bianca Cita (Milano), Mauro Cremaschi (Milano), Carlo Doglioni (Roma), Derek Ford (Hamilton), Paolo Forti (Bologna), Alexander Klimchouk (Kiev), Walter Landini (Pisa), Nevio Pugliese (Trieste), Domenico Rio (Padova), Benedetto Sala (Ferrara), Ugo Sauro (Verona), Enrico Serpagli (Modena), Andrea Tintori (Milano), James C. Tyler (Washington D.C.)

PREISTORIA: Carlo Baroni (Pisa), Alberto Broglio (Ferrara), Leone Fasani (Verona), Giacomo Giacobini (Torino), Jean Guilaine (Paris), Janusz K. Kozłowski (Kraków), Bernd Kromer (Heidelberg), Venceslas Kruta (Paris), Franco Nicolis (Trento), Carlo Peretto (Ferrara), Luciano Salzani (Verona), Christian Strahm (Freiburg), Vincenzo Tiné (Verona).

In copertina: *Mene rhombea* (Volta) Perciformes Menidae. Uno degli ittioliti più facilmente reperibili nei calcari eocenici della Pesciara (Bolca, Val d'Alpone, Monti Lessini orientali). Ciottolo inciso con raffigurazione di stambecco rinvenuto nel sito del Paleolitico superiore di Riparo Tagliente (Verona), conservato presso il Museo Civico di Storia Naturale di Verona.

Mene rhombea (Volta) Perciformes Menidae. One of the most easily found Ichthyolites in the Eocene Limestones of the Pesciara locality (Bolca, Alpone Valley, eastern Lessini hills). Engraved pebble with ibex found in the Upper Palaeolithic site of Riparo Tagliente near Verona (Northern Italy), exposed at the Museo Civico di Storia Naturale di Verona.

GRAFICA COPERTINA: Damir Jellici

© Copyright 2022 - Comune di Verona

Tutti i diritti sono riservati. Nessuna parte di questa pubblicazione può essere riprodotta in qualsiasi forma, sia meccanica che elettronica senza il permesso scritto degli Editori e degli Autori.

Direttore responsabile: Angelo Brugnoli

Autorizzazione del Tribunale di Verona, 31.XII.1985. Reg. n. 61

BOLLETTINO
DEL MUSEO CIVICO
DI STORIA NATURALE
DI VERONA

Volume 46

Geologia Paleontologia Preistoria

Cronistoria delle ricerche sull'età del Ferro nel territorio veronese (parte 1): tra il collezionismo antiquario e la nascita della paletnologia veronese

GIOVANNI ADAMI¹, MASSIMO SARACINO²

1. Archeologo, libero professionista – giovanni.adami@outlook.it

2. Musei Civici di Verona, Museo di Storia Naturale, Sezione di Preistoria – Lungadige Porta Vittoria, 9– 37129 Verona
massimo.saracino@comune.verona.it

ABSTRACT

In this first paper concerning the history of research of the Iron Age in the Verona area, we would like to offer a first look at the beginnings of the first interests towards this period. Antiquarian collectionism, which was mainly interested in acquiring artistic masterpieces from the Etruscan, Greek and Roman periods behind which artistic personalities could be identified, showed no particular interest in the pre-Roman phases and the occasional discoveries and studies are quite rare. From the second half of the 19th century, however, the great cultural fervour characterising the birth of prehistoric archaeology also affected the Verona area around two important local institutions: the Accademia di Agricoltura, Commercio e Arti and the Museo Civico. Several episodes, including the prehistoric exhibition of 1876 in Verona and the contemporary discoveries of Alessandro Prosdocimi in Este, stimulated the researches on this period, which however were never systematic. Such events, which indirectly involved also the first members of Veronese paletnology, contributed on one hand to bring to light a new civilization worthy of note in the panorama of Iron Age Italy and on the other hand to give impulse to the researches on the field and to better frame, from a chronological and cultural point of view, the discoveries that followed one another in the Veronese territory (from Lessini to the plain).

Key words: Verona, history of the studies, paletnology, protohistory.

RIASSUNTO

In questo primo contributo sulla storia delle ricerche sull'età del Ferro nel territorio veronese, si vuole offrire un primo sguardo sugli albori dei primi interessi a questo periodo. Il collezionismo di matrice antiquaria, interessato principalmente alla raccolta di bellezze artistiche di epoca etrusca, greca e romana dietro alle quali erano ravvisabili personalità artistiche, non mostrava particolare interesse verso le fasi pre-romane e alquanto rari sono gli episodi di scoperte e studi. Dalla seconda metà dell'800, invece, il grande fermento culturale che caratterizzò la nascita dell'archeologia preistorica interessa anche il territorio veronese intorno a due importanti istituzioni locali: l'Accademia di Agricoltura, Commercio e Arti e il Museo Civico. A stimolare le ricerche, che però non ebbero mai un carattere di sistematicità, su questo periodo furono essenzialmente più episodi, tra cui l'Esposizione preistorica del 1876 a Verona e le contemporanee scoperte estensi di Alessandro Prosdocimi. Tali avvenimenti, che videro indirettamente coinvolti anche i primi rappresentanti della paletnologia veronese, contribuirono da un lato a mettere sempre più in luce una nuova civiltà degna di nota nel panorama dell'Italia dell'età del Ferro e dall'altro a dare impulso alle ricerche sul campo e meglio inquadrare, da un punto di vista cronologico e culturale, le scoperte che si susseguivano nel territorio veronese (dai Lessini alla pianura).

Parole chiave: Verona, storia degli studi, paletnologia, protostoria.

INTRODUZIONE

Il presente contributo prende spunto da una tesi di laurea magistrale discussa da uno degli scriventi (G.A.) presso l'*Alma Mater Studiorum* Università di

Bologna (*Il territorio veronese durante l'età del Ferro: storia degli studi e dinamiche del popolamento*, relatrice professoressa Elisabetta Govi, co-relatore

1. Il presente testo è stato discusso, condiviso ed elaborato da entrambi gli autori.

Massimo Saracino) e incentrata sull'evoluzione del popolamento nella provincia di Verona durante l'età del Ferro. In quella occasione uno dei capitoli era stato dedicato alla storia degli studi e delle ricerche sul campo e si è deciso, vista la mole, di rielaborarlo in tre parti differenti: la prima incentrata sul collezionismo e sugli albori della paletnologia veronese, la seconda relativa al periodo che va dagli inizi del XX secolo al secondo dopoguerra e la terza riguardante le fasi più recenti (dagli anni '60 del XX secolo a oggi).

Se da un lato il presente lavoro non ha pretese di aggiungere nulla di nuovo al dibattito scientifico (v. Guidi, 2014), dall'altro vuole comunque raggruppare selettivamente i numerosi lavori sull'argomento e ben delineare un quadro circostanziato sulle principali attività di collezionismo, studio e ricerca sull'età del Ferro (dalla seconda metà del X al III sec. a.C.) nel territorio veronese susseguitesesi dal XIV al XIX secolo, che hanno contribuito all'evoluzione del rapporto fra studiosi e materia.

IL COLLEZIONISMO TRA XIV E L'UNITÀ D'ITALIA

A Verona il collezionismo artistico-antiquario, limitato a poche categorie di reperti legati alla storia romana, quali epigrafi, monete e statue, sembra avere la sua più antica attestazione agli inizi del Trecento (Franzoni, 1981: 208). La sua nascita, relativamente precoce nel panorama del Veneto, va ricondotta al notevole potere attrattivo che la Biblioteca del Capitolo, ricca di antichi manoscritti, esercitò sugli intellettuali a partire dalla fine del Duecento (Billamovich, 1976). Non a caso in passato è stato sostenuto che proprio qui Petrarca, nella stessa città in cui aveva scoperto le lettere di Cicerone *Ad Atticum*, cominciò a collezionare monete e forse favorì la nascita di altre raccolte (Franzoni, 1981: 207-208; Bolla, 2019: 8).

Come nel resto d'Italia, nei secoli seguenti le collezioni si moltiplicarono, divenendo, insieme al mecenatismo verso le arti, uno *status symbol* dell'aristocrazia. Col loro crescere gli vennero dedicati degli spazi appositi all'interno delle dimore signorili, nello specifico Studi e Gallerie, nei quali frequentemente l'oggetto antico aveva un mero valore decorativo (Franzoni, 1981: 264-266).

Tra le personalità più ragguardevoli del collezionismo cinquecentesco veronese, come ricordò più tardi lo stesso Scipione Maffei (1675-1755), fu il conte Mario Bevilacqua (1536-1593). Questi iniziò

a formare il suo museo nel palazzo dei SS. Apostoli (oggi su Corso Cavour) intorno al 1570 con l'aiuto del prozio Girolamo Canossa (m. 1592), creando una collezione che spaziava molto geograficamente e tematicamente: oltre ad antichità comprendeva anche dipinti, in particolare ritratti e codici, sia a stampa che manoscritti. Tra le altre cose sarebbe stato proprietario, come ci tramanda un testo della fine del secolo, di un bronzetto con incise delle "lettere etrusche" rinvenuto a Bionde di Visegna, nell'attuale comune di Salizzole (Berro, 1964; Franzoni, 1980, 1981; Salzani, 1985a).

Mentre in questa fase il collezionismo artistico-antiquario si trovava in una condizione matura, cominciò ad affacciarsi sulla scena uno nuovo, incentrato sulle "cose della natura" e che trovò fra i suoi primi esponenti, insieme al bolognese Ulisse Aldrovandi (1522-1605) e al napoletano Ferrante Imperato (1559-1631), il farmacista veronese Francesco Calzolari (1521/22-1609/10), quest'ultimo allievo del medico umanista Girolamo Fracastoro (1476/78-1553) (Ruffo, Curi, 2005: 12-16). Il museo, allestito nella sua abitazione, conteneva materiale estremamente eterogeneo (animali imbalsamati, fossili, vasi), fatto che lo accomunò alle *Wunderkammern* o *Raritätenkammern* ben diffuse in Nord Europa, in cui la curiosità fungeva da primo movente della loro composizione e la meraviglia dello spettatore era il loro fine (Trigger, 1989: 47-54; Schnapp, 1993: 131-137). Diversamente da altre città dell'Italia settentrionale dove il collezionismo sembra essere una caratteristica nobiliare, a Verona la situazione pare più variopinta con famiglie e personaggi privi di titoli nobiliari affascinati dal fenomeno (Bolla, 2019: 17).

Col Seicento il collezionismo cambiò: mentre da un lato si redigevano i primi inventari, attività raramente svolta nel secolo precedente, dall'altro aumentò l'interesse verso il collezionismo naturalistico. A Verona la sintesi di questo cambiamento fu rappresentata dal conte Lodovico Moscardo (1611-1681). Egli creò una collezione che oltre a essere composta da trecento fra dipinti e incisioni, cinquemila fra monete e medaglie e seicentocinquanta sculture, bronzi e oggetti di scavo, includeva anche gran parte della collezione Calzolari. Di questa pubblicò nel 1656 a Padova una descrizione in due volumi con il titolo *Note overo memorie del Museo di Lodovico Moscardo nobile veronese*, fatto raro in un'epoca in cui cataloghi o simili lavori rimanevano solitamente inediti. In questa notevole quantità di oggetti interessa menzionare quello che è stato interpretato come uno spiedo votivo in bronzo con impugnatura romboi-

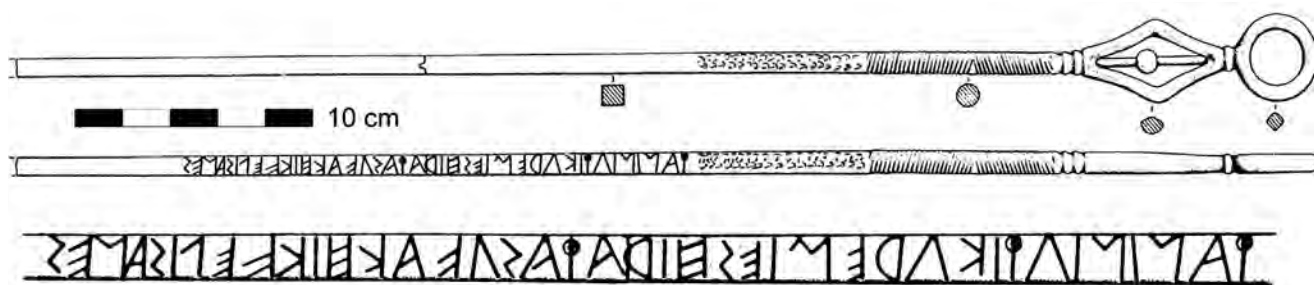


Fig. 1 – Spiedo votivo con iscrizione retica da Ca' dei Cavri (elaborazione da Salzani, 1987a: 182)

Votive skewer with Rhaetian inscription from Ca' dei Cavri (elaboration from Salzani, 1987a: 182)

dale e terminazione a losanga e anello, recante un'iscrizione retica (Figura 1), rinvenuto durante dei lavori agricoli nel 1672 o negli anni immediatamente precedenti, a *Ca' dei Cavri* (a ovest di Verona) insieme a quattro dischi di bronzo. Il primo, oggi conservato nel Museo Miniscalchi-Erizzo, venne interpretato inizialmente dallo stesso Moscardo come un'armagota, passando alla storia come la *Spada di Verona*, mentre i dischi di bronzo, oggi dispersi, come dei finimenti di cavalli (Franzoni, 1981; Pomian, 1986; Marinetti, 1987; Salzani, 1987a; Ruffo, Curi, 2005). Nel recente *corpus* delle iscrizioni retiche (MLR nr. 290) l'iscrizione, incisa con tratto sottile e molto accurato, viene datata con seriazione epigrafica tra la metà del V e la fine del III sec. a.C. (fase II di Sanzeno) e, come ben chiarisce la parola *uφiku* (*donato*, variante del più noto *utiku*) si tratta di un dono (Marchesini, 2015: 255-256). Anche la parola *φanini*, che compare anche nella situla di Providence (*φanin*), potrebbe indicare l'oggetto donato (Marchesini, Zaghetto, 2019: 338-339). Per le altre parole, alcune caratterizzate da marca di possesso -s, non vi sono al momento spiegazioni soddisfacenti.

Il vero cambio di passo avvenne col Settecento quando, oltre a un notevole aumento delle collezioni naturalistiche, in particolare di fossili e minerali (Pomian, 1986: 31-53), crebbe l'interesse verso le curiosità antropologiche, in particolare orientali, e, già dalla fine del Seicento, verso la numismatica medievale, che di conseguenza contribuì a una parziale rivalutazione di quest'epoca storica (Pomian, 1986: 53-70). In questo periodo si registra altresì un lento e inevitabile indebolimento economico dell'aristocrazia, che comportò lo smembramento di importanti collezioni, accelerato sul finire del secolo dai trafugamenti operati dai francesi durante l'occupazio-

zione della città. Figura emblematica di questa fase fu il sopra menzionato Scipione Maffei, collezionista e celebre intellettuale che, spinto dalla concezione illuministica dell'universalità della cultura, realizzò un nuovo museo lapidario «universale e pubblico» nel cortile dell'Accademia Filarmonica di Verona (Pomian, 1986: 53-56). Il suo contributo, insieme a quello di altri intellettuali coevi e ben più famosi come Caylus e Winckelmann, fece sì che «una cultura antiquaria a prevalenza filologica si» trasformasse «in una cultura antiquaria a prevalenza archeologica e artistica, prima del massiccio ritorno della filologia agli inizi del secolo XIX» (Pomian, 1986: 56).

Oltre a Maffei ci furono molti altri collezionisti a Verona in questo secolo, che tuttavia non diedero mai un contributo culturale pari al suo: uno di questi fu Iacopo Verità (1744-1827), che qui ricordiamo in quanto fu in possesso di due alari in bronzo decorati con teste leonine e un coperchio di situla rinvenuti nel 1763 a Gazzo dal conte Ercole Giusti. In assenza di riferimenti archeologici del contesto di ritrovamento, la cronologia incerta dei due reperti, attualmente conservati nel Museo Archeologico al Teatro Romano di Verona (d'ora in poi MATR), si basa essenzialmente sulla datazione dei pendenti a figura umana con barca solare, attaccati alle protomi di felino e, secondo diversi autori, va inquadrata tra la fine dell'VIII e il V sec. a.C. (Marchini, 1972; Salzani, 1983a; Pomian, 1986; Bolla, 2021: 20-22). Come ci informa Carlo Cipolla (1854-1917), del «Museo Verità» facevano parte anche sei vasi ossuari zonati, tre coperchi e tre coppe (una a vernice nera), di provenienza ignota, caratteristici «del terzo periodo euganeo, giusta la classificazione proposta dal ch. Prosdocimi» (Cipolla, 1884a: 10). Luciano Salzani (2014) recentemente è inoltre riuscito a ricostruire

la pertinenza a questa collezione di tre asce in bronzo che, sulla base di certe informazioni storiche ed elementi crono-tipologici, potrebbero provenire dal territorio veronese, anche se non vi è la certezza piena. Nella fattispecie, trattasi di due asce ad alette superiori inquadrare al VII sec. a.C. (Salzani, 2014: 139, figg. 3, 2-3) e un'ascia a occhio tipo Cuma data tra IX e VIII sec. a.C. (Salzani, 2014: 142, fig. 4, 3).

Al 1785 risale invece la segnalazione del sacerdote Marco Pezzo, ripresa un secolo più tardi dal De Stefani (1885a), di tombe dell'età del Ferro sul Monte Loffa, nei pressi di Sant'Anna d'Alfaedo, la cui presenza risulta incerta e da verificare (Salzani, 2001-2002).

A cavallo tra il XVIII e il XIX secolo operò invece l'abate Giuseppe Venturi (1766-1841), noto erudito e collezionista di libri e anticaglie, del cui museo, nel catalogo dell'Esposizione preistorica del 1876, figurano 6 vasi (3 ossuari zonati e 3 coppe decorate) attribuiti all'età del Ferro, ma di provenienza ignota (Goiran, 1876: 36). Tali materiali furono lasciati in eredità alla Biblioteca civica e nel 1863, per ordine del podestà Ottavio di Canossa, ne fu disposto il trasferimento al Museo (Marchini, 1972: 71-72).

Con l'Ottocento il collezionismo, sempre legato soprattutto al mondo classico, passò da essere un fenomeno principalmente aristocratico a uno borghese. Una delle differenze che contraddistinse questa fase rispetto alla precedente fu la mancata ereditarietà all'interno della famiglia, a cui venne preferita la vendita o cessione a enti pubblici come il Municipio di Verona. Da questa pratica nacque l'esigenza di creare un luogo che raccogliesse questa grande varietà di oggetti e così, con la delibera del Consiglio comunale del 30 dicembre 1854, venne istituito il Museo Civico della città con sede a Palazzo Pompei, lasciato alla città dal conte Alessandro, e inaugurato tra dicembre del 1860 e gennaio del 1861 (Marchini, 1972: 37; Franzoni, 1981: 266; Ruffo, Curi, 2005: 45-46).

LA NASCITA DELLA PALEOTNOLOGIA VERONESE (1861-1899)

Negli anni dell'unità nazionale, grazie a contatti e collaborazioni con studiosi d'oltralpe, cominciò a diffondersi in Italia una nuova concezione dello studio delle antichità, nata alcuni decenni prima in Danimarca, che permise al collezionismo antiquario di compiere i primi significativi passi per diventare una scienza autonoma (Guidi, 1988: 12-17, 25-29;

Schnapp, 1993: 260-268). I più sensibili a queste novità furono i cultori della paleoetnologia, ovvero di preistoria e protostoria, mentre i classicisti rimasero ancora fortemente legati al modello filologico settecentesco (Guidi, 1988: 26-27; Schnapp, 1993: 269-274). Così in questo periodo in Italia comparve per la prima volta una generazione di intellettuali che si dedicò allo scavo e alla pubblicazione di siti e materiali relativi alle fasi più antiche della storia dell'uomo e pertanto definiti *pionieri* della paleoetnologia.

Tale entusiasmo fu legato in parte a un considerevole aumento di ritrovamenti e segnalazioni anche nel seno di importanti opere pubbliche che nel caso del veronese riguardarono, ad esempio, la bonifica delle Valli Grandi, la realizzazione della ferrovia Mantova-Legnago e Verona-Caprino, l'esecuzione dei canali Camuzzoni e Garda-Mincio, la costruzione di alcuni forti, come quello di San Briccio (Brugnoli, 1997: 175), tutte opere che dovevano mettere la città di Verona e del suo territorio al passo della rivoluzione industriale (Zangarini, 1991).

Molti membri di questa generazione di idealisti e positivisti operarono anche a Verona: radunatisi all'interno dell'Accademia di Agricoltura, Commercio e Arti, composero un gruppo estremamente variegato per formazione e professioni, che operò sul territorio per circa un trentennio dalla metà del XIX secolo (Facchi, 2005a: 108, 2014: 105-106). In seguito all'annessione al Regno d'Italia nel 1866, sancita con il famoso plebiscito del Veneto, il loro interesse nei confronti dell'archeologia portò alcuni di loro a rivestire cariche di tutela del patrimonio culturale che proprio in quegli anni vennero istituite dal Ministero (Biondani, 2005: 153-162; Brugnoli, 2005: 293-299), come la *Commissione consultiva conservatrice di belle arti ed antichità*, a cui seguì nel 1876 l'istituzione della figura dell'*Ispettore agli scavi e ai monumenti della provincia*, di nomina ministeriale (Brugnoli, 1997: 166-167). Personalità come Pier Paolo Martinati (1812-1878) – «iniziatore e maestro» della paleoetnologia veronese (Pigorini, 1878b: 105), «divulgatore della nuova scienza, coordinatore e motore propositivo» (Facchi, 2014: 106) – e Stefano De Stefani (1822-1892), oltre a occupare tali ruoli, vennero coinvolti anche nella gestione del Museo Civico contribuendo a farvi confluire materiali provenienti da siti preistorici e protostorici emersi in quei decenni o facenti parte di collezioni private (Facchi, 2005a: 112; Brugnoli, 2001-02: 21-26; Ruffo, Curi, 2005: 45-46). A tali personaggi eminenti vanno aggiunti anche il naturalista Gaetano Pellegrini (1824-1883), il botanico Agostino Goiran (1835-

1909), lo storico Carlo Cipolla e l'insegnante di liceo Francesco Dal Fabbro (1838-1904). Nonostante non siano stati incisivi per la storia degli studi italiani, come lo fu il gruppo emiliano, e talvolta nemmeno troppo rigorosi nella metodologia di scavo e documentazione, a questi *pionieri* va riconosciuto il merito di aver attirato per la prima volta l'attenzione, non soltanto della comunità scientifica, ma anche del grande pubblico, verso la preistoria e protostoria di un territorio che vantava una lunga e consolidata tradizione di studi classici e naturalistici.

La loro iniziativa più celebre fu indubbiamente l'*Esposizione Preistorica Veronese* presso il Museo Civico in Palazzo Pompei, dove Martinati come conservatore dal 1871 al 1878 aveva nel frattempo costituito la sotto-sezione di Paletnologia (Facchi, 2005b: 112). L'evento, ispirato a quello organizzato a Brescia l'anno precedente, si tenne fra il 20 febbraio e il 3 aprile 1876. Fu ardentemente desiderato da Martinati, curato da Agostino Goiran e definito poco più tardi da Pellegrini (1878: 3) come «un potente mezzo per istimolare i cultori di questa scienza e per propagare nel pubblico la conoscenza delle nostre antichità. Dopo questa mostra, tanto le collezioni pubbliche quanto le private si accrebbero di nuovi oggetti, e si conobbero nuovi strati archeologici». Nel corso dell'inaugurazione Pietro Paolo Martinati proferì un discorso, nel quale faceva il punto delle conoscenze sulla paletnologia veronese e concludeva con un'esortazione a «Credere e discutere [...], perché il Vero non teme ma sfida, non fugge ma accetta la discussione, e il libero e ragionevole ossequio del sapiente gli è più gradito che il cieco e tremante omaggio del servo» (Martinati, 1876: 199).

Nel corso dell'Esposizione ebbero occasione di esporre le proprie collezioni diversi enti e collezionisti privati (Facchi, 2005a e b). Tra questi l'ingegner Antonio Mazzotto che era in possesso di diversi palchi di cervidi, uno di capriolo e un «parallelepipedo di argilla [...] ornato in testa di una croce diagonale profondamente incisa» (Martinati, 1876: 179) rinvenuti nel 1846 alle falde del colle di San Briccio di Lavagno. Tra i materiali del Museo Civico esposti si trovava anche un coltello datato all'VIII sec. a.C. rinvenuto a Bovolone nel 1871 insieme a un palco di corna di cervide, dono di Bernardino Biondelli per celebrare l'Esposizione (Goiran, 1876).

È interessante notare come in questa occasione fu data molta importanza all'aspetto topografico (Facchi, 2005b), caratteristica per cui i *pionieri* veronesi sembrano distinguersi anche nelle ricerche successive (Boaro, 2001-02: 41-43).

Nello stesso anno, a Este nel podere Boldù-Dolfin, si scoprirono casualmente sette tombe, di cui due contenenti ricchi corredi e situle bronzee decorate a sbalzo. Tale rinvenimento indusse Alessandro Prosdocimi (1843-1911), conservatore del museo locale, a intraprendere ulteriori scavi e a sottolineare il riconoscimento di un'importante civiltà, definita allora «atestina», degna di nota nel quadro dell'Italia pre-romana (Fogolari, 1981: 28). A complimentarsi con Prosdocimi vi fu, tra gli altri, lo stesso Martinati, che in una lettera del 12 ottobre 1876, oltre a dare suggerimenti sulle modalità di recupero delle tombe, lo esortava a proseguire le ricerche aggiungendo che, nel considerare le situle laminate simili a quelle etrusche, escludeva che potesse trattarsi di «una civiltà più remota ed immatura» (Chieco Bianchi, 2002: 26-27).

Tra il 1876 e il 1878, anno di morte di Martinati, vennero effettuati alcuni rinvenimenti nel veronese dai suoi familiari e collaboratori: nel 1876 fu scoperta una sepoltura in località Madonna dell'Uva Secca a Povegliano, le cui fibule, datate all'ultimo quarto del VII sec. a.C., sono oggi conservate al Museo delle Civiltà di Roma (Peroni, 1975); nel 1877 Gaetano Pellegrini consegnò a Luigi Pigorini (1842-1925) un'ascia ad alette rinvenuta alla Rocca di Garda, datata tra secondo e terzo quarto del VI a.C. (Pigorini, 1877; Carancini, 1984) e nel 1878 si rinvenne una sepoltura nel Fondo Guasti di Valle Burgan, presso Sorgà, consegnata dall'arciprete di Castel D'Ario don Francesco Masè (1808-1884) sempre a Pigorini (Pigorini, 1878a).

Tra i ritrovamenti più eclatanti avvenuti in questo periodo, vi fu sicuramente l'elmo conico di Oppeano datato al V sec. a.C. e rinvenuto «alla profondità di circa un metro fra ghiaie e sabbia dell'Adige nel fondo degli eredi M. Carlotti» (Pigorini, 1878b: 105-106). L'oggetto in lamina bronzea doveva far parte della collezione privata del Martinati che, in uno scambio epistolare con Pigorini (suo genero), scrive di averlo visto per la prima volta nel 1877 a casa di una delle sue figlie a Cerea. Alla sua morte, la vedova vendette la collezione archeologica allo Stato italiano, che depositò l'elmo nel 1880 presso il Museo Archeologico Nazionale di Firenze dov'è tuttora conservato (Salzani, 2013: 42). Della suddetta collezione facevano parte anche altri reperti (principalmente fibule bronzee) donati da Giambattista Maleساني di Verona, rinvenuti nel fondo Consolo, detto la Montara, e precisamente ai Sabbioni, datati tra IX e VI sec. a.C. (Pigorini, 1878b). In tale scritto Pigorini, ribadendo la sua secolare teoria, sottolineava come

i reperti, a eccezione dell'elmo, mostrassero affinità stilistiche sia con l'ambito Felsineo che con quello Euganeo, «ma a veder bene e per le loro specialità appartengono all'Euganeo» (Pigorini, 1878: 123). Si data infine genericamente a questi anni un appunto di Pigorini, rinvenuto nell'archivio conservato all'Università di Padova, che documenta il recupero da parte di una figlia di Martinati, Antonietta, di un'urna cineraria zonata, due fibule e una coppetta, datate al V sec. a.C. e provenienti da un nucleo di sepolture a San Vito di Cerea sulla strada verso Asparetto (Prosdocimi, 2005).

Con la morte di Martinati e di altre due figure cardinali come Gaetano Pellegrini nel 1883 e don Francesco Masè nel 1884, uno degli scopritori del sito di Coazze di Gazzo Veronese (Trevisan, Saccoccio, 2015), l'unico che rimase a occuparsi di paleoetnologia fu Stefano De Stefani che solo dopo l'*Esposizione Preistorica Veronese* si avvicinò alla ricerca archeologica più compiutamente (Salzani, 2005: 136), nonostante Martinati avrebbe preferito non affidargli incarichi prettamente scientifici, ma soltanto rappresentativi e burocratici (Boaro, 2001-02: 40).

Nel corso della sua attività, che si concentrò per la maggior parte tra il 1879 e il 1889, pubblicò a più riprese nel 1879, 1882 e 1888 il rinvenimento di alcune sepolture rinvenute nel Fondo Bellinato di Minerbe, oggi localizzato grazie allo studio dell'archivio privato De Stefani. Tutti i materiali, datati fra la metà del VII e la metà del VI sec. a.C., vennero consegnati al Museo Civico tranne un piccolo nucleo che nel 1980 venne esposto nel Museo Fioroni di Legnago (De Stefani, 1879; Salzani, 2005; Salzani, De Stefani, 2013). Tra 1880 e 1881 pubblicò il rinvenimento di nuovi materiali dal Fondo Coazze di Gazzo Veronese che furono donati al Museo Civico (De Stefani, 1880, 1881a). Sempre nel 1881, in seguito alla prima comunicazione al Congresso Geografico Internazionale di Venezia del ritrovamento nel territorio di Breonio di oggetti in selce dalle forme più svariate, De Stefani diede inizio alla controversia sulle cosiddette «selci strane» tra sostenitori dell'autenticità (tra cui De Stefani, Martinati, Chierici e Pigorini) e oppositori (De Mortillet, Mantegazza, Orsi, Setton Karr), manufatti che più tardi si rivelarono essere falsificazioni realizzate dai locali contadini (Longo, Chelidonio, 2001-02). Nel 1884 segnalò il rinvenimento di due probabili sepolture a Palazzina di Isola della Scala datate tra la seconda metà del VI e la seconda metà del IV sec. a.C. (De Stefani, 1884a; Aspes *et al.*, 1976: 162). Nei pressi di Rivoli, in seguito ai rinvenimenti nel 1880 di un *dolio* in

località Castello (Cipolla, 1881; Salzani, 1985-86), nel 1883 di un bronzetto di un ammantato con in capo un *tutulus*, datato al V sec. a.C. e successivamente confluito nel MATR (Fogolari, 1950-51: 370, n. 44; Franzoni, 1980: 46, n. 29; Salzani, 1985-86), De Stefani (1885c) menzionò la scoperta di alcuni frammenti di vasellame oggi dispersi ancora in località Castello e in una cava di sabbia ai piedi del Forte di materiali riconducibili su base tipologica a due o più sepolture datate tra VIII e VII sec. a.C. (De Stefani, 1885a, 1885b; Carancini, 1975: 265, n. 2002; Aspes *et al.*, 1976: 101-110; Salzani, 1985-86; Von Eles Masi, 1986: nrr. 1324 e 1384a; Macellari, 2001-02).

Un'altra zona in cui concentrò notevolmente i suoi sforzi e le sue ricerche fu nell'allora Comune di Breonio, il cui territorio è oggi diviso fra quelli di Sant'Anna d'Alfaedo e Fumane. Nel 1881 acquistò da un contadino una serie di oggetti, probabilmente parte di un rogo votivo, o *Brandopferplatz*, provenienti da Campo Paraiso (Figura 2) e datati tra la fine del VII e la seconda metà del V sec. a.C. (De Stefani, 1881b; Aspes *et al.*, 1976; Salzani, 1979a, 1981; Von Eles Masi, 1986; Gleirscher, 1991-93; Macellari, 2001-02). Quello stesso anno cominciò a interessarsi al sito di Monte Loffa, ricadente nelle proprietà dell'allora sindaco Michele Morandini. Qui, tra il 1883 e il 1888, furono organizzati degli scavi programmatici, che portarono alla luce 27 fondi di «capanna», come afferma nella pubblicazione del 1885-86, pertinenti a un abitato datato fra il V e il I sec. a.C. di cui il geometra Pietro Arieti fece un rilievo edito soltanto recentemente (De Stefani, 1885a; Salzani, De Stefani, 2013). Col passare degli anni De Stefani, probabilmente a causa di impegni di lavoro, problemi di salute e della vicenda delle «selci strane» (Boaro, 2001-02), perse progressivamente interesse per questo sito, fatto che giustifica la mancanza di documentazione in particolare per gli ultimi scavi. Così spesso si trovò a delegare la loro supervisione a terzi: nelle migliori occasioni questi furono studiosi del calibro di Pigorini e Pompeo Castelfranco (1843-1921), in altre era gente del posto, come lo stesso sindaco Morandini (De Stefani, 1885-86; Salzani, 1981, 2001-02; Bianchi, Lincetto, 2001-02; Macellari, 2001-02; Migliavacca, 2001-02). Nella sua pubblicazione del 1885 colse l'occasione per menzionare il rinvenimento di una fibula La Tène scoperta durante la costruzione del vicino Forte Masua (tra Cavalo e Breonio) e oggi irreperibile (Salzani, 1981). L'anno seguente pubblicò una carta archeologica del Comune (De Stefani, 1886), come sintesi delle sue ricerche, in cui, oltre a figurare i siti

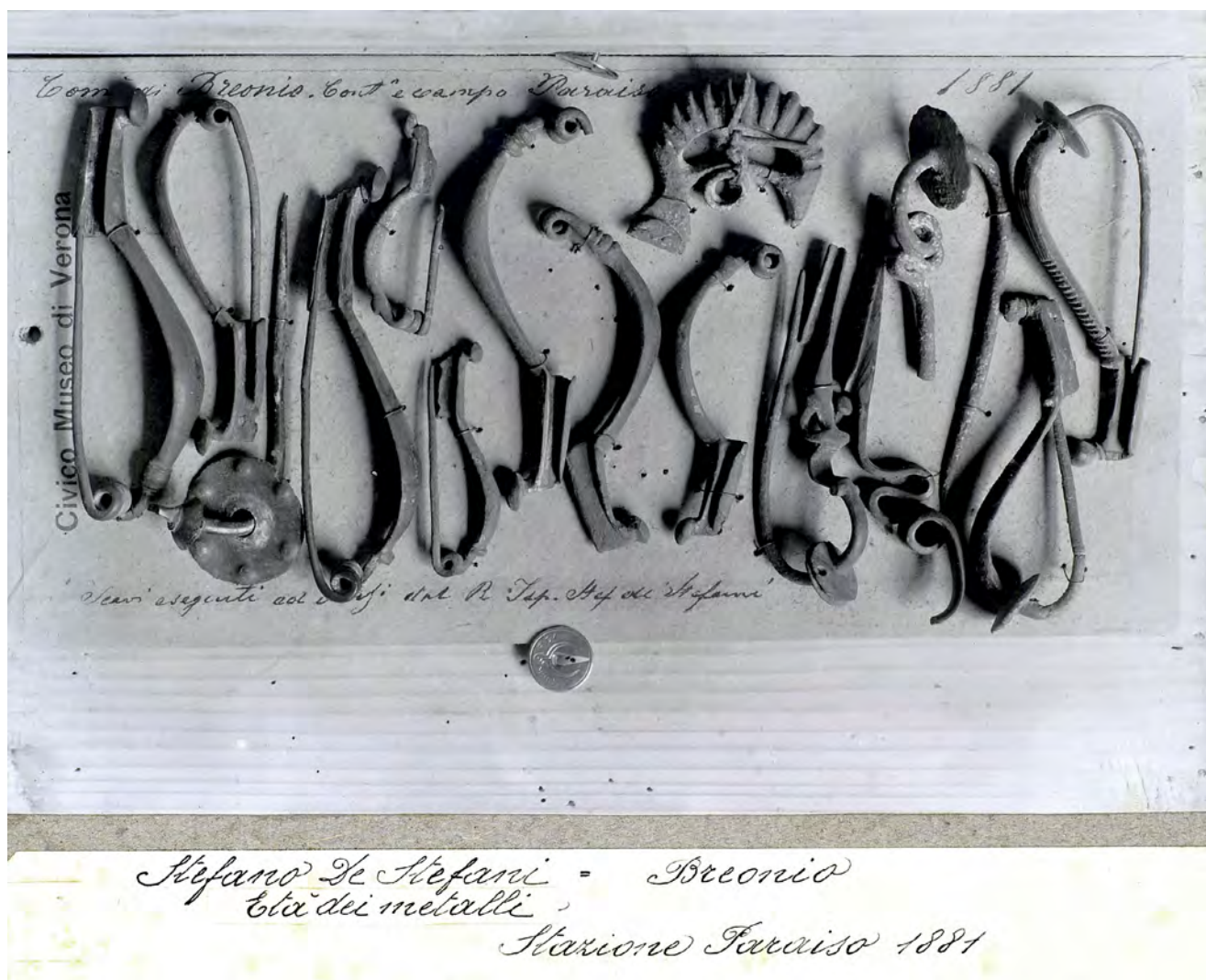


Fig. 2 – Immagine fotografica in mostra alla 1ª Esposizione Scientifica del 1929 di Firenze riguardante il cartone espositivo originale di alcuni reperti provenienti dal sito di Campo Paraiso (Archivio fotografico del Museo Galileo di Firenze)
 Picture exhibited at the 1st Scientific Exhibition of 1929 in Florence showing the original display board of some artefacts from the Campo Paraiso site (Photographic archive of the Museo Galileo, Florence)

appena menzionati, ne troviamo altri da lui definiti «misti» per la presenza sia di manufatti in bronzo che in ferro come «Covolo della Roba» (Salzani, 1979b, 1981), «Vajo della Merla» (De Stefani, 1884b; Salzani, 1979b), che restituirono materiali sporadici di V sec. a.C., e «Colarè» e «Covolo Camerini» di cui non resta altra testimonianza (De Stefani, 1888; Salzani, 1981).

Altri materiali, che non pubblicò mai ma che ci sono giunti grazie alla sua mediazione, sono due armille e un bracciale a spirale rinvenuti in data ignota a Valeggio sul Mincio (Zorzi, 1960; Salzani, 1987b), un nucleo di oggetti inquadrabili fra VI e IV sec.

a.C. oggi conservati presso il MATR con indicazione «tra S. Zeno e Colognola. Stefano De Stefani 1886» (Salzani, 1983b, 1985d), altri che si trovano nei depositi del Museo di Storia Naturale con indicazione «Stefano De Stefani. Settembre 1891. Le Franchine di Oppeano» (Salzani, 1985a) e un appunto del 1889, rinvenuto nel suo archivio privato, che ha rivelato i primi rinvenimenti della necropoli in località Caneviera nel Comune di Albaredo all'Adige (Salzani, 2005a). A questi si aggiunge che forse sono stati da lui scoperti anche i materiali datati al V sec. a.C. provenienti da Ca' del Vecio, nel Comune di Sant'Anna

d'Alfaedo, oggi conservati nei depositi del Museo Civico di Storia Naturale (Salzani 1979b, 1981).

Negli stessi anni in cui De Stefani compiva le sue ricerche e i suoi studi, il conte Carlo Cipolla, dal 1881 Ispettore degli Scavi e Monumenti del circondario di Verona, nonostante si dedicasse per lo più ad antichità classiche, non mancò di comunicare alcune importanti rinvenimenti dell'età del Ferro. Oltre al già menzionato rinvenimento di Castello di Rivoli, nel 1880 diede notizia della scoperta di alcune sepolture a Povegliano, in località Campi Magri della Bora e Madonna dell'Uva Secca, datate tra III e II sec. a.C. (Cipolla, 1880; Aspes *et al.*, 1976). Nel 1883, durante i lavori di costruzione del forte di San Briccio di Lavagno, diede notizia del rinvenimento di diversi materiali archeologici divisibili in due gruppi: il primo inquadrabile verso la fine del VI sec. a.C. e il secondo fra III e II sec. a.C. a cui si aggiungono due palchi di cervo con un'iscrizione retica (Cipolla, 1883, 1884a, 1885a; Aspes *et al.*, 1976; Rizzetto, 1977). Infine nel 1885 pubblicò il rinvenimento di una necropoli emersa durante i lavori della ferrovia Mantova-Legnago nei pressi di San Vito di Cerea (Cipolla, 1885b; Pigorini, 1886).

In questo periodo non mancarono comunque ritrovamenti casuali da parte di appassionati e studiosi locali, come quello del 1881 da parte di don Domenico Carcerieri durante i lavori di costruzione di un rustico a sud del Castejon di Colognola ai Colli, datati tra V e I sec. a.C. e consegnati al Museo Civico (Solinas, 1973; Rizzetto, 1973; Aspes *et al.*, 1976). Lo stesso anno in un fondo di proprietà Giusti, probabilmente a Gazzo Veronese, si rinvenne una cista a cordoni in lamina di bronzo che in seguito divenne parte della collezione Ancona (Capuis *et al.*, 1990: 214, n. 161.1). Nel 1884, Bernardino Biondelli (1804-1886) segnalò i resti di un colossale muro di cinta a Bosco Chiesanuova (Lessinia) attribuendone la realizzazione agli abitanti dell'Etruria circumpadana (Biondelli, 1884), ma la notizia è stata solo di recente smentita (Salzani, Ragnolini Sauro, 2014). Nel 1886, a Dolcè, in una località non precisata, viene rinvenuto un bronzetto raffigurante un lanciatore di giavellotto datato al V sec. a.C. (Franzoni, 1980: 188). Nel 1888 a Caprino Veronese si rinvenne un bronzetto confluito nel MATR raffigurante un gio-

vane stante con corona radiata in testa, interpretato da Giulia Fogolari come *Helios* e datato al III sec. a.C. (Fogolari, 1950-51: 373, n. 51; Franzoni, 1980: 72 n. 54; Salzani, 1985-86). Sempre nel 1888 furono rinvenute una fibula e due armille databili all'VIII sec. a.C. a Verona nei pressi di Porta San Giorgio, oggi conservate al MATR (Salzani, 1976; Saracino *et al.*, 2021). Nel 1889 si rinvenne a Isola Rizza un attacco d'ansa configurato a testa di bovide con anello soprastante datato al VI sec. a.C. e ora al MATR (Salzani, 1985a). Nel 1890 durante i lavori di sterro dei muraglioni della Binastrova, tra Piazza Isolo e Lungadige Re Teodorico a Verona, si rinvenne un colino in bronzo databile alla fine del IV sec. a.C. (Salzani, 1985b, 1985c), sebbene di recente la sua provenienza sia stata messa in dubbio (Bolla, Castoldi, 2016: 150). Dopo che Cipolla (1884a) aveva già segnalato il rinvenimento di materiali preromani, nel 1892 iniziarono a Baldaria, frazione di Cologna Veneta, i lavori di escavazione per la realizzazione di un nuovo alveo per il Fiume Guà. In questa occasione l'allora segretario comunale Cesare Gardellini salvò dei materiali pertinenti a una necropoli e databili fra fine IX e inizi VI sec. a.C., divenendo per questo merito Ispettore onorario di Cologna (Rossi, 2005).

Soltanto nel 1895 venne informato della scoperta Gherardo Ghirardini (1854-1920), all'epoca professore all'Università di Pisa, che si occupò della loro prima edizione (Gardellini, 1896; Ghirardini, 1897; Visentin, 1969). Questi costituirono inoltre il primo nucleo di oggetti del Museo Civico di Cologna Veneta (Dal Cero, 2005). Al Ghirardini, profondo conoscitore delle antichità felsinee ed etrusche, va riconosciuto il merito di aver posto grande attenzione alla civiltà dei Veneti antichi nell'ambito delle culture pre-romane.

Nel frattempo, nel 1892 con la morte di De Stefani si era chiusa l'esperienza dei *pionieri* veronesi e, sebbene non venissero più organizzate delle indagini mirate a risolvere delle problematiche scientifiche come era accaduto nei decenni precedenti, le notizie di rinvenimenti relativi all'età del Ferro si ridussero notevolmente, ma non scomparvero.

Nel 1893 a Verona sotto il pavimento «nella ex Chiesa di San Giovanni Decollato / Via Disciplina in Verona. Croce di Malta» (oggi Via Carducci)², D.G.

2. Conformemente a quanto già riportato in Saracino *et al.* (2021: 335), è verosimile che il ritrovamento sia stato fatto nella chiesa di Santa Maria della Neve (o della Giustizia), non più esistente. Sopra al primo altare laterale di destra, era collocato il dipinto della *Decollazione di San Giovanni Battista* di Alessandro Turchi, detto l'Orbetto (Lanceni, 1720: 239). L'opera dal 1811 era a Brera e dalla metà del XIX secolo nella chiesa italiana di San Pietro a Clerkenwell, Londra (Scaglietti Kalescian, 1999: 207-208). Da qui forse l'equivocità della notizia di Giovanni Belviglieri.

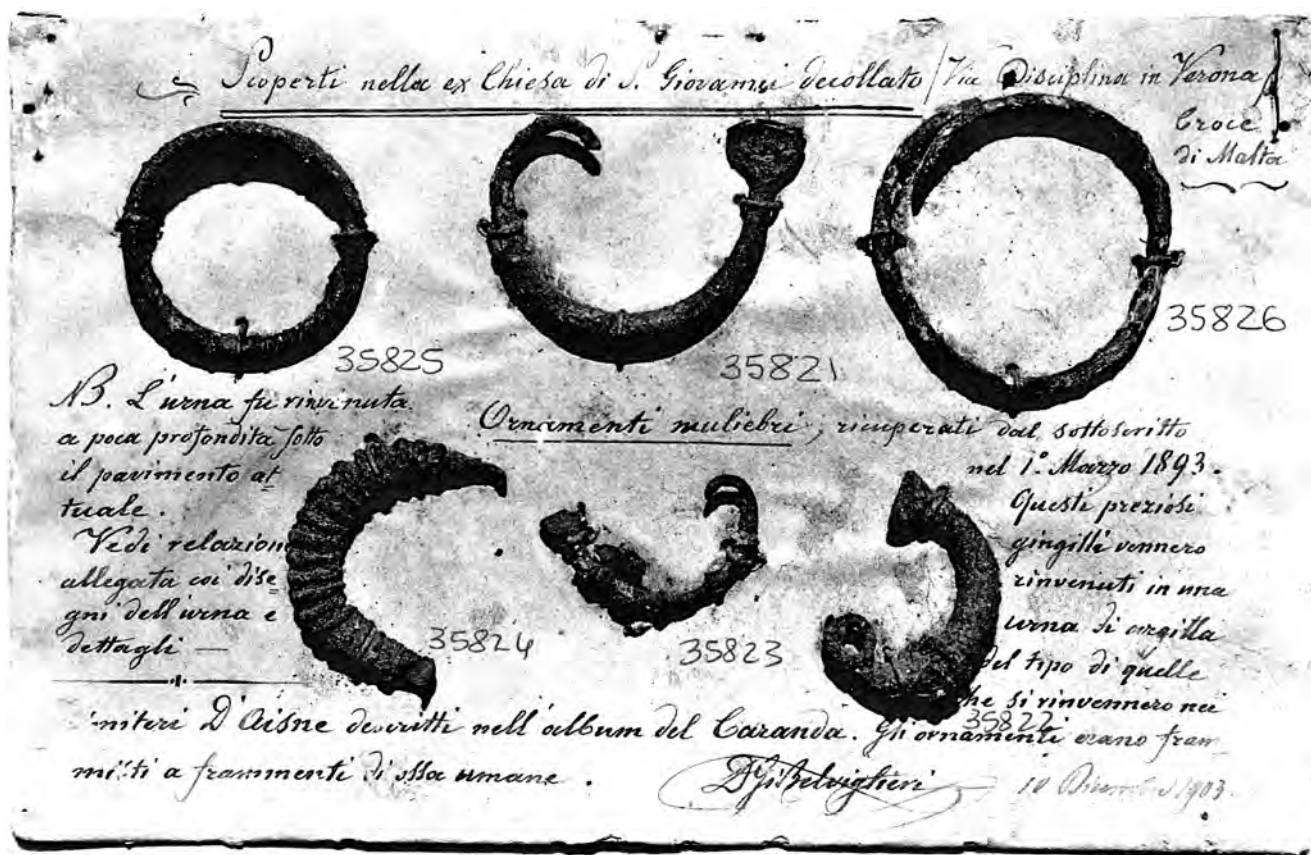


Fig. 3 – Fibule e armille rinvenute nel 1893 in Via Disciplina/Via Croce di Malta (ora Via Carducci) sul cartone espositivo originale e relativi disegni: nn. di inventario da 35821 a 35826 (Archivio del Museo Archeologico al Teatro Romano di Verona)
 Fibulae and armillae found in 1893 in Via Disciplina/Via Croce di Malta (now Via Carducci) on the original display board and related drawings: inventory numbers from 35821 to 35826 (Archives of the Archaeological Museum at the Roman Theatre in Verona)

Belviglieri rinvenne dei bronzi frammisti a ossa umane entro un'urna (andata dispersa), datati tra X e IX sec. a.C. (Salzani, 1985c; Saracino *et al.*, 2021: 335) (Figura 3). Nel 1899 venne rinvenuta a Villabartolomea una paletta rituale in bronzo datata tra seconda metà del VII e metà IV sec. a.C., oggi conservata al Museo Civico di Padova (Salzani, 1978).

Alla fine di questo secolo abbiamo la vaga notizia del rinvenimento di materiali a Ca' del Ferro di Oppeano in seguito consegnati al Museo Civico di Storia Naturale e a quello Nazionale di Este (Capuis *et al.*, 1990: 195, n. 54.9). Sempre senza precise indicazioni delle circostanze di rinvenimento sono una fibula e due pendagli provenienti da Pradelle di Gazzo Veronese, datate al passaggio tra VI e V sec. a.C. e conservati al Museo Civico di Storia Naturale (Aspes *et al.*, 1976: 169). Nel corso dei numerosi scavi svoltisi nelle palafitte di Peschiera tra la seconda metà dell'Ottocento e inizi del Novecento si rinvennero tre *sympula* in bronzo, uno dalla palafitta di «Bacino Marina» e due da quella di «Imboccatura di Mincio», e una fibula lateniana, senza un'indicazione più precisa, oggi conservati al Museo di Storia Naturale e datati agli inizi della tarda età del Ferro (Zorzi, 1960; Aspes *et al.*, 1976: 174). Infine nell'attuale Comune di Brentino – Belluno venne rinvenuta una fibula databile al V sec. a.C. oggi conservata nel Museo Civico di Rovereto (Capuis *et al.*, 1990: 35, n. 18.4).

CONCLUSIONI

Come si è visto, fin da quando i paradigmi dell'archeologia iniziarono a delinearsi in Italia, a Verona le indagini sulla preistoria del territorio vennero intraprese principalmente da studiosi della medio-alta borghesia locale (e non solo) provvisti di un bagaglio culturale plurimo (di professione notai come Martinati, naturalisti come De Stefani, Pellegrini e Goiran o storici come Cipolla) che li spinse a occuparsi anche di paleoetnologia. Il fervore positivista verso la disciplina (riconosciuta accademicamente solo nel 1875), così come una radicata cultura naturalistica erano fortemente presenti a Verona già alla metà del XIX secolo. Tali aspetti erano testimoniati da tutta una serie di attività, come le iniziative dell'Accademia di Agricoltura, Commercio e

Arti (ben frequentata dai padri nobili della preistoria veronese), la scoperta casuale della palafitta di Peschiera nel 1851³ a opera del genio militare austriaco e oggetto di ricerche già dal 1860 su iniziativa del Martinati e grazie a un finanziamento di 200 fiorini da parte dell'Accademia (von Sacken, 1865: 7-9; De Mortillet, 1865: 188; Martinati, 1876: 174-176; De Stefani, 1883: 258-259) e dalla nascita del Museo Civico (inaugurato ufficialmente nel 1861) verso cui confluirono numerose collezioni anche su impulso dell'Accademia.

Alcuni eventi culturali post-unitari (v. ad esempio: il V Congresso Internazionale di Antropologia e Archeologia Preistoriche di Bologna del 1871, l'uscita nel 1875 del I numero del *Bullettino di Paleontologia Italiana*, l'inaugurazione nel 1876 del Museo Nazionale Preistorico ed Etnografico di Roma) e le attività di ricerca e istituzionali da parte di figure emblematiche come Pigorini, Chierici e Strobel (per citarne alcuni), non fecero che rafforzare l'importanza e l'interesse per la nuova scienza, rivelatasi presto «utile elemento di unificazione» (Guidi, 1988: 26). In tale quadro, l'interesse mostrato dallo stesso Pigorini verso il territorio veronese in relazione alla sua teoria sulla migrazione degli Italici (Facchi, 2005: 127-131), ma anche per aggirare potenziali conflitti di competenza tra Stato ed enti locali (Facchi, 2014: 106), lo spinse a legarsi agli studiosi e ai collezionisti locali e soprattutto alle loro ricerche e ai loro ritrovamenti. Tale vicinanza e interesse lo portò a intessere una profonda amicizia col Martinati, di cui sposò nel 1879 la figlia Nilla.

Tuttavia, i *pionieri* della paleontologia veronese non erano particolarmente attratti dall'età del Ferro, mentre lo erano maggiormente da altri contesti, come ad esempio le palafitte del Lago di Garda e la Lessinia, rispettivamente molto più ricche in manufatti bronzei e in selce. Territori verso i quali venivano maggiormente e preferibilmente dirottati i finanziamenti ministeriali, grazie anche all'interessamento di Pigorini (Salzani, 2005a: 137). Nemmeno i ritrovamenti della civiltà villanoviana a opera di Giovanni Gozzadini (sposato con la veronese Maria Teresa Serego Alighieri, amica personale di De Stefani) e di quelli a Este da parte di Prosdocimi, alterarono di molto i loro interessi.

I 46 siti dell'età del Ferro segnalati e/o indagati (Tabella 1 e Figura 4) nel corso dei due ma-

3. I primi rinvenimenti di «molti cocci di grossolani vasi di argilla» (Martinati, 1876: 175), riferibili a quella che solo 30 anni più tardi sarà riconosciuta come palafitta, avvennero nel 1830.

cro-periodi storici compresi tra XIV e XIX secolo (4 per il periodo legato al collezionismo antiquario e 42 riferiti alle attività dei primi paleoetnologi), sovente casuali e isolati, riferiti a bronzi o a sepolture, raramente contestualizzati dal punto di vista stratigrafico, spesso nei possedimenti degli studiosi o in quelli di amici e parenti, venivano comunque raccolti, studiati, pubblicati e costituivano anche oggetto di scambi con altri ricercatori o erano venduti a Musei per finanziare altri sca-

vi e ricerche, come da prassi consolidata in quei tempi. Tali numeri esigui sono anche da mettere in relazione con la difficoltà di controllare il territorio di competenza che li portava spesso a fidarsi delle comunicazioni che ricevevano dai locali sindaci, come nel caso dei primi inventari di oggetti d'arte ed edifici di interesse archeologico, per i quali spesso gli amministratori locali rispondevano negativamente o non davano alcun riscontro (Brugnoli, 1997: 168-169).

Tabella 1 – Elenco dei siti menzionati nel testo distinti per tipologia: I/S = isolato/sporadico, A = abitato, T = tomba/e, LC = luogo di culto

Table 1 – Sites mentioned in the text and listed by typology: I/S = isolated/sporadic, A = settlement, T = tomb(s), LC = cult site

ID	Sito	Comune	Tipologia sito	Anno della scoperta o edizione	Scopritore
1	Belluno Veronese	Brentino-Belluno	I/S	1857 o 1867	Fortunato Zeni
2	Covolo della Roba	Sant'Anna d'Alfaedo	I/S	1886	Stefano De Stefani
3	Covolo dei Camerini	Sant'Anna d'Alfaedo	I/S	1888	Stefano De Stefani
4	Campo Paraiso	Sant'Anna d'Alfaedo	LC	1881	Stefano De Stefani
5	Monte Loffa	Sant'Anna d'Alfaedo	A	1883-1888	Stefano De Stefani
6	Ca' del Vecio	Sant'Anna d'Alfaedo	I/S	1887	Stefano De Stefani
7	Vajo della Merla	Fumane	I/S	1884	Stefano De Stefani
8	Colarè	Fumane	I/S	1888	Stefano De Stefani
9	Forte Masua	Fumane	I/S	1885	Stefano De Stefani
10	Dolcè	Dolcè	I/S	1886	Ignoto
11	Caprino Veronese	Caprino Veronese	I/S	1888	Ignoto
12	Forte di Rivoli	Rivoli Veronese	T	1885	Stefano De Stefani
13	Rivoli Veronese, loc. Castello	Rivoli Veronese	I/S	1880, 1881 e 1883	Carlo Cipolla, Stefano De Stefani
14	Rocca di Garda	Garda	I/S	1877	Gaetano Pellegrini
15	Bacino Marina	Peschiera del Garda	I/S	1892-1906	Arrigo e Gustavo Balladoro o loro conoscenti
16	Imboccatura di Mincio	Peschiera del Garda	I/S	1892-1906	Arrigo e Gustavo Balladoro o loro conoscenti
17	Peschiera del Garda	Peschiera del Garda	I/S	1870 circa-1906	Ignoto
18	Ca' dei Cavri	Bussolengo	I/S	1672 circa	Conoscenti del conte Lodovico Moscardo
19	Porta San Giorgio	Verona	I/S	1888	Ignoto

ID	Sito	Comune	Tipologia sito	Anno della scoperta o edizione	Scopritore
20	Muraglioni della Binastrova	Verona	I/S	1890	Ignoto
21	Ex Chiesa San Giovanni Decollato (ora Via Carducci)	Verona	T	1893	D. Giovanni Belviglieri
22	San Briccio	Lavagno	I/S	1846 e 1883	Carlo Cipolla
23	San Zeno-Colognola	Colognola ai Colli	I/S	1886	Stefano De Stefani
24	Castejon	Colognola ai Colli	A	1881	Don Domenico Carcerieri
25	Fondo Camera	Cologna Veneta	T	1896 circa	Cesare Gardellini
26	Chiesa di Santa Giustina	Cologna Veneta	I/S	1884	Carlo Cipolla
27	Fiume Nuovo di Baldaria	Cologna Veneta	T	1892	Cesare Gardellini
28	Desmontà-Caneviera	Veronella-Albaredo d'Adige	T	1889	Stefano De Stefani
29	Fondo Carlotti	Oppeano Veronese	I/S	1877 circa	Pietro Paolo Martinati
30	Montara	Oppeano Veronese	A	1878	Giambattista Malesani (?)
31	Franchine	Oppeano Veronese	T	1891	Stefano De Stefani
32	Ca' del Ferro	Oppeano Veronese	T	Fine Ottocento	Camillo Dal Fiume
33	Isola Rizza	Isola Rizza	I/S	1889	Ignoto
34	Madonna dell'Uva Secca	Povegliano Veronese	T	1876 e 1880	Collaboratori del Martinati, Carlo Cipolla
35	Valeggio sul Mincio	Valeggio sul Mincio	I/S	Fine Ottocento	Stefano De Stefani
36	Campi Magri della Bora	Povegliano Veronese	T	1880	Carlo Cipolla
37	Palazzina	Isola della Scala	T	1884	Stefano De Stefani
38	Bovolone	Bovolone	I/S	1871	Bernardino Biondelli
39	Fondo Bellinato	Minerbe	T	1879	Stefano De Stefani
40	Villa Bartolomea	Villa Bartolomea	I/S	1899	Ignoto
41	San Vito	Cerea	T	1876-1878	Antonietta Martinati
42	Bionde di Visegna	Salizzole	I/S	Fine Cinquecento	Conoscenti di Alessandro Canobbio
43	Valle Burgan	Sorgà	T	1878	Don Francesco Masè
44	Pradelle	Gazzo Veronese	I/S	Fine Ottocento	Ignoto
45	Gazzo Veronese	Gazzo Veronese	I/S	1763	Ercole Giusti
46	Coazze	Gazzo Veronese	A	1867-1873	Vincenzo Giacometti, Don Francesco Masè

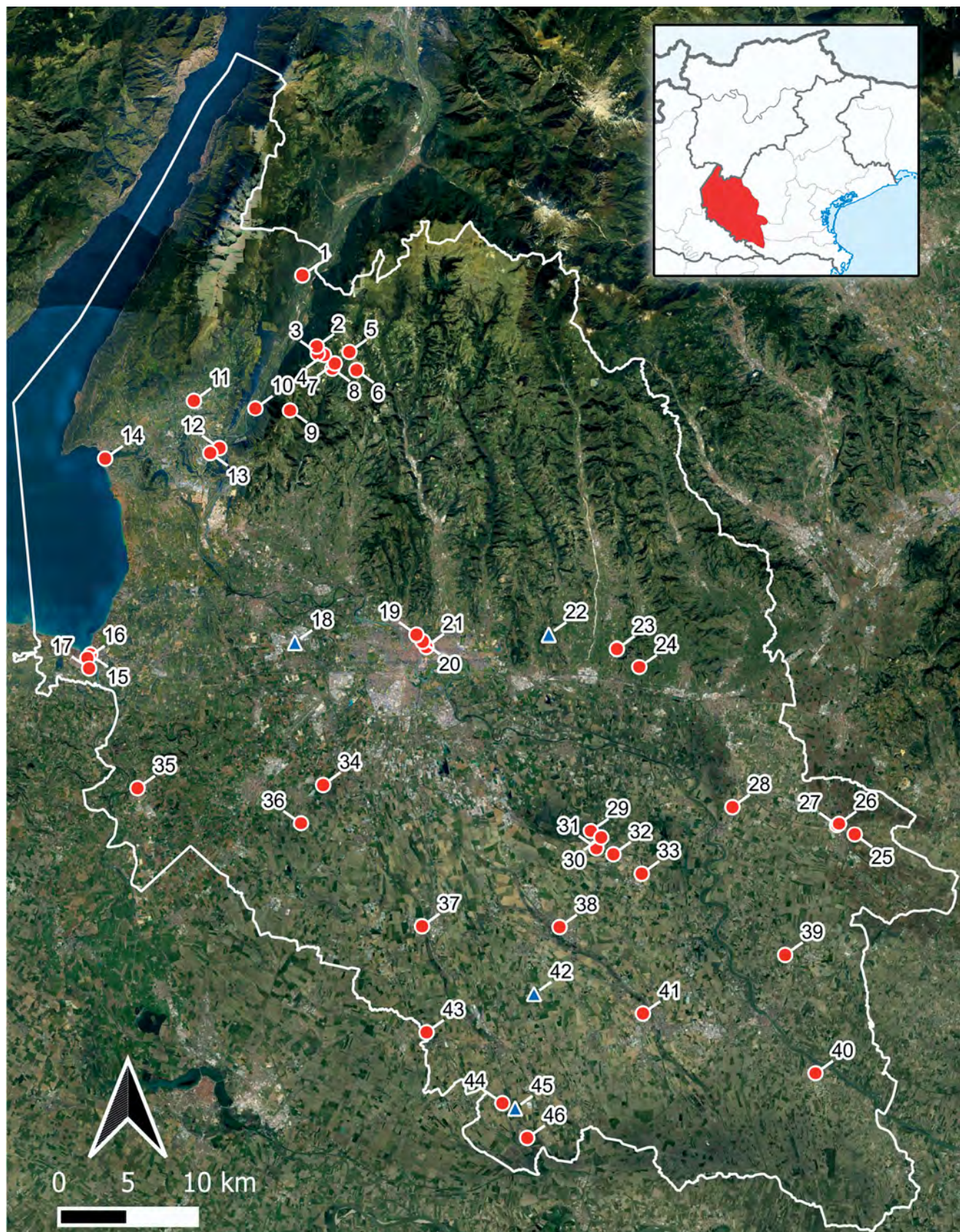


Fig. 4 – Localizzazione dei siti dell'età del Ferro riferiti alla Tabella 1. Con il triangolo blu i siti segnalati durante le fasi del collezionismo antiquario, con il cerchio rosso quelli individuati nel corso dell'800 (elaborazione a cura di G. Adami tramite QGIS)

Localization of Iron Age sites referred to Table 1. With the blue triangle the sites reported during the phases of antiquarian collecting phase, with the red circle those identified during the 19th century (processing by G. Adami via QGIS)

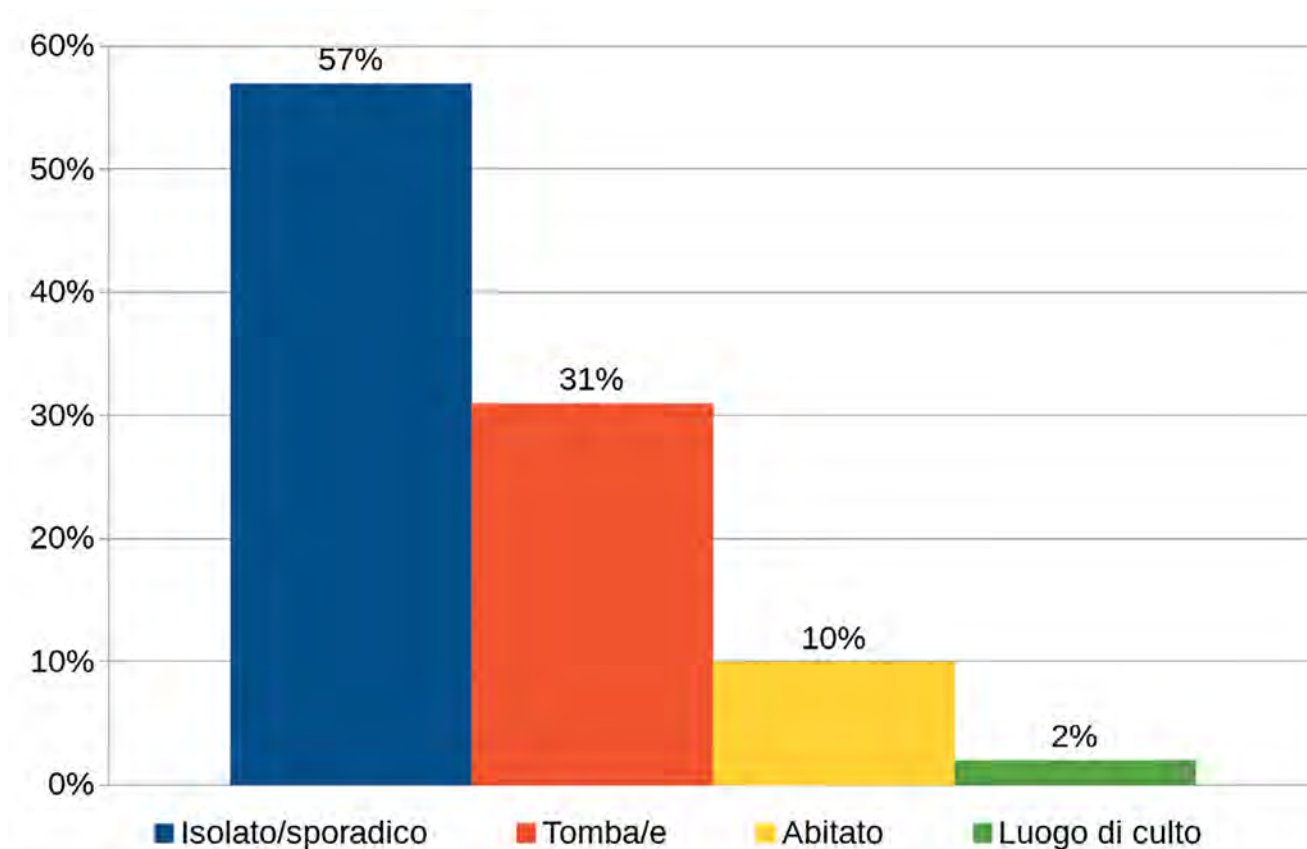


Fig. 5 – Differenziazione percentuale delle tipologie di ritrovamento avvenute nel corso del XIX secolo. Su 42 siti, 24 si riferiscono a rinvenimenti isolati o sporadici, 13 a sepolture, 4 ad abitati e 1 a luogo di culto

Percentage distinction of finding typologies occurred during the 19th century. Out of 42 sites, 24 refer to isolated or sporadic finds, 13 to burials, 4 to settlements and 1 to a cult site

Dal punto di vista della concentrazione delle ricerche, un territorio particolarmente esplorato e/o che ha restituito maggior numero di scoperte è la Lessinia occidentale, ben nota e frequentata dal De Stefani (seppure avesse origini legnaghese), a cui segue il territorio del Comune di Oppeano, famoso a quei tempi per l'elmo bronzeo. Analoghe concentrazioni numeriche tra loro riguardano invece i territori comunali di Gazzo Veronese, Peschiera, Verona e Colognola ai Colli: tutte aree oggetto di ricerche più approfondite anche in tempi più recenti.

Come si può invece evincere dal grafico (Figura 5), in termini percentuali gran parte delle scoperte dei primi paleoetnologi erano isolate o disperse su più aree (57%); seguono ritrovamenti riferibili a contesti funebri (31%), a insediamenti (10%) e infine a quello che è stato interpretato come un luogo di culto (2%) e cioè Campo Paraiso.

L'unico studioso che si cimentò nello studio dell'età del Ferro in maniera però del tutto episodica fu De Stefani in seguito alla scoperta nel 1879 delle tombe a Minerbe (fondo Bellinato) e nel 1884 a Pallazzina di Isola della Scala, cui però non seguirono approfondimenti con progetti di ricerca o di scavo più ampi. Nel primo caso, ignaro delle scoperte in Este, le associava al villanoviano bolognese, mentre con il secondo iniziava i rapporti con Prosdocimi, la cui influenza scientifica ben si coglie soprattutto nella seconda pubblicazione della necropoli, di dieci pagine più ricca dell'iniziale rapporto (Salzani, 2005a: 139-140). Anche Carlo Cipolla, nella sua duplice veste di Ispettore Governativo agli Scavi della Commissione Consultiva Conservatrice di Belle Arti e Antichità e di membro della locale sezione archeologica della Commissione per la Conservazione del Museo Civico, negli anni compresi tra il 1879

e il 1906, diede un contributo alle scoperte e pubblicazioni dei siti dell'età del Ferro. La sua predilezione e la sua inclinazione scientifica verso la storia medievale e moderna, di cui dal 1882 teneva la docenza all'Università di Torino, lo portò però a occuparsi di protostoria in quanto referente culturale del Governo centrale e dell'Amministrazione comunale, senza velleità di approfondire la tematica.

De Stefani fu, senza ombra di dubbio, lo studioso più prolifico del gruppo, attivo soprattutto in Lessinia, dove le ricerche erano rivolte a diversi aspetti della preistoria: la realizzazione di una carta archeologica del territorio, il campignano e infine la risoluzione della questione delle «selci strane». Quest'ultima *tragicomica* storia incise notevolmente sulla personalità scientifica di De Stefani, a cui va dato comunque «il merito di aver con la sua appassionata attività richiamato l'attenzione degli studiosi ufficiali alle ricerche in una zona di così rilevante interesse» (Leonardi P., 1963: 341) e sulla base della quale sono poi iniziati importanti progetti di ricerca tuttora in corso.

RINGRAZIAMENTI

Si ringraziano Elisabetta Govi (*Alma Mater Studiorum* Università di Bologna, Dipartimento di Storia Culture Civiltà), Sabina Bernacchini (Laboratorio fotografico del Museo Galileo, Istituto e Museo di Storia della Scienza di Firenze), Margherita Bolla (Museo Archeologico al Teatro Romano di Verona) e Simona Marchesini (Alteritas, Verona).

BIBLIOGRAFIA

- ASPES A., BUCHI E., FASANI L., RIZZETTO G., SALZANI L. (a cura di), 1976. 3000 anni fa a Verona. Dalla fine dell'Età del Bronzo all'arrivo dei romani nel territorio veronese, Verona: 261 pp.
- BATTAGLIA R., 1932. Notizie preliminari sulle ricerche preistoriche eseguite nei monti Lessini (anno 1930). *Archivio per l'antropologia e l'etnologia*, 60-61: 3-31.
- BATTAGLIA R., 1934. S. Anna d'Alfaedo. Resti di un santuario veneto-gallico sul Monte Loffa. *Notizie degli Scavi di Antichità*: 116-143.
- BERRO E., 1964. Nogara Salizzole, Verona, Ghidini e Fiorini: 5-58.
- BIANCHI P., LINCETTO S., 2001-02. Monte Loffa. Materiali della collezione Castelfranco nelle Civiche Raccolte Archeologiche di Milano. *Annuario storico della Valpolicella*, XVIII: 245-256.
- BILLANOVICH G., 1976. Tradizione classica e cristiana e scienza antiquaria. In: Folena G. (a cura di). *Storia della cultura veneta. Dalle origini al Trecento*, 1, Vicenza: 124-134.
- BIONDANI F., 2005. Ricerca e tutela archeologica nel basso Veronese alla fine dell'Ottocento: l'attività di Stefano De Stefani. In: Leonardi G., Rossi S. (a cura di). *Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004)*. Cologna Veneta: 153-166.
- BIONDELLI B., 1884. Di una scoperta archeologica nei monti Lessini presso Verona. *Rendiconti del R. Ist. Lomb. di SS.LL.AA.*, s. II, XVII: 729-730.
- BOARO S., 2001-02. L'Epistolario De Stefani nel fondo Pigorini di Padova. Il caso Breonio e la paleontologia veronese nell'elaborazione delle teorie pigoriniane. *Annuario storico della Valpolicella*, XVIII: 39-86.
- BOLLA M., 2019. Collezioni di antichità a Verona fino al XVI secolo. *Studi Veronesi. Miscellanea di studi sul territorio veronese*, IV: 7-44.
- BOLLA M., 2021. Animali di bronzo del Museo Archeologico al Teatro romano di Verona. *Memorie del Museo Civico di Storia Naturale di Verona*. 2 Serie. Scienze dell'Uomo, 14: 238 pp.
- BOLLA M., CASTOLDI M., 2016. I recipienti di bronzo in Italia settentrionale tra IV e I secolo a.C. e il caso del territorio veronese. *Arheološki vestnik*, 67: 121-175.
- BRUGNOLI A., 1997. Ettore Scipione Righi ispettore agli scavi. In: AA.VV. Ettore Scipione Righi (1833-1894) e il suo tempo. Atti della Giornata di studio. Verona: 165-184.
- BRUGNOLI A., 2001-02. Stefano De Stefani tra ricerca e tutela. La documentazione degli archivi veronesi. *Annuario storico della Valpolicella*, XVIII: 17-38.
- BRUGNOLI A., 2005. L'evoluzione degli organi di tutela del patrimonio archeologico a Verona dall'Unità al Novecento e la loro documentazione archivistica. Il caso di Cologna Veneta e del territorio veronese sud orientale. In: Leonardi G., Rossi S. (a cura di). *Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004)*. Cologna Veneta: 293-302.
- CAPUIS L., LEONARDI G., PESAVENTO MATTIOLI S., ROSADA G., (a cura di), 1990. Carta archeologica del Veneto. II, Modena: 387 pp.
- CARANCINI G.L., 1975. Gli spilloni nell'Italia continentale. *Prähistorische Bronzefunde*, XIII, 2, Monaco di Baviera: 381 pp.
- CARANCINI G.L., 1984. Le asce nell'Italia continentale II. *Prähistorische Bronzefunde*, IX, 12, Monaco di Baviera, p. 139.
- CHIECO BIANCHI A.M., 2002. Il museo nazionale atestino: dalla nascita al 1985. In: Chieco Bianchi A.M., Ruta Serafini A. (a cura di). 1902-2002. Il museo di Este: passato e futuro, Treviso, Canova: 15-90.
- CIPOLLA C., 1880. Povegliano Veronese. *Notizie degli Scavi di Antichità*: 236-241.
- CIPOLLA C., 1881. Rivoli Veronese. *Notizie di Scavi di Antichità*: 309-310.

- CIPOLLA C., 1883. Lavagno. *Notizie degli Scavi di Antichità*: 363-365.
- CIPOLLA C., 1884a. Lavagno. *Notizie degli Scavi di Antichità*: 4-13, 97, 170-171, 232, 414-416.
- CIPOLLA C., 1884b. Cologna Veneta. *Notizie degli Scavi di Antichità*: 232-234.
- CIPOLLA C., 1885a. Lavagno. *Notizie degli Scavi di Antichità*: 396-397.
- CIPOLLA C., 1885b. Cerea. *Notizie degli Scavi di Antichità*: 489.
- DAL CERRO B., 2005. Il Museo Civico Archeologico di Cologna Veneta (Verona). In: Leonardi G., Rossi S. (a cura di). *Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004)*. Cologna Veneta: 87-103.
- DE MORTILLET G., 1865. *Matériaux pour l'histoire positive et philosophique de l'homme*, Paris.
- DE STEFANI S., 1879. Legnago. *Notizie degli Scavi di Antichità*: 132-133.
- DE STEFANI S., 1880. Gazzo-Veronese. *Notizie degli Scavi di Antichità*: 236.
- DE STEFANI S., 1881a. Gazzo-Veronese. *Notizie degli Scavi di Antichità*: 310.
- DE STEFANI S., 1881b. Sopra molti e diversi oggetti di alta antichità scoperti a Breonio nel Veronese. *Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti*, s. V, VII: 1327-1335.
- DE STEFANI S., 1883. Sopra gli scavi fatti nella palafitta centrale del golfo di Peschiera ed in quella del Mincio. *Memorie dell'Accademia di Agricoltura, Arti e Commercio di Verona*, s. III, LX: 257-292.
- DE STEFANI S., 1884a. Isola della Scala. *Notizie di scavi di antichità*: 15-16 e 139.
- DE STEFANI S., 1884b. Breonio. Antichi oggetti trovati nel Vaio della Merla, presso il Vaio della Pizzolana, e nel Vaio Campostrin, descritti dall'ispettore cav. St. de Stefani. *Notizie degli Scavi di Antichità*: 137-139.
- DE STEFANI S., 1885a. Sopra gli scavi fatti nelle antichissime capanne di pietra del Monte Loffa a Sant'Anna del Faedo. *Atti e memorie dell'Accademia di Agricoltura, Arti e Commercio di Verona*, s. III, LXII: 3-40 (estratto).
- DE STEFANI S., 1885b. Sopra la scoperta di oggetti di alta antichità scavati a Rivoli Veronese. *Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti*, s. VI, III: 1-14 (estratto).
- DE STEFANI S., 1885c. Rivoli Veronese. Nota del R. ispettore cav. De Stefani. *Notizie degli Scavi di Antichità*: 239-241.
- DE STEFANI S., 1885-86. Intorno un dodecaedro quasi regolare di pietra a facce pentagonali scolpite con cifre scoperto nelle antichissime capanne di pietra del Monte Loffa. *Notizie di Stefano de' Stefani r. ispettore degli scavi e monumenti. Atti del Reale Istituto Veneto di Scienze, Lettere e Arti*, s. VI, IV: 3-25.
- DE STEFANI S., 1886. Notizie storiche delle scoperte paleontologiche fatte nel comune di Breonio-Veronese. Memoria di Stefano De Stefani. *Atti della Reale Accademia dei Lincei. Memorie della Classe di Scienze Morali, Storiche e Filologiche*, s. IV, II, 1: 238-249.
- DE STEFANI S. 1888. Intorno alle scoperte fatte nella Grotta dei Camerini nel Comune di Breonio. *Bullettino di Paleontologia Italiana*, XIV: 81-91.
- FACCHI A., 2005a. 1876: la prima carta archeologica del Veronese. In: Leonardi G., Rossi S. (a cura di). *Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004)*. Cologna Veneta: 303-314.
- FACCHI A., 2005b. Pietro Paolo Martinati (1812-1878) e le prime ricerche di paleontologia nella pianura veronese. In: Leonardi G., Rossi S. (a cura di). *Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004)*. Cologna Veneta: 105-133.
- FACCHI A., 2014. Persone e istituzioni nella genesi e nello sviluppo della scienza preistorica alla periferia del Regno: il caso della provincia di Verona. In: Guidi A. (a cura di). *150 anni di preistoria e protostoria in Italia. Atti XLVI Riunione Scientifica I.I.P.P., Studi di Preistoria e Protostoria*, 1, Firenze: 105-110.
- FERRARI C., 2008. Cronistoria degli scavi e delle scoperte archeologiche. In: Guidi A., Salzani L. (a cura di). *Oppeano. Vecchi e nuovi dati sul centro protourbano*. Treviso: 11-15.
- FOGOLARI G., 1972. Castion di Erbè (Prov. di Verona). *Rivista di scienze preistoriche*, 27: 449-450.
- FOGOLARI G., 1981. Padova preromana. In: Padova antica. Da comunità paleoveneta a città romano-cristiana. Padova, Ed. Lint: 27-45.
- FOGOLARI G., 1950-51. Per un *Corpus* dei bronzetti etruschi. Bronzetti etruschi e italici nel Museo del Teatro Romano di Verona. *Studi etruschi*, s. II, XXI: 343-374.
- FRANZONI L., 1980. Bronzetti etruschi e italici del Museo Archeologico di Verona, Roma: 242 pp.
- FRANZONI L., 1981. Antiquari e collezionisti del Cinquecento. In: Arnaldi G., Pastore Stocchi M. (a cura di). *Storia della cultura veneta. Dal primo Quattrocento al Concilio di Trento*. 3/III, Vicenza: 207-266.
- GARDELLINI C., 1896. Cologna Veneta. Antichità scoperte presso la frazione comunale di Baldaria. *Notizie degli Scavi di Antichità*: 507-511.
- GHIRARDINI G., 1897. Il sepolcreto primitivo di Baldaria presso Cologna Veneta. *Bullettino di Paleontologia Italiana*, XXIII: 122-147.
- GLEIRSCHER P., 1991-93. Campo Paraiso, un *Brandopferplatz* tipo Rugger Egg? *Annuario storico della Valpolicella*: 111-134.
- GOIRAN A., 1876. Catalogo degli oggetti presentati alla Esposizione preistorica veronese inaugurata il 20 febbraio 1876, Verona: 61 pp.
- GUIDI A., 1988. *Storia della Paleontologia*: 336 pp.
- GUIDI A. (a cura di), 2014. *150 anni di Preistoria e Protostoria in Italia. Studi di Preistoria e Protostoria*, 1, Firenze: 615 pp.
- GUIDI A., SALZANI L., 2008. *Oppeano. Vecchi e nuovi dati sul centro protourbano*. Treviso: 180 pp.
- LANCENI G.B., 1720. Ricerca pittorica o sia Notizia universale delle pitture nelle chiese, e luoghi pubblici di

Verona. Opera presentata al pubblico in favore de' dilettanti dall'incognito conoscitore, vol. 1. Verona: 334 pp.

LEONARDI G., 1975. Castion di Erbè (Verona), *Preistoria alpina*, 11: 337-338.

LEONARDI G., 1976. Castion di Erbè (com. di Erbè) (Verona), *Studi Etruschi*, XLIV: 412.

LEONARDI G., 1977. Castion di Erbè (Verona), *Rivista di scienze preistoriche*, 32: 326.

LEONARDI G., 2002. Castion di Erbè. In: A. Aspes (a cura di). *Preistoria veronese contributi e aggiornamenti*: 185-186.

LEONARDI G., ROSSI S. (a cura di), 2005. Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004), Cologna Veneta: 414 pp.

LEONARDI P., 1963. Il contributo dei Veneti alla conoscenza della preistoria e protostoria delle Venezie. *Studi Etruschi*, XXXI: 332-350.

LONGO L., CHELIDONIO G., 2001-02. Le "selci strane": un caso fra etnoarcheologia e implicazioni socio-economiche. *Annuario storico della Valpolicella*, XVIII: 125-146.

MACELLARI R., 2001-02. "Il vostro amico preistorico". La corrispondenza fra Gaetano Chierici e Stefano De Stefani. *Annuario storico della Valpolicella*, XVIII: 109-118.

MARCHESINI S., 2015. *Monumenta Linguae Raeticae*. Scienze e Lettere, Roma: 337 pp.

MARCHESINI S., ZAGHETTO L., 2019. The Situla in Providence. A comprehensive analysis of inscription and decorative program. In: Hye S., Töchterle U. (eds.), UPIKU: TAUKE. Festschrift für Gerhard Tomedi zum 65. Geburtstag. *Universitätsforschungen zur prähistorischen Archäologie* 339. Bonn, Verlag Dr. Rudolf Habelt GmbH: 329-341.

MARCHINI G., 1972. Antiquari e collezioni archeologiche dell'Ottocento veronese, Verona: 316 pp.

MARINETTI A., 1987. L'iscrizione retica (PID247) da Ca' dei Cavri (Verona). In: AA.VV. *Prima della storia inediti 10 anni di ricerche a Verona*. Verona: 131-140.

MARTINATI P.P., 1876. Storia della paleoetnologia veronese. *Atti e Memorie dell'Accademia di Verona*, LIII: 171-206.

MIGLIAVACCA M., 2001-02. I materiali del Monte Loffa dagli scavi De Stefani conservati al Museo di Storia Naturale di Verona. *Annuario storico della Valpolicella*: 223-228.

PELLEGRINI G., 1878. Di un sepolcro preromano scoperto a Povegliano Veronese. *Memorie dell'Accademia d'Agricoltura e Commercio di Verona*, vol. LVI, XII della serie II, fasc. I: 1-45.

PERONI R., 1975. Studi di cronologia delle civiltà di Este e Golasecca, Firenze: 410 pp.

PIGORINI L., 1877. Notizie diverse. *Bullettino di Paleontologia italiana*, III: 64.

PIGORINI L., 1878a. Brescia, Mantova, Verona, Padova. *Notizie degli Scavi di Antichità*: 75-81.

PIGORINI L., 1878b. Oggetti della prima età del ferro scoperti in Oppeano nel Veronese. *Bullettino di Paleontologia italiana*, IV: 105-124 e tavv. VI e VII.

PIGORINI L., 1886. Cerea. *Bullettino di Paleontologia italiana*, XII: 67.

POMIAN K., 1986. Collezionisti d'arte e curiosità naturali. In: Arnaldi G., Pastore M. Stocchi (a cura di). *Storia della cultura veneta*. Il Settecento. 5/II, Vicenza: 1-70.

PROSDOCIMI B., 2005. "Nuove notizie" di necropoli veneta a S. Vito di Cerea: un ritrovamento nell'archivio Pigorini. In: Leonardi G., Rossi S. (a cura di). *Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004)*. Cologna Veneta: 379-386.

RIZZETTO G., 1973. Testimonianze archeologiche a Casteggi di Colognola ai Colli. *Vita Veronese*, XXVI, 11-12: 354-363.

RIZZETTO G., 1977. Una nota aggiornativa su S. Briccio di Lavagno (Verona). *Bollettino del Museo Civico di Storia Naturale di Verona*, IV: 575-591.

ROSSI S., 2005. La "necropoli del Fiume Nuovo". Topografia dei rinvenimenti, aggiornamento e spunti critici sulla protostoria di Baldaria di Cologna Veneta. In: Leonardi G., Rossi S. (a cura di). *Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004)*. Cologna Veneta: 267-290.

RUFFO S., 1964. Francesco Zorzi e il Museo di Storia Naturale di Verona. *Natura e montagna*, IV, n. 3: 121-126.

RUFFO S., 1967-68. Francesco Zorzi e Angelo Pasa. *Atti e Memorie dell'Accademia di Agricoltura Scienze e Lettere di Verona*, s. VI, XIX: 1-10 (estratto).

RUFFO S., CURI E., 2005. Il Museo civico di storia naturale di Verona dal 1862 a oggi. Venezia: 171 pp.

SALZANI L., 1976. Verona – Porta San Giorgio. In: AA.VV., *3000 anni fa a Verona*. Catalogo della mostra, Verona: 156, fig. 21.

SALZANI L., 1978. Villabartolomea (Verona). In: AA.VV., *L'arte preistorica nell'Italia settentrionale dalle origini alla civiltà paleoveneta*. Verona: 119-120.

SALZANI L., 1979a. Il ripostiglio di Campo Paraiso (Breonio). *Bollettino del Museo Civico di Storia Naturale di Verona*, VI: 501-598.

SALZANI L., 1979b. Breonio (Verona). *Bollettino del Museo Civico di Storia Naturale di Verona*, VI: 619-622.

SALZANI L., 1981. Preistoria in Valpolicella. Verona: 149 pp.

SALZANI L., 1983a. Gazzo Veronese. *Bollettino del Museo Civico di Storia Naturale di Verona*, X: 531-533.

SALZANI L., 1983b. Colognola ai Colli. Indagini archeologiche. Vago di Lavagno: 118 pp.

SALZANI L., 1985a. Preistoria e protostoria nella media pianura veronese. Oppeano (Verona): 89 pp.

SALZANI L., 1985b. Castel S. Pietro. Le documentazioni protostoriche. *Civiltà veronese*, 2: 9-14.

SALZANI L., 1985c. Contributi per la conoscenza della Tarda Età del Ferro nel Veronese. *Atti e Memorie dell'Accademia di Verona*, s. VI, XXXV: 353-381.

SALZANI L., 1985d. S. Zeno di Colognola ai Colli. *Bollettino del Museo Civico di Storia Naturale di Verona*, XII: 520-521.

SALZANI L., 1985-86. Rassegna di ritrovamenti preistorici nella Valdadige veronese. *Annuario storico della Valpolicella*, V: 53-78.

SALZANI L., 1987a. Ca' dei Cavri. In: AA.VV., Prima della storia: inediti di 10 anni di ricerche a Verona. Verona: 181-182.

SALZANI L., 1987b. La preistoria lungo la Valle del Tartaro. Vago di Lavagno (VR): 195 pp.

SALZANI L., 2001-02. Note sul Monte Loffa dall'archivio privato De Stefani. *Annuario storico della Valpolicella*, XVIII: 229-234.

SALZANI L., 2005. Le ricerche preistoriche di Stefano De Stefani nella pianura veronese. In: Leonardi G., Rossi S. (a cura di). Archeologia e idrografia del Veronese a cent'anni dalla deviazione del fiume Guà (1904-2004). Cologna Veneta: 135-152.

SALZANI L., 2013. L'elmo di Oppeano. In: Bismara C., Chiappa B., Varanini G. M. (a cura di). Oppeano, il territorio e le comunità. Scripta Ed., Verona: 42-43.

SALZANI L., 2014. Per una storia della Paletnologia veronese: i bronzi protostorici della Collezione Verità e del Museo Civico. *Bollettino del Museo Civico di Storia Naturale di Verona*, 38: 133-151.

SALZANI L., 2018. Necropoli dei veneti antichi a Ca' del Ferro di Oppeano (Verona). SAP ed., Mantova: 192 pp.

SALZANI L., DE STEFANI R. (a cura di), 2013. Atlante delle ricerche e scoperte nelle stazioni litiche di Breonio e altri scritti inediti di Stefano De Stefani. *Memorie del Museo Civico di Storia Naturale di Verona - 2. Serie. Sezione Scienze dell'Uomo*, 12: 152 pp.

SALZANI L., RAGNOLINI SAURO L., 2014. Le vicende di una scoperta archeologica discussa e dimentica. *La Lessinia. Ieri, Oggi, Domani*, 37: 63-70.

SARACINO M., SALZANI P., MARTINELLI N., 2021. Verona prima di Verona: preistoria e protostoria dell'area urba-

na. In: Latella L. (a cura di). Storia naturale della città di Verona. *Memorie del Museo Civico di Storia Naturale di Verona*, 2. serie. *Monografie Naturalistiche*, 6: 323-340.

SCAGLIETTI KALESCIAN D. (a cura di), 1999. Alessandro Turchi detto l'Orbetto 1578-1649. Scripta edizioni, Trento: 534 pp.

SOLINAS, G. 1973. L'altare sotto l'asfalto. Verona: 31 pp.

SCHNAPP A., 1993. La conquista del passato. Alle origini dell'archeologia. Parigi: 367 pp.

TARANTINI M., 2014. Continuità, rinnovamenti, contaminazioni. Preistoria e protostoria in Italia dal 1925 al 1962. In: Guidi A. (a cura di). 150 anni di preistoria e protostoria in Italia. Atti della XLVI Riunione Scientifica I.I.P.P., *Studi di Preistoria e Protostoria*, 1, Firenze: 363-372.

TREVISAN D., SACCOCCIO F., 2015. I siti di Coazze, Sorgà-Tione e Moratica (Verona): storia degli studi e materiali inediti dai Musei di Bologna, Parma e Mantova. In: Leonardi G., Tinè V. (a cura di). Preistoria e Protostoria del Veneto. *Studi di Preistoria e Protostoria*, 2, Firenze: 909-914.

TRIGGER B.G., 1989. Storia del pensiero archeologico. Cambridge: 532 pp.

VISENTIN M., 1969. Cologna preromana e la sua necropoli. La civiltà dell'età del Ferro a Baldaria. Cologna Veneta (Verona).

VON ELES MASI P., 1986. Le fibule dell'Italia settentrionale. *Prähistorische Bronzefunde*, XIV, 5, Monaco di Baviera: 258 pp.

VON SACKEN E.F., 1865. Der Pfahlbau im Garda-see. Vienna: 40 pp.

ZORZI F., 1960. Preistoria veronese. Insediamenti e stirpi. In: AA.VV. Verona e il suo territorio, I: 73-153.

ZANGARINI M. (a cura di), 1991. Il Canale Camuzzoni. Industria e società a Verona dall'Unità al Novecento. Verona, Cierre edizioni: 267 pp.

Palaeophysiology of reproduction in fossil fishes: an overview and new insights, with the description of four new ichnotaxa

LUIGI CAPASSO

University Museum, State University "Gabriele D'Annunzio" – Piazza Trento e Trieste, 1 – 66100 Chieti (Italy)

ABSTRACT

Many recent discoveries have overturned some deep-rooted beliefs in the field of palaeophysiology regarding reproduction in fossil fish and have made it appropriate to propose this new synthesis on the subject, in which the author has integrated current literature with information also deriving from unpublished material. The most primitive and ancient fish, the Agnatha, had already adopted the model of internal fertilization, through the development of well differentiated copulatory organs: a fertilization model that still persists today in living jawless fishes. Thus it can be said with certainty that internal fertilization preceded external fertilization and that copulatory organs appeared before jaws, along the evolution of Vertebrates. From an anatomical point of view, the copulatory organs in Agnatha are (and were) connected directly to the skeleton of the pelvic girdle, which indicates that the pelvic girdle initially developed to support the copulatory organs rather than the pelvic appendages (fins). Also, in the Placoderms a sexual dimorphism is well established with intromittent organs in the males, which certainly involved internal fertilization. However, some Placoderms certainly laid eggs (in special egg sacs containing multitudes of eggs), but in most cases they believed the eggs to be fertilized, as evidenced by the numerous paleontological records of embryos within the female oviducts. Internal fertilization also developed in the Chondrichthyans, but on different anatomical bases than those adopted by the Placoderms, demonstrating that these characters evolved autonomously in the two groups. We have fossil evidence showing that the Chondrichthyans adopted the feature of laying fertilized eggs as early as the Devonian, and the egg capsules of the Chondrichthyas are known from the Devonian to the Miocene. However, many Chondrichthyans already in the Lower Carboniferous were viviparous, or at least ovoviviparous, as evidenced by the presence of embryos in some species of sharks belonging to the ichthyofauna of Bear Gulch, Montana, USA. In Osteichthyans external fertilization is the rule and this also applies to fossil species. There are few paleontological examples of intromittent organs in Actinopterygii, and very few are those of fossil eggs, as well as of embryos developed inside oviducts belonging to fossil bony fishes. However, among the Sarcopterygii, in which a regime of ovoviviparity is still demonstrated today, there is evidence that this modality dates back at least to the Late Carboniferous in which some very young Coelacanthus with a large yolk sac were raised. In addition, paleontological evidence shows that many fishes practiced particular care of their fertilized eggs and offspring, and there is much evidence that demonstrates a true oviposition strategy (habitat shift, nursery area, site fidelity) pursued by the fish belonging to all major groups, both extinct and living. In examining the paleontological evidence of paleofertility, including the study of new fossil finds, the author has the opportunity to describe here four new ichnotaxa belonging to the Veterovata grouping of ichnofossils.

Key words: Sexual dimorphism, Copulatory organs, Egg capsules, Embryos, Parental care.

INTRODUCTION

In the last two decades, paleontologists have shown great interest in the topic of reproduction in fossil species, which has also been supported by new, unexpected discoveries of fossil traces of the reproductive capabilities and modalities in extinct animals. Thus, the paleontology of reproduction has become a recurring theme, resulting in both the launch of new lines of research as well as a large increase in publications on this topic.

The reconstruction of the palaeophysiological aspects of reproduction in fossil animals is an interdisciplinary issue, because it must take into consideration at least three of the following different aspects:

- (i) intersex differences within the same fossil species, also in relation to possible interpretations of the fertilization modality;
- (ii) traces of pregnancy *vs* eggs;

- (iii) identification and study of embryonic and newborn individuals, also to investigate possible parental care.

This great variability of aspects means that even studied material as well as the techniques necessary for the analysis and the reconstruction of the palaeophysiology of reproduction are quite various, ranging from (i) a detailed study of the anatomical variability within the same fossil species (such as the biological value of the morphotypes), to (ii) the search for traces of fossil eggs (which are now the object of a separate parataxonomy: *Veterovata*: Mikhailov *et al.*, 1996), and to (iii) the study of the ontogenesis of individual paleontological species and their ways of interacting with the environment, which also involves some aspects of ichnopaleontology (nesting traces, or *Calichnia*: Buatois & Mangano, 2011).

The focus of these research papers was above all the reconstruction of the palaeophysiology of reproduction in the large Cenozoic Reptiles, for which detailed knowledge (i) of their fossil eggs, (ii) of the states of maturation of the embryos, (iii) of their nesting methods and models, and (iv) of the parental care, was reached (Gregory, 2010). Unfortunately for fossil fish such knowledge is still far away, and almost all the mentioned areas are still largely speculative.

In this pioneering context, the present work aims to summarize the current situation regarding the main areas that contribute to the reconstruction of the palaeophysiology of reproduction in fossil fish, by examining and updating the following main aspects: (i) the anatomical intersexual differences, with (ii) their consequences in the interpretation of the copulation model (internal or external), but also through possible interpretations that may allow (iii) the hypothesis of possible courtship; (iv) the paleontological documentation of pregnancy and embryonic development, for viviparous species, and (v) of fossil records of eggs, possibly with traces of embryos for ovoviviparous and oviparous species; and, finally, (vi) the paleontological documentation and interpretation of the anatomy and ontogenesis of newborns, and of any (vii) parental care reserved for the fry and juvenile, immature fishes.

Despite the fact that some particularly complete reviews have been published on this same topic (Trinajstić *et al.*, 2014; 2019), some very relevant recent discoveries have made all the old syntheses suddenly obsolete. One of these extraordinary discoveries certainly concerns the documentation of

specific copulatory organs in jawless fishes (Agnatha), both fossil and living (Chevrinais *et al.*, 2018). These past and recent discoveries have compelled us to completely rewrite the argument of the origin and evolution of reproduction physiology in fossil fish, thus requiring a new updated synthesis.

The synthesis proposed here is fundamentally based on a review of current knowledge present in literature, but the previous knowledge is also substantially integrated by some new unpublished material which is presented and interpreted here for the first time.

SEXUAL DIMORPHISM, COURTSHIP AND COPULATION

Sexual dimorphism is a common and well-known phenomenon in living fish (Tortonese, 2000). However, in fossil fish it can be difficult to detect and demonstrate, and therefore it is not well known how widespread this phenomenon was in past times.

From an anatomical point of view, sexual differences are primary or secondary, depending on whether they are already present at birth or whether they occur only after reaching sexual maturity. Among the primary sexual characteristics there are undoubtedly those concerning the copulatory organs which, for fish, are those which (only in the male sex) favor the penetration of sperm into the female cloaca. These copulatory organs, (combining our knowledge on living species and those on fossil species, which is at a very primitive stage) are of the following four types (Table 1): (i) *gonopodium*, consisting of some modified anal fin rays; (ii) *mixopterygia* (or *pelvic clasper*), consisting of a pair of structures connected to the rays of the pelvic fins and/or to the pelvic girdles, in the presence of regularly, structured pelvic fins; *intromittent organ*, consisting of a pair of special organs, (iii) independent of the pelvic and anal fins (so called "*Placoderm's type*") or (iv) connected with the pelvic girdles in absence of the pelvic fins (so called "*Lamprey's type*").

- (i) The "gonopodium", a unique median structure composed of the anterior rays of the anal fin, odd and median organs, is present today only in some groups of living bony fish (Poeciliidae, Anablepidae, Cyprinodontiformes); even sporadic Osteichthyan fish have a gonopodium-like structure with hooks, and is known from some Middle Triassic Neopterygii of Europe (Bürgin, 1990; Nelson, 2006; Hurley *et al.*, 2007; Friedman, 2015).

Table 1

Type of fertilization	Model of reproduction	Fecondation model	Copulatory organs in males		
			Name	Structure	Taxonomic distribution
External	Oviparity or ovoviviparity	Spawning	---	No	The majority of living Actinopterygii
		Vent-to-vent	---	No	Some living Actinopterygii
Internal	Ovoviviparity or viviparity	Mating (female penetration)	Mixopterygia (or pelvic claspers)	Modified or special structures connected with pelvic girdles and fins	Many living and fossil Chondrichthyes, and the only Placoderm <i>Incisoscutum</i>
			Intromittent organs	Special simmetric abdominal organs, independent by both pelvic fins and anal fin	Placoderms
				Simmetrical abdominal organs connected with pelvic girdles in assence of pelvic fins	Some both living (<i>Petromyzon marinus</i>) and fossil (<i>Euphanerops longaevus</i>) jawless fish (lampreys)
			Gonopodium	Modified one/some anal fin ray(s)	Few living and very few fossil Actinopterygii

(ii) The “mixopterygia” (or pelvic claspers) represent the male couple of copulatory organs, connected to the pelvic fins and/or to the pelvic girdles, and are present in most living and in some fossil Chondrichthyans. Mixopterygia represent a modification of the distal part of the metapterygium of the pelvic fin, that are tranformed into a specialised reproductive structure for internal fertilisation (Lund, 1982, 1985; Grogan & Lund, 2004; Grogan *et al.*, 2012). Due to the above mentioned anatomical situation, the pelvic claspers are articulated with the posterolateral margin of the pelvic girdles via the metapterygium (Grogan & Lund, 2004; O’Shaughnessy *et al.*, 2015). In extant sharks, usually only one pelvic clasper is employed in copulation to convey sperm into the female’s cloaca (Pratt & Carrier, 2001; Conrath & Musick, 2012), though there are some species described (such as *Scyliorhinus canicula* and *Rhinoptera javanica*) which employ both pelvic claspers during mating

(Leigh-Sharp, 1920; Uchida *et al.*, 1990). In the Placoderms, to date we have the description of a single paleontological case of intromittent organs unequivocally connected to the pelvic skeleton: *Incisoscutum*, of the Australian Late Devonian, in which the males possessed well ossified claspers connected to the pelvic girdle skeleton through basipterygia (Trinajstić *et al.*, 2014; 2019).

Finally, the “intromittent organs” are also symmetrical organs, which (however) are special organs, functionally specialized in coupling. Today we know two types of intromittent organs: the “Placoderm’s type” and the “Lamprey’s type”.

(iii) The intromittent organs of the Placoderm’s type are exclusive of the primitive gnathostomes, that is of some Placoderms. In contrast to Chondrichthyans, these appear to lack any association with the pelvic fins, instead articulating with the posterior cephalo-trunk shield (Antiarchi) or being clearly separated posteriorly from the pelvic fin/girdle (Ptyctodontida,

Arthrodira) (Long *et al.*, 2009; Trinajstić *et al.*, 2014). In Placoderms (with the exception of the *Incisoscutum*) the couple of intromittent organs developed laterally to the ventral mid-line, in the space between the pelvic fins/girdles and the anal fin.

- (iv) The intromittent organs of the Lamprey's type are exclusive of some fossil and living Agnatha. In fact, in the Late Devonian jawless anaspid-like fish *Euphanerops longaeus* (Miguasha Lagerstätte, eastern Canada) Chevrinais *et al.* (2018) showed paired intromittent organs preserved in close association with the pelvic girdles, but in absence of the pelvic fins (Figure 1). “It is difficult to determine whether the intromittent organs articulate to the pelvic girdles, but pelvic fins are absent” (Chevrinais *et al.*, 2018). Exactly the same anatomical situation was well demonstrated in the living lamprey *Petromyzon marinus*, in which the couple of intromittent organs is closely connected with the pelvic girdles, but the pelvic fins are absent; such pelvic girdles serve to support only the intromittent organs, and not the pelvic fins (Chevrinais *et al.*, 2018). This suggests that the intromittent organs develop independently from the pelvic fins (as in nearly all the Placoderms), but in close association with the pelvic girdles (as in jawless fish, both fossil and living), and this represents the plesiomorphic condition for jawed vertebrates (Figure 1).

All these described male, copulatory organs represent the anatomical basis of internal fertilization, which leads to ovoviviparity or viviparity, both rare conditions in living and fossil fish (Table 1); although it must be emphasized that internal fertilization can occur, in exceptional cases, even in the absence of intromittent organs in male fish (Watson, 1927; Balon *et al.*, 1988). Nonetheless, the most common reproductive process in fish occurs through oviparity, that is, the laying and fertilization of eggs in an extracorporeal environment. In this process, special copulatory organs are not necessary and reproduction takes place through the simple emission (through the cloaca) of the eggs by the females and of the sperm by the males.

Therefore, being oviparous, most of the fish do not mate and perform the laying and fertilization of the eggs with a process called “spawning”. Rarely there can be a “pseudo-copulation”, which consists

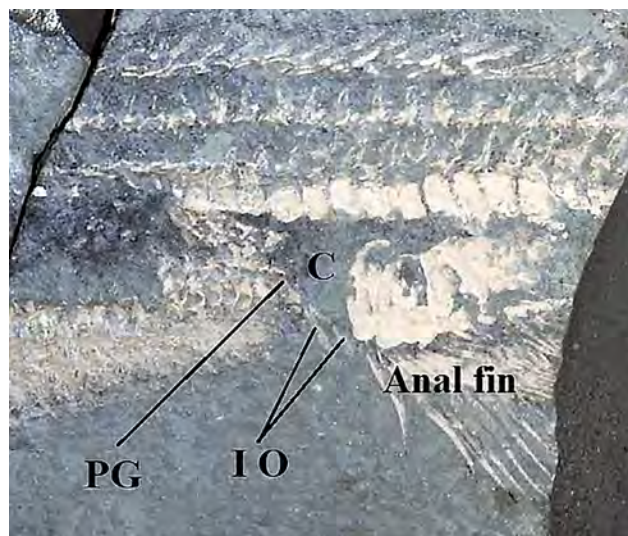


Fig. 1 – Intromittent organs and their relationship with pelvic girdles in *Euphanerops longaeus* (Miguasha Lagerstätte, eastern Canada), Late Devonian; specimen no. 01-123 of the Musée d'Histoire Naturelle de Miguasha, Canada; from Chevrinais *et al.* (2018). C: Cloaca; PG: pelvic girdle; IO: intromittent organs

in the two partners approaching and rubbing each other lightly for a long time on the sides of the abdomen, favouring the emission of eggs and sperm, respectively. This phenomenon is called “vent-to-vent” (Table 1). Evidently, neither “spawning” nor “vent-to-vent” require special anatomical structures suitable for coupling and therefore do not involve structural changes.

The secondary sexual characteristics, which appear (with the only exception of the genus *Echinochimaera*, that we will describe later) only after the achievement of sexual maturity, consist of peculiar morphologies of dermal or bony spines, supernumerary skin plates or plates with special ornaments, dimensional differences (even considerable) between adults of each sex. All these anatomical arrangements do not (generally) have direct involvement in mating.

According to present state knowledge, the phenomenon of sexual dimorphism in fossil fish was demonstrated about eighty years ago for the Placoderm *Rhamphodopsis* (Watson, 1938), and was confirmed in another Palaeozoic Placoderm, *Ctenurella*, about sixty years ago by Ørvig (1960). Finally, forty years ago Lund (1990) reported that a number of Chondrichthyan fishes from the Missis-

sipian (about 320 million years old) of Bear Gulch Limestone, Montana (USA), were highly sexually dimorphic.

Copulation organs in jawless fish (Agnatha)

One of the most ancient paleontological cases of unequivocal presence of male copulatory organs was reported by Chevrinais *et al.* (2018) and concern the case of *Euphanerops longaevus*, a jawless fish from Late Devonian. In this fossil fish, Chevrinais *et al.* (2018) demonstrated that the pelvic region is composed of two sets of morphologically distinct paired structures, representing small pelvic girdles and intromittent organs, in absence of pelvic fins (Figure 1). Notwithstanding the fact that there is a lack of information about the corresponding female subjects of this same species, the presence of paired intromittent organs represents a masculine condition, as it is also present in living jawless fish, as *Petromyzon marinus* (Chevrinais *et al.*, 2018).

In light of these recent discoveries, both in fossil and living jawless fishes, it really seems that internal fertilization was the rule in these first and primitive vertebrates. Looking at the detailed anatomy of many fossil jawless fishes in this new light, especially the Silurian and Lower Devonian, it is possible that new discoveries may be made in the near future. In particular, the Anaspida show the presence of paired fins in the ventral region and many scales or groups of scales interposed between these paired fins and the anus. For example, *Rhyncholepis* possessed a shorter paired fin-fold, a large preanal plate, a large post-anal plate, and a highly developed anal fin first spine (Figure 2 A). All these median and well ossified structures were not associated with reproductive functions (Blom *et al.*, 2002), but could be compared with the disposition of the intromittent organs in living jawless fishes to verify their possible involvement in these sexual functions. In fact, if we look in detail at the arrangement of the plates located along the ventral midline between the base of the region of the brachial openings and the anus, for example in *Birkenia*, we can easily notice the existence of a large number of relatively large plates with a special morphology (Blom *et al.*, 2002), whose origin and comparative anatomy has yet to be addressed (Figure 2 B and C). With great probability these studies will lead to the identification of some plates with reproductive functions also in the Silurian genus *Birkenia*.

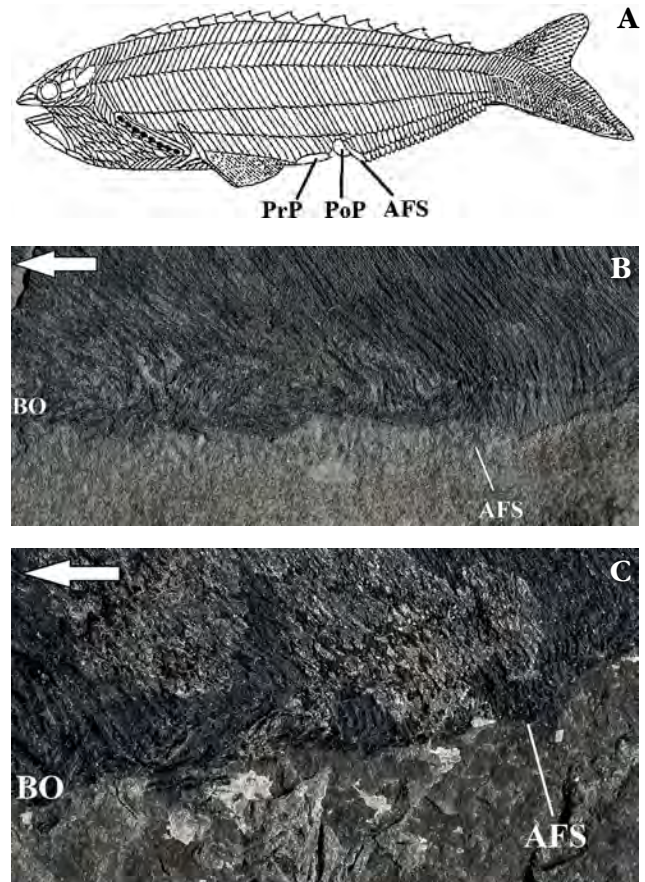


Fig. 2 – **A**: reconstruction of the body of *Rhyncholepis parvula* (from Blom *et al.*, 2002); **B** and **C**: the ventral profile between the most inferior branchial opening (BO), and the anal fin in two specimens of *Birkenia elegans*, from Upper Silurian of Lesmahagow, Scotland. **PrP**: preanal plate; **PoP**: postanal plate; **AFS**: Anal fin first spine. The arrow is directed to the head of the fish

Copulation organs and sexual dimorphism in Chondrichthyan fish

In many of the fish belonging to the class of Chondrichthyes living today, the males have characteristic copulation organs, such as the “pelvic claspers”, which serve to facilitate the internal fertilization via transfer of sperm from males to females. Although they are present at birth, its presence in young males is very difficult to demonstrate in fossil specimens, because claspers in juvenile and immature subjects are small in size and are not yet calcified or ossified. In fact, the pelvic claspers achieve full size and calcify or ossify at sexual maturity (Dodd & Dodd, 1985).

The most ancient unquestionable case of intromittent organs in Chondrichthyans is the well-developed copulatory pelvic claspers present in the Upper Devonian filter-feeding shark *Diademodus hydei*, from the late Famennian Cleveland Shale of Ohio, USA (Harris, 1951); the intromittent organs of this fossil Chondrichthyans consist in a modification of the pelvic fins.

Concerning the Mississippian of Bear Gulch Limestone, Montana, USA, many genera and species from the Carboniferous Chondrichthyan fishes, characteristic of this locality, present sexual dimorphism. In fact, clear and numerous anatomical characters have been described as sexual differences in a number of species pertinent to some groups of Chondrichthyes: Cladodontid, Hybodontid and Holocephalan (Lund, 1982; 1985; 1990). Lund himself has clearly demonstrated on several occasions that the intersex anatomical differences (with the single exception of *Echinochimaera*) are secondary sexual characteristics, and absent in younger subjects, and therefore these characteristics appear only in adult and sexually mature individuals. These anatomical differences between the two sexes are evident only in the Holocephalian *Echinochimaera meltoni*, even in very small size individuals, demonstrating that they are primary sexual characteristics (Lund, 1990). These secondary sexual differences have been examined and described in detail and concern at least the following morphological and structural aspects: squamation, shape and structure of the fins, shape and size of the spines and of the body as a whole. Lund (1990) has shown that all these differences are documentable only in individuals who demonstrate that they have reached sexual maturity, that is, in those individuals whose pelvic claspers are ossified or calcified.

The most evident example of this sexual dimorphism is undoubtedly represented by the two species of Holocephalian fish pertaining to the genus *Echinochimaera*, namely *E. meltoni* and *E. snyderi*. Lund (1990) asserts that in *Echinochimaera meltoni* “sexual dimorphism is elaborate and extreme, and sexes can be determined on the shape of the distal end of the dorsal fin spine of the smallest of juvenile specimens. An adult male is twice the size of the largest females, and bears 4 pairs of antler-like supraorbital denticles, an extended dorsal spine by enlarged, forwardly protruding denticles, brush-like extensions of the first radials of the first dorsal fin, and enlarged

paired dorsal denticles extending from the second dorsal fin to the caudal fin. Additionally, paired prepelvic tenaculae are present and the male body is somewhat less rounded than that of the females. Dorsal spines of subadult and adult males are invariably preserved in a forwardly flexed position, a condition never seen in juveniles of females” (Lund, 1990). This complex description of sexual dimorphism in *Echinochimaera meltoni* demonstrates how in this species almost all sexual differences are very elaborate and are also primary sexual characteristics, that is clearly visible only known case, even in juvenile individuals.

In the Bradyodont *Harpagofututor volsellorhinus*, (characteristic of the same Bear Gulch Carboniferous limestone beds in Montana, USA), both primary and secondary sexual characteristics are present. The primaries consist of well differentiated pelvic claspers connected to the pelvic fins, while the secondary ones are concentrated on the pectoral fins and on the antero-superior part of the head. In fact, males have large paired, distally biramous head claspers, quite developed in the region located in front of the orbits, and they were certainly very mobile, which articulate to the ethmoid region of the braincase. They are robust appendages, certainly equipped with muscle bundles, and covered with skin shields. It is possible that these couple of head claspers assist males in holding females during mating. But it is equally possible that, like the large well-developed spines, they had only one display function for males. In fact, Lund (1982) wrote “While a display function can be assumed in view of the alteration in body form produced, display alone might be better enhanced by increased surface area than by structural strength”. Furthermore, the pelvic fins of females are reduced, but the pectoral fins are hypertrophied in males (Lund, 1982).

Similar differences have also been described in another Bradyodont, *Chondrenchelys problematica*, from the Lower Carboniferous of Glencartholm, Scotland. Pelvic claspers and hypertrophic pectoral fins have also been shown in males of this species (Carroll, 1988; Lund, 1982).

Finally, it is worth remembering the *Falcatus falcatus* case, Cladodontida, Stethacanthidae, in which sexual dimorphism was very evident (Figure 3). In the male individuals of this species, in fact, the first dorsal spine and fin are massively hypertrophic (Figure 3 A). Males also have elongated rostra and dorsal cranial and fin denticles,

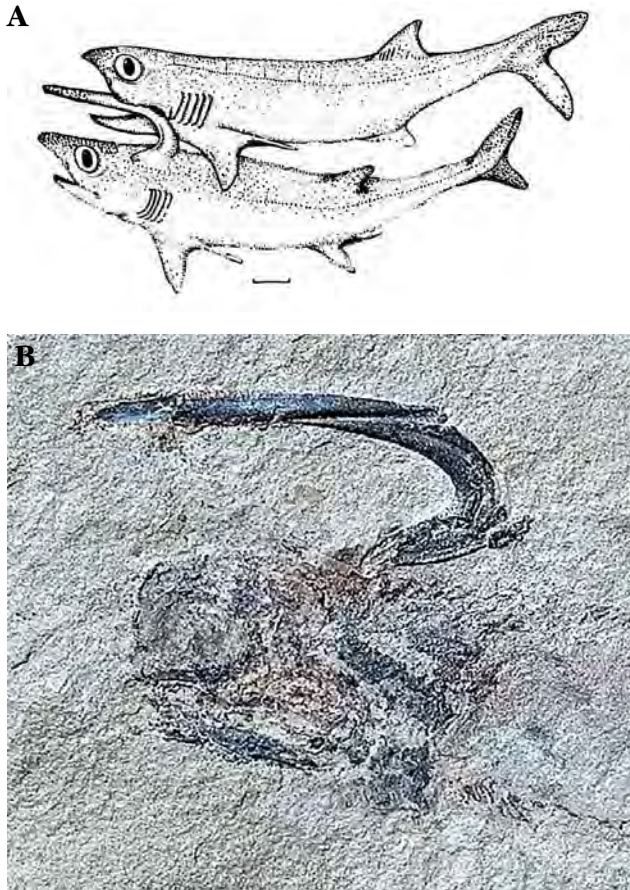


Fig. 3 – *Falcatus falcatus* from the Bear Gulch (Montana, USA) Mississippian limestone. **A:** detail of the characteristic modified hypertrophic first dorsal spine in an adult male subject; **B:** mating scene, with female, above, and male, below (scheme drawn by Lund, 1985, on the basis of a fossil specimen, preserved at the University of Montana Geological Museum, Missoula, USA)

while females and juveniles lack denticles and the first dorsal fin and spine. The function of this enormous spine in the dorsal region that characterizes the anatomy of males has been the subject of discussion, but as an extraordinary fossil it certainly provides unexpected information about it, and connects the presence of this dorsal spine to the act of copulation. In fact, in this fossil Lund (1990) demonstrated a close intersexual inter-relationship (Figure 3 B) with the female being placed above the male, and was fossilized in the act of biting the dorsal spine of the underlying male (Maisey, 2009). This would indicate that the modified structures of *Falcatus* would have had a function in the sphere

of sexual and courtship behavior. In this same regard, it is also necessary to reconnect information relating to the reciprocal frequency of the two sexes within the Bear Gulch deposit. Indeed, among these aspects of the sexual dimorphism in *Falcatus falcatus*, Lund (1985) noted that in the fossil community there were many more males than females, and that this fits with the behavioural model of male display/courtship and female choice. This evidence should be interpreted as possible so-called “lek mating aggregations”, such as the form of ritualized courtship in which females choose their partner at the expense of numerous other males (Lund, 1985).

Thus, the example of *Falcatus falcatus* really seems to demonstrate the fossil existence of anatomical sexual differences aimed at the completion of courtship and copulation between some Paleozoic fish (Maisey, 2009).

Copulation organs and sexual dimorphism in Placoderms

Watson (1934; 1938) was the first palaeontologist to describe the presence of intromittent organs in Palaeozoic fish, the Ptyctodont Placoderm *Rhamphodopsis* from the Middle Old Red Sandstone of Scotland. In this genus both sexes have dermal plates, placed posterior to the pelvic fins, along the midline. In males, this couple of plates are curved laterally, representing true intromittent organs while in females these dermal plates are more rounded and short (genital plates) (Miles, 1967).

In 1960 the Norwegian paleontologist Tor Ørvig described a new genus of Ptyctodont Placoderm, *Ctenurella gladbachensis*, from late Devonian of Germany. In this armoured fish many elements of dimorphism were identified and described, both of the secondary type such as cranial claspers, and of the primary type i.e. real intromittent organs (Ørvig, 1960), positioned near the ventral midline in the space between the pelvic fins and the origin of the anal fin (Figures 4 A and B).

A series of recent discoveries demonstrate that intromittent organs are more widespread than previously thought in Placoderms (Ahlberg *et al.*, 2009), and today we know that all three main groups of Placoderms, namely the Ptyctodontids (as the quoted *Rhamphodopsis* and *Ctenurella*), the Antiarchs and the Arthrodira, exhibited sexual dimorphism.

In contrast to Chondrichthyans, these intromittent organs (improperly called “claspers”) have two fundamental differences: (i) in Placoderms the cop-

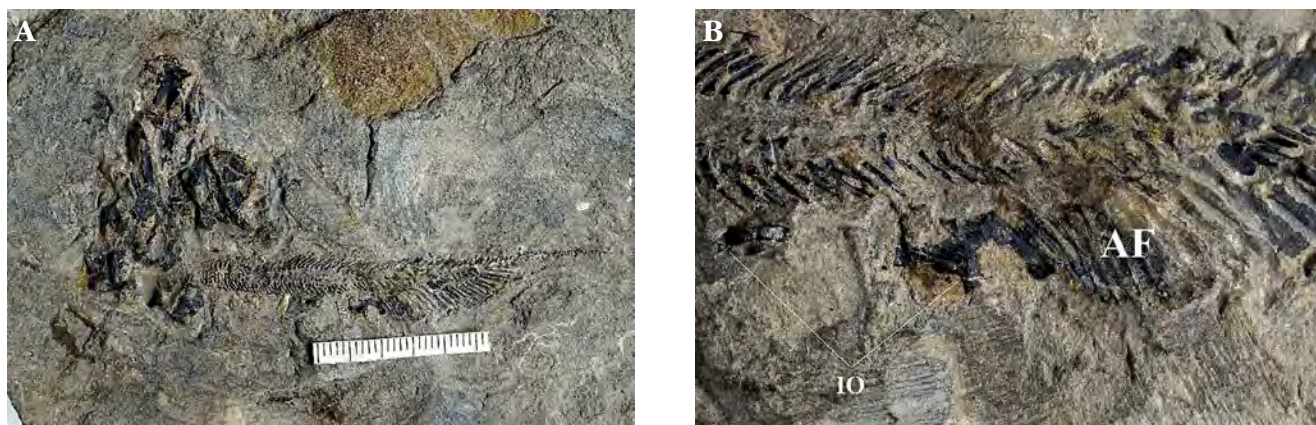


Fig. 4 – **A:** *Ctenurella gladbachensis*, from the Late Devonian of Bambach, Germany; **B:** detail of the ventral profile with intro-mittent organs, preserved partially in negative (IO) situated anteriorly to the anal fin (AF)

ulatory organs are bony paired structures, but in the modern sharks and rays the claspers are cartilaginous. In addition, in Placoderms the intro-mittent organs have a very different position and topographic relationship, as it appears to lack any association with the pelvic fins, instead articulating with the posterior cephalo-trunk shield (in the Antiarchs) or being clearly separated posteriorly from the pelvic fins/girdles, positioned between the pelvic fins and the anal fin (in the Ptyctodontids, and in the Arthrodira, with the exception of the genus *Incisoscutum*) (Long *et al.*, 2009, 2015; Trinajstić *et al.*, 2014).

Many more recent studies have demonstrated that a high number of Placoderms had intromittent organs in the males, while the females had paired dermal plates (called “genital plates”) that were inferred to have facilitated internal fertilization (copulation). As said previously, in both sexes, these structures are not associated with the pelvic fins (with the exception of the genus *Incisoscutum*). Thus, the similarities between the male intromittent organs and their morphology in the Placoderm group and in modern sharks are actually not the same anatomical structures, but most probably evolved independently.

Somewhat surprising therefore is this great diffusion of intromittent organs in Placoderms which demonstrates that the first model of fertilization in the most ancient gnathostomes was internal fertilization: “*This implies that external fertilization and spawning, which characterizes most extant aquatic gnathostomes, must have derived from internal fer-*

tilization, even though this transformation has been thought implausible” (Long *et al.*, 2015).

In fact, several Placoderms, representing the basal phylogenetic nodes of the jawed vertebrate clade, possess intromittent organs and primary characters of sexual dimorphism also in females. It is worth listing here the fundamental species in which these differences have unequivocally been demonstrated in the last decades. Excellent examples of sexual dimorphism, in fact, have been found also in other Devonian Placoderms Ptyctodonts, in addition to that already described in *Ctenurella*. The two best known and most significant cases are probably *Campbellodus* and *Rhynchodus*.

Both the *Campbellodus*, from the Gogo Formation in Australia, and *Rhynchodus* from Delaware County in New York, appear to be known only through female individuals, who are distinguished by having large and short plates in the posterior region to the pelvic fins, in front of the anus (Trinajstić *et al.*, 2014). Two other Ptyctodonts from the Devonian of the same Gogo Formation, Australia, have equally well differentiated and developed intromittent organs: *Austroptyctodus* and *Kymbryanodus* (Trinajstić *et al.*, 2014).

As far as the Antiarchs are concerned, the presence of a pair of well developed post-pelvic plates located at the posterior margin of the cephalo-trunk shield has been demonstrated in *Pterichthyodes milleri*, a classical Placoderm from the Devonian of Scotland, since 1972 (Figure 5 A) and were interpreted as female genital plates by Hemmings & Roston (1972). I observed similar plates also in presumed

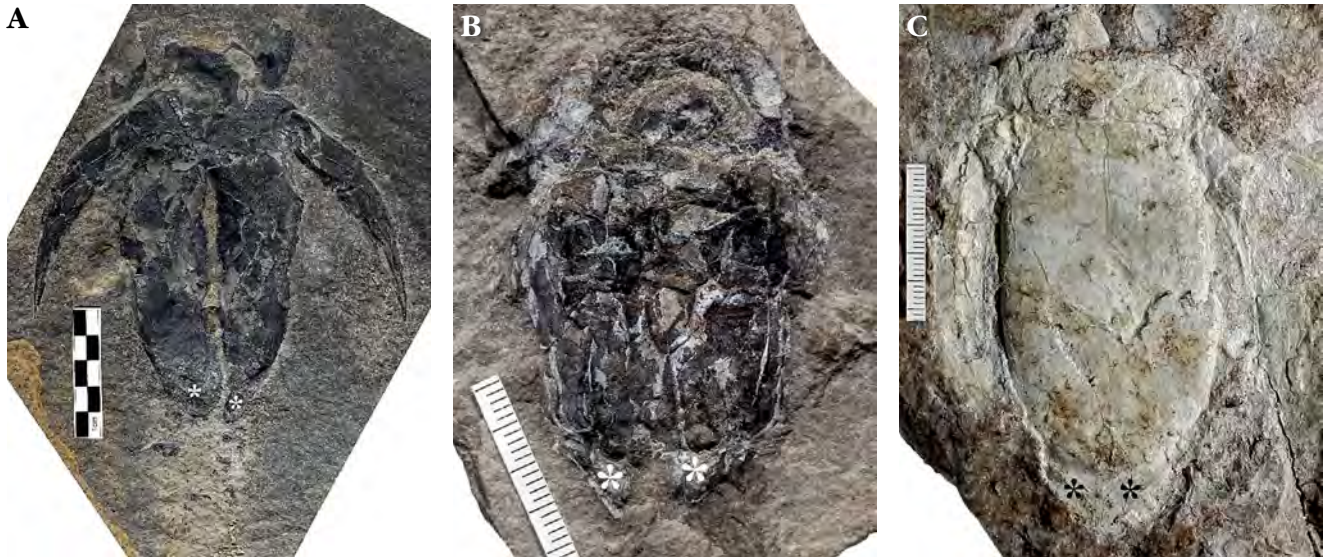


Fig. 5 – Some examples of female Devonian Antiarchs with a pair of well developed post-pelvic plates (asterisks), located at the posterior margin of the cephalo-trunk shield. **A:** *Pterichthyodes milleri* from Achanarras Quarry, Scotland; **B:** *Pterichthyodes cornutus* from Lethen Bar, Scotland; **C:** *Remigolepis zhongweiensis*, from Niushoushan area, Ningxia, China (late Frasnian-Famennian)

female individuals of the species *Pterichthyodes cornutus*, from the Devonian of Scotland (Figure 5 B). Long *et al.* (2015) confirmed this interpretation, but to date there is no evidence of corresponding claspers in male subjects, that could be interpreted as intromittent organs. It is probable that this lack is due to the anatomical position of the claspers in males, evidently covered by some element of the cephalo-trunk shield. Also in *Bothriolepis*, practically a cosmopolitan Devonian Antiarch, Long *et al.* (2015) demonstrated the presence of small semicircular plates only in some subjects (interpreted as female), sitting on the distal area of the subanal lamina. In some local Devonian *Bothriolepids* of China, such as *Remigolepis zhongweiensis* (Figure 5 C), and *Hunanolepis tieni*, I personally observed the presence of similar plates (moreover already described by Zhao & Zhu, 2010), present only in subjects that can be interpreted as female. In no case have corresponding intromittent organs been documented in presumably male subjects.

Recent studies conducted on another Antiarch, *Microbrachius dicki*, have impressively increased the anatomical features of sexual dimorphism in this small Placoderm (already well known since the end of the 19th century), due to numerous new discoveries both in Estonia and, above all, in the

Orkney Islands, U.K. Indeed, the abundance of recently discovered specimens has demonstrated the presence of notable differences in the arrangement and morphology of the dermal plates placed behind the cephalic and cephalo-trunk shield (Long *et al.*, 2015).

In *Microbrachius* males, in fact, there is a pair of well developed dermal intromittent organs, located on the posterior border of the cephalo-trunk shield. They consist of two strong bones, in contact with each other along the median line, by means of a real suture (which suggests that they were not mobile), folded laterally and pointed. In the same region, in females, there are instead two dermal bony plates in post-pelvic position, blade-like, which probably covered the cloaca (Figure 6 A and B). Long *et al.* (2015) reconstructed these copulatory structures in detail, and hypothesized their role in mating, suggesting that intromittent organs attached themselves to female post-pelvic plates (genital plates) during mating. The two components could remain adherent to each other as the internal face of both the intromittent organs and the female genital plates were covered with small spines and tubercles which, therefore, favoured their mutual anchoring, allowing a better transfer of the sperm inside the female cloaca.

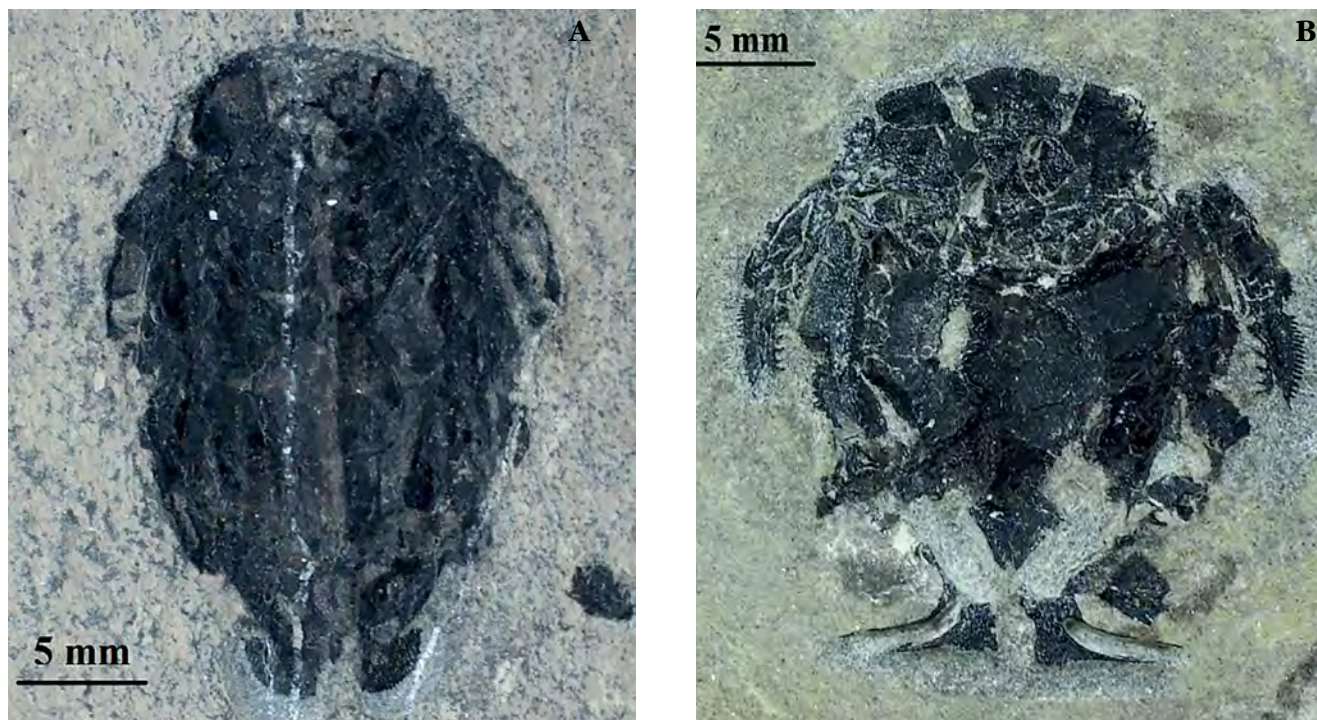


Fig. 6 – *Microbrachius dicki* from the upper Givetian, Devonian, of Orkney Island, Scotland. **A**: female (with a pair of well developed post-pelvic plates, located at the posterior margin of the cephalo-trunk shield); **B**: male (with a pair of intromittent organs, located at the posterior margin of the cephalo-trunk shield). Courtesy of Dr. John P. Adamek, Mundelein, Illinois (Fossilmall.com)

Among the same Placoderm group of the Arthrodira, there is the *Millerosteus minor* of the Middle and Late Devonian of Scotland, which in some individuals (interpreted as male) show a well developed intromittent organ in the form of elongated curved elements, located just posterior to the cephalo-trunk shield (Figure 7 A and B). In other individuals (interpreted as female) this organ is lacking (Figure 7 C and D), and instead the posterior margin of the cephalo-thoracic shield is prolonged with a pair of wide plates, even if in any case tapering backwards.

In the Devonian genus *Coccosteus*, such as the most common genus of Arthrodira pertaining to the Coccosteomorphi, both the composite nature of the pelvic girdle (Watson, 1934) and the presence of well-developed and differentiated intromittent organs positioned at the posterior margin of the cephalo-trunk shield, immediately behind the pelvic girdles (Figure 8 A and B), have been well demonstrated (Trinajstić *et al.*, 2014). A very similar situation was observed also in the following genera

of Arthrodira, *Compagopiscis*, *Camuropiscis*, *Eastmanosteus*, and *Holonema*, of the Late Devonian of the Gogo Formation, Australia (Trinajstić *et al.*, 2014).

From the same Gogo Formation derives the Arthrodire *Incisoscutum ritchiei*, in which embryos inside both female individuals and intromittent organs in male ones were demonstrated. In fact, in males these copulatory organs are completely ossified and consist of a thin rod attached to a square basal plate that articulates directly with the pelvic girdles. The tip of the distal end has a small cap of dermal bone with small pits and denticles to cling to the female during copulation, in addition to some anatomical details indicating the presence of muscle insertions that have led to interpret these copulatory organs as real erectile structures (Trinajstić *et al.*, 2019). In female subjects there are a couple of large basipterygia which are typical of the Chondrichthyan anatomical structures, with characteristic claspers connected to the pelvic fins, and represent an unicum inside the Placoderms.

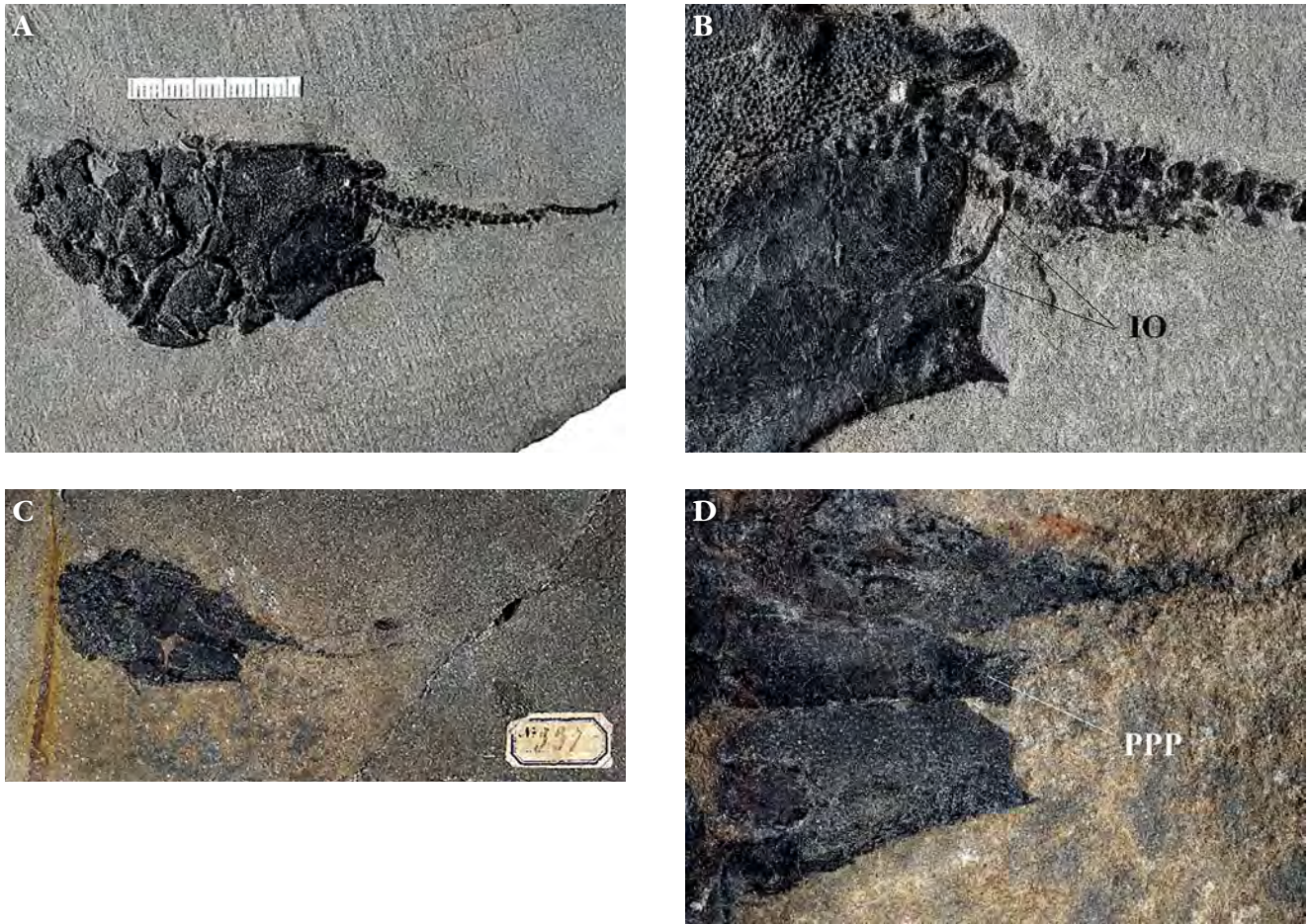


Fig. 7 – Primary sexual diorphism in Placoderm Arthrodira *Millerosteus minor*, from the Middle Devonian of Caithness quarry, Scotland. **A:** male individual; **B:** detail of the region posterior to the cephalo-trunk shield with evident intramittent organ (IO); **C:** female individual; **D:** detail of the region posterior to the cephalo-trunk shield, with evident post-pelvic plate (PPP)

Finally, in the two other Arthrodira of the Australian Devonian, *Austrophyllolepis* and *Cowralepis*, two plates placed at the posterior margin of the cephalo-trunk shield are described, but (being present in all individuals) no sexual role has been assigned to these plates, which are also present in the smaller sized subjects, though these plates do not appear to have any connection with the elements pertaining to the pelvic girdles (Ritchie, 2005). However, Ritchie (2005), having been able to examine a very large population of *Cowralepis maclachlani* specimens, noted the presence of two morphotypes: one with a shorter and wider cephalo-trunk shield, the other with a more elongated and narrow cephalo-trunk shield. Ritchie (2005) commented that these differences may be due to distortions related to the di-

agenesis of the layers. However, at least two specimens each represent a pair of individuals (each belonging to a morphotype) that fossilized side by side, partially overlapping, leaving us to imagine a copulation attitude. It is not sure if these fossils (Figure 9 A and B) are positioned so due to random overlaps of two fishes, but actually in both cases the presumed mating occurs between different morphotypes, and this supports the copulation hypothesis. Naturally, the question can be resolved only when anatomical elements distinct by sex, such as copulatory organs *vs* supra-cloaca genital plates, are eventually demonstrated. In this regard, it should be added in fact that in the genus *Australophyllolepis*, Long *et al.* (2009) reinterpreted some structures of the post-pelvic region as basipterygium, i.e. as real

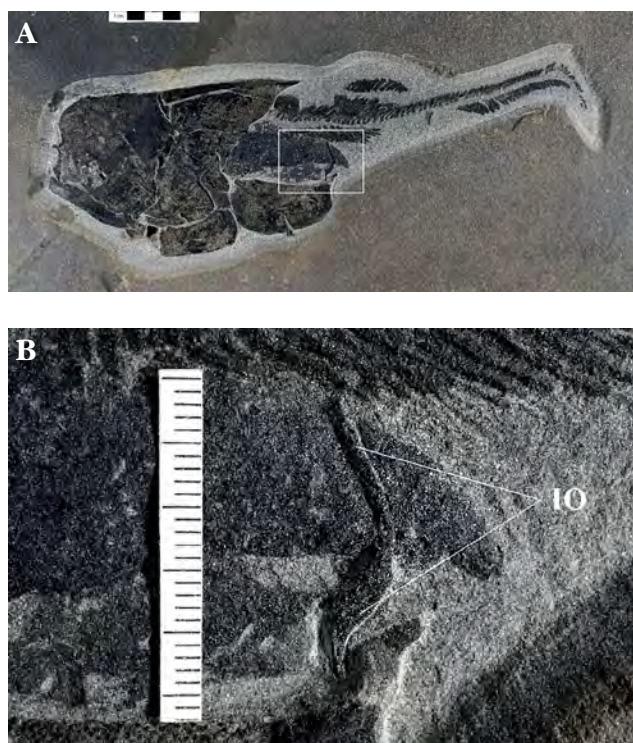


Fig. 8 – **A**: Male individual of Placoderm Arthrodira *Coccosteus cuspidatus*, from the Middle Devonian of Caithness quarry, Scotland; **B**: detail of the region posterior to the cephalo-trunk shield with evident intromittent organs (IO)

intromittent organs. Therefore, a review of the large *Cowralepis* population awaits to be studied in detail from this point of view as well.

As can be easily understood from the long list reported so far, it seems that internal fertilization was indeed a characteristic common to all Placoderms. This functional feature was evidently supported by anatomical structures which certainly represent a primary sexual dimorphism. Emblematically, Trinajstić *et al.* (2019) demonstrated the presence of a small, completely ossified, styliform, intromittent organ in a male embryo found in the visceral cavity of a female of *Incisorostrum* from the Upper Devonian of Gogo (Australia). This clearly demonstrates that this Placoderms was viviparous, with internal fertilization and the intromittent organs in males were completely ossified even before birth.

All these paleontological elements have strengthened the idea that the intromittent organs developed at the same time as the jaws. Lund himself wrote: “Jaws appeared around the same time as claspers in

Placoderms, and so might also have been connected to this early reproductive behavior in some way”.

The most recent paleontological evidence shows that even the Agnatha fossil, as well as the living jawless fishes, possess an internal fertilization which represents the first fossil evidence of the existence of intromittent organs also in Agnatha of the Lower Devonian (*Euphanerops longaevus*). Therefore, the origin of internal fertilization must be anticipated prior to the origin of the jaws along the evolution of Vertebrates.

Furthermore, the phylogenetic relationships between internal fertilization in the Chondrichthyes and that in the Placoderms must be clarified. In fact, there is no doubt that the male claspers in present-day sharks and rays, as well as those in fossil Choandrichthyans, are anatomically and ontogenetically different structures from the Placoderms intromittent organs, and the two anatomical structures probably evolved in a completely independent way, although they achieved the same functionality, that of internal fertilization.

Copulation organs and sexual dimorphism in Acanthodians

Moreover, the role that the Acanthodians may have played, which in any case represent the most ancient gnathostomes to have appeared on Earth, remains completely obscure, at least at the moment (Watson, 1937). The Acanthodians, which are extinct fishes possibly genetically related with the origin of the Chondrichthyans, were endowed with characteristics, multiple spines, so much so that unequaled, but the presence of tracks to support the even fins is currently doubtful, even if a pelvic structure girdle was tentatively described in the genus *Acanthodes* (Zidek, 1976b). It is even more difficult to establish whether at the base of these structures, along the ventral midline, there could be some that could also perform reproductive functions. Nevertheless, Watson (1937) had already described the presence of calcified elements near the base of the pelvic fin spines in *Ischnacanthus*. The field of investigation of the anatomy of the even spines of the most ancient Acanthodians, those of the Chinese Silurian (*Sinacanthus*) must still to be fully explored (Zhu, 1998), both from a topographical point of view of the single spines (which are almost always found isolated, Figure 10), and in particular under the point of view of the structure of their base (which could be connected to the presence of structures with reproductive functions).

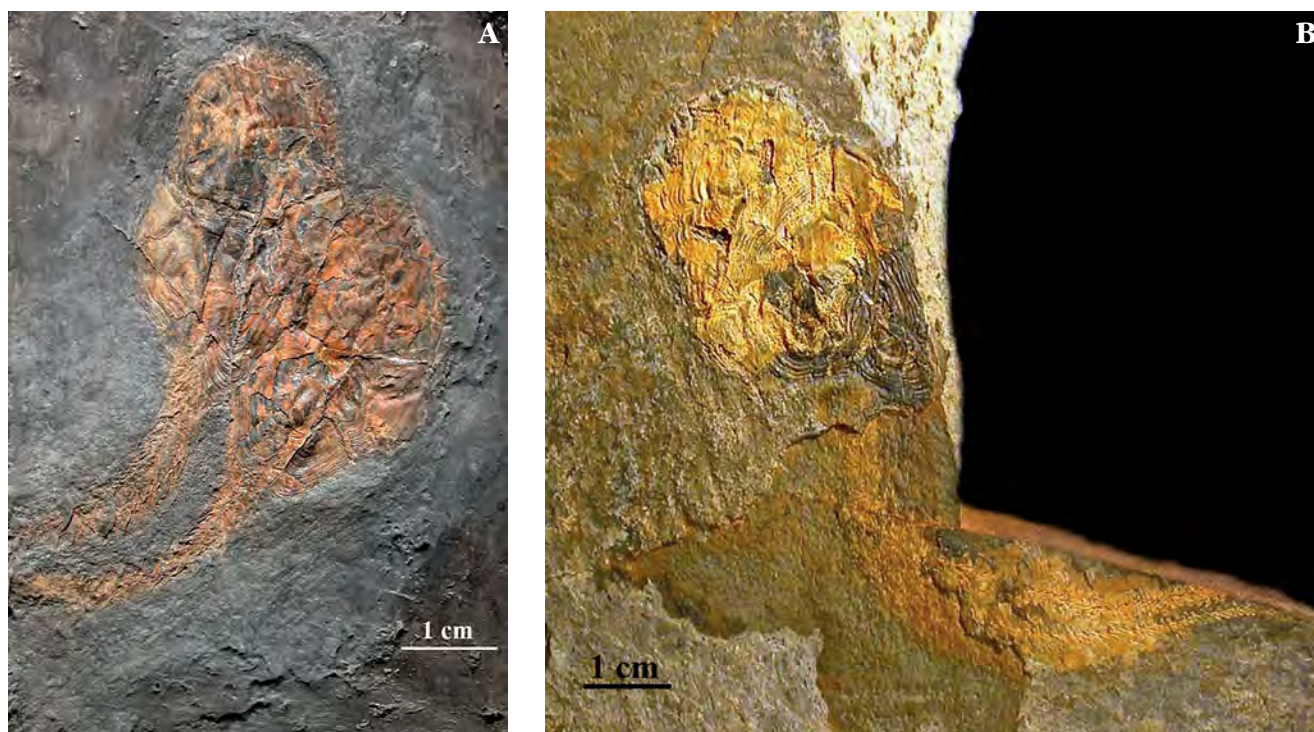


Fig. 9 – Two examples in which the two known morphotypes of *Couralepis mclachlani*, from the Devonian (Givetian) of Cowra, New South Wales, Australia, have fossilized overlapping, strongly recalling an attitude of mating. Courtesy of Dr. Roger Jones, London

Copulation organs and sexual dimorphism in Osteichthyes

In the Osteichthyes fossil we have little evidence of primary sexual dimorphism, such as the fossil record of intromittent organs. Gonopodium-like structures, possibly with hooks, is known from some Middle Triassic Neopterygii of Europe and China (Bürgin, 1990; Nelson, 2006; Hurley *et al.*, 2007; Friedman, 2015). In fact, both in Middle Triassic Swiss-Italian species *Peltopleurus nutialis* (Lombardo, 1999) and *Peltopleurus lissocephalus* (Bürgin, 1990), as well as in Middle-Triassic of China species *Peltopleurus nitidus*, a gonopodium-like structure comprising two segmented elements is present rather than a single elongated ray (Xu & Ma, 2016).

Concerning the secondary sexual characters, we only have six certain cases of sexual dimorphism in Mesozoic fossil Actinopterygian fishes, all of which belong to the Pycnodontiformes. Three of the six cases in question, as follows, are specimens from the deposits of Cenomanian Sannine limestone in Lebanon (Haqel and Hjoula), which are well known for the excellent state of conservation of the fos-

sils they contain (Capasso, 2017). The fourth case of sexual dimorphism was observed in a large series of samples collected from the world famous Monte Bolca locality. The fifth case is from a true sample of a population of Pycnodonts that also provides statistical data, and the sixth case is from Jurassic of Solnhofen, Germany. The six cases are the following:

1. *Nursallia tethysensis*;
2. *Hensodon spinosus*;
3. *Pankowskithys libanicus*;
4. *Pycnodus apodus*;
5. “*Coelodus*” *danae*;
6. *Gyrodus hexagonus*.

In the species *Nursallia tethysensis*, Capasso *et al.* (2009) showed that the number of spines of each individual scale that forms the dorsal ridge (in the region between the parietal and dorsal fins) differs in a bimodal manner within the same species. Capasso *et al.* (2009) examined 12 specimens of the species *Nursallia tethysensis*, and demonstrated the presence of two different morphology patterns of the single scales of the dorsal ridge. In the first group of specimens each scale is surmounted by three spines:



Fig. 10 – Isolated spine of the ventral midline of *Sinacanthus wuchangensis*, from the Late Silurian (Wenlock), Yimugantawu Formation, Tarim, China

the anterior one is directed anteriorly, while the second and third are directed posteriorly. In these specimens the total number of scutes that composed the dorsal ridge is 6 or 7, which is lower than that characteristic of the second group of specimens. In this second group, the scales of the dorsal ridge are surmounted by only one spine, which has a rounded tip. In these specimens, the total number of scutes that compose the dorsal ridge is 8 or 9, which as indicated, is higher than that characteristic of the first group of specimens. Capasso *et al.* (2009) related these differences to sexual dimorphism inside the species *Nursallia tethysensis*.

Concerning *Hensodon spinosus*, Capasso *et al.* (2010) demonstrated the bimodal variability in the number and morphology of the patterning, and in the number and arrangement of the spinous processes of the bones of the splanchnocranium, and above all, of

the cleithrum. Some additional differences were also seen regarding the vertebral column. Capasso *et al.* (2010) examined four specimens of *Hensodon spinosus*, and took into consideration also the holotype described by Hennig (1907), which was re-examined by Kriwet (2004). On the basis of the observations made on these materials, the characters that distinguish the two sexes can be summarized as follows:

- (i) there are two patterns of the frontal region and horns, which most likely represent sexual dimorphism. In the supposed male specimen, the frontals are rather narrow above the orbit and support two large, elongated, anteriorly directed conic horns, with a pointed pit, one on each frontal. Above this horn, the frontal margin has a series of eight small spines that contribute to provide a serrated aspect on the superior margin of the frontal, while ventrally, at the base of the large horn, there are another two smaller spines. As already mentioned, this morphology can be interpreted as the male pattern. In the holotype, the frontal has two smaller horns, one dorsally, the other more ventrally (Hennig, 1907), and we believe that is the female pattern;
- (ii) the frontal is much broader above the orbit in the supposed female than in the male;
- (iii) the long anterior margin of the dermosupraoccipital is serrated, and its superior margin has two well-developed spines (this serration is less pronounced in the supposed female than in the male);
- (iv) the dorsal margin of the supratemporal also has a few spines. This character is the same in both sexes, but the anterior margin of the process follows the frontal profile in the supposed male, while it forms a marked angle with the frontal profile in the three female specimens (Capasso *et al.*, 2010), and in the holotype (Kriwet, 2004);
- (v) the dermopterotic is very long, although not high, and it bears a long horizontal crest. Its acuminate, anterior extremity overhangs the orbit in the male specimen. In all three of the female specimens described by Capasso *et al.* (2010), the dermopterotic is a little shorter and less acuminate;
- (vi) the dermhyomandibula is semi-lunar, and thus relatively distinguishable from the preopercle in the male specimen, while it is in complete continuity with the preopercle in the female specimen;

- (vii) the posterior margin of the preopercle shows some small spines in the male specimen. It appears that the three supposed female specimens described by Capasso *et al.* (2010), as well as the holotype (Kriwet, 2004), do not have these preopercular spines;
- (viii) in the supposed male specimen, the cleithrum is noticeably more robust, with many elongated and robust spines. Despite this, the number and general arrangement of the spines and the general shape of the bone is exactly the same in both sexes. However, the three supposed female specimens have a cleithrum that is generally more delicate;
- (ix) the dorsal and ventral arcocentra are more developed in the presumed male specimen than in the three other (female) specimens;
- (x) another very relevant bone in the anatomy of the skeleton of this species is the post-coelomic bone. In both the presumed male and female specimens this bone is well developed. Despite this, in the supposed females it appears to be more delicate. The post-coelomic bone is sinuous, and stays in contact with the first haemal spine, as well as with the first anal axonosts. It extends from the ventral profile of the fish and reaches the inferior border of the vertebral column. The ventral part is expanded, clave-shaped, and its ventral margin has two large spines. The relevant dimensions of these post-coelomic spines are nearly the same in the two sexes. In the supposed male, two additional small spines are present on the anterior margin of the bone, facing the abdominal cavity;
- (xi) there is an important difference between the two sexes concerning the last neural and haemal arches. In the three supposed female specimens, these arches are small and the notochord is not covered. In the supposed male specimen, the last neural and haemal arches have wing-like expansions that completely cover the notochord, with some arches are ankylosed together.

The combination of these anatomical differences results in two morphotypes according to sex. These appear very different from each other (Figure 11 A-D), so much so that according to the state of our knowledge at present, the case of *Hensodon spinosus* is the most striking example of sexual dimorphism, not only in the restricted field of Pycnodonts, but also in fossil fish as a whole.

Concerning *Pankowskichthys libanicus*, on the basis of a single specimen, Cawley & Kriwet (2017b) described a second specimen of the same species, and were the first to identify the presence of two distinct morphotypes within the same species. This was demonstrated by some anatomical details of the splanchnocranial bones, and the presence of spinous processes of the parietal bone, which were interpreted as characteristic of the male specimens, though lacking any supporting scientific evidence. Taverne & Capasso (2020) described a third specimen of the same species, which confirmed that there are two sex-related morphotypes in this Pycnodont.

Taverne & Capasso (2020) also defined in great detail the anatomical differences that distinguish these male and female individuals. The male specimen and the female holotype share the same general morphology. At first sight, the two specimens appear to be very similar. However, as we will see here, the differences between the two sexes of *Pankowskichthys libanicus* are numerous, and are indeed much more numerous than the four differences mentioned by Cawley & Kriwet (2017). In more detail, these sexual differences include the following:

- (i) the mesethmoid is well exposed in the male, while it is almost entirely hidden by the prefrontal in the female;
- (ii) the frontal reaches the dermosupraoccipital and the dermopterotic in the male, but not the parietal. In the female, the posterior region of the frontal is elongated. The bone is sutured to the dermosupraoccipital and the parietal, and reaches the dermopterotic at only one point;
- (iii) the frontal bears a well-developed horn in the male, while it only has a medium protuberance in the female;
- (iv) the parietal is much smaller in the male than the female;
- (v) the dermopterotic is much wider in the male than the female;
- (vi) the parasphenoid is very long and greatly outstretches the level of the hypercleithrum in the female, while it does not outstretch the rear of the skull in the male;
- (vii) the orbitosphenoid is pressed against the mesethmoid in the male, while this bone is hook-like and well separated from the mesethmoid in the female;
- (viii) the premaxilla has a short anterior hook-shaped process that is not attached to the prefrontal in the female, but has an acuminate, anterior extremity sutured to the prefrontal in the male;

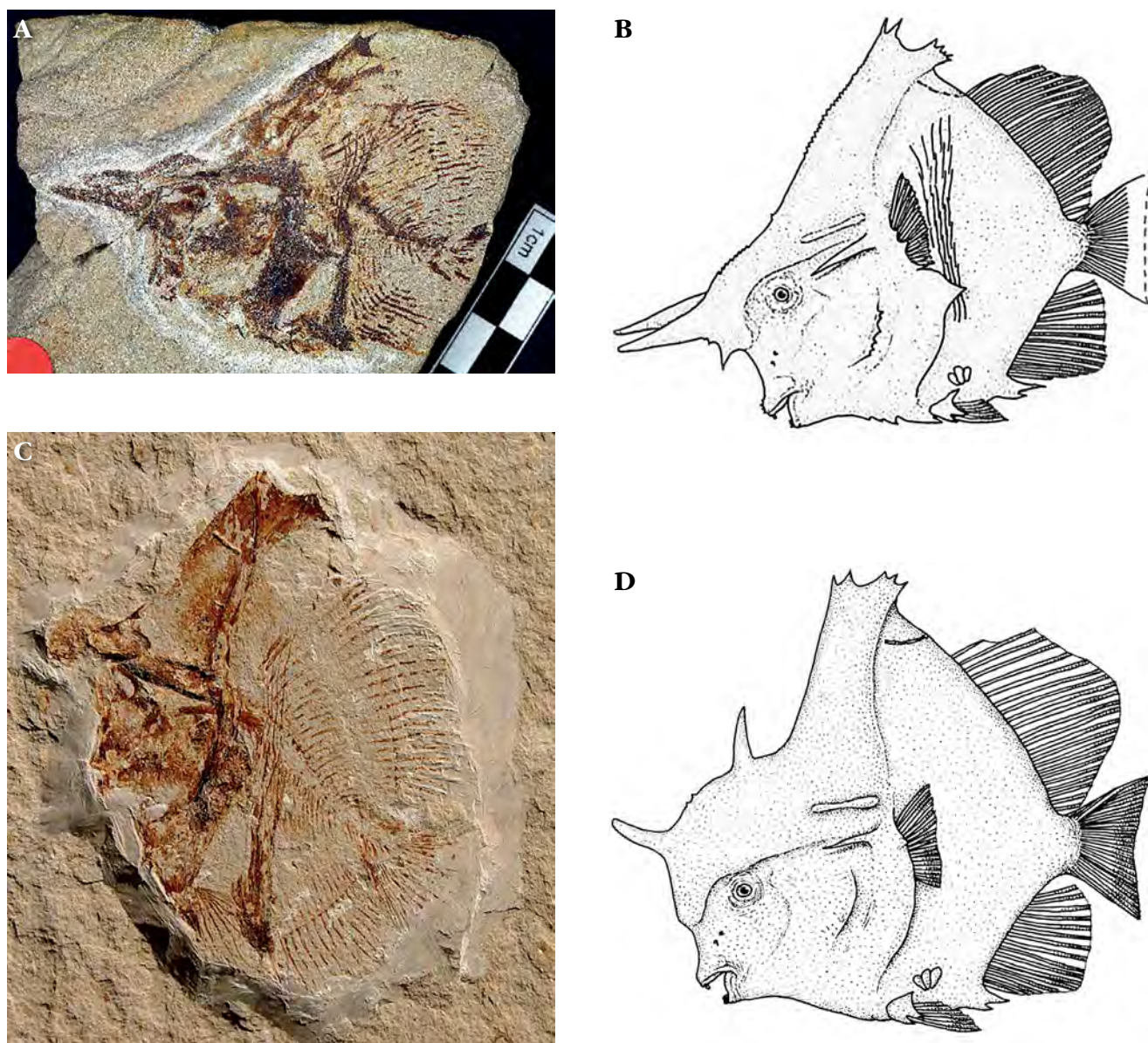


Fig. 11 – Sexual dimorphism in *Hensodon spinosus* from the Cenomanian Sannine limestone of Haqel, Lebanon. **A:** An assumed male specimen (TL = 50 mm). **B:** Reconstruction of the entire living fish, as the assumed male pattern. **C:** An assumed female specimen (TL = 64 mm ca.). **D:** Reconstruction of the entire living fish, as the assumed female pattern. From Capasso, Taverne & Nohra (2010)

- (ix) the dentary has two very small teeth in the female, while it is toothless in the male;
- (x) the ventral margin of the dentary has four or five well-developed spines in the male, but has only a series of microspines on the female;
- (xi) the hyomandibula is almost as deep as the preopercle in the male, but is much more reduced in the female;
- (xii) the preopercle completely covers the metapterygoid and the entopterygoid in the female. A large part of the entopterygoid is visible in the male;
- (xiii) the nuchal horn is proportionally shorter (72.2% the standard length) in the male than the female (83.5% the standard length);
- (xiv) the nuchal horn is more upright in the male than the female, which has an obliquely directed horn;

- (xv) the spaces between the spines of the nuchal horn are concave in the male, but almost straight in the female;
- (xvi) the abdominal cavity, the pelvic girdle and the post-coelomic bone are entirely covered by the dorsal branch of the cleithrum in the male. In the female, portions of the ribs, parts of the ventral fins and the post-coelomic bone are exposed behind the cleithrum;
- (xvii) the ventral anterior branch of the cleithrum is broad in the male, but narrow in the female;
- (xviii) a broad process with a spiny ventral margin is seen for the male, on the ventral border of the cleithrum, just before the pectoral spine, while this process is not present in the female;
- (xix) the dorsal and anal fin rays are much longer in the male than the female;
- (xx) there are three spiny dorsal ridge scutes between the nuchal horn and the dorsal fin in the male. In the female, there is no dorsal ridge scute, and the dorsal fin begins immediately after the nuchal horn.

The 20 characters of the *Pankowskichthys libanicus* skeleton represent the phenotypic expression of sexual dimorphism, even if each of these differences relate to a minor anatomical detail. These 20 characters together define the very articulated and relevant differences in the morphologies of the two sexes, as is clearly seen by comparing the profile of the male head with that of the female head.

Concerning the Pycnodonts collected from the famous Eocene deposit of Monte Bolca, Northern Italy, (revised by Blot, 1987), the specimens assigned to the genus *Pycnodus* appeared to belong to two different species: *Pycnodus apodus* (Volta) (not *Pycnodus platessus* Agassiz) and *Pycnodus gibbus* Agassiz. Heckel (1856) confirmed the validity of these two separate species, clarifying that the distinctive characters between them was the general shape of the body and the proportions between the maximum height and the total length of the body. Indeed, as described by Heckel (1856), *Pycnodus gibbus* is characterized by a body height that is two-thirds its length, while *Pycnodus apodus* is characterized by a body height that is half its length. It follows that *Pycnodus gibbus* has a higher general shape of the body, which appears almost shortened, while *Pycnodus apodus* has a more tapered and elongated body.

Blot (1987) examined a total of 50 specimens, and based on the classifications shown on the tags

and in the catalogues of the museums and collections to which they belong, he assigned these both to *Pycnodus apodus* and *Pycnodus gibbus*. These included specimens of very different sizes, where the smallest was only 2.9 cm long (National Museum of Natural History of Paris, No. 0130-0131), the largest was 26.3 cm long (Civic Museum of Natural History of Verona; no. II D 170-171). Blot (1987) performed a complete metric analysis of all of these specimens, showing among other things that in the smaller specimens the body is relatively high in relation to the length, and that the specimens have a more oval general appearance and are shortened. At the same time, in the larger specimens, the height of the body is less than the length, and so the specimens have a more tapered general appearance.

On the basis of these data, Blot (1987) was able to demonstrate that the two presumed species, namely *Pycnodus apodus* and *Pycnodus gibbus*, are in reality only one species, namely *Pycnodus apodus*. *Pycnodus gibbus* corresponds to a body morphology that is characteristic of the more youthful development phases of *Pycnodus apodus*, which are also characterised, among other things, by a more angular morphology of the frontal profile, as well as by the general morphology of the taller and shorter body, thus appearing more squat.

In addition to the differences in size that were evidently linked to the growth phase, Blot (1987) also underlined, as indicated above, that between the two hypothetical species there are also small morphological differences. First, *Pycnodus gibbus* has a more angular aspect of its frontal profile, and this major gibbosity does not always correlate well with the general somatic measurements and indices. Blot (1987) himself demonstrated this by relating the length of the body, the body height, and the angle of gibbosity of the frontal profile (in degrees).

To explain these small differences, Blot (1987) hypothesized a role for sexual dimorphism, in the sense that the females might also have been those of the smaller body size, with a higher body, and with a more humped frontal profile. As Blot (1987) said: “*Peut-être s’agit-il, tout au plus, d’une différentiation en relation avec le sexe des exemplaires ainsi que l’on peut l’observer de nos jours chez un certain nombre d’espèces de poissons, surtout parmi celles qui présentent un corps élevé*”.

The case of “*Coelodus*” *danae*, reported by Capasso *et al.* (2021), currently represents the only paleontological case of sexual dimorphism in a population of fossil fish. Bravi (1996) described the new species

“Coelodus” danae on the basis of a great number of small sized Pycnodonts collected from the Aptian (Lower Cretaceous) of Caserta (southern Italy). Indeed, there are 135 individuals and almost every one of them is very well preserved and complete.

Simple macroscopic examinations of this population of specimens known as *“Coelodus” danae* clearly distinguish the presence of two separate body morphologies, as two “morphotypes”: individuals that are defined as the ‘short’ type, and individuals that are defined as the ‘long’ type. Despite the obvious differences that can be highlighted by a simple comparison of the two individuals, detailed analysis of the skeletal anatomy did not demonstrate any substantial differences, either in the morphology of the individual bone elements, or in the relationships between them. Therefore, there is little or no doubt that these two morphotypes belong to the same species, even when taking into consideration the individuals for which the morphological and somatometric differences are the most extreme.

In the short morphotype presented as the prototype of this population, there are 31 vertebral bodies, of which 16 pertain to the caudal pedicel. In the prototype of the long morphotype, there are 28 vertebral bodies, of which 15 are caudal. Therefore, it can be concluded that the different body lengths (as compared to the maximum heights) are the result of longer individual bones, rather than a greater number of bones within the spine. The same situation is seen for the other elements of the axial skeleton (i.e. the ribs), as well as for the uneven fins, and even for the elements relevant to the coating scales. For example, the dermal shields that make up the dorsal hull (in front of the dorsal fin) and connect the neural apophyses of the vertebrae with the bar scales are characteristic of the pycnodonts. These are more numerous for the short morphology (11 elements), as compared to the long morphology (10 elements).

Finally, it is worth noting that there are no important differences in the cloacal region, which is of great importance in the evaluation of sexual dimorphism of some extant fish, as the copulatory organs are positioned in this region (Tortonese, 2000). No differences were seen within the population of *“Coelodus” danae* in terms of the numbers, morphologies and arrangements of the bones in this region. The dermal elements (i.e. the scales) of the anal region consist of two small scales that are positioned posterior to the anus and anterior to

the beginning of the anal fin. These are almost constant, and show only minimal differences across these two morphotypes. One such difference is seen for the long morphotype, where the anterior scale is smaller and is surmounted by two spinous processes, while in the short morphotype, it is a little more robust and surmounted by three spinous processes. However, the posterior scale is more robust and surmounted by three spinous processes in both of these morphotypes. Also, these spinous processes, and especially those for the posterior anal scales, are longer for the short morphotype than for the long morphotype.

The total length of the longest individual is 61.5 mm, with a maximum body height of 50.5 mm. The representation of the relationships between the total lengths measured with respect to the maximum heights measured on a Cartesian plane show dispersion around a single central (median) area, thus demonstrating the overall homogeneity of the population examined.

The morphological and the somatometric data demonstrate that this population of *“Coelodus” danae* includes individuals that belong to the same species. This is supported by both the anatomical structures and the arrangement of the skeleton and the tegumentary elements, along with the unimodal and monocentric distribution of the main somatometric parameters.

In this context, the most obvious interpretation would be to consider the variability as the normal expression of individual differences at the population level. However, the presence of only two morphotypes is equally evident, each of which appears to be well characterised, from both a morphological and a somatometric point of view. This variability can therefore certainly be defined as intraspecific, and thus is most likely sexual. Furthermore, in favour of this interpretation, for the small-sized individuals that evidently correspond to the juvenile phases of the life cycle of this species, both the somatometric and the morphological characteristics show intermediate values between those of the two extreme morphotypes. Thus, this suggests that in the juvenile specimens the characteristics of sexual dimorphism were not yet developed.

In summary, the variability described by Capasso *et al.* (2021) within the population of *“Coelodus” danae* from the Aptian (Lower Cretaceous) of Profeti (Caserta, Italy) shows minimal morphological and somatometric differences of the main skeletal segments (especially of the skull and axial skeleton),

accompanied by small morphological differences of the scales of the cloacal region, and some somatometric differences. Overall, this variability identifies two extreme morphotypes: a ‘short’ morphotype and a ‘long’ morphotype. Somatometric analyses clearly demonstrate that this population is homogeneous, as it shows a single mean and data that are evenly dispersed around the values that are most representative of the population. These include unimodality and monocentricity for the distribution of both the main somatometric measurements, and the index derived from them. Finally, it should be emphasised that all of these characteristics of dimorphism, both morphological and somatometric, appear during the ontogenetic maturation process, as they are absent in the more juvenile individuals.

Therefore, the example of “*Coelodus*” *danae* refers to a population of Pycnodontiformes in which both the morphological and somatometric sexual differences were slight differences, while they were absent in the juvenile specimens and present to various degrees only in the adults. This population thus shows extreme configurations in only some of the specimens and therefore all of the data shown here support the interpretation that the variability shown within this population is dependent on sexual dimorphism. However, this case contrasts with the case of *Pankowskichthys libanicus*, in which the supposed sex of each specimen was identified only on the basis of the morphological minutiae detected in a very low number of specimens. In the present study, despite the reasonable number of individuals, we are not able to link a specific sex to a specific somatometric morphotype with any certainty (Capasso *et al.*, 2021).

Finally, concerning the case of *Gyrodus hexagonus*, we report that Lambers (1991) studied a number of Pycnodonts pertaining to the genus *Gyrodus* that were collected in the lithographic limestone of Solnhofen (Germany), including the exceptionally well preserved type specimen of *Gyrodus dichactinius* of Teylers Museum, and other well-preserved materials. Lambers (1991) carried out a quantitative analysis of morphometric data of two small Jurassic “species” of *Gyrodus*, and demonstrated that they represent only one species. Indeed, the two previously described formal species called *Gyrodus hexagonus* (including *Gyrodus frontatus*, as a synonym) and what was usually called *Gyrodus macrophthalmus* (including *Gyrodus dichactinius*, as a synonym) actually all belong to the same species: *Gyrodus hexagonus*. The differences thus represent

two morphotypes that were previously described as automonus species, *Gyrodus hexagonus* and *Gyrodus macrophthalmus*. Lambers (1991) assumed that sexual dimorphism had a role in the configuration of these two morphotypes within the population of Solnhofen’s *Gyrodus*.

A recently described case could represent a further example of sexual dimorphism in Pycnodonts. Indeed, Stinnesbeck *et al.* (2019) observed a large population of *Nursallia gutturosa* from the Latest-Cenomanian-middle Turonian of Vallecillo, Mexico, observing the presence of two different morphotypes, distinguishable only by the dimensions of the dorsal fin: very elongated in the presumed male subjects, very short in the presumed female ones.

In addition to the review made so far regarding sexual dimorphism and possible mating modes in fossil fish, it is also necessary to mention the possibility of finding behavioral fossil traces that represent potential clues to sexual dimorphism and mating practices in the vent-to-vent modality of pseudo-copulation. We have already seen that the relationship between two individuals, representing different morphotypes, can exceptionally be preserved in the fossil state, as in the case of *Cowralepis*. In addition to this extraordinary Paleozoic example, according to the author’s experience, other exceptional cases can be cited regarding fossil traces of vent-to-vent relationships in Mesozoic, Cenozoic and even Quaternary Osteichthys. Here are only a few:

- (i) a pair of *Australosomus merlei*, from the Lower Triassic of Madagascar (Figure 12 A);
- (ii) a pair of *Ctenodentelops striatus*, from the Cenomanian of En Nammoura, Lebanon (Figure 12 B);
- (iii) a pair of *Dapalis macrurus*, from the Oligocene of Cereste, France (Figure 12 C);
- (iv) a pair of *Mallotus villosus*, from Green Creek Pleistocene, Canada (Figure 12 D).

It is clear that the interpretation of these fossils in the sense of behavioral traces linked to pseudo-mating is an inference, but some contextual elements support this interpretation: (i) the two specimens belong to the same species, and (ii) they generally show minimal differences, especially from the point of view of some somatic proportions. Moreover, (iii) both specimens are fossilized side by side, and (iv) are oriented in the same direction, but (v) never completely overlapping. Furthermore, it is very important to underline that overlaps of this kind are very rare events, almost never described, despite

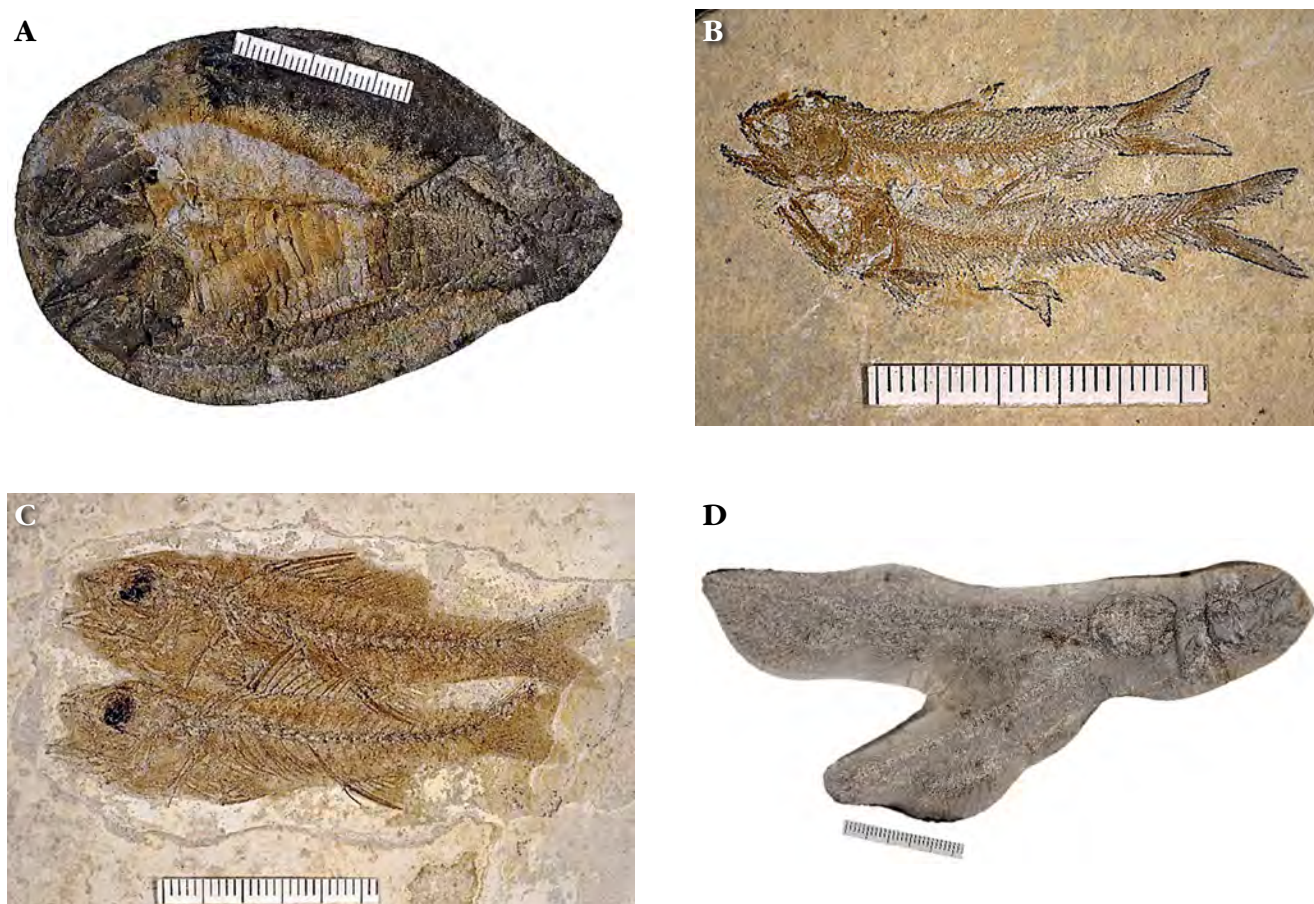


Fig. 12 – Four examples of fossil behavioral traces of possible vent-to-vent pseudo-copulation in some Actinopterygii of various antiquity. **A:** a pair of *Australosomus merlei*, from the Lower Triassic of Madagascar; **B:** a pair of *Ctenodentelops striatus*, from the Cenomanian of En Nammoura, Lebanon; **C:** a pair of *Dapalis macrurus*, from the Oligocene of Cereste, France; **D:** a pair of *Mallotus villosus*, from Green Creek Pleistocene, Canada

the fact that, especially in some deposits (such as in Haqel, Lebanon), fossil fish are very thickened, and overlaps are the norm. For this reason it is of great significance to consider that no specimen with the characteristics indicated above, however, has been described up to now, for example, from the Haqel locality. On the other hand, we must consider that in other deposits the opposite condition occurs: thus in the case of the deposit of En Nammoura (Lebanon), in which the density of fossil fish is very small, and the possibility of finding two specimens of fossil fish in the same square meter of surface of limestone stratum is absolutely remote (Capasso, 2017). These considerations encourage the interpretation of the described four cases that really represent true traces of pseudo-mating, in the vent-to-vent mode, limited to fossil Osteichthyes.

VIVIPAROUS AND OVOVIVIPAROUS SPECIES: PREGNANCY

Beyond the modalities of internal or external fertilization, there are three types of development of the fertilized eggs in fish (Wourms, 1981):

- (i) viviparity, in which the fertilized eggs (with or without a yolk sac) are retained by the mother, and the embryo feeds on direct connections (such as a single “umbilical cord” or multiple “trophonemes”) with the mother’s circulatory system (so called “matrotrophicity”); all embryonic development is intra-maternal, and the newborns are expelled alive and fully developed;
- (ii) ovoviviparity, in which the eggs are fertilized internally and remain in the maternal oviducts where the embryos develop in the yolk sac,

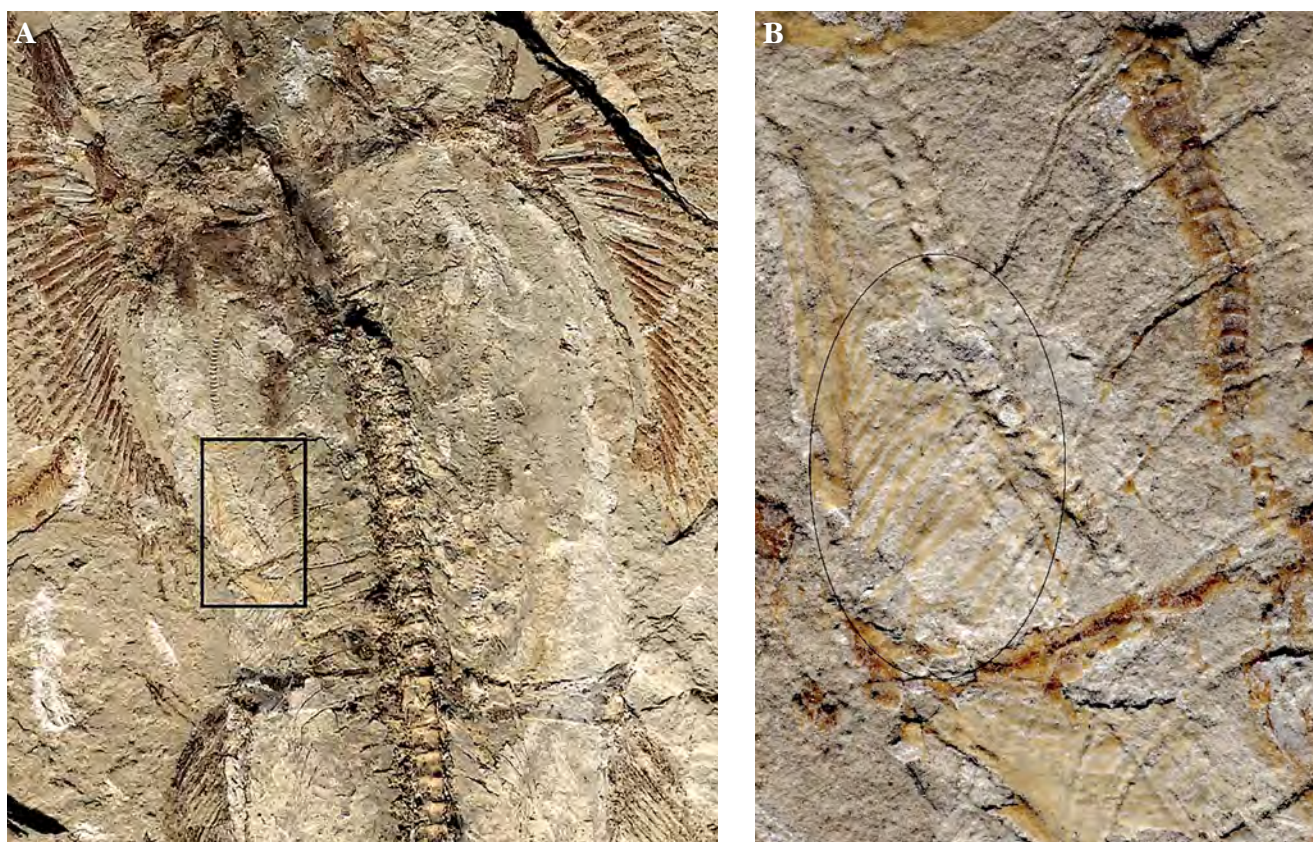


Fig. 13 – **A**: a partial specimen of the fossil ray *Rhinobatos maronita*, from the Cenomanian (Late Cretaceous) of Hjoula, that preserved five embryos in the visceral cavity, situated between the toracic girdle and the pelvic one, two at the left side of the vertebral column and three at the right side; **B**: the detail (the area included in the rectangle in figure A) of the region between the most lateral left side embryo and the wall of the ventral cavity of the mother (oviducts) shown the presence of little filamentous structure that perfectly correspond to trophonemes

without connections with the mother's circulatory system; the eggs hatch inside the oviducts and the newborns are expelled alive and fully developed;

- (iii) oviparity, in which the eggs (already fertilized or will be fertilized outside) are laid and embryos develop outside the mother.

The condition of pregnancy in female fish therefore consists both in the (temporary) retention of eggs (awaiting fertilization or recently fertilized), and in the retention and growth of embryos, or in the yolk sac (ovoviviparity) or directly dependent on the maternal bloodstream (viviparity).

Viviparity is easily observed and well documented in many living Chondrichthyan fishes (sharks and rays), as well as in few Neopterygian fishes (only 14 teleostean families), but they are very difficult to identify in extinct taxa, due to limited fossil records

and, most of all limited interpretation in a paleophysiological key.

Viviparity and/or ovoviviparity have been confirmed many times in specimens whose embryos were recovered inside a pregnant, fossil female fish (Long *et al.*, 2008; 2009), but remain rare events, and require an analysis to distinguish embryos from internal food items in the female abdominal cavity. Even when it is possible to clarify the doubt between the remains of small prey and embryos, the remains of embryos in the visceral cavity of a female fossil fish are almost never convincing to assert whether it is an ovoviviparity or a true viviparity. Only in conditions of exceptional conservation can remains of yolk sac be found, which indicate an ovoviviparity, or remains of the umbilical chord or of the trophonemes, which indicate a direct connection between the circulatory stream of

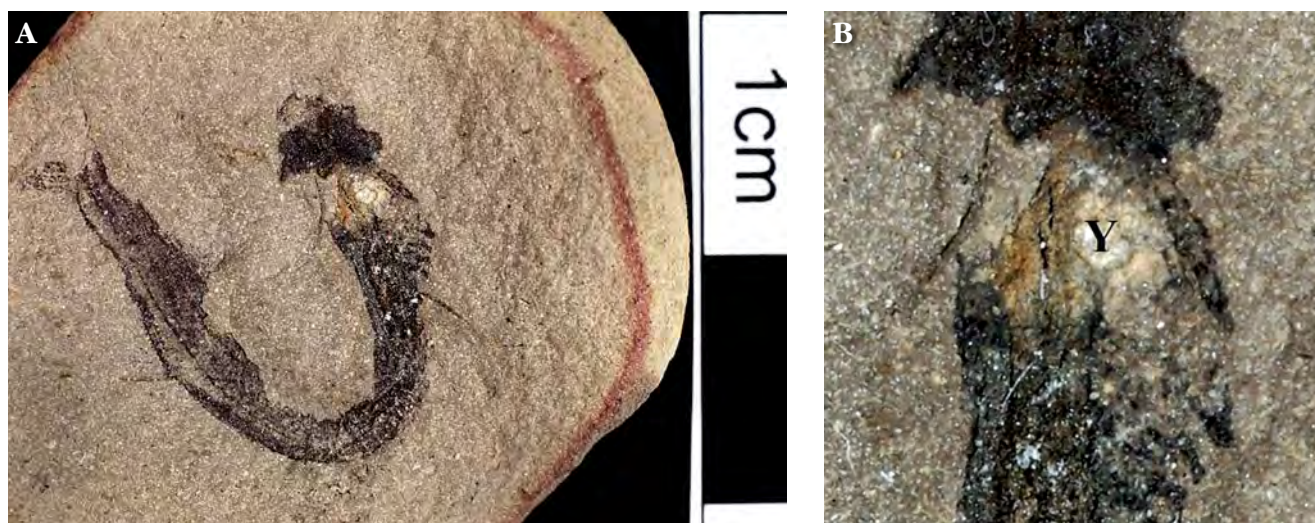


Fig. 14 – A specimen of *Acanthodes* sp. ind. of very small size, curved on itself, that shown the remains of a yellowish mass, with a dense yellow granule in the center, located in close connection with the abdominal region of the small fry, that is interpretable of the fossilized yolk sac (Y). From the Late Carboniferous Francis Creek Shale, Braidwood, Illinois, USA

the mother and that of the fetus, and therefore are the unequivocal trace of viviparity.

To present date knowledge, only two cases have clearly demonstrated the presence of umbilical chord *vs* trophonemes. The first consists of a specimen of *Rhinobatos maronita*, from the Cenomanian of Lebanon, described by Capasso (2003), in association with five embryos (Figures 13 A and B). The second represents the discovery of traces of umbilical cord, which again represents another unique find. These are the skeletal remains of an embryo documented in the abdominal cavity of the Placoderm Ptyctodont *Materpiscis attenboroughi*, from the Upper Devonian of the Gogo Formation, Australia. The ‘embryo’ was associated with recrystallized material, which was interpreted as remains of the yolk sac, and by a vascular structure that was interpreted as the fossilized umbilical cord. This mixed condition was called “yolk-sac viviparity” (Long *et al.*, 2008).

In the all other cases, the interpretative doubt between viviparity and ovoviviparity always remains.

Viviparity vs ovoviviparity in Acanthodians

Initial information in this regard seems to come from some recent discoveries made in the deposit of the so-called Pit 11, which was located southwest of the town of Braidwood, Illinois, a deposit similar and coeval to that of the Mazon Creek area, and belonging to the same Upper Carboniferous Francis Creek Shale.

A very small sized specimen of *Acanthodes* sp. ind. in fact is kept curved on itself inside a tiny ferrite nodule and clearly presents the remains of a yellowish mass, with a dense yellow granule in the center, located in close connection with the abdominal region of the small fry. There is little doubt that this out-of-body structure represents the remains of this acanthodian’s yolk sac (Figure 14 A and B). Moreover, even the chromatism of these fossil remains can be superimposed on that described for the remains of the yolk sacks of Coelacanth *Rhabdoderma*, coming from the same deposit. Thus, this outstanding new fossil, that I presents here for the first time, demonstrates that some of the Carboniferous Acanthodians were at least ovoviviparous as well.

Viviparity vs ovoviviparity in Chondrichthyans

In the Chondrichthyans, internal fertilization developed independently of what happened in the Placoderms (homoplasy), and there have been numerous examples of viviparity versus ovoviviparity, since the Carboniferous. Indeed Grogan & Lund (2004; 2011) reported numerous female specimens of the *Harpagofututor volsellorhinus* shark containing multiple embryos in the visceral cavity. Also in this case, it was shown that the same mother was managing embryos at different stages of development. In fact, due to the different sizes of the embryos, it was possible



Fig. 15 – **A**: The fossil ray *Rajorhina expansa*, from Cenomanian (Late Cretaceous) of Hjoula, Lebanon; **B**: detail of the abdominal region of the specimen in which three semicircular hollows (asterisks) are well evident in correspondence of the abdominal cavity could correspond to the external cast left by three advanced growth-stage eggs (which unfortunately were lost during the excavation of this fossil); note that both the metapterygia (MP) are posteriorly divaricated

to distinguish at least two generations corresponding to separate fertilization events. The lack of yolk sac traces also suggests, in the case of *Harpagofututor*, a true viviparity, with tropism of the embryos of the directly maternal type (matrotrophicity). Although neither the umbilical cords nor trophonemes were noticed, preserved organic pigments that enveloped the embryos, suggests that a nutritional material of maternal origin was still provided to each embryo (Grogan & Lund, 2011).

Some further examples of embryos inside the abdominal cavity of fossil Chondrichthyans are also present, as we have already said, in the marie Cenomanian (Cretaceous) ichthyofauna of Lebanon. In addition to the clear example of *Rhinobatos maronita* (Capasso, 2003) (see Figure 13),

traces of material probably connected to embryos are also evident in *Rajorhina expansa*. In fact, in a case from Hjoula (Figure 15), in correspondence to the abdominal cavity, there are at least three semi-ovoid hollows, all approximately the same size, two located to the left of the vertebral column and one located to the right of it. The hollows could correspond to the external cast left by three masses (which unfortunately were lost during the excavation of this fossil), with a near ovoid shape, whose presence in the abdominal cavity of the ray has actually posteriorly divaricated the two metapterygia. It is highly likely that these semi-ovoid hollows were actually left by three advanced growth-stage eggs inside the abdominal cavity of this fossil ray.

In addition, Fanti *et al.* (2019) described the presence of four oval masses, with a concentric pattern, located in correspondence with the abdominal cavity of the stingray *Tethytrigon muricatus* of the Eocene of Monte Bolca, Italy. Their asymmetrical position with respect to the vertebral column, the homogeneous dimensions, and the topographical position of these masses have made it possible to describe them as fertilized eggs in growth.

Finally, Carvalho *et al.* (2004) described a new stingray from the Green River Formation, Wyoming, dated to the Early Eocene, namely *Asterotrygon maloneyi*. This freshwater ray is known in many specimens, some of very small size and are interpreted as newborns, though still found in the vicinity of their mother (which will be covered in the paragraph dedicated to parental care); even the holotype of this stingray is a female individual whose abdominal cavity contains a perfectly preserved embryo, perhaps even with traces of a yolk sac (see Figure 30 A).

Viviparity vs ovoviviparity in Placoderms

The oldest known embryo to date has been very recently described in a Placoderm Arthrodira, *Watsonosteus fletti*, from the Givetian (Middle Devonian) of the Orkney Island, Scotland, representing at the same time the oldest trace of an embryo in all Vertebrates (Newman *et al.*, 2021). Other remains of embryos in Placoderm Arthrodira *Rhamphodopsis threiplandi* have also been documented in the Devonian of Scotland (Trinajstić *et al.*, 2014).

Long *et al.* (2009) demonstrated the presence of embryos also in at least two female specimens of the Arthrodira *Incisoscutum ritchieri*, and in a female specimen of the Ptyctodont *Australoptytodus gardneri*, both of which found in the Upper Devonian of the Gogo Formation, Australia. In these cases the remains of very small specimens were initially interpreted as “intestinal contents”, but a more careful analysis of the topographical position inside the abdominal cavity of the mothers showed that it was the contents of the oviducts. In *Incisoscutum ritchieri*, however, the simultaneous presence of embryos of different sizes was demonstrated, which presumptively correspond to different stages of foetal maturation. However, this circumstance is difficult to explain, even if it is compared with different fertilization times or with sperm storage with ongoing fertilization, phenomena that are also observed in some modern sharks (*Callorhynchus*, *Prionace*,

Chiloscyllium, *Galeocerdo*, *Mustelus*). Of course, the adelphophagy phenomenon is also a possible explanation of the asynchronous development of cohabiting embryos of predatory fishes.

Viviparity vs ovoviviparity in Osteichthyes

Actinopterygii

As regards the Actinopterygii, where internal fertilization is currently an exception, there are very few traces of viviparity with embryos or ovoviviparity with eggs, presumably fertilized, inside the oviducts.

A very small individual was found in the visceral cavity of an adult of the same Actinopterygii species *Birgeria nielsenii*, a predator belonging to the Lower Triassic ichthyofauna of Madagascar (Beltan, 1977). Some authors have interpreted this case as the remains of a meal, even if there are no signs of alterations related to digestion of the scaly lining of the endo-abdominal individual (Beltan, 1996). For this reason, it could actually be an embryo (Beltan, 1980).

There is no doubt, however, that another genus of Triassic predators, the *Saurichthys*, was viviparous (Bürgin, 1990). Griffith (1977) had already reported the presence of embryos in specimens of this species from the Upper Triassic of Lunz, Austria. Rieppel (1985) and Furrer (2003) had equally demonstrated the presence of an adult of *Saurichthys curionii* with embryos in the abdominal cavity also in the Middle Triassic ichthyofauna of Monte San Giorgio (Italy and Switzerland), and Renesto & Stockar (2009) described three further specimens of adult females from this same locality, each with multiple embryos present in the abdominal cavity, perfectly preserved, even with the presence of remains of soft tissues pertaining to at least one embryo.

Furthermore, D’Erasmus (1914-15) described a specimen of *Hypsospondilus bassanii* from the Lower Cretaceous limestone of Pietraroja in Benevento, southern Italy, whose abdominal cavity had small spheroidal, monomorphic and one-dimensional masses, which were interpreted as eggs retained in the oviducts, also according to what is microscopically documented by Capasso (2007).

Finally, some examples of Actinopterygii still remain to be documented and it must be ascertained whether the “swelling” of the abdominal cavity, which appears filled with a substance apparently devoid of macroscopic anatomical structures (in which therefore the presence of embryos is exclud-

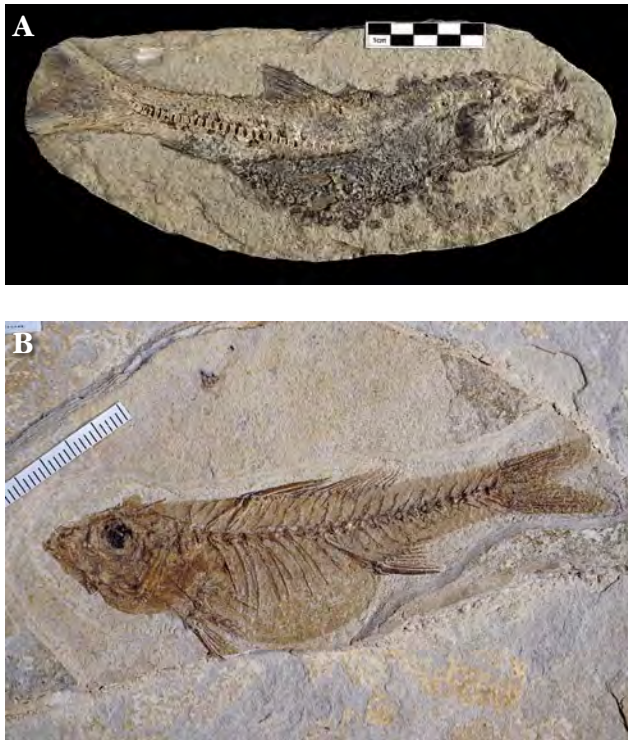


Fig. 16 – Two cases of abdominal “swelling”, possibly related to egg retention (fertilized or unfertilized) in fossil Actinopterygii. **A:** *Tharrias araripis*, from the Lower Cretaceous of Ceara, Brazil; **B:** *Dapalis macrurus*, from the Oligocene of Provence, France

ed) could represent cases of mature egg remains, already fertilized or not yet fertilized, in presumably female individuals (but in whose species, at the moment, anatomical traits pertinent to sexual dimorphism have not been documented). Two cases are reported in this paper so as to show the anatomical evidence of this genus of swellings, whose true origin and nature still awaits clarification: an example is *Tharrias araripis*, from the Lower Cretaceous of Ceara, Brazil (Figure 16 A), and a specimen of *Dapalis macrurus*, from the Oligocene of Provence, France (Figure 16 B).

Sarcopterygii

There is paleontological information regarding Coelacanth, which was not mentioned in the previous paragraph as no form of sexual dimorphism was present, both in the living forms and in the fossil ones, and the males do not possess any copulatory organ but, compared to the females, have only minimal differences in the structure and size

of the scales around the cloaca. Despite the absence of intromittent organs, Coelacanth are fishes with internal fertilization. The females retain the fertilized eggs, and the embryos fully feed on their yolk sacs inside the mothers, thus the living Coelacanth are ovoviviparous fish (Smith *et al.*, 1975). It seems that gestation lasts about 5 years and leads to the birth of two to five mature newborns. Recent studies have shown, however, that at a certain point in the development of intrauterine life, embryos take in food through the mouth, feeding on (in addition to the substances present in the yolk sac) maternal substances present in the oviducts, around the embryos (Balon, 1991). This double system of nutrition appears to be a great advantage in producing the complete growth of embryos.

The earliest information regarding reproduction in Coelacanth dates back to the Carboniferous. In fact, the Coelacanth *Rhabdoderma exiguum* of the Pennsylvanian of Illinois, is known above all through a large number of juvenile specimens, some of very small size, which also contain well-preserved, fossilized yolk sac still adhering to the abdominal region (Figure 17). Some authors have considered that these fry are hatchlings, not least because no embryos have ever been found

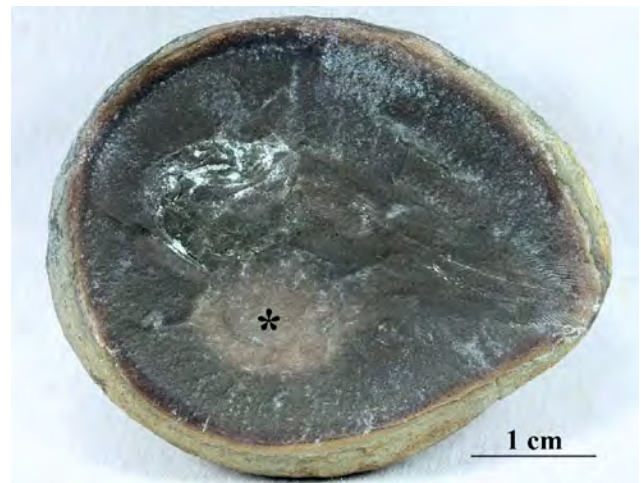


Fig. 17 – A specimen of *Rhabdoderma elegans* in a ferrite nodule from the Pennsylvanian (Late Carboniferous) Francis Creek Shale, Braidwood, Illinois (USA), with a great dimension yolk sac preserved (asterisc). Courtesy of Dr. John P. Adamek, Mundelein, Illinois (Fossilmall.com)

in connection to possible adults. Furthermore, the comparison of the proportions of the yolk sac with respect to the length of the fish shows that in *Rhabdoderma* the yolk sac had much smaller proportions than those of the living Coelacanth. Therefore, according to Balon (1991) *Rhabdoderma* had eggs of much lesser yolk volume and may represent an earlier form of oviparity with hiding, guarding or brooding type of parental care.

On finds of these numerous juveniles beside eggs of the Carboniferous Coelacanth *Rhabdoderma*, Schultze (1972) argued that this little Coelacanth was oviparous. Therefore, according to this hypothesis the ovoviviparity of the living Coelacanth would derive from a Paleozoic condition of oviparity. Even if we accept this hypothesis, we still have to admit that the Coelacanth had achieved ovoviviparity at least in the Triassic.

Indeed, Wen *et al.* (2013) described the Coelacanth fossil *Luopingcoelacanthus eurylacrimalis*, collected in the so-called Luoping Biota, Yunnan, South China, dated to the Middle Triassic. In a specimen of this species, two embryos were found, positioned in the abdominal cavity and whose dimensions suggest they were individuals close to birth, based on comparisons with previously reported embryos of the fossil Coelacanth *Rhabdoderma* and *Holophagus* (see the next lines), and the living genus *Latimeria*. Certainly this discovery demonstrates that Coelacanth was ovoviviparous as early as the Triassic.

Furthermore, Watson (1927) had already described a specimen of the Coelacanth, *Undina penicillata* (today transferred to the genus *Holophagus*), from the Late Jurassic lithographic limestone of Solnhofen (Germany), with two well developed embryos in the abdominal cavity.

Recently Cavin *et al.* (2021) described a pair of small basisphenoids (bones of the base of the skull, positioned at the end of the notochord) of the giant Coelacanth *Trachymetopon* sp., originating from the Middle Jurassic of Normandy, France. The dimensions and some anatomical details suggest that they are a couple of embryos or at most of newborns.

Finally, embryos have also been demonstrated at the level of the abdominal cavity of a Coelacanth of the Lower Cretaceous of the Crato Formation, Ceara deposit, Brazil. In fact, the holotype of the Coelacanth *Axelrodichthys araripensis* is a pregnant female with three embryos located in her abdominal cavity, immediately below the calcified swim bladder (Maisey, 1986).

OVIPARUS SPECIES: EGGS

It is difficult to assign a specific fossil egg capsule to a single fossil fish taxon, however this attribution is supported by, at least in some cases, (i) the morphological similarities of a peculiar structure and/or morphology between fossil and living forms (as is the case for the Chimaeras), (ii) a close and univocal association between the remains of eggs and the remains of fish in a single geological layer (as in *Couralepis*), (iii) the coincidence of the chronological extension of a given morphology of the fossil eggs and certain taxa of fossil fish, or (iv) the combination of several of these factors.

Due to these uncertainties of correlation between fossil species of eggs and fish, a parataxonomy has been created that considers the fossil eggs of fish as real ichnofossils. For the application of this parataxonomy a selection of the following works, which are both concise and very clear, is suggested: Mikhailov *et al.* (1996) and Wittry (2018), such as the “*Guide to the identification of fossil shark egg cases*” published by The Field Museum, which can also be easily consulted via the internet.

Due to the difficulties that the authors have described in the previous lines, in this paragraph the taxonomic division of the main and most significant taxa of fossil fish eggs is necessarily approximate and, above all, arguable.

Oviparity in Placoderms

We have already reported that all the paleontological evidence demonstrates that Placoderms had internal fertilization and viviparous or at most ovoviviparous reproduction. Nonetheless, at least two cases have been described in which fossil remains of eggs have been assigned to Placoderms.

Ritchie (2005) described a sack-like structure, containing more than 200 tightly packed oval structures, which he himself interpreted as an egg sac. This finding comes from the Middle Devonian (Givetian) of Cowra, New South Wales, Australia, and has been found in association with a multitude of individuals of the Placoderm Arthrodire *Couralepis mclachlani*: thousands of individuals have been collected from this location, including individuals with a total size of about 1 cm. The association of possible eggs, the absence of traces of sexual dimorphism, and the presence of an abundant and complete ontogenetic series of individuals (which also includes very small individuals), led Ritchie (2005) himself to infer that the *Couralepis* was an oviparous Placoderm, and

Table 2

Main valid ichnogenera	Number of described species (approximately)	Group of Chondrichthyans assumed as producers	Chronological range of fossil records		Deposition environment (deposits)
			First appearance	Extinction	
<i>Beargulchtotheca</i> *	1	?Chondrichthyan	Mississippian		Marine
<i>Chimaerotheca</i>	12	Chimaeroids	Devonian	Oligocene	Marine
<i>Crookallia</i>	5	?	Pennsylvanian		Paralic
<i>Fayolia</i>	16	Xenacanthiformes	Late Devonian	Middle Triassic	Freshwater
<i>Palaeochimaerotheca</i> *	1	Chimaeroids	Pennsylvanian		Freshwater
<i>Palaeoxyris</i>	26	Hybodonts	Middle Mississippian	Late Cretaceous	Freshwater to brackish
<i>Parascylliotheca</i> *	1	Parascyllidae	Cenomanian		Shallow marine
<i>Rajithec</i> a	4	Rajiformes	Late Jurassic	Miocene	Shallow marine
<i>Scyliorhiniotheca</i>	1	Scyliorhinid sharks	Late Eocene		Deep marine
<i>Theutonicotheca</i> *	1	?	Lower Devonian		Marine
<i>Vetacapsula</i>	12	???Helodontidae	Pennsylvanian		Paralic

* Ichnogenus established in this paper.

that the locality of Cowra was a true nursery for this genus.

More recently Carr & Jackson (2018) described a sack-like structure about 25 cm long collected in the Cleveland Shale, Ohio, USA, and dated to the Late Devonian (Famennian) that has been interpreted as an egg case. In this case, the presence of embryonic dermal bones with the same microscopic structure and biochemical composition (collagen fibers) of fossil bones of Placoderm Arthroires was demonstrated in the same deposit.

Thus, today we have sufficient paleontological evidence to affirm that even some species of Placoderms, already in the Late Devonian, had adopted oviparity. Therefore, we can accept the conclusion proposed by Carr & Jackson (2018) themselves: “Both egg-case oviparity and viviparity represent early and successful strategies following the origin on internal fertilization”.

Oviparity in Chondrichthyans

As we have seen, there is no univocal correspondence between species of fossil fish and ichnospecies of fossil egg capsules, therefore these correspondences are only hypothesized, based on different charac-

teristics from case to case. Nevertheless, at least the group of origin has almost always been hypothesized, that is, that taxonomic grouping of Chondrichthyans that could probably have laid a certain type of egg capsule, characterized by a well-defined and univocal morphology. In summary, based on our current paleontological knowledge on the egg cases of Chondrichthyans we will follow this criterion of correlation between the paleontological taxonomic group that produced the eggs and presumptively corresponding ichnospecies (Table 2).

Holocephalans

In light of the most recent findings, the belief expressed by Trinajstić *et al.* (2019) according to which “Fossilized egg capsules from the Late Devonian provide evidence that oviparity occurred prior to viviparity and ovoviviparity in Chondrichthyans” is no longer sustainable, at least not completely.

This belief is fundamentally based on some helical fossils from the Famennian (Late Devonian) of Belgium, which were initially interpreted as algae remains (Stainier, 1894), and then interpreted as selaceous eggs (Pruvost, 1919; Crookall, 1928), which have been assigned to the species *Spiraxis inter-*

strialis. Further findings of the same type were subsequently collected and described in equally Famennian strata of North America, and were assigned to two further distinct ichnospecies: *Spiraxis major*, from New York State, and *Spiraxis randalli*, from Pennsylvania. Most recently Mottequin *et al.* (2021) have analytically re-examined this material, also in light of many new specimens found in Belgian museums, and have excluded that the genus *Spiraxis* may have anything to do with fossil eggs and, even if they haven't exactly determined the nature of these fossil helical structures, they proposed a range of alternative interpretations. Therefore, with Mottequin *et al.* (2021), we can assert that: “*The first evidence of oviparity in the fossil record of chondrichthyans is thus not as old as previously thought and is close to the first occurrence of viviparity in this group, both being recognized now in the Mississippian*”.

The need to interpret a further find remains, described as “*Holocephalian (Chimaeroid) egg-case*”, found in the stratigraphic series of Bokkeveld, Cape Province, South Africa, currently dated to the Middle-Upper Devonian (Chaloner *et al.*, 1980). The morphology of this egg case (Figure 18) is absolutely characteristic and repeats the eggs of Holocephalans pertaining to the families Callorhynchidae and Rhinochimaeridae, both fossil and living.

In the interpretation of this find we can fully apply both the criteria of the comparative morphology between fossils and living beings, and the criterion of the chronological extension of the presumed species involved. Of all the fossil eggs assigned to fish, those of Holocephalans are certainly among the most characteristic and correspond very well to types E (Callorhynchidae) and F (Rhinochimaeridae), according to the morphological catalog presented by Fischer *et al.* (2014): structurally constituted by a central body, elongated and tapered at one end, surrounded by characteristic and thick, wavy, lateral collarettes (Didier, 1995). The South African Devonian specimen matches this model perfectly. Furthermore, the Holocephalan fishes are still alive and their first appearance must be traced back to the Middle Devonian, as evidenced by the reports of the Middle Devonian of Boulonnais, Pas-de-Calais, France (Darras *et al.*, 2008).

Despite all these similarities, Fischer *et al.* (2014) believe that the South African Devonian specimen is actually a Placoderm egg. In our opinion, this interpretation is highly questionable, both due to the demonstrated morphological and chronological extension similarities of the oothaecs of Hol-



Fig. 18 – The fossil egg capsule of a “Chimeroid” from the Middle-Upper Devonian of the Bokkeveld Series, Cape Province, South Africa (from Chaloner *et al.*, 1980)

ocephalans, and both (i) to the increasingly documented and extensive knowledge of viviparity in Placoderms, and (ii) to the morphology of possible egg sacs found in association with Devonian Placoderms in both Australia and the USA (as mentioned in the previous paragraph). Finally the only two supposed oothecas assigned to Placoderms demonstrate a saccular-shape, and contain a multitude of eggs, very different from the structure and shape of the South African record.

So we could conclude that the hypothesis of Trinajstić *et al.* (2019) can only be shared with Holocephalans, for which the fossilized egg capsules from the Late Devonian provide evidence that oviparity occurred in the Holocephalans since their first

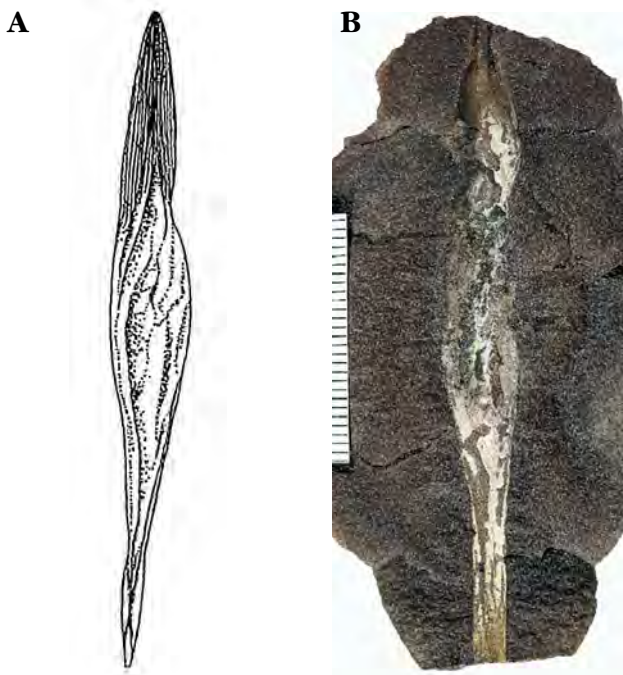


Fig. 19 – *Palaeochimaerootheca browni*, gn. et sp. nov. These egg capsules pertain to Holocephalians fish of the family Chimaeridae. **A**: a specimen characterized by an elongate body, a conical beak, a very elongated pedicle, two thin and smooth lateral collarettes (flanges), without (or with minimal) twisting along the major axis, from the Pennsylvanian of Mazon Creek area, Illinois, USA (from Brown, 1950); **B**: The holotype, such as an egg capsule recently found at Knob Naster, Johnson County, Missouri, USA, dated to Pennsylvanian-Desmoinesian, Upper Carboniferous, which confirms the morphology described by Brown (1950), and assigned to a Holocephalian of the family Chimaeridae

appearance, while for the other Chondrichthyans, paleontological evidence demonstrates that viviparity was prevalent already in the past, starting from the Carboniferous.

Moreover, after the Devonian case from South Africa, the egg capsules with a morphology conforming to that of the living Holocephalans have been documented as fossils almost continuously from the Carboniferous to the Cenozoic. In fact, we have a uncertain specimen collected in the Mazon Creek locality in Illinois, dated to the Pennsylvanian and consisting of a very elongated egg case with little, if any, spiral twist (Figure 19 A), described and figured by Brown (1950). This morphology differs from that of the egg cases of the

living Holocephalans related to the Callorhynchidae and Rhinochimaeridae families (having the feature of finely folded, lateral collarettes), but is similar to the egg cases of the Holocephalans of the Chimaeridae family. Some recent findings made in the ferrite nodules from Cherokee Shale of Knob Naster, Johnson County, Missouri, USA, dated to Pennsylvanian-Desmoinesian, confirm the previous observations by Brown (1950), and show that indeed in this locality, which provided a great variety of fossil Chondrichthyans eggs, there are egg capsules with a very elongated morphology, a fusiform body with very thin and, above all, smooth flanges (lateral collarettes) (Figure 19 B): these egg capsules may actually correspond to Chimaeridae eggs. Considering the brief description made by Brown (1950) without carrying out a systematic determination of the find, but also in light of the new discovery, I think it appropriate to establish a new ichnotaxon that systematically fixes the morphology and systematic position of this egg capsule, to which I have given the name *Palaeochimaerootheca browni*, gn. and sp. nov. (see the Appendix of Systematic Paleontology to this paper).

However, among the eggs of Holocephalins (apart from those rare ones belonging to the Chimaeridae family), many species of fossil egg capsules are referable to the other two families, Callorhynchidae and Rhinochimaeridae. The fundamental genus is *Chimaerotecha*, described by Brown (1946), to which numerous species from Triassic to Cenozoic times belong: *Chimaerotecha arenicola*, from the Lower Triassic of Yakutia, Russia (Vozin, 1968) (Figure 20 A); *Chimaerotecha farensis*, from the Lower Triassic of Iran (Dashtban, 2005); *Chimaerotecha germanica*, from Dogger (Middle Jurassic), of Heiningen, Württemberg, Germany (Jaekel, 1901); *Chimaerotecha besselsi*, from Dogger (Middle Jurassic), near to Heiningen, Württemberg, Germany (Jaekel, 1901); *Chimaerotecha newmexicana*, from the sandstone of Trinidad (Upper Cretaceous) near Raton and Koehler, both in New Mexico (USA) (Brown, 1949) (Figure 20 B); *Chimaerotecha montanana*, from the sandstone of the Horsethief member of the Montana group (Upper Cretaceous), along the river Two Medicine, Montana (USA) (Brown, 1949); *Chimaerotecha gilli*, from the Cliff House Sandstone of the Late Cretaceous, in Soda Canyon and in Mcassin Mesa, both localities in Colorado (USA) (Harrison IV *et al.*, 2021); *Chimaerotecha wyomingana*, from the Mesaverde Formation (Upper Cretaceous), ad

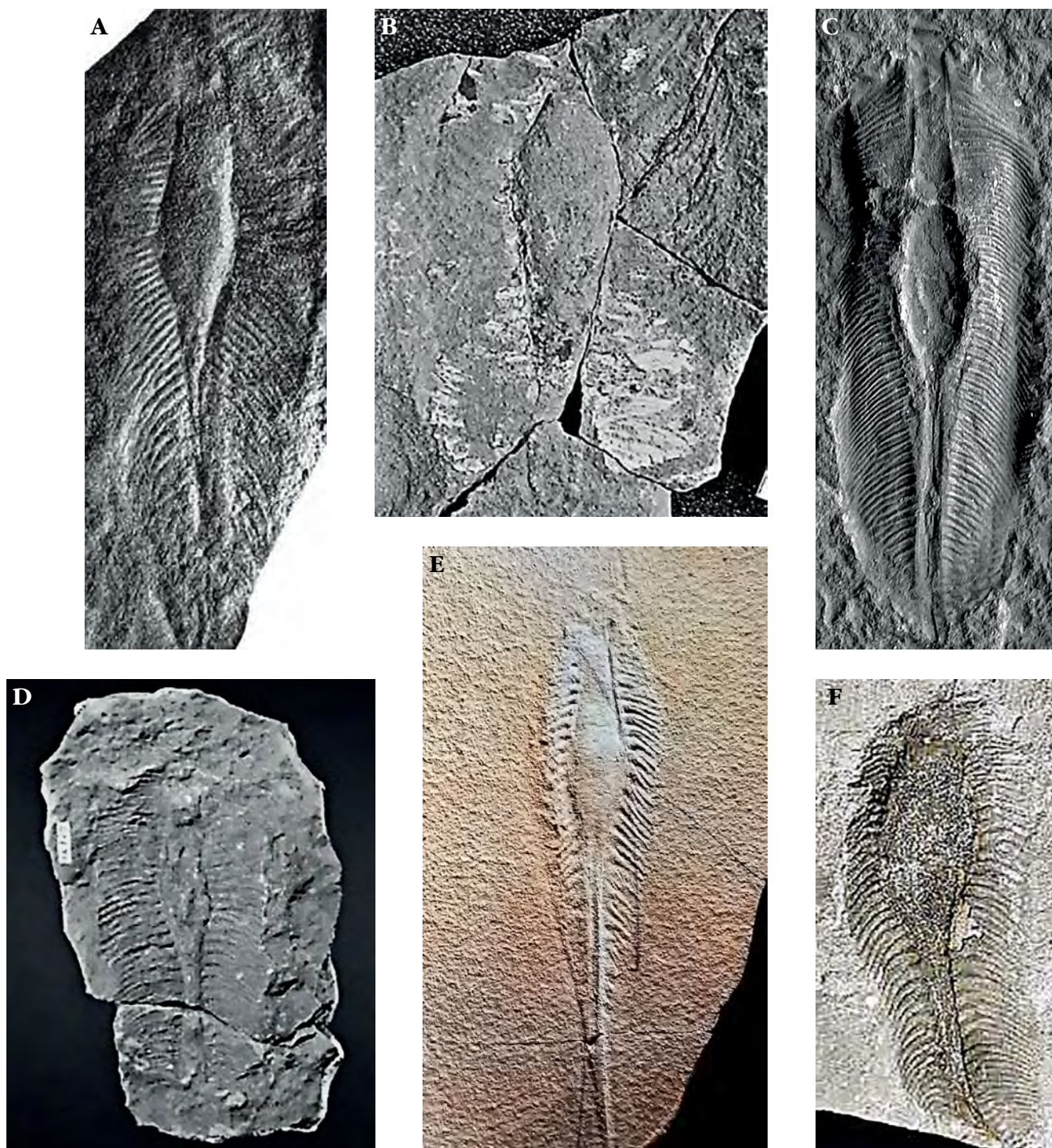


Fig. 20 – Some egg capsules of fossil of Holocephalan fishes pertaining to the families Callorinchidae and/or Rhinochimaeridae: **A:** *Chimerothaeca arenicola*, from the Lower Triassic of Yakutia, Russia (from Vozin, 1968); **B:** *Chimaerotheca new-mexicana*, from the sandstone of Trinidad (Upper Cretaceous) near Koehler, New Mexico (USA) (from Brown, 1949); **C:** *Chimaerotheca caucasica*, from the strata of North Caucasus, Russia, tentatively dated to Lower Cretaceous (from Obruchev, 1967); **D:** *Chimaerotheca alaskana*, from the sandstone member of Split Creek, of the Katalla Formation (Oligocene), collected at north-east of Katalla, Alaska (USA) (from Brown, 1949); **E:** egg capsule of an undetermined Chimaeridae from the Upper Jurassic Lithographic Limestone of Solnhofen, Germany (courtesy of Dr. K.A. Frickinger); **F:** egg capsule of an undetermined Chimaeridae from Keasey Formation of the Oligocene, near Vernonia, Oregon, USA (from the web site www.myfossil.org/chimaeroid-egg-capsule)

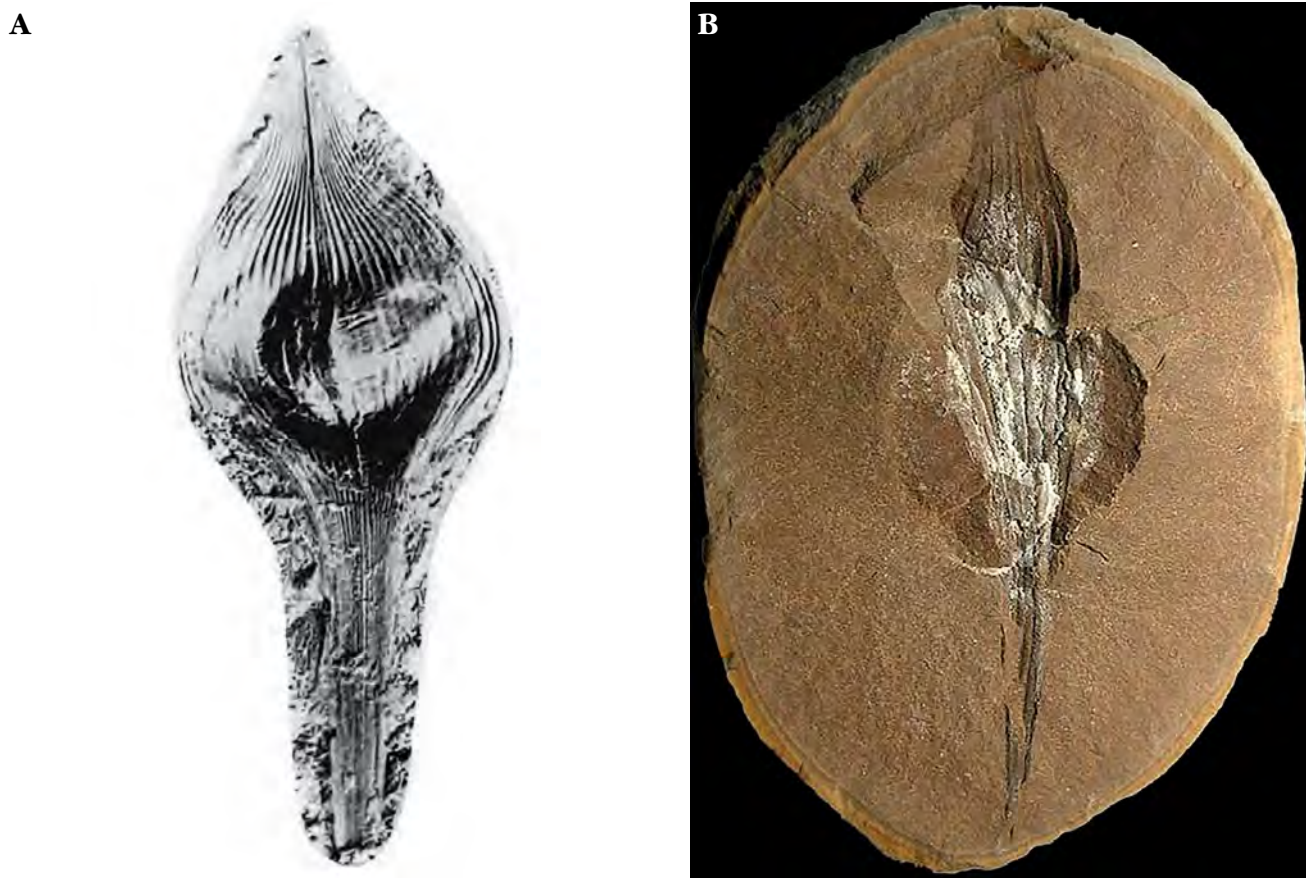


Fig. 21 – **A**: the egg capsule *Vetacapsula cooperi*, total length = 89 mm (after Crookall, 1928); **B**: a specimen of *Vetacapsula* sp. from Crock Hey (USA), Carboniferous, total length = 3 cm (after <https://steurb.bome.xs4all.nl/engdier/eeikaps.html>)

West of Laramie, Wyoming (USA) (Brown, 1949); *Chimaerotheca caucasica*, from the strata of North Caucasus, Russia, tentatively dated to Lower Cretaceous (Obruchev, 1967) (Figure 20 C); *Chimaerotheca alaskana*, from the sandstone member of Split Creek, of the Katalla Formation (Oligocene), collected at north-east of Katalla, Alaska (USA) (Brown, 1949) (Figure 20 D). Some of these species collected in the Lower Triassic of Iran and in the Cretaceous of USA (Bock, 1949), have been questioned as their “butterfly” morphology does not exactly correspond to the canonical morphology of the Holocephalan fish egg cases (Fischer *et al.*, 2014). Additional ichnospecies have been described (but not determined taxonomically) in sediments of marine origin of Solnhofen, Germany (Stahl, 1999; Frickhinger, 1994) (see Figure 20 E), and of Canada, including the Keasey Formation of the Oligocene of Vernon, Oregon, USA (Figure 20 F).

Finally, the ichnogenus *Vetacapsula* is a very rare form of egg capsule. Nevertheless, 12 ichnospecies assigned to this ichnogenus have been described, which come from sedimentary deposits exclusively of the Pennsylvanian period, both in North America and Europe. Sediments containing egg capsules of this ichnogenus were formed in a paralic environment (along or near coastlines, including deltas, shoreline, shelf systems and estuaries).

Morphologically, the egg capsules of the ichnogenus *Vetacapsula* are characterized by a very large body, expanded laterally, and pointed at the extremities. The beak is twice as long as the pedicle and both are tapered conical in shape. The whole surface of the egg capsule is deeply striated by longitudinal grooves and free of collarettes (Figure 21 A and B).

The type of Chondrichthyan that laid the egg houses of the genus *Vetacapsula* remains unknown to this day (Fisher & Kogan, 2008), though Stainier

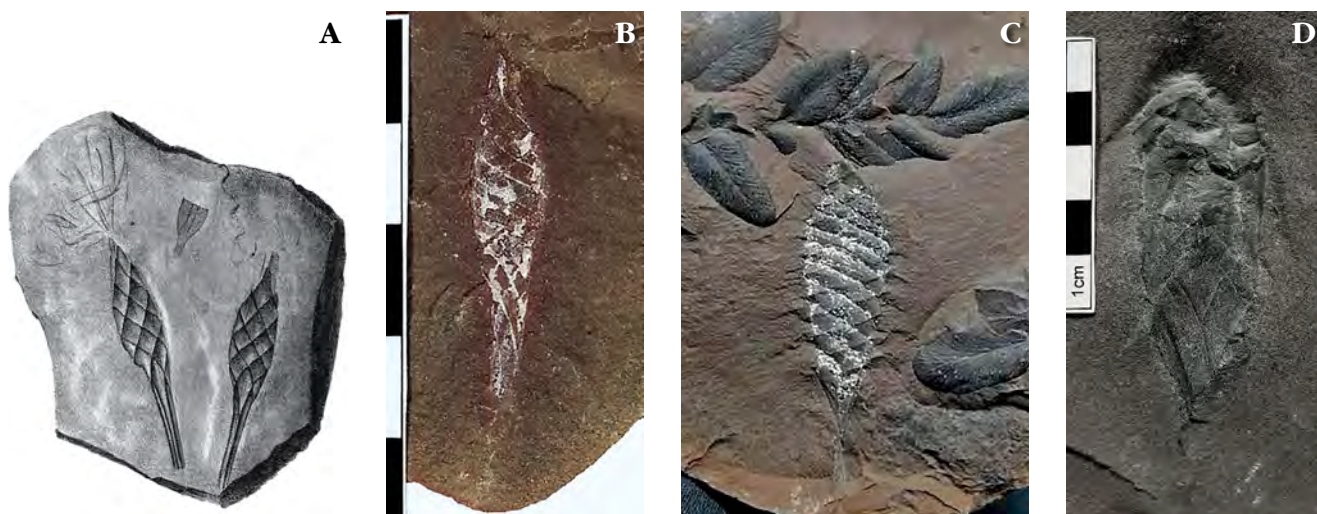


Fig. 22 – **A:** The fist illustration of egg capsules, originally described as plant remains, by Brongniart (1828) as the new species *Palaeoxyris regularis*, from the Middle Triassic (Anisian) of Sultz-les-Bains, Vosges, France; **B:** *Palaeoxyris levisii* in a ferrite nodule from Mazon Creek area, Illinois, USA, of the Carboniferous (Pennsylvanian); **C:** the egg capsule *Palaeoxyris* sp. from the Carboniferous (Westphalian) of Crock Hey Open Cast, Wigan, Lancashire, UK. It can be seen that in both cases (B and C) the egg capsules are anchored to a branch of a plant by means of their tendrils. **D:** An egg capsule with short, squat morphology, apparently without a beak, could belong to a similar undetermined ichnogenus, but different from *Palaeoxyris*, collected in Coal Measures, England

(1938) described the presence of this ichnogenus of egg houses in close connection with the teeth of Helodontidae, pertaining to Holocephalan group (Permian and Carboniferous).

Hybodontiform sharks

The Hybodonts are an extinct group of Elasmobranchii which existed from the late Devonian to the Late Cretaceous, and the fossil egg capsules of ichnogenus *Palaeoxyris*, (which has an exactly overlapping chronological extension), were already described by Brongniart (1828) as plant remains (Figure 22 A), and have been associated with this group of fossil sharks. Today there is general agreement in interpreting the egg capsules of the ichnogenus *Palaeoxyris* as eggs of the Hybodontid sharks (Crookall, 1932; Fischer *et al.*, 2014).

The eggs belonging to this ichnogenus are undoubtedly the most widespread and best known fossils of Chondrichthyans eggs. To date, 26 species have been described, deriving from sedimentary deposits of fresh water and brackish water (they are not present in deposits of marine origin), from all continents (Zidek, 1976a; Böttcher, 2010; McLean, 2014).

Morphologically, the ichnogenus *Palaeoxyris* is characterized by a fusiform, elongated body,

which extends posteriorly into a very long pedicle, while anteriorly to the body there is a short and pointed beak, with a thin and long tendril(s), at its apex. However, there are certainly some forms with very shortened or even absent pedicles, such as those from the English Carboniferous, which could belong to a different ichnogenus, but which still await to be studied and compared in detail (Figure 22 D).

The collarettes (also called flanges) also extend posteriorly on the pedicle, appearing spirally twisted on the pedicle in the pre-Permian species, and with parallel arrangements in the Mesozoic species (Fischer *et al.*, 2014). At the level of the body there are 3 (sometimes 4) membranous collarettes wound in a spiral around the body itself. These collarettes also continue anteriorly, also covering the pedicle, almost parallel to each other.

Generally the *Palaeoxyris* eggs are found unattached, but there are many examples in which they have fossilized adhering to the substrate, that is with their tendrils rolled up around a small vegetable branch (Figures 22 B and 22 C). Sometimes small groups of associated eggs have been preserved, anchored to the same point of the substrate (Figure 22 A).

Xenacanthiform sharks

Xenacanthiformes sharks first appeared in the Late Devonian and became extinct in the Middle Triassic. According to various authors (Renault & Zeiller, 1888; Pruvost, 1919; Schneider & Reichel, 1989) these sharks were the most likely producers of the egg capsules belonging to the ichnogenus *Fayolia*, described for the first time, as a fossil plant, by Renault & Zeiller (1884). Egg houses of this genus are considered relatively rare, nevertheless 16 species have been assigned to this genus to date. Fossils have been found in sediments mainly of freshwater origin, both from Europe, Asia and the USA, with a stratigraphic distribution ranging from the Late Devonian to the Middle Triassic (Table 2), i.e. exactly identical to that of the Xenacanthiformes sharks.

From a morphological point of view, the *Fayolia* egg capsules are very similar to the ichnogenus *Palaeoxyris* since the main difference consists in the general shape. *Fayolia* is a much more squat egg case with a cylindrical aspect, less tapered at the ends. Both the beak (with one or two tendrils) and the pedicle are short and a pair of smooth collarettes are tightly coiled around the entire egg capsule, which gives it a screw-like appearance (Figure 23).

Batoidea

In 1866, the Swiss naturalist Karl von Fischer-Ooster described the first fossil of an egg case of a truly modern-looking Rajiformes, collected in the Miocene molasses of Châtel-Saint-Denis, near Freiburg, Switzerland. The same author reported that the morphology of this egg case, about 4 cm long, was practically identical to that of the eggs of the genus *Raja* still living today, hypothesizing that the Miocene ootecta of Freiburg could have been deposited by a genus of Miocene ray, such as *Zygobates* or *Aetobatis*. Nevertheless, Fischer-Ooster (1866) determined this egg case as a new species of the genus *Raja*, such as *Raja* [sic] *helvetica* (Figure 24).

Peyer (1928) described a similar specimen, also collected in the Oligocene subalpine molasse outcropping near Lucerne, Switzerland, and Kubacka (1932) described another ichnospecies quite similar to the previous ones, collected from the Miocene of Hungary. Furthermore, Steininger (1966), in describing a further specimen of the Switzerland Oligocene, established the new fossil ichnogenus *Rajitecha*, in which all the fossil species known to date have been brought together. Finally, Fischer *et al.* (2014) reported the presence of this same genus in the Late Jurassic of Germany.



Fig. 23 – The egg capsule of the ichnogenus *Fayolia* sp. from the Coal measure of Westphalian A (Upper Carboniferous) from Crockhey Pit, Wigan, Lancashire, U.K.

Thus we can assert that the Rajoidea, which appeared in the Lower Jurassic, left fossil traces of their eggs starting from the Late Jurassic and up to the Miocene, to a limited extent. These egg capsules were found exclusively in shallow marine deposits, limited to the Central European geographical area.

It should be noted that all fossil forms closely resemble the recent egg capsules of the living Rajiformes. In fact, these egg capsules are characterized by a central sub-rectangular body, equipped with two narrow and smooth side collarettes with four horns implanted at each corner of the body: two directed anteriorly and two posteriorly, elongated,



Fig. 24 – Drawing of the holotype of the ootheca of *Raia* [sic] *helvetica* (today *Raijtheca helvetica*), the first described fossil batoid egg (from Fischer-Ooster, 1866)

tapered, with tendrils originating from the base of each horn. This morphology has remained virtually unchanged from the Late Jurassic to the present, although this observation is currently based only on very few fossil samples.

Scyliorhinidae

Living sharks belonging to the family Scyliorhinidae lay large egg capsules (consisting mainly of collagen) of caliciform shape, equipped with two coarse and rounded posterior horns, dorso-ventrally flattened, which have two narrow and smooth lateral collarettes, and a tuft of at least two tendrils both to the anterior pole than to the posterior one.

A group of fossil egg capsules has recently been described with a very similar morphology to that of living Scyliorhinidae oothecae, collected in deep-water marine deposits of Bear River Cold-Seep, western Washington State, USA, and dated to the Late Eocene (Kiel *et al.*, 2013). The authors established a new ichnogenus and a new ichnospecies for these fossils: *Scyliorhinotheca goederti*. This is an exceptional case, because these oothecae have been preserved thanks to a complicated and very rare process of fossilization, which started in taphonomic conditions of anoxia.

? Parascylliidae

In the last thirty years, the Sannine limestone quarries of central Lebanon have returned millions of fossil remains of fish among which a few hundred new genera and new species have been identified and described, despite the fact that these deposits have been known for almost half a millennium (Capasso, 2017). Over the last three decades, some sub-oval



Fig. 25 – *Parascylliootheca libanica* n. gen. and n. sp. from the Sannine limestone of Hjoula, Central Lebanon, dated to the Cenomanian (Late Cretaceous). **A**: paratype; **B**: holotype. These two sub-oval fossil structures have a globular shape and a surface crossed by concentric streaks; in the holotype (B) a newborn specimen of the *Pararhincodon lehmani* shark is superimposed on the surface of the globular structure which, moreover, seems to show a break in the continuity of its profile at the upper left pole (asterisk), due to supposed exit of the embryo from its capsule

fossil structures have been found from the locality of Hjoula (among other things), and have a globular shape with a surface crossed by concentric streaks (Figure 25 A). Although these structures lack any visible horns, they have been interpreted as possible egg capsules of sharks, also in consideration of the fact that these selaceans are particularly abundant in the Hjoula deposit (Capasso, 2017).

A series of considerations and comparisons with oothaecas of living sharks, and above all the association between one of these fossil sub-ovsal structures and a newborn specimen of the *Pararhinodon lebmami* shark (which has fossilized above the surface of the globular structure) (Figure 25 B), reinforce the idea that these fossil sub-globular structures from Hjoula are actually egg capsules laid by Parascylliidae sharks. Therefore, in this same paper, the author establishes a new ichnogenus and a new ichnospecies for these fossils, *Parascylliootheca libanica* n. gen. and n. sp. (see Appendix of Systematic Paleontology).

Undetermined group

A certain number of specimens of various origins and of different ages certainly or most likely represent fossil egg capsules of Chondrichthyans, but either there is uncertainty on whether they are actually egg capsules or there isn't any evidence that can indicate which paleontological species laid these eggs. A certain number of specimens fall into this group of uncertain egg capsules, either by nature or by origin, some already described in literature, others presented here for the first time. We will mention only three below.

First of all we must remember the case of the ichnogenus *Crookallia*, established by Chabakov (1949). Morphologically, these egg capsules are very similar to those of the ichnogenus *Vetacapsula*, but differ for the absence of the robust median rib, the presence of a smaller number of longitudinal striations along the body and along the pedicle, and finally for a less bulbous body; there are no collarettes, except in one species. Five ichnospecies belonging to this ichnogenus have been described to date.

Crookallia is an exclusive ichnogenus of the Pennsylvanian whose remains have been found in Belgium (Stainier, 1938), in Holland (Crookall, 1930) and in Ukraine (Chabakov, 1949). The Chondrichthyan fish that produced this kind of egg remains unknown to this day (Stainier, 1938).

From the famous Early Devonian (Emsian) deposit of Bundenbach, Germany, some fossil fish have been collected, belonging to the Agnatha (for example, *Drepanaspis*) and to the Placoderms (for example, *Gemuendina*, *Lunaspis*, *Stensioella*). Among the numerous enigmatic fossil structures collected from this deposit in the course of lengthy excavation activities, I have identified a fossil remnant that could represent an example of fossil egg capsule. It is a hypothetical case with a total length

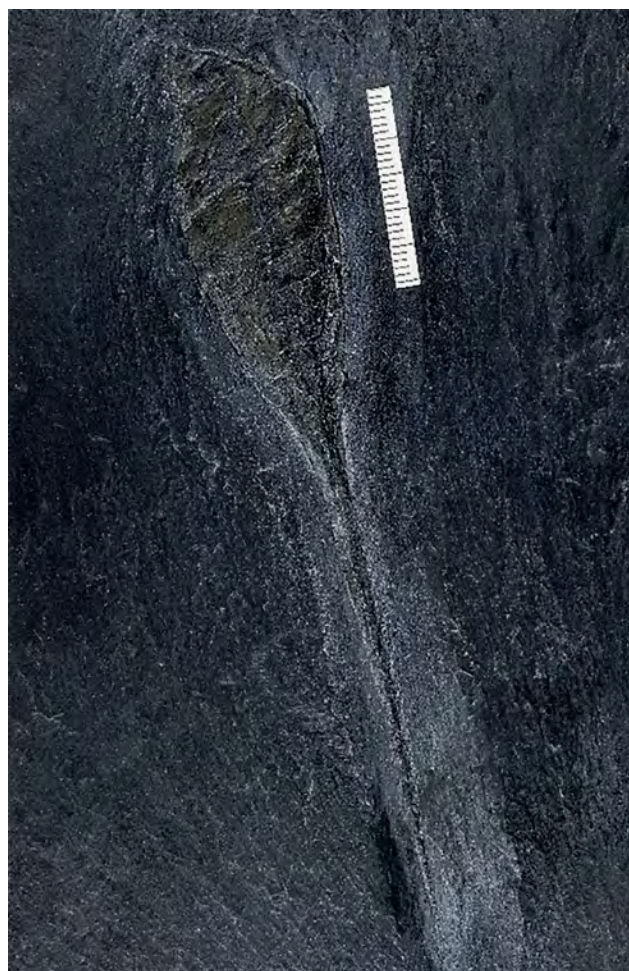


Fig. 26 – The holotype of the ichnotaxon *Theutonicootheca primigenia*, n. gen. and n. sp., a presumed egg capsule from the Early Devonian of Bundenbach, Germany, with a very tapered shape; the beak is conical and shortened, the pedicle enormously elongated, and the body is short and stocky, spindle-shaped, crossed by an uninterrupted furrow which appears to be a pair of spiral-wound collarettes

of 127 mm, and a very tapered shape. The beak is conical and shortened, the pedicle is enormously elongated, and the body is short and stocky, spindle-shaped, crossed by an uninterrupted furrow which appears to be a pair of spiral-wound collarettes (Figure 26). There are, of course, many uncertainties, and we currently have no evidence that this fossil structure actually represents an egg capsule. Nonetheless, and awaiting further finds or new possible alternative interpretations, I believe I must in any case codify this fossil structure from a taxonomic point of view, especially in consid-



Fig. 27 – Holotype of the presumed egg capsule of unknown Chondrichthyan of the ichnospecies *Beargulchootheca carbonifera*, n. gn and n. sp., from the Mississippian of the Bear Gulch Limestone, Montana, USA

eration of the absolute rarity of the find and its relevance also in terms of its antiquity. Therefore I have established for this fossil the new ichnotaxon *Theutonicootheca primigenia* (see the Appendix of Systematic Paleontology).

Finally, it is worth remembering Grogan *et al.* (2012) who reported the presence of a single example of possible egg capsule in the Bear Gulch, Montana, Lower Carboniferous deposit: “Our 41 years of excavation across all areas and sections of the Bear Gulch deposit have resulted in the discovery of only one possible egg case (Grogan and Lund, *in prep.*). Microscopic examination suggests a similarity to some euselachian egg cases in its general appearance and in details, including a series of respiratory-type apertures. A preliminary CT scan of the fossil indicated a structure within the fossilized mass, but a higher resolution examination is necessary for further evaluation. At this stage, the data suggest that this fossil may be an egg case, and, if so, it is more likely to have belonged to a chondrichthyan than a non-chondrichthyan. If it is eventually confirmed as an egg case, then the low recovery rate of this material may simply indicate that these egg cases do not fossilize well or that egg cases were not typically de-

posited in the confines of the Paleozoic Bear Gulch bay. Alternatively, it could be interpreted as an indication that oviparity with an egg case was a rarity at best for the resident chondrichthyan fishes within this bay”.

Unfortunately the paper that Grogan *et al.* (2012) announced (i.e., Grogan & Lund, *in prep.*) has not been published yet, and during the drafting of this overview I contacted Dr Eileen D. Grogan directly, who confirmed that the finding in question, according to her experience, represents an egg capsule of a Chondrichthyan, but no paper has been published to date and no evidence, not even regarding the general morphology of this specimen, is known to date.

In this context, therefore, it is important to report and briefly describe a second specimen collected in the 70s of the last century in the same Bear Gulch deposit. It is a pair of ribbon-like structures, both of a cylindrical aspect, wound in a spiral on themselves (one conspicuously, the other much less), ending in a rounded way at both ends. Near one of the extremities (which we presume to be the anterior one) some very elongated, densely twisted tendrils are attached, and they appearance as a pair of elongated and twisted sack-like objects, ending with twisted and imbricated tendrils (Figure 27).

These characteristics, with all evidence, trace the general morphology of selaceous eggs.

In this paper, since a comparison is not possible between this specimen and E.D. Grogan’s pending specimen description, and despite having no possibility to hypothesize a correlation between this potential egg capsule and one of the numerous Chondrichthyan species present in the Lower Carboniferous ichthyofauna of Bear Gulch, I still believe it appropriate to impose a binomial nomenclature on this ichnofossil, such as *Beargulchootheca carbonifera*, n. gn and n. sp. (see the Appendix of Systematic Paleontology).

Oviparity in Osteichthyes

To date, no fossil structures have been described for which a possible interpretation in the sense of Actinopterygian fish eggs has been proposed. However, Godfrey (1995) described clusters of impressions of small eggs preserved in some siderite nodule concretions from the Middle Pennsylvanian, Francis Creek Shale (Carbondale Formation, Desmoinesian Series, Westphalian C-D), in the Mazon Creek area, Will-Kankakee Counties,

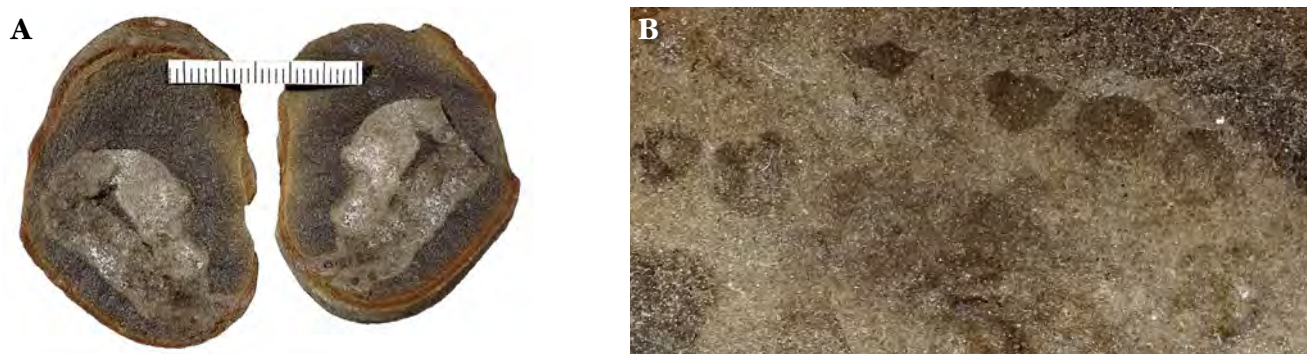


Fig. 28 – The eggs of the ichnotaxon *Mazonova helichnus* were originally spawn within gelatinous ribbon-like structure, containing 1 or 2 rows of eggs, suggesting that the animal that these eggs were laid by an Actinopterygian fish or by an Amphibian. From the Middle Pennsylvanian, Francis Creek Shale, Mazon Creek area, Illinois, USA

Illinois, USA. For these remains Godfrey (1995) established the new ichnotaxon *Mazonova helichnus* (Figure 28). The same Godfrey (1995) said that “*Differential staining of the matrix suggests that the eggs were originally spawn within gelatinous strings containing 1 or 2 rows of eggs. Unfortunately, these egg impressions lack the diagnostic features needed to identify the zoological taxon (taxa) from which they originated*”, but certainly the fact that the eggs are contained in a gelatinous ribbon reinforces the interpretation that these eggs were laid by an Actinopterygian fish or by an amphibian, according to the criteria established by Capasso *et al.* (2013).

Mamay (1994) described unequivocal egg cluster attached to pteridosperm *Sphenopteridium manzanitanum* collected from the upper Pennsylvanian rocks of the Kinney Brick Quarry, New Mexico (USA); these monomorphic spherical structures were attributed to Osteichthyan fish, but recently Lucas *et al.* (2021) demonstrate that these eggs were produced by gasteropods.

NURSERY, NEWBORNS AND PARENTAL CARE

Many present day fish have a nursery solution for their offspring. Thanks to a long series of recent discoveries, but also thanks to a more careful interpretation of paleontological data already known for some time, in the last two decades we have collected very clear evidence that demonstrates the existence of real nurseries relevant to almost all the main groups of fossil fish.

The main element that makes it possible to interpret a mass of fossil fish in a given location or in a given layer is in any case the high number of immature or juvenile subjects compared to the total number of individuals of a given species. This condition has been well documented since the Devonian.

Beyond these striking and hitherto unpublished cases, we will cite below just a few examples (listed in chronological sequence) to provide a quick summary of case studies in this field, which is in full development and to which an ever-increasing number of scientific papers are dedicated.

There is no doubt that real nurseries have been preserved in the fossil state, that is clusters of fish (i) all belonging to the same species, (ii) all of the same size and (iii) all newborns. In my personal experience, I have been able to observe only a few of these examples in which the enormous multitude of fry leaves no doubt that they are real fossil nurseries. I will mention here only two examples: a top layer level of the Sannine limestone sequence outcropping in Hjoula, central Lebanon, dated to the Cenomanian (Figure 29 A) and a basal layer of the bluish gray marls outcropping near Fara Vicentino (Chiavon River), Veneto, North Italy, dated to Oligocene (Figure 29 B). In both these cases, the extreme immaturity of the individuals does not allow a systematic determination of the species involved which, however, certainly belong to the Clupeiformes.

An absolutely convincing example of a Devonian nursery is one described in the Tioga Country, Pennsylvania, USA, dated to the Late Devonian, in which the fossil assemblage is dominated by new-

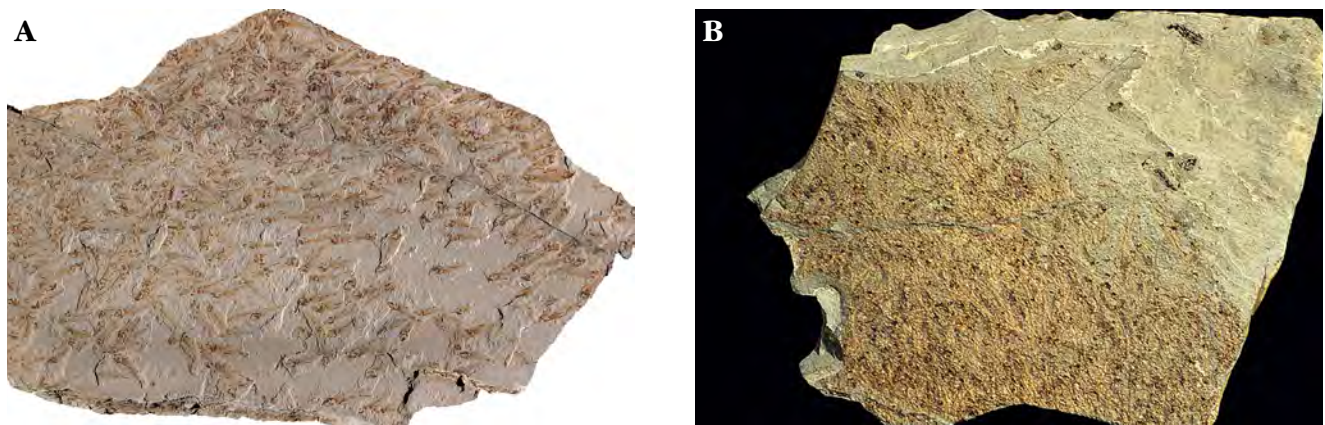


Fig. 29 – Two examples of fossil nurseries in which have been preserved clusters of fish (i) all belonging to the same species, (ii) all of the same size and (iii) all newborns in any case of absolutely young age. **A**: a top layer level of the Sannine limestone sequence outcropping in Hjoula, central Lebanon, dated to the Cenomanian; **B**: a basal layer of the bluish gray marls outcropping near Fara Vicentino (Chiavon River), Veneto, North Italy, dated to Oligocene. In both cases the extreme immaturity of the individuals does not allow a systematic determination of the species involved which, however, certainly belong to the Clupeiformes

born and immature individuals of the Placoderm Antiarchs pertaining to the genus *Bothriolepis* (Downs *et al.*, 2011).

Carr (2010) has shown that the Devonian fossil assemblage found in Marriganowry, Australia, is evidently constituted by immature and juvenile individuals of Placoderm *Couralepis*, present in this locality (as we have already seen) even with very small individuals of less than 1 cm in size. Therefore Carr (2010) concludes that the locality of Marriganowry represented a nursery area for this species.

The presence of a large number of immature and juvenile individuals has led to the hypothesis that also the locations of Miguasha, Canada, and Lode, Latvia, both of Devonian age (Frasnian), were nursery areas for the Placoderms, respectively of the genus *Bothriolepis* (Cloutier *et al.*, 2009; Cloutier, 2010) and of the genus *Asterolepis* (Upeniec, 2011; Upeniece & Upeniece, 1992).

Olive *et al.* (2016) described a nursery area used by some genera of Placoderms, i.e. *Turrisaspis*, *Grossilepis* and *Phyllolepis*, in the locality of Strud, Belgium, dated to Late Devonian (Famennian). In fact, a large number of very small specimens, newborn or young, have been found in this deposit, so Olive *et al.* (2016) concluded that “the Strud depositional environment corresponds to a channel in an alluvial plain, and the presence of a nursery in such environment could have provided nutrients and protection to the placoderm offspring”.

Gess & Coates (2015) described a new Coelacanth harvested in the Waterloo Farm locality, South Africa, dated to Famennian (Late Devonian), *Serenichthys kowiensis*. All complete individuals are small in size, with a length of 3–6 cm. Only a few larger isolated operculae were collected and therefore, the majority of individuals were presumed juveniles and the deposit was deemed a nursery area. Thus, Gess & Coates (2015) conclude that “The presence of abundant juveniles within an estuarine setting strongly parallels the discovery of similarly sized juveniles of *Rhabdoderma exiguum* together with eggs and yolk-sack larvae in the Upper Carboniferous Mazon Creek biota. It is therefore argued that *Serenichthys*, like *Rhabdoderma*, was using the sheltered estuarine environment as a nursery”.

The environment in which sediments from the Mazon Creek area, that were deposited during the Pennsylvanian, has also been interpreted as a brackish environment in which many elasmobranchs gave birth to their offspring. In the case of the genus *Ban-dringa*, of which many juvenile individuals have been found, it has been assumed that the brackish and marine environment of Mazon Creek was a nursery used while waiting for the young sharks to face migration towards the freshwaters, which represent the environment of these Chondrichthyans (Sallan & Coates, 2014).

However, in the Upper Carboniferous Mazon Creek the Chondrichthyans population is not the

only population composed of young individuals, but also the Coelacanth (*Rhabdoderma*) are represented by a large numbers of eggs, yolk sac juveniles and juveniles (Schultze, 1972). Moreover, a lack of non-juvenile Coelacanths as well as a scarcity of adult Coelacanth remains suggest, as proposed by Schultze (1972; 1980) and by Sallan & Coates (2014), that “the Mazon Creek estuarine environment provided a safe spawning ground and nursery for a variety of fish” (Gess & Coates, 2015).

In the Madygen Formation, Kyrgyzstan, dated from the Middle to Late Triassic, Fischer *et al.* (2011) demonstrated the presence of abundant remains of egg capsules assigned to the new ichnospecies *Fayolia sharovi* and *Palaeoxyris alternna*. The depositional environment, as demonstrated by the isotopic analyses, is that of littoral conditions. In this case, the egg capsules were found in association with a multitude of tiny teeth belonging to juvenile subjects of the Chondrichthyan *Lonchidion ferganensis*; only a few teeth belonging to adult individuals of the same species were found. This paleontological complex allowed Fischer *et al.* (2011) to hypothesize that, during the Middle and Upper Triassic, the freshwater environment of Madygen was a true nursery for Chondrichthyan fish, both Hybodontid sharks (which probably produced the egg capsules of the ichnogenus *Palaeoxyris*), and Xenacanthid ones (which probably produced the egg capsules of the ichnogenus *Fayolia*). Evidently these sharks, inhabitants of freshwater, periodically swam through the littoral zones to reproduce, shed their fertilized eggs, and let their fry carry out the first phases of their life (Fischer *et al.*, 2011).

Krüger *et al.* (2021) demonstrated the presence of egg capsules belonging to the ichnogenus *Palaeoxyris* in a Swedish Early Jurassic deposit. In this location, the egg capsules were associated with the remains of fossil plants of the horsetail type. So the authors suggested an “estuarine depositional setting, and potentially that newborn sharks were living in habitats comparable to modern mangroves, as is often the case today” (Krüger *et al.*, 2021).

Cavin *et al.* (2020) developed the hypothesis that the Pycnodonts lived in marine warm waters and in the breeding season they migrated to the continental freshwaters where they mated and reproduced. This hypothesis is based on the presence, within continental freshwater sediments, of remains of juvenile specimens of species where the

adults are well known in marine sediments. This is the case for a fragment sample of prearticular and one of vomer referred to cf. *Phacodus* that were collected from the Lower Campanian continental deposits of the Villeveyrac, L'Olivet site, in southern France. The specimens are very small in size and correspond to tiny individuals of Pycnodonts, as juveniles. The palaeontological interest in these remains appears to be linked to the interpretation that Cavin *et al.* (2020) assigned to the presence of juvenile individuals of the genus *Phacodus* in the sedimentation of a freshwater environment. Indeed, they said: “Because most of the larger sized specimens of *Phacodus* found in the Upper Cretaceous of England, Spain, Morocco and the United States come from marine deposits, while the small specimens described here lived in a continental palaeoenvironment, we hypothesise that this species bred in freshwaters and spent its adult life in the sea, or alternatively that reproduction happened in the sea and juveniles then spent a while in freshwaters”. They also discussed other discoveries of freshwater Pycnodonts worldwide, and they believed that the Pycnodonts temporarily passed from marine to freshwater, corresponding to their reproductive period.

Capasso *et al.* (2021) demonstrated a large abundance of immature and juvenile individuals in a population of Pycnodontiformes of the Aptian (Lower Cretaceous) from Profeti (Province of Caserta, Southern Apennines, Italy), and hypothesized that the deposit was a nursery area, in a lagoon environment.

A fascinating example of possible parental care was illustrated by Grande (1980) in an Early Eocene stingray from the Green River Formation, Wyoming, USA; it is an extraordinary fossil in which an adult female about 34 cm long is surrounded by three newborns of the same species, each about 7.7 cm long (Figure 30 B). Grande (1980) interpreted this extraordinary fossil as a multiple birth that had just occurred. Moreover, this fossil, which at the time belonged to the private collection of Mr. Tom Maloney (after his death it was donated by his wife Hilda Mae Maloney to the American Museum of Natural History), was used to establish the new taxon *Asterotrygon maloneyi*, whose holotype is a female whose abdominal cavity contained a perfectly preserved single embryo (Carvalho *et al.*, 2004) (Figure 30 A).

The study of the relative frequencies of juvenile specimens compared to adults, has led us to suppose that the so-called “Messel lake” was also a nursery

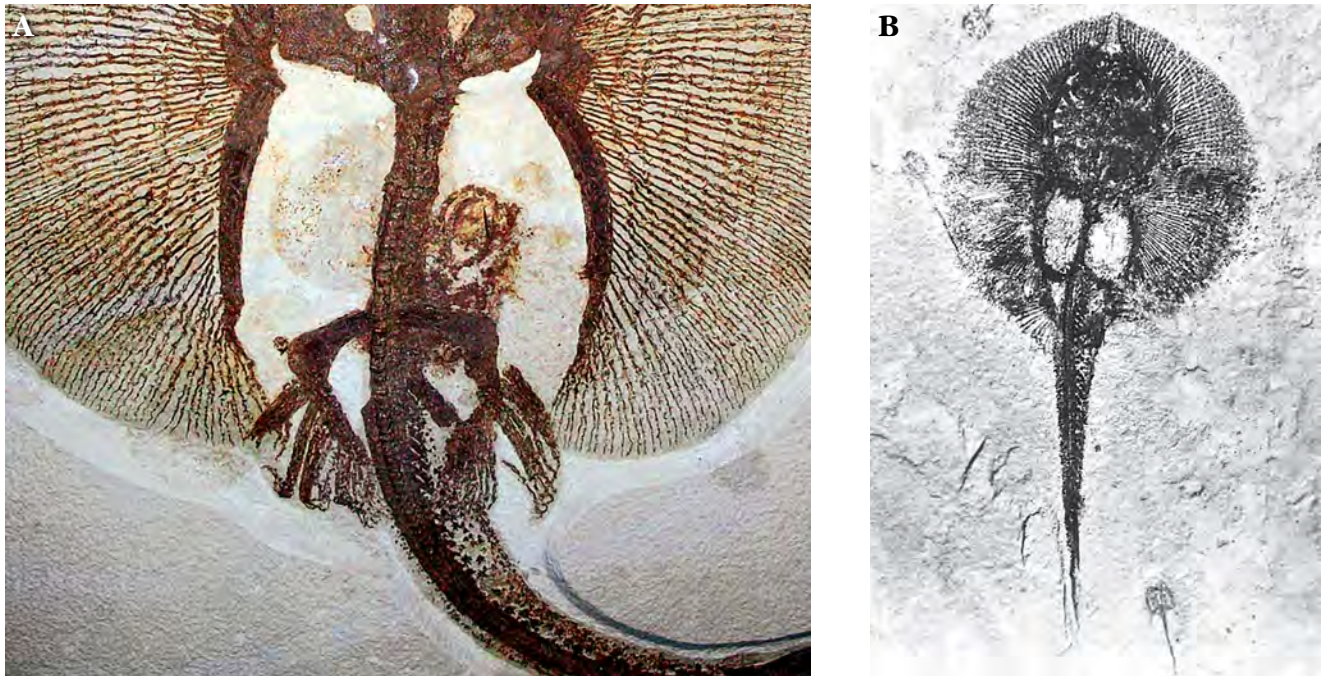


Fig. 30 – The stingray *Asterotrygon maloneyi* from the Green River Formation, Wyoming, USA. **A**: the holotype with the perfectly preserved embryo inside the abdominal cavity; **B**: the “scene of parturition” fossilized on this slab as reported by Grande (1980) (the “mother” has a Total Length of 34 cm, and the three newborns have a Total Length of about 7.7 cm)

area (Micklich, 2002). With the exception of the only species of gar (*Lepisosteus*) and for species known through practically unique specimens (*Anguilla* and *Masillosteus*), most of the fossil fishes coming from the Messel lake deposit, in Southern Germany dated to the Middle Eocene, were newborn or juvenile specimens. This led to the hypothesis that the Messel Eocene lake had, at least periodically, effective contacts with a drainage system, which could actually allow the migration of fish populations in the mating season (Micklich, 2002).

Kiel *et al.* (2013) described the new ichnotaxon *Scyliorhinotheca goederti*, as egg capsules pertaining to a fossil shark, from the Bear River Cold-Seep deposit, western Washington State, USA, dated to the Late Eocene. Since these egg capsules were found in large groups of specimens, Treude *et al.* (2011) inferred that the locality was a nursery area, used by marine deep-water predators.

Finally, the large sharks, so-called “megatoothed sharks” (Otodontidae) are currently cosmopolitan, but they often use shallow, dynamic ecosystems as nurseries. In fact, these environments are characterized by a particular abundance of small preys, suitable for the growth of newborns and young people. To date we have at least three paleontological ex-

amples of nurseries occupied by fossil megatoothed sharks, all identified thanks to the great abundance of teeth of newborns or young adults compared to the dental remains pertaining to adults. For *Carcharocles megalodon*, Miocene and Pliocene nurseries have been described in Panama, Spain and the US Atlantic coast (Maryland and Florida) (Pimiento *et al.*, 2010; Herraiz *et al.*, 2020). For *Carcharocles angustidens* (through the use of accurate odontometric measurements) a nursery has been hypothesized both in the Chandler Bridge Formation of Charleston, South Carolina, USA, and in the Ashley Formation, both deposited during the Oligocene (Miller *et al.*, 2021). Finally, as regards *Carcharodon carcharias*, Villafañe *et al.* (2020) showed that the Pliocene deposit in Coquimbo, Chile, was a nursery area, based on the concentration of teeth of immature and young individuals.

Regarding the Paleozoic and Mesozoic freshwater sharks of the continental European basins, Fischer (2012) was the first to reconstruct the migratory movements between the freshwater and marine basins, based on the variations in the concentrations of stable isotopes of hydroxyapatite of the fossil teeth (which indicate in which type of water the dental growth took place). Combining this informa-

tion with the distribution of the egg capsules, Fischer (2012) himself was able to conclude that these freshwater sharks, in the Mesozoic, performed temporary migrations to saltwater in order to reproduce; in fact he states: “*The oviposition strategy (habitat shift, nursery area, site fidelity) inferred from fossil egg capsule and shark teeth [stable isotopes proportions] are remarkably similar to those of modern relatives, suggesting that the reproductive patterns seen in extant sharks originated well before the Cenozoic*” (Fischer, 2012).

CONCLUSIONS

During the last two decades many important discoveries have been made in the field of palaeophysiology of reproduction in fossil fish and these discoveries have led to a certain quantity of knowledge that now allows us to delineate this topic more clearly than in the past and, above all, in a more complete and better documented way. In this paper the author has tried to summarize this knowledge, implementing it with new paleontological data, and this has resulted in the following concise conclusions.

First of all, today we can assert that since their first appearance the fish have adopted a type of internal fertilization. In fact, in addition to representing the most primitive and most ancient fish, the fossil Agnatha also represents the first vertebrate and features copulatory organs. This condition is documented at least in the Devonian, but it is possible that the Agnatha of the Silurian also possessed copulatory organs, and this undoubtedly represents one of the most appealing themes to investigate in the near future, so as to broaden our knowledge on the origin of fertilization in fish and, therefore, in Vertebrates.

Certainly the process of internal fertilization has remained unchanged in the Agnatha starting from the Devonian to present, both from an anatomical and functional point of view. In fact, even in living jawless fishes internal fertilization and the presence of special copulatory organs in the male subjects remain. This information has allowed us to assert at least two general principles, which have overturned previous opinions: (i) internal fertilization preceded (and does not follow) external fertilization and, moreover, (ii) the appearance of copulatory organs preceded (and not accompanied) the appearance of jaws. From an anatomical point of view, in Agnatha the copulatory organs are (and were) directly con-

nected to the skeleton of the pelvic girdle, which indicates that the pelvic girdle initially developed to support the copulatory organs, rather than the pelvic appendages (fins).

In the Placoderms the constant presence of well developed and well distinct copulatory organs between males and females has been ascertained, with well-defined, characteristic intromittent organs in males. With some exceptions (*Incisoscutum*), in the Placoderms these intromittent organs are unique, symmetrical, abdominal structures, independent from both to pelvic girdles and/or pelvic fins and to anal fins. Internal fertilization was generally followed by embryonic development within the maternal oviducts, so that most of the Placoderms were probably viviparous or ovoviviparous, as evidenced by the presence of embryos in many species, starting from the lower Devonian. Nevertheless, some species were oviparous and laid a large number of small eggs, collected in large sack-like capsules (*Cowralepis* from Devonian of Australia, and an undetermined taxon from Devonian of Cleveland, USA).

Internal fertilization, which in living fishes represents the usual reproduction modality, was also present in the Chondrichthyans since the lower Paleozoic. However, in Chondrichthyans the male intromittent organs, with the same functional process, have a very different anatomical structure from that generally adopted by the Placoderms: modified or special structures connected with pelvic girdles and/or pelvic fins, called claspers. This structural/anatomical difference demonstrates that the reproductive strategy of the Chondrichthyes developed separately from that of the Placoderms and the intromittent organs appeared autonomously in the two groups of fish (omoplasy).

Among the Chondrichthyans, internal fertilization could be followed by both the spawning of fertilized eggs (oviparity), or the retention of fertilized eggs (ovoviviparity) or even perhaps a true viviparity (matrotrophy). The most ancient testimonies on this topic concern the group of Chimaeriformes (Holocephalians), whose eggs (structurally and morphologically very similar to those of living Chimaerae) are known starting from the Devonian, and fossils have been found practically uninterrupted up to the Miocene.

However, many Chondrichthyes of the lower Carboniferous (Mississippian) have shown the presence of embryos inside the maternal oviducts, even in varying degrees of development. This suggests

a great complexity of the reproductive system of the Carboniferous Chondrichthyans, which could also include the preservation of the sperm in the maternal oviducts, in order to develop various and successive waves of egg fertilization, or also the possibility of an adelphophagic practice, with which a kind of endo-uterine natural selection was carried out.

Naturally, Ovoviviparity *vs* viviparity in the Chondrichthyans started from the Carboniferous and has continued to present day, and there are numerous examples of embryo retention both in the sharks and in the rays, both in the Mesozoic (with striking examples coming from the Cenomanian of Lebanon) and in the Cenozoic. Likewise, there are numerous examples of oviparity among fossil Chondrichthyans, with examples of well documented egg capsules from the Carboniferous to the Miocene. A congerie of ichnotaxa have been described in this context, and today we have convincing paleontological evidence of the correspondence between these ichnotaxa, which belong to the so called Veterovata group, and the Chondrichthyans groups that have emitted them, as summarized in Table 2.

We have very little information about the paleophysiology of reproduction in Acanthodians. We certainly know that the characteristic spines, known as fossils since the Silurian, had a hollow structure and were also present in the stretch of the ventral midline between the pelvic fins and the anus. Certainly some of them had a well-defined, complex, hollow, internal structure but we have no information on the possibility that any of these structures also had reproductive functions. A new datum in this regard, presented here for the first time, concerns the discovery of absolutely undeveloped individuals, still endowed with yolk sac, coming from the Late Carboniferous (Pennsylvanian) of the Francis Creek Shale deposit, Illinois, USA. This represents a first indication of oviparity among the Acanthodians.

Finally, among the Osteichthyes we have a lack of information and this can certainly be linked to the fact that these fish had abundantly adopted the external fertilization process, which obviously (not providing for the presence of intromittent structures) does not involve anatomical characteristics. Nonetheless, there are some rare exceptions with few species that actually carry out a proper coupling with internal fertilization, both among living Osteichthyes and among very few fossil species. Paleontological examples of Actinopterygii with intromittent organs, in fact, are known from the Triassic of China (*Pelto-*

pleurus); while excellent examples of ovoviviparity, if not true viviparity, are known through the numerous fossils of *Saurichthys* in which many embryos, in various stages of development, have been documented.

The most common method of fertilization among Osteichthyes is that of the laying of eggs by the females in an external environment and the simultaneous emission of sperm by the males. This spawning process can be facilitated by a vent-to-vent behavior between the two partners who rub each other's abdomen for a long time. Perhaps this reciprocal attitude has been preserved in the fossil state, as shown by cases also described among the Placoderms (*Cowralepis*), among the Carboniferous Chondrichthyan (*Falcatus*), and possibly among some Mesozoic, Cenozoic, and Quaternary Actinopterygii (*Australosomus*, *Ctenodentelops*, *Dapalis*, *Mallotus*), here shown for the first time.

Even rarer among the Osteichthyans are the examples of presumed eggs, both possibly believed in the maternal oviducts (*Hypsospondilus*, *Tharrias*, *Dapalis*) and emitted externally, inserted in presumably gelatinous ribbons (*Mazonova*).

Among the Osteichthyans, a separate chapter is reserved to the Coelacanth, for which paleontological documentation collected to date clarifies some aspects of their reproductive strategy. Living Coelacanth, as recently discovered, have internal fertilization, even though the males do not possess any intromittent organ. The mother retains the fertilized eggs, and the embryos are endowed with a conspicuous yolk sac for the entire duration of gestation (5 years), while nutrition for the embryos takes place through nutritional substances that the mother passes into the oviducts. We have evidence of the existence of fossil Coelacanth embryos from Carboniferous (*Rhabdoderma*) with well developed yolk sacs, which demonstrate how reproduction of these fish has possibly remained unchanged at least from the Carboniferous to today.

Finally, the fry of many fish certainly received parental care. Sufficient evidence has been collected showing that some species of selaceans and certainly some groups of bony fishes performed seasonal migrations in order to reach suitable places for reproduction, for protection from predators and for richer food resources for the offspring. These migratory flows have been demonstrated both on the basis of the distribution of the egg capsules and on the basis of the microchemical analysis of the chemical elements contained in the apatite of their teeth.

The large concentration of fry in layers that do not contain/or contain few adults is another demonstration of the existence of real nurseries, which have been demonstrated in the fossil state since the Devonian. In addition to the numerous examples present in literature, at times based on morphological and on biometric analyses, there is unequivocal paleontological evidence of real impressive clusters of fry, that is of fossil nurseries, in peculiar layers of some classical and highly conservative deposits, such as those of the Cenomanian of Lebanon (Hjoula) and the Oligocene of northern Italy (Chiavon), which I have documented here for the first time.

APPENDIX: SYSTEMATIC PALEONTOLOGY

Ichnogroup:

Veterovata Mikhailov *et al.*, 1996

Ichnogenus:

Theutonicootheca n. gen.

Type species

Theutonicootheca primigenia, n. gen. and n. sp.

Type locality

Bundenbach, Hunsrück, SW Germany.

Type horizon

Kaib Formation, Lower Emsian, Lower Devonian.

Etymology

The name of the new ichnogenus refers to the Latin adjective "Theutonicus", which means "German", "coming from Germany", and to its nature as an egg capsule ("ootheca": word of Latin derivation, usually used to indicate the protein shell with which the oviparous fishes coat their individual eggs).

Diagnosis

The same as the type species.

Ichnospecies:

Theutonicootheca primigenia n. gen. and n. sp.

Figure 26

Type locality

The same as the genus.

Type horizon

The same as the genus.

Etymology

The Latin adjective "primigenius", which means "the first child", "the first of his race".

Holotype

CPC #S-1729; a very tapered shape egg capsule similar structure (Figure 26).

Other material

No other material.

Diagnosis

The new ichnotaxon is presumably an egg capsule of medium size, with a maximum length of about 130 mm, and the maximum width (in correspondence of their body) of 22 mm, with a tapered shape; the beak is conical and shortened (despite its apex being damaged and partially missing), and the enormously elongated pedicle. The body is short and stocky, spindle-shaped, crossed by an uninterrupted furrow which appears to be a pair of spiral-wound collarettes (lateral fringes). There are no traces of tendrils (also in relation to the lack of the most anterior part of the beak).

Discussion

The presumed egg capsule described shows the characteristics of the egg capsules pertaining to the *Palaeoxyris* and *Fayolia* model. If this structure actually represents an egg capsule, it was laid by an Agnatha or a Placoderm, the only two types of fish fossilized in the Bundenbach deposit. The confirmation of this interpretation, based on any new findings actually seem very unlikely, given the absolute rarity of such a finding (this structure, in fact, does not allow comparisons with any other fossil coming from the same deposit and not yet described).

Conclusion

Theutonicootheca primigenia n. gen. and n. sp. represents a possible egg capsule emitted by an Agnatha or a Placoderms of the Lower Devonian, one of the oldest examples of egg capsules known to date.

Ichnogenus:

Beargulchootheca, n. gn.

Type species

Beargulchootheca carbonifera, n. gn and n. sp.

Type locality

Bear Gulch, Montana, USA.

Type horizon

Bear Gulch Limestone of the Heath Formation, the upper part of the *Chesterian* stage, Mississippian (Early *Carboniferous*).

Etymology

The name of the new ichnogenus refers to the name of the location, Bear Gulch, and to its nature as an egg capsule (“*ootheca*”: word of Latin derivation, usually used to indicate the protein shell with which the oviparous fishes coat their individual eggs).

Diagnosis

The same as the type species.

Ichnospecies:

Beargulchootheca carbonifera n. gen. and n. sp.

Figure 27

Type locality

The same as the genus.

Type horizon

The same as the genus.

Etymology

The adjective “carboniferous” is referred to the geological period to which this ichnospecies pertains.

Holotype

CPC #S-762; a pair of ribbon-like structures approximately 60 and 35 mm long respectively, joined together by a complex and repeatedly rolled up pair of tendrils (Figure 27).

Other material

No other material.

Diagnosis

The new ichnotaxon is a pair of ribbon-like structures approximately 60 and 35 mm long respectively, each with both rounded ends. The largest is gently curved on itself (and for this reason its total length is greater = about 60 mm); the minor is rolled up, wound in a spiral on itself (and for this reason its shorter length = 35 mm). Small chromatic differences are present within each ribbon-like structure, with a discontinuous darker area located towards

the center of each ribbon. The average thickness of each ribbon-like structure is about 7-8 mm. The two ribbon-like structures are joined together by a complex and repeatedly rolled up pair of tendrils. The tendrils are also ribbon-like, with an average thickness of about 2.5 mm.

Discussion

The presumed egg capsule described shows the characteristics of the ribbon-like eggs, coated with gelatinous substance, of many living bony fishes and of many amphibians. However, some characters recall those of the oothecas of the Chondrichthyes: (i) the clearly spiraled structure, of both oothecas, and of the long and filament tendrils; (ii) the presence of a highly twisted complex of tendrils, which is characteristic of many living shark egg capsules (Mancusi *et al.*, 2021).

Conclusion

So that *Beargulchootheca carbonifera* n. gen. and n. sp. represents a possible egg capsule deposited presumably by a Chondrichthyan of the Early Carboniferous of the Bear Gulch, Montana, USA.

Ichnogenus:

Palaeochimaerootheca n. gen.

Type species

Palaeochimaerootheca browni n. gen. and n. sp.

Type locality

Knob Naster, Johnson Country, Missouri, USA.

Type horizon

Cherokee Shale of the Pennsylvanian-Desmoinesian, Late Carboniferous.

Etymology

The name of the new ichnogenus refers to its special antiquity (“palaeo-”), to the systematic position of the fish that presumably produced the egg capsule (“Chimaera”: referring to the Holocephalan pertaining to the Chimaeridae family), and finally to its nature as an egg capsule (“*ootheca*”: word of Latin derivation, usually used to indicate the protein shell with which the oviparous fishes coat their individual eggs).

Diagnosis

The same as the type species.

Ichnospecies:

Palaeochimaerootheca browni n. sp.

Figure 19 A and B

Type locality

The same as the genus.

Type horizon

The same as the genus.

Etymology

The name of the new species is inspired by Dr. Ronald W. Brown, who first reported and briefly described it in 1950, and reproduced this same egg capsule in a drawing, coming from the Mazon Creek area, Illinois, USA, without carrying out the taxonomic attribution.

Holotype

CPC #S-71; an egg capsule without the apex of both the beak and the tip of the pedicle, preserved in a ferrite nodule (Figure 19 B).

Other material

A complete egg case, coming from the Middle Pennsylvanian, Francis Creek Shale (Carbondale Formation, Desmoinesian Series, Westphalian C-D), in the Mazon Creek area, Will-Kankakee Counties, Illinois, USA, described by Brown (1950), page 596 and Figure 1.1 (Figure 19 A).

Diagnosis

The new taxon is an egg capsule of medium size, with a maximum length of about 71 mm and a maximum width of 9 mm, with a very elongated general appearance; the body is elongated and fusiform; the beak is conical, elongated, crossed by a clear and deep median longitudinal notch, equipped with a superficial ornamentation consisting of very thin longitudinal lines, parallel to the axis of the egg capsule. The pedicle is very elongated, crossed by two longitudinal ribs. The lateral flanges (collarettes) are only two, very narrow and show that the capsule is possibly rotated around its longitudinal axis of only perhaps about 90°. There are no traces of tendrils (Brown does not report any in his drawing, while the apex of the beak and the tip of the pedicle are missing in the holotype). Although Brown (1950) did not insert a metric scale in the specimen he depicted, the length of the body is about half the total length of the capsule; while the length of the beak

is about a quarter of the total length of the capsule.

Discussion

The egg capsule described shows the characteristics of the egg capsules of the Holocephalans belonging to the family Chimaeridae; in fact, it corresponds to “Type G” of the morphological classification described by Fisher *et al.* (2014).

The holotype of *Palaeochimaerootheca browni* corresponds almost perfectly to the egg capsule depicted by Brown (1950) in Figure 2.1: the only appreciable difference lies in the fact that in Brown's specimen (1950) the beak appears more deeply decorated by longitudinal lines than in the holotype, and they are much more attenuated so as to make the surface of the ootheca appear almost smooth in correspondence with the beak.

Brown (1950) had only very briefly described this specimen, bringing it closer to the genus *Palaeoxyris*, but without facing an in-depth taxonomic discussion, since his paper was devoted to the description of another ichnospecies from the Cretaceous of Kansas. He added that this egg capsule has some similarity with the European genus *Fayolia*, in regards to the almost total absence of torsion.

A further difference between the specimen described by Brown (1950) and the holotype of the new ichnospecies described here, lies in the discovery location and in the geological formation from which the two specimens were collected. In fact, the specimen described by Brown (1950) comes from the Francis Creek Shale (Carbondale Formation, Desmoinesian Series), dated to Middle Pennsylvanian (Westphalian C-D), while the holotype of the new species comes from Knob Naster, Johnson County, Missouri, USA, pertaining to the Cherokee Shale, dated to Pennsylvanian-Desmoinesian.

Conclusion

Palaeochimaerootheca browni n. gn. and n. sp., is the egg capsule of a Holocephalan pertaining to the family Chimaeridae widespread in North American Pennsylvanian-Desmoinesian.

Ichnogenus:

Parascylliootheca n. gen.

Type species

Parascylliootheca libanica n. gen. and n. sp.

Type locality

Hjoula, Central Lebanon.

Type horizon

Marine Sannine limestone, dated to the Cenomanian, Late Cretaceous.

Etymology

The name of the new ichnogenus refers to the name of the shark family Parascylliidae, that includes both living and fossil forms, due to the systematic position of the shark that presumably produced the egg capsule, such as *Pararhincodon lehmami*, and to its nature as an egg capsule ("ootheca": word of Latin derivation, usually used to indicate the protein shell with which the oviparous fishes coat their individual eggs).

Diagnosis

The same as the type species.

Ichnospecies:

Parascylliootheca libanica n. gen. and n. sp.

Figure 25 A and B, and Figure 31 A

Type locality

The same as the genus.

Type horizon

The same as the genus.

Etymology

The name of the new ichnospecies is inspired by the name of the country where these fossils were collected, such as Lebanon.

Holotype

CPC #S-1375; a sack-like structure with an approximately oval profile, with a maximum length of 127 mm, and a maximum width of approximately 80 mm (Figure 25 A).

Other material

CPC #736; a section of sack-like structure with an approximately circular, partial profile, lacking at least one polar part, with a maximum diameter of approximately 91 mm (Paratype) (Figure 25 B).

Diagnosis

The new ichnotaxon is presumably an egg capsule of relatively large size, with a maximum length of

about 127 mm, with a globular, saccular general appearance. The body is smoothly and gently convex. Its surface is crossed by thin, slightly deepened, concentric lines. There are no traces of anterior (beak) or posterior (pedicle) extensions; traces of horns and tendrils are also missing. In the holotype the profile is ovoid, a little narrower towards one end (?anterior), wider and wider towards the opposite (posterior); the profile of the capsule is interrupted due to the lack of a portion of the capsule itself, just in proximity to the likely anterior pole. In the holotype the profile of the capsule is doubled, because there is a homogeneous border, separated from the mass of the body by a deep groove; this border completely surrounds the capsule, even it is wider in the presumptively posterior part, narrower in the presumptively anterior part. This border can be interpreted as a thin, tight, continuous lateral flange (collarettes). A newborn specimen of the *Pararhincodon lehmami* shark is superimposed on the surface of the egg capsule (Figure 25 B).

Discussion

The egg capsule described shows the characteristics of those of the extant shark pertaining to the family Parascylliidae (Mancusi *et al.*, 2021). The eggs of these sharks are characteristically sack-like, devoid of horns and equipped with reduced flanges, developed only near the anterior and posterior poles (Figure 29 B). In our case we have interpreted this structure as an egg case of a Parascylliidae shark, both for the analogies with the current egg capsules of present day sharks (genera *Cirrhoscyllium* and *Parascyllium*), and for the close association between the fossil egg capsule and the newborn of *Pararhincodon lehmami*, belonging to the only extinct genus of the Parascyllidae family, that is the genus *Pararhincodon*. The association between the egg capsule and the newborn of *Pararhincodon* is very close: not only is the newborn shark superimposed on the egg capsule, but also the egg capsule itself shows a discontinuity of its presumptively anterior margin, from which the newborn shark could have hatched from its egg. It should also be noted that the newborn of *Pararhincodon lehmami* shows a broken vertebral column at the level of the pectoral fins; this injury could be the cause of the death of this newborn who evidently suffered a serious trauma, with the rupture of the spinal column, either at the moment of hatching from the egg or immediately after.



Fig. 31 – Comparison between (A) the fossil egg capsule pertaining to the ichnospecies *Parascylliootheca libanica* n. gen. and n. sp., from the Sannine Cenomanian marine limestone of Hjoula, Lebanon, and (B) a specimen of the extant egg of the living nurse shark, *Ginglymostoma cirratum*, from the waters of the Fernando de Noronha Marine National Park, Chico Mendes Institute for Biodiversity Conservation, Brazil (www.zenger.news/2021/09/21/video-diver-finds-one-of-the-oceans-rarest-shark-eggs)

Conclusion

Parascylliootheca libanica n. gen. and n. sp. is the egg capsule of a shark, pertaining to the family Parascylliidae, widespread in a shallow marine environment of Lebanon during the Cenomanian (Late Cretaceous).

ACKNOWLEDGEMENTS

First of all, I thank my colleague Prof. Louis Paul Taverne, who scientifically revised the text thus improving it. I thank Dr Christopher Berry, who performed the English language review of this long paper. I particularly thank Dr. John P. Adamek, of Mundelein, Illinois (Fossilmall.com), and Dr. Roger

Jones, of London, both of whom have allowed me to examine and publish here the images of some rare fossil items belonging to their private collections. Finally, I thank Donatella Del Pizzo and Luciano Lullo who took the photographs illustrating this paper.

REFERENCES

- AHLBERG P.E., TRINAJSTIC K., JOHANSON Z., LONG J.A., 2009. Pelvic claspers confirm chondrichthyan-like internal fertilization in arthrodires. *Nature*, 460: 888-889.
- BALON E.K., 1991. Probable evolution of the coelacanth's reproductive style: lecithotrophy and orally feeding embryos in cichlid fishes and in *Latimeria chalumnae*. *Environ Biol Fish*, 32: 249–265.

- BALON E.K., BRUTON M.N., FRICKE H., 1988. A fiftieth anniversary reflexion on the living coelacanth, *Latimeria chalumnae*: some new interpretations of its natural history and conservation status. *Environ Biol Fish*, 23: 241-250.
- BELTAN L., 1977. La parturition d'un actinoptérygien du Nord-Ouest de Madagascar. *C R Acad Sci Sér D*, 284: 2223-5.
- BELTAN L., 1980. Eotrias du Nord-Ouest de Madagascar: Étude de quelques poissons, dont un est en parturition. *Ann. Soc géol Nord*, 99: 453-64.
- BELTAN L., 1996. Overview of systematics, paleobiology, and paleoecology of Triassic fishes of northwestern Madagascar. In: Arratia G. & Viehl G. (Editors): *Mesozoic fishes – Systematics and paleoecology*. München: Verlag Dr. Friedrich Pfeil: p. 479-500.
- BLOM H., MÄRSS T., MILLER C.G., 2002. Silurian and earliest Devonian birkeniid anaspids from the Northern Hemisphere. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 92: 263-323.
- BLOT J., 1987. L'Ordre des Pycnodontiformes. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 5: 211 pp.
- BOCK W., 1949. Triassic chimaeroid egg capsules from the Connecticut Valley. *Journal of Paleontology*, 23: 515-517.
- BÖTTCHER R., 2010. Description of the egg capsule *Palaeoxyris friessi* n. sp. from the Ladinian (Middle Triassic) of SW Germany and discussion of all known egg capsules from the Triassic of the Germanic Basin. *Palaeodiversity*, 3: 123-139.
- BRAVI S., 1996. *Ricerche sui livelli ad ittioliti in facies di piattaforma carbonatica dell'Italia meridionale*. Tesi di Dottorato, Università di Napoli Federico II: 396 pp.
- BRONGNIART A., 1828. Essai d'une Flore du grès bigarré. *Annales des Sciences Naturelles*, 15: 435-460.
- BROWN R.W., 1946. Fossil egg capsules of chimaeroid fishes. *Journal of Paleontology*, 20 (3): 261-266.
- BROWN R.W., 1949. Triassic chimaeroid egg capsules from the Connecticut Valley. *Journal of Paleontology*, 23: 515-517.
- BROWN R.W., 1950. Cretaceous fish egg capsule from Kansas. *Journal of Paleontology*, 24: 594-600.
- BUATOIS L., MANGANO M.G., 2011. *Ichnology, Organism-Substrate Interactions in Space and Time*. Cambridge University Press, Cambridge.
- BÜRGIN T., 1990. Reproduction in Middle Triassic actinopterygians; complex fin structures and evidences of viviparity in fossil fishes. *Zoological Journal of the Linnean Society*, 100: 379-391.
- CAPASSO L., 2003. Embryos and trophonemes in Cenomanian rays from Lebanon (Batomorphi, Pisces). *Atti del Museo Civico di Storia Naturale di Trieste*, 50: 23-39.
- CAPASSO L., 2007. *Pietraraja, pietre e memorie*. Edigrafita Editore, Teramo.
- CAPASSO L., 2017. The history and the situation of the world famous fossil fish quarries in Lebanon. *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 41: 53-76.
- CAPASSO L., ABI SAAD P., TAVERNE L., 2009. *Nursallia tethysensis* sp. nov., a new pycnodont fish (Neopterygii: Halecostomi) from the Cenomanian of Lebanon. *Bullettin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 79: 117-136.
- CAPASSO L., DEL RE M.C., BRAVI S., TAVERNE L.P., 2021. Sexual dimorphism in a population of Pycnodontiformes of the Aptian (Lower Cretaceous) from Profeti (Province of Caserta, Southern Apennines, Italy). *Bollettino del Museo Civico di Storia Naturale di Verona (Geologia, Paleontologia, Preistoria)*, 45: 31-41.
- CAPASSO L., PALIZZI A., MILIA L., D'ANASTASIO R., 2013. *Archaeoovulus palenae*, n. gn., n. sp. (Icnofossilia): A fossil amphibious ootheca from the pre-evaporitic Messinian site of Capo di Fiume, Palena (Abruzzo). *Atti della Società Toscana di Scienze Naturali, Memorie, Serie A*, 120: 25-38.
- CAPASSO L., TAVERNE L., NOHRA R., 2010. A re-description of *Hensodon spinosus*, a remarkable coccodontid fish (Actinopterygii, †Pycnodontiformes) from the Cenomanian (Late Cretaceous) of Haql, Lebanon. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 80: 145-162.
- CARR R.K., 2010. Placoderm reproductive strategies. *J. Vertebr. Paleontol. Abstr. Programme A.*, 70.
- CARR R.K., JACKSON G., 2018. A preliminary note of egg-case oviparity in a Devonian placoderm fish. *Acta Geologica Polonica*, 68 (3): 381-389.
- CARROLL R.L., 1988. *Vertebrate paleontology and evolution*. W.H. Freeman and Company, New York: 698 pp.
- CARVALHO M.R., MAISEY J.G., GANDE L., 2004. Freshwater stingrays of the Green River Formation of Wyoming (Early Eocene), with the description of a new genus and species and an analysis of its phylogenetic relationship (Chondrichthyes: Myliobatiformes). *Bulletin of the American Museum of Natural History*, 284: 1-136.
- CAVIN L., GARCIA G., VALENTIN X., 2020. A minute freshwater pycnodont fish from the Late Cretaceous of southern France: Palaeoecological implications. *Cretaceous Research*, 106 doi.org/10.1016/j.cretres.2019.104242
- CAVIN L., PIUZ A., FERRANTE C., GUINOT G., 2021. Giant Mesozoic coelacanths (Osteichthyes, Actinistia) reveal high body size disparity decoupled from taxic diversity. *Sci. Rep.*, 11: 11812.
- CAWLEY J.J., KRIWET J., 2017. Possible sexual dimorphism in *Pankowskichthys libanicus* (Neopterygii, †Pycnodontiformes) from the Cenomanian of Lebanon. *Research & Knowledge*, 3 (1): 33-35.
- CHABAKOV A.W., 1949. O dwóch nowych formach problematycznych iskropayemych *Crookallia* i karbona Donetzkogo basseyina i *Palaeoxyris* i jury Krima [About two new problematic fossils *Crookallia* from the Carboniferous of Donezk Basin and *Palaeoxyris* from the Jurassic of Crimea]. *Annual of the All-Union Paleontological Society*, 13: 83-87 [in Russian].
- CHALONER W.G., FOREY P.L., GARDINER B.G., HILL A.J., YOUNG V.T., 1980. Devonian fish and plant from the Bokkeveld series of South Africa. *Annals of the South African Museum*, 81: 128-157.

- CHEVRINAIS M., JOHANSON Z., TRINAJSTIC K., LONG J., MOREL C., RENAUD C.B., CLOUTIER R., 2018. Evolution of Vertebrate postcranial complexity: axial skeleton regionalization and paired appendages in Devonian Jawless fish. *Palaeontology*, 61 (6): 949-961.
- CLOUTIER R., 2010. The fossil record of fish ontogenies: Insights into developmental patterns and processes. *Seminars in Cell & Developmental Biology*, 21: 400-413.
- CLOUTIER R., BÉCHARD I., CHAREST F., MATTON O., 2009. La contribution des poissons fossiles de Miguasha à la biologie évolutive du développement. *Nat Can.*, 133: 84-95.
- CONRATH C.L., MUSIK J.A., 2012. Reproductive Biology of Elasmobranchs. In: Carrier J.A., Heithaus M.R. (Editors). *Biology of Sharks and their Relatives*. Boca Raton: Florida CRC Press: 739-746.
- CROOKALL R., 1928. The genus *Fayolia*. *The Naturalist*, 1928: 325-332.
- CROOKALL R., 1930. Further morphological studies in *Palaeoxyris*, ect. *Summary of Progress of Geological Survey of Great Britain and the Museum of Practical Geology for 1929*, 3: 8-36.
- CROOKALL R., 1932. The nature and affinities of *Palaeoxyris*, ect. *Summary of Progress of Geological Survey of Great Britain and the Museum of Practical Geology for 1931*, 2: 123-140.
- D'ERASMO G., 1914-15. La fauna e l'età dei calcari ad ittioliti di Pietraroja. *Paleontographia Italica*, 21: 29-111.
- DARRAS L., DERYCKE C., BLIECK A., VACHARD D., 2008. The oldest holocephalan (Chondrichthyes) from the Middle Devonian of the Boulonnais (Pas-de-Calais, France). *C. R. Palevol*, 7: 297-304.
- DASHTBAN H., 2005. *Chimaerotheca farensis* (n. sp.) – new species of chimaera egg capsule. *Geosciences*, 14 (56): 146-151.
- DIDIER D.A., 1995. Phylogenetic systematics of extant chimaeroid fishes (Holocephali, Chimaeroidei). *American Museum Novitates*, 3119: 1-86.
- DODD M., DODD M.H.I., 1985. Evolutionary aspects of reproduction in cyclostomes and cartilaginous fishes. In: Foreman R.E., Gorbman A., Dodd J.M. (Editors). *Evolutionary Biology of Primitive Fishes*. USA, Springer, pp. 295-319.
- DOWNS J.P., CRISWELL K.E., DAESCHLER E.B., 2011. Mass mortality of juvenile antiarchs (*Bothriolepis* sp.) from the Catskill Formation (Upper Devonian, Famennian Stage), Tioga County, Pennsylvania. *Proc Acad Nat Sci Phila.*, 161 (1): 191-203.
- FANTI F., MAZZUFERI G., MARRAMÀ G., 2019. Egg preservation in an Eocene stingray (Myliobatiformes, Dasyatidae). *Journal of Vertebrate Paleontology*, 39 (2): 1-5.
- FISCHER J., 2012. Palaeoecology, migration behavior, and reproductive pattern of Palaeozoic to Mesozoic freshwater sharks revealed by stable isotopes. Doctoral Dissertation, Technischen Universität Bergakademie Freiberg.
- FISCHER J., AXSMITH B.J., ASH S.R., 2010. First unequivocal record of the hybodont shark egg capsule *Palaeoxyris* in the Mesozoic of North America. *N.Jb. Geol. Paläont. Abb.*, 255 (3): 327-344.
- FISCHER J., LICHT M., KRIWET J., SCHNEIDER J.W., BUCHWITZ M., BARTSCH P., 2014. Egg capsule morphology provides new information about the interrelationships of chondrichthyans fishes. *Journal of Systematic Palaeontology*, 12 (3): 389-399.
- FISHER J., KOGAN I., 2008. Elasmobranch egg capsules *Palaeoxyris*, *Fayolia* and *Vetacapsula* as subject of palaeontological research – an annotated bibliography. *Freiberger Forschungshfte C*, 528: 75-91.
- FISCHER J., LICHT M., KRIWET J., SCHNEIDER J.W., BUCHWITZ M., BARTSCH P., 2014. Egg Capsule morphology provides new information about the interrelationships of chondrichthyan fishes. *Journal of Systematic Palaeontology*, 12 (3): 389-399.
- FISCHER J., VOIGT S., SCHNEIDER J.W., BUCHWITZ M., VOIGT S., 2011. A selachian freshwater fauna from the Triassic of Kyrgystan and its implication for Mesozoic shark nurseries. *Journal of Vertebrate Paleontology*, 31 (5): 937-953.
- FISCHER-OOSTER C. von, 1866. Paläontologische Mitteilungen. 2. Ueber fossile Seemäuse. *Mitteilungen der Naturforschenden Gesellschaft in Bern*, 603-618: 265-268.
- FRICKHINGER K.A., 1994. *Die Fossilien von Solnhofen*. Goldschneck-Verlag, Weidert, pp. 1-332.
- FRIEDMAN M., 2015. The evolution of ray-finned fishes. *Palaeontology*, 58: 213-228.
- FURRER H., 2003. Der Monte San Giorgio im Südtessin – vom Berg der Saurier zur Fossil-Lagerstätte internationaler Bedeutung. *Neues Jahrbuch der Naturforschenden Gesellschaft in Zürich*, 206: 1-64.
- GESS R.W., COATES M.I., 2015. Fossil juvenile coelacanths from the Devonian of South Africa shed light on the order of character acquisition in actinistians. *Zoological Journal of the Linnean Society*, 175 (2): 360-383.
- GODFREY S.J., 1995. Fossilized Eggs from the Pennsylvanian of Illinois. *Ichnos: an international journal for plant and animal traces*, 4 (1): 71-75.
- GRANDE L., 1980. Paleontology of the Green River Formation, with a review of the fish fauna. *Bulletin of the Geological survey of Wyoming*, 63: 1-334.
- GREGORY P.S., 2010. *Princeton Field Guide to Dinosaurs*. Princeton University Press, Princeton.
- GRIFFITH J., 1977. The Upper Triassic fishes from Polzberg bei Lunz, Austria. *Zoological Journal of the Linnean Society*, 60: 1-93.
- GROGAN E.D., LUND R., 2004. The origin and relationships of early Chondrichthyans. In: Carrier J.C., Musick J.A., Heithaus M.R. (Editors). *Biology of Sharks and their Relatives*. Boca Raton, CRC Press: 3-31.
- GROGAN E.D., LUND R., 2011. Superfoetative viviparity in a Carboniferous chondrichthyan and reproduction in early gnathostomes. *Zoological Journal of the Linnean Society*, 161 (3): 587-594.
- GROGAN E.D., LUND R., ALLEN E.G., 2012. The Origin and Relationships of Early Chondrichthyans. In: Carrier G.C., Music J.A., Heithaus M.R. (Editors). *Biology of Sharks and Their Relatives*. CRC Press.

- HARRIS J.E., 1951. *Diademodus hydei*, a new fossil shark from the Cleveland Shale. *Journal of Zoology*, 120: 683-697.
- HARRISON IV G.W., KIRKLAND J.I., FISCHER J., SAN MIGUEL G., WOOD J.R., SANTUCCI L., 2021. Two chimaeroid egg case remains from the Late Cretaceous, Mesa Verde National Park, Colorado, USA. *New Mexico Museum of Natural History and Science Bulletin*, 82: 113-120.
- HECKEL J.J., 1856. Beiträge zur Kenntniss der fossilen Fische Österreichs. II. Abhandlung. *Denkschriften der kaiserlichen Akademie der Wissenschaften, Math.-Naturwiss. Classe*, 11 (1): 187-274.
- HEMMINGS S.K., ROSTON J., 1972. A multivariate analysis of measurements on the Scottish Middle Old Red Sandstone antiarch fish genus *Pterichthyodes* Bleeker. *Biol. J. Linn. Soc.*, 4: 15-28.
- HENNIG E., 1907. Ueber einige Pycnodonten vom Libanon. *Centralblatt für Mineralogie, Geologie und Paläontologie, Stuttgart, Jahrgang*, 1907: 360-371.
- HERRAIZ J.L., RIBÉ J., BOTELLA H., MARTINEZ-PÉREZ C., FERRÓN H.G., 2020. Use of nursery areas by the extinct megatooth shark *Otodus megalodon* (Chondrichthyes, Lamniformes). *Biology Letters*, 16: 202000746.
- HURLEY I.A., MUELLER R.L., DUNN K.A., SCHMIDT E.J., FRIEDMAN M., HO R.K., PRINCE V.E., YANG Z., THOMAS M.G., COATES M.I., 2007. A new time-scale for ray-finned evolution. *Proc. R. Soc. B*, 274: 489-498.
- JAEKEL O., 1901. Ueber jurassische Zähne und Eier von Chimariden. *Neues Jahrb. Beilage*, 14: 540-564.
- KIEL S., PECKMANN J., SIMON K., 2013. Catshark egg capsules from a Late Eocene deep-water methane-seep deposit in western Washington State, USA. *Acta Palaeontologica*, 58 (1): 77-84.
- KRIWET J., 2004. A new pycnodont fish genus (Neopterygii: Pycnodontiformes) from the Cenomanian (Upper Cretaceous) of Mount Lebanon. *Journal of Vertebrate Paleontology*, 24 (3): 525-532.
- KRÜGER A., SLATER S., VAJDA V., 2021. 3D imaging shark egg case (*Palaeoxyris*) from Sweden with new insights into Early Jurassic shark ecology. *GFF*, 143 (2-3): 229-247.
- KUBACSKA A., 1932. Paläobiologische Untersuchungen aus Ungarn. B) Fossile Rochen-Eikapseln aus dem Mitteloligozän Ungarns. *Geologica Hungarica, Series Palaeontologica*, 10: 41-55.
- LAMBERS P.H., 1991. The Upper Jurassic actinopterygian fish *Gyrodus dichactinius* Winkler 1862 (*Gyrodus hexagonus* Blainville 1818) from Solnhofen, Bavaria and anatomy of the genus *Gyrodus* Agassiz. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 94 (4): 489-544.
- LEIGH-SHARP W.H., 1920. The comparative morphology of the secondary sexual characters of elasmobranch fishes. *Journal of Morphology*, 35: 359-380.
- LOMBARDO C., 1999. Sexual dimorphism in a new species of the Actinopterygian *Peltopleurus* from the Triassic of Northern Italy. *Palaeontology*, 42: 741-760.
- LONG J.A., MARK-KURIK E., JOHANSON Z., LEE M.S., YOUNG G.C., ZHU M., AHLBERG P.E., NEWMAN M., JONES R., DEN BLAAUWEN J., CHOO B., TRINAJSTIC K., 2015. Copulation in antiarch placoderms and the origin of gnathostome internal fertilization. *Nature*, 517: 196-199.
- LONG J.A., TRINAJSTIC K., YOUNG G.C., SENDEN T., 2008. Live birth in the Devonian period. *Nature*, 453: 650-652.
- LONG J.A., TRINAJSTIC K., JOHANSON Z., 2009. Devonian arthrodire embryos and the origin of internal fertilization in vertebrates. *Nature*, 457: 1124-1127.
- LUCAS S.G., SIMPSON E.L., LIGHTIG A.J., LERNER A.J., ABBASS N., 2021. Fossil eggs from the Kinney Brick Quarry Lagerstätte, Pennsylvanian of New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 84: 229-240.
- LUND R., 1982. *Harpagofututor volsellorhinus* new genus and species (Chondrichthyes, Chondrenchelyiformes) from the Namurian Bear Gulch Limestone, *Chondrenchelys problematica* Traquair (Visean) and their sexual dimorphism. *Journal of Paleontology*, 56: 938-958.
- LUND R., 1985. The morphology of *Falcatus falcatus* (St. John and Worthen), a Mississippian stethacanthid chondrichthyan from the Bear Gulch Limestone of Montana. *Journal of Vertebrate Paleontology*, 5: 1-19.
- LUND R., 1990. Chondrichthyan life history style as revealed by the 320 million years old Mississippian of Montana. *Environmental Biology of Fishes*, 27: 1-19.
- MAISEY J.G., 1986. Coelacanths from the Lower Cretaceous of Brazil. *American Museum Novitates*, 2866: 1-30.
- MAISEY J.G., 2009. The spine-brush complex in symmoriiform sharks (Chondrichthyes; Symmoriiformes), with comments on dorsal fin modularity. *Journal of Vertebrate Paleontology*, 29: 14-24.
- MAMAY S.H., 1994. Fossil eggs of probable piscine origin preserved on Pennsylvanian Sphaenopteridium foliage from the Kinney Quarry, Central New Mexico. *Journal of Vertebrate Paleontology*, 14 (3): 320-326.
- MANCUSI C., MASSI D., BAINO R., CARIANI A., CROBE V., EBERT D.A., FERRARI A., GORDON C.A., HOFF G.R., IGLESIAS S.P., TITONE A., SERENA F., 2021. An identification key for Chondrichthyes egg cases of the Mediterranean and Black Sea. *The European Zoological Journal*, 88 (1): 436-448.
- MCLEAN G., 2014. A Comparative Study of the Australian Fossil Shark Egg-Case *Palaeoxyris duni*, with Comments on Affinities and Structure. *Proceedings of the Linnean Society of New South Wales*, 136: 201-218.
- MICKLICH N., 2002. The fish fauna of Messel Pit: A nursery school? *Cour. Forsch.-Inst. Senckenberg, Frankfurt a.M.*, 237: 97-127.
- MIKHAILOV K.E., BRAY E.S., HIRSCH K.E., 1996. Parataxonomy of Fossil Egg Remains (Veterovata): Principles and Applications. *Journal of Vertebrate Paleontology*, 16: 763-776.
- MILES R.S., 1967. Observations on the ptyctodonts fish, *Rhambodopsis* Watson. *Zool. J. Linn. Soc. London*, 47: 99-120.
- MILLER A.E., GIBSON M.L., BOESSENECKER R.W., 2021. A megatoothed shark (*Carcharocles angustidens*) nursery in the Oligocene Charleston Embayment, South Carolina, USA. *Palaeontologia Electronica*, 24 (2): a19.

- MOTTEQUIN B., GOOLAERTS S., HUNT A.P., OLIVE S., 2021. The erroneous chondrichthyan egg case assignments from the Devonian: implications for the knowledge on the evolution of the reproductive strategy within chondrichthyans. *The Science of Nature*, 108: 36-44.
- NELSON J.S., 2006. *Fishes of the world*. 4th Edition. Hoboken: John Wiley & Sons, pp 1-610.
- NEWMAN M.J., BLAAUWEN J.D., BURROW C., JONES R., 2021. Earliest vertebrate embryos in the fossil record (Middle Devonian, Givetian). *Palaeontology*, 64 (1): 21-30.
- O'SHAUGHNESSY K.L., DAN R.D., COHN M.G., 2015. Molecular development of Chondrichthyans claspers and the evolution of copulatory organs. *Nat Comm*, 6: 6698.
- OBRUCHEV D.V., 1967. Fossil Chimaera egg capsules. *International Geology Review*, 9: 567-573.
- OLIVE S., CLÉNT G., DAESCHLER E.B., DUPRET V., 2016. Placoderm Assemblage from the Tetrapod-Bearing Locality of Strud (Belgium, Upper Famennian) Provides Evidence for a Fish Nursery. *PlosONE*, DOI: 10.1371/journal.pone.0161540
- ØRVIG T., 1960. New Finds of Acanthodians, Arthrodires, Crossopterygians, Ganoids and Dipnoans in the Upper Middle Devonian Calcareous Flags (Oberer Plattenkalk) of the Bergisch Gladbach-Paffrath Trough: Part 1". *Paläontologische Zeitschrift*, 34 (3-4): 312.
- PEYER B., 1928. Rochen-Eikapseln aus den Horwerschishten (unteres Stampien) von Grisigen, Kt. Luzern. *Ecologiae Geologicae Helveticae*, 21: 407-413.
- PIMIENTO C., EHRET D.J., MACFADDEN B.J., HUBBELL G., 2010. Ancient nursery area for the extinct giant shark *Megalodon* from the Miocene of Panama. *PLoS ONE*, 5:e10552.
- PRATT H.L. JR., CARRIER J.C., 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. In: Tricas TC & Gruber SH (Editors): *The Behavior and Sensory Biology of Elasmobranch Fishes*. Springer Netherlands, pp. 157-188.
- PRUVOST P., 1919. Introduction à l'étude du terrain houiller du Nord et du Pas-de-Calais. La Faune continentale du terrain houiller du Nord de la France. In: *Mémoires pour servir à l'explication de la Carte Géologique détaillée de la France*. Imprimerie Nationale, Paris: 439-453.
- RENAULT B., ZEILLER R., 1884. Sur un nouveau genre de fossiles végétaux. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, 98: 1391-1394.
- RENAULT B., ZEILLER R., 1888. Sur l'attribution des genres *Fayolia* et *Palaeoxyris*. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, 98: 1022-1025.
- RENESTO S., STOCKAR R., 2009. Exceptional preservation of embryos in the actinopterygian *Saurichthys* from the Middle Triassic of Monte San Giorgio, Switzerland. *Swiss J. Geosci.*, 102: 323-330.
- RIEPEL O., 1985. Die Gattung *Saurichthys* (Pisces, Actinopterygii) aus der mittleren Trias des Monte San Giorgio, Kanton Tessin. In: Die Triasfauna der Tessiner Kalkalpen XXV. *Schweizerische Paläontologische Abhandlungen*, 108: 1-103.
- ITCHIE A., 2005. *Cowralepis*, a new genus of Phyllolepid fish (Pisces, Placodermi) from the late Middle Devonian of New South Wales, Australia. *Proc. Linn. Soc. NSW*, 126: 1-215.
- SALLAN L.C., COATES M.I., 2014. The long-rostrum elasmobranch *Bandringa* Zangerl, 1969, and taphonomy within a Carboniferous shark nursery. *Journal of Vertebrate Paleontology*, 34 (1): 22-33.
- SCHULTZE H-P., 1972. Early growth stages in coelacanth fishes. *Nature New Biology*, 236: 90-92.
- SCHULTZE H-P., 1980. Eier legende und lebend gebarende Quastenflosser. *Natur und Museum*, 110: 101-108.
- SCHNEIDER J.W., REICHEL W., 1989. Chondrichthyer-Eikapseln aus dem Rotliegenden (Unterperm) Mitteleuropas Schlussfolgerungen zur Paläobiologie paläozoischer Süßwasserhaie. *Freiberger Forschungshefte C*, 436: 58-69.
- SMITH C.L., RAND C.S., SCHAEFFERAND B., ATZ J.W., 1975. *Latimeria*, the living Coelacanth, is ovoviparous. *Nature*, 190 (4219): 1105-1106.
- STAHL B.J., 1999. *Chondrichthyes III – Holocephali. Handbook of Paleichthyology 4*. Verlag Dr. Friedrich Pfeil, München: 164 pp.
- STAINIER X., 1894. Un *Spiraxis* nouveau du Devonien Belge. *B. Soc. Belg. Géol. Paléont. Hydrol.*, 7: 23-28.
- STAINIER X., 1938. *Belinurus* et *Vetacapsula* nouveaux du Houiller belge. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 14 (32): 1-13.
- STEININGER F., 1966. Zur Kenntnis fossiler Euselachier-Eikapseln aus dem Ober-Oligozän von Mitteleuropa. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, 6: 37-49.
- STINNESBECK E.S., RUST J., HERDER F., 2019. Paleobiology and taphonomy of the pycnodont fish *Nursallia gutturosus*, based on material from the Latest-Cenomanian-middle Turonian Vallecillo platy limestone, Mexico. *Paläontologische Zeitschrift*, 93 (4): 659-668.
- TAVERNE L., CAPASSO L., 2020. New data on *Pankowskichthys libanicus* (Pycnodontiformes, Gladiopycnodontidae), a fossil fish from the marine Upper Cretaceous of Lebanon. *Geo-Eco-Trop.*, 44 (1): 185-193.
- TORTONESE E., 2000. Fauna d'Italia: Volume 1 (Chondrichthyes), and Volume 2 (Osteichthyes). Calderini Editore, Bologna.
- TREUDE T., KIEL S., LINKE P., PECKMANN J., GOEDERT J., 2011. Elasmobranch egg capsules associated with modern and ancient cold seeps: a nursery for marine deep-water predators. *Marine Ecology Progress Series*, 437: 175-181.
- TRINAJSTIC K., BOISVERT C., LONG J., MAKIMENKO A., JOHANSON Z., 2014. Pelvic and reproductive structures in placoderms (stem gnathostomes). *Biol. Rev.*, 90: 467-501.
- TRINAJSTIC K., BOISVERT C., LONG J., JOHANSON Z., 2019. Evolution of Vertebrate Reproduction. In: Johansons Z., Underwood C., Richtet M. (Editors). *Evolution and development of fishes*. Cambridge University Press: 207-226.
- TRINAJSTIC K., LONG J.A., 2009. A new genus and species of ptyctodont (Placodermi) from the Late Devonian

Gneudna Formation, Western Australia, and an analysis of ptyctodont phylogeny. *Geol. Mag.*, 146: 743-760.

UCHIDA S., TODA M., KAMEI Y., 1990. Reproduction of elasmobranchs in captivity. In: Pratt H.L. Jr, Gruver S.H., Taniuchi T. (Editors): *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematic, and the Status of Fisheries*. NOAA Tech Rep NMFS, 90: 327-346.

UPENIECE I., 2011. *Palaeoecology and juvenile individuals of the Devonian placoderm and acanthodian fishes from Lode site, Latvia*. Doc. Thesis. University of Latvia.

UPENIECE I., UPENIECE J., 1992. Young Upper Devonian antiarch (*Asterolepis*) individuals from the Lode quarry, Latvia. In: Mark-Kurik E. (Editor): *Fossil Fishes as Living Animals*. Tallinn: Academy of Sciences of Estonia, 1992: 167-176.

VILLAFANA J.A., HERNANDEZ S., ALVARADO A., SHIMADA K., PIMIENTO C., RIVADENEIRA M.M., KRIWET J., 2020. First evidence of a palaeo-nursery area of the great white shark. *Scientific Reports*, 10: 8502.

VOZIN F.V., 1968. Yaitseyve kapsuly khimer iz triasa Yakutii. *Geologiya i Geofizika*, 8: 67-77 [in Russian].

XU G.H., MA X.Y., 2016. A Middle Triassic stem-neopterygian fish from China sheds new light on the peltopleuriform phylogeny and internal fertilization. *Science Bulletin*, 61 (22).

WATSON D.M.S., 1927. The reproduction of the coelacanth fish *Undina*. *Proc. Zool. Soc. Lond.*, 1: 453-457.

WATSON D.M.S., 1934. The interpretation of arthrodires. *Proceedings of the Zoological Society of London*, 3: 437-464.

WATSON D.M.S., 1937. The acanthodian fishes. *R. Soc. London Phil. Trans. B*, 228: 49-146.

WATSON D.M.S., 1938. On *Rhamphodopsis*, a Ptyctodont from the Middle Old Red Sandstone of Scotland. *Earth Environ Sci Trans R Society Edinb*, 59: 397-410.

WEN W., ZHANG Q.-Y., HU S.-X., BENTON M.J., ZHOU C.-Y., TAO X., HUANG J.-Y., CHEN Z.-Q., 2013. Coelacanths from the Middle Triassic Luoping Biota, Yunnan, South China, with the earliest evidence of ovoviviparity. *Acta Palaeontologica Polonica*, 58 (1): 175-193.

WITTRY J., 2018. *Pennsylvanian Age Fossils of Northeastern Illinois, USA 1: Fossil Shark Egg Cases of the Mazon Creek Region*. Fieldguides.fieldmuseum.org [978] 2/2018.

WOURMS J.P., 1981. Viviparity: the maternal-fetal relationship in fishes. *Amer. Zool.*, 21: 473-515.

ZHAO W.J., ZHU M., 2010. Siluro-Devonian vertebrate biostratigraphy and biogeography of China. *Palaeoworld*, 19: 4-26.

ZHU M., 1998. Early Silurian sinacanths (Chondrichthyes) from China. *Palaeontology*, 41 (1): 157-171.

ZIDECK J., 1976a. Kansas Hamilton Quarry (Upper Pennsylvanian) *Acanthodes*, with remarks on the previously reported North American occurrences of the genus. *University of Kansas Paleontologica Contributions*, 83: 1-41.

ZIDECK J., 1976b. A new shark egg capsule from the Pennsylvanian of Oklahoma, and remarks on the chondrichthyan egg capsules in general. *Journal of Vertebrate Paleontology*, 50 (5): 907-915.

NOTE ON MATERIAL AND ABBREVIATIONS

The fossil specimens examined and described in this work belong predominantly to the “Luigi Capasso Public Collection” (Abbreviation = CPC). This is a Public Collection that was established in past century, and is protected by the Italian State. It is legally registered by two Decrees of the Ministry for Cultural Heritage and Activities, under the dates of October, 11, 1999, and April 29, 2020, no. 14, both according to Italian law 1089/39. The specimens of this collection were also subject to prescription in order of availability to studies on the basis of the Article 30 of Italian law N° 42/2004. Below I provide the correspondence of the individual specimens with the numbers of the official catalogue of the “Capasso Collection” deposited at the Ministry of Cultural Heritage. The fossil specimens examined and described in this work are the following, the provenance of which is described in detail in the captions of the figures, as indicated below: Figure 2B: CPC # S-247; Figure 2C: CPC #S-799; Figure 3A: CPC #S-78; Figure 4A and 4B: CPC #S-57; Figure 5A: CPC #S-48; Figure 5B: CPC #S-1106; Figure 5C: CPC #S-1294; Figure 7A and 7B: CPC #S-382; Figure 7C and 7D: CPC #S-1800; Figure 8A and 8B: CPC #S-587; Figure 10: CPC #S-1238; Figure 12A: CPC #S-1555; Figure 12B: CPC #S-1955; Figure 12C: CPC #S-1612; Figure 12D: CPC #S-1736; Figure 13A and 13B: CPC #S-436; Figure 14A and 14B: CPC #S-997; Figure 15A and 15B: CPC #S-606; Figure 16A: CPC #S-727; Figure 16B: CPC #S-943; Figure 19B: CPC #S-71; Figure 21B: CPC #S-581; Figure 21D: CPC #S-704; Figure 22: CPC #S-741; Figure 25A: CPC S-736; Figure 25B: CPC #S-1375; Figure 26: CPC #S-1729; Figure 27: CPC #S-762; Figure 28A and 28B: CPC #S-1698; Figure 30A: CPC #S-334; Figure 30B: CPC #I-174; Figure 31 A: CPC #S-1375.

Furthermore, some specimens belong to other private collections: Figure 6A, Figure 6B and Figure 17 from the Collection of Dr. John P. Adamek, of Mundelein, Illinois, USA (Fossilmall.com); Figures 9 at the Collection of Dr. Roger Jones, of London, England.

For the figures not indicated in the previous lists, the source of the images is cited in the relative captions.

The marine Upper Santonian (Late Cretaceous) of Apricena (Gargano Promontory, southern Italy) and its fossil fish fauna

LOUIS TAVERNE¹, PIETRO DOMENICO DE COSMO², MICHELLE MORSILLI³, VALERIA LUCIANI³

1. Institut Royal des Sciences Naturelles de Belgique – Directoire Terre et Histoire de la Vie

Rue Vautier, 29 – B-1000 Bruxelles, Belgique – louis.taverne@skynet.be

2. University of Ferrara – Department of Earth Sciences, Block B – Room 409, 410 Via Saragat, 1 – I-44100 Ferrara, Italy and Via Piangipane, 21 – I-44121 Ferrara, Italy – pietrodomenico.decosmo@gmail.com

3. University of Ferrara – Department of Earth Sciences, Block B – Room 409, 410 Via Saragat, 1 – I-44100 Ferrara, Italy – mrb@unife.it

ABSTRACT

*The Santonian of Apricena (Gargano Promontory, Apulia, southern Italy) is described, and more especially a new marine lithostratigraphic unit recently discovered and located south-east to Apricena which is depicted and illustrated in details. For the first time also, the complete list of its ichthyofauna is given. It includes ten teleost genera. All are new except two. The trophic relationships of this piscine community are considered. Comparisons are made with other Senonian ichthyofaunas from the Eurafrian Mesogea and with that of the Campanian-Maastrichtian of Nardò, another bed from southern Italy. The ichthyofauna of Apricena is highly endemic. However, the genera *Chanoides* (Ostariophysi, Chanoididae) and *Nardodercetis* (Aulopiformes, Dercetidae) are present in both faunas of Apricena and Nardò. The families Ichthyodectidae and Clupeidae also are common to both beds but the genera and species are different.*

Key words: Apricena, Gargano Promontory, Apulia, southern Italy, marine Upper Santonian, ichthyofauna.

RÉSUMÉ

Le Santonien d'Apricena (Promontoire de Gargano, Les Pouilles, Italie du Sud) est décrit et tout spécialement une nouvelle unité lithostratigraphique marine récemment découverte et située au sud-est d'Apricena qui est dépeinte et illustrée en détails. Pour la première fois aussi, la liste complète de son ichthyofaune est donnée. Celle-ci se compose de dix genres de téléostéens, tous nouveaux sauf deux. Les rapports trophiques de cette communauté de poissons sont envisagés. Des comparaisons sont faites avec d'autres ichthyofaunes du Santonien de Mésogée eurafricaine ainsi qu'avec celle du Campano-Maastrichtien de Nardò, un autre gisement de l'Italie du sud. L'ichthyofaune d'Apricena est très endémique. Néanmoins, les genres *Chanoides* (Ostariophysi, Chanoididae) et *Nardodercetis* (Aulopiformes, Dercetidae) sont présents dans les deux faunes d'Apricena et de Nardò. Les familles des Ichthyodectidae et des Clupeidae sont aussi communes aux deux gisements mais les genres et les espèces sont différents.

Mots-clefs: Apricena, Promontoire de Gargano, Les Pouilles, Italie du Sud, Santonien supérieur marin, ichthyofaune.

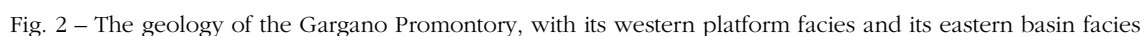
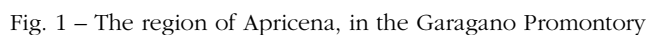
INTRODUCTION

New discoveries about the Santonian beds of Apricena (Gargano Promontory, Province of Foggia, Apulia, southern Italy) were made during the Ph. D. geological researches of one of us (De Cosmo, 2002). Some interesting fossil fishes also were discovered on that occasion (Taverne, De Cosmo, 2008; Taverne, 2009, 2011, 2013a, b, c, 2014, 2015, 2021).

The aim of our paper is to describe those new discoveries in the Santonian Formation of Apricena and to comment on its ichthyofauna.

GEOLOGICAL SETTING

The study area is located near the Apricena town, in the Apulia Region, at the toe of the western part of the Gargano Promontory, that represents the foreland area of the southern Apennine orogenic system (Figure 1). The Gargano Promontory belongs to the Apulia Carbonate Platform, a Mesozoic and Tertiary paleogeographical elements of the southern Tethys margin (Bernoulli, 1972, 2001; D'Argenio, 1976; Eberli *et al.*, 1993; Bosellini, 2002).



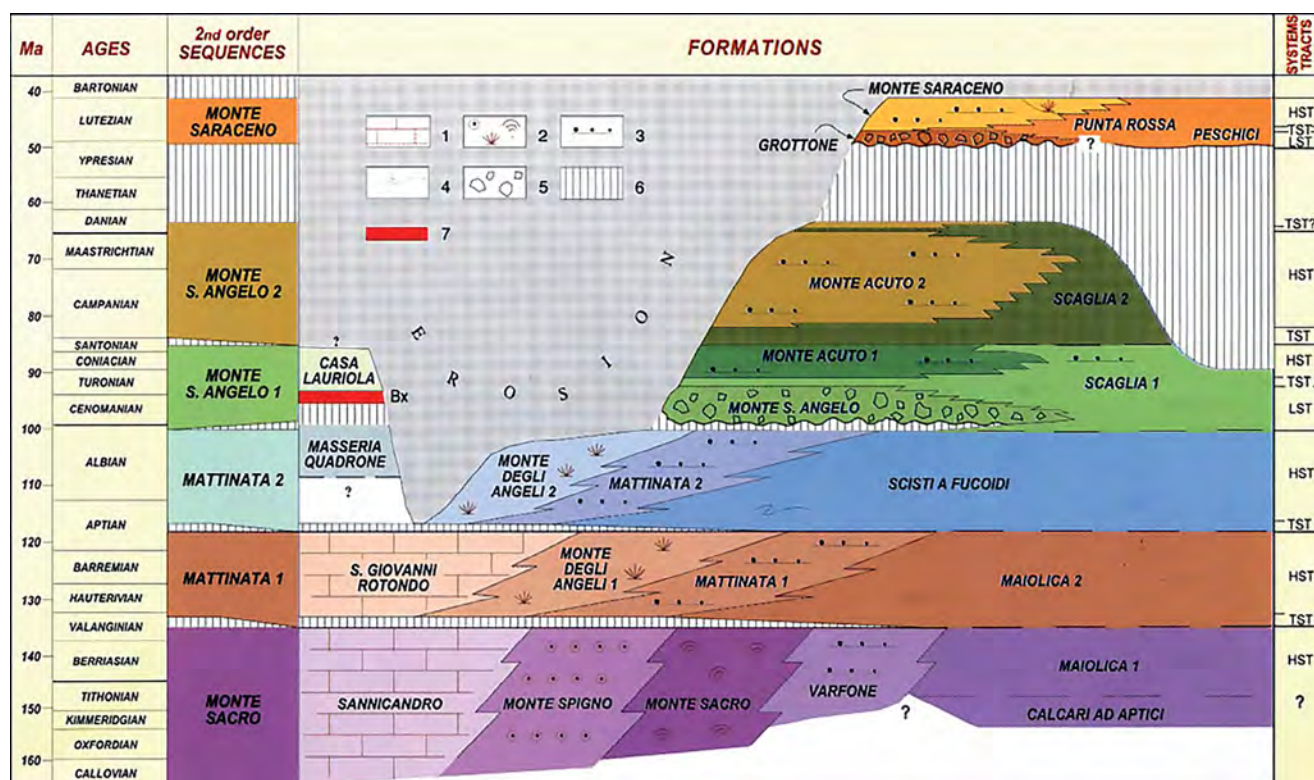


Fig. 3 – The chrono-stratigraphy of the Gargano Promontory

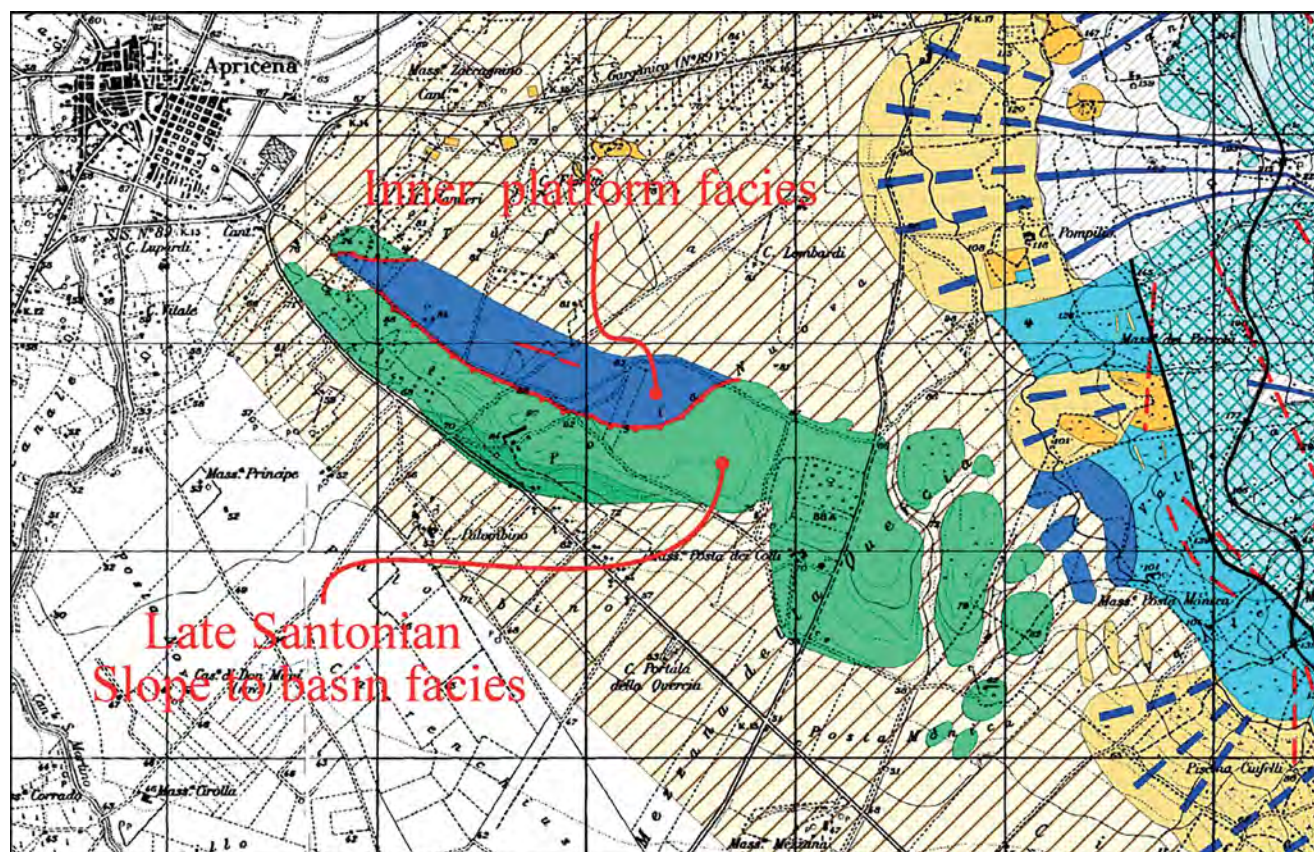


Fig. 4 – The chrono-stratigraphy of the Gargano Promontory.

Geologically, the Gargano Promontory could be roughly divided in two main parts (Figure 2): a western part made mainly by platform facies and the eastern part made by slope to basin facies (Morsilli, Bosellini, 1997, and references therein). The Upper Jurassic to Eocene outcropping carbonate succession, on the occurrence of various regional to local events, has been divided in various second order depositional sequences (supersequences), summarized in a chronostratigraphic scheme (Bosellini *et al.*, 1999) (Figure 3). These elements are deformed in a gentle anticline with a NW-SE axis with a deformation history not yet fully understood (Bertotti *et al.*, 1999; Billi, Salvini, 2000; Chilovi *et al.*, 2000; Branckman, Aydin, 2004; Tondi *et al.*, 2005).

In the Apricena area all cropping out Mesozoic stratigraphic units were previously attributed to inner platform facies belonging respectively to Lower Cretaceous San Giovanni Rotondo Limestone (Bari Limestone eq.) and Upper Cretaceous Coniacian-Santonian p. p. in age attributable to the medium lower part of the Altamura Limestone made mainly by peritidal cycles (Luperto Sinni, Masse, 1986; Luperto Sinni, 1996; Laviano, Marino, 1996; Bosellini *et al.*, 1999).

Recently, sedimentological and micro-paleontological analysis have permitted to recognize a new stratigraphic unit, interpreted as representing base-of-slope to basin settings, that lies disconformably on the previously inner platform facies of Altamura Limestone (Morsilli *et al.*, 2002, 2003). The whole characters of this unit and its age permit to ascribe it to the Monte Acuto Formation (Unità 3 *sensu* Neri, 1993), a well known Upper Cretaceous base-of-slope unit of the Gargano Promontory (Bernoulli, 1972; Bosellini *et al.*, 1993, 1999). Inside this unit in the Apricena area, and more precisely in the upper part, recent study has brought to discover a variegated fossil flora and ichthyofauna (De Cosmo, 2002) (Figure 4).

CHARACTERS OF THE MONTE ACUTO LIMESTONE IN THE APRICENA AREA

The stratigraphic succession is approximately 60 meters thick and shows a fining-upward trend that can be subdivided in two distinct parts (Figure 5).

The lower part consist of m-thick breccia bodies with clasts of 10 to 50 cm (platform derived clasts with rudists shells and fragments), interbed-

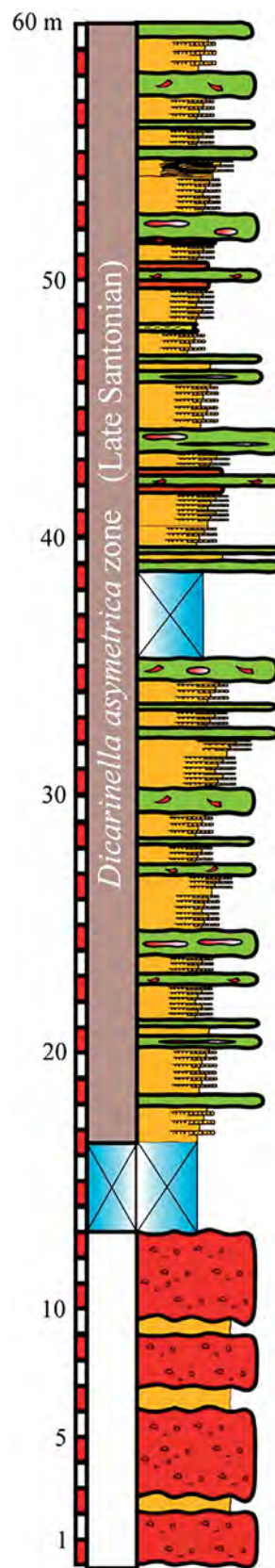


Fig. 5 – The stratigraphy of the Monte Acuto Limestone in the Apricena area



Fig. 6 – The breccia bodies of the lower stratigraphical part of the Monte Acuto Limestones at Apricena



Fig. 7 – The thinly bedded white mudstone, laminated wackestone-packstone, and grainstone-packstone with lightly convoluted laminae in the upper stratigraphical part of the Monte Acuto Limestones at Apricena



Fig. 8 – The chert nodules in the upper stratigraphical part of the Monte Acuto Limestones at Apricena



Fig. 9 – Some remains of plants from the upper stratigraphical part of the Monte Acuto Limestones at Apricena

ded with medium to thick beds (30-80 cm) of normally-graded skeletal rudstones and grainstones, sometimes with well developed even laminations (Figure 6).

The upper part consists of thinly bedded (2-5 cm) white mudstone alternated with weakly cemented, even laminated wackestone-packstone, and thin beds (3-10 cm) of grainstone-packstone with lightly wavy to convoluted laminae (Figure 7). Scattered thin beds (5-20 cm) of skeletal grainstone with

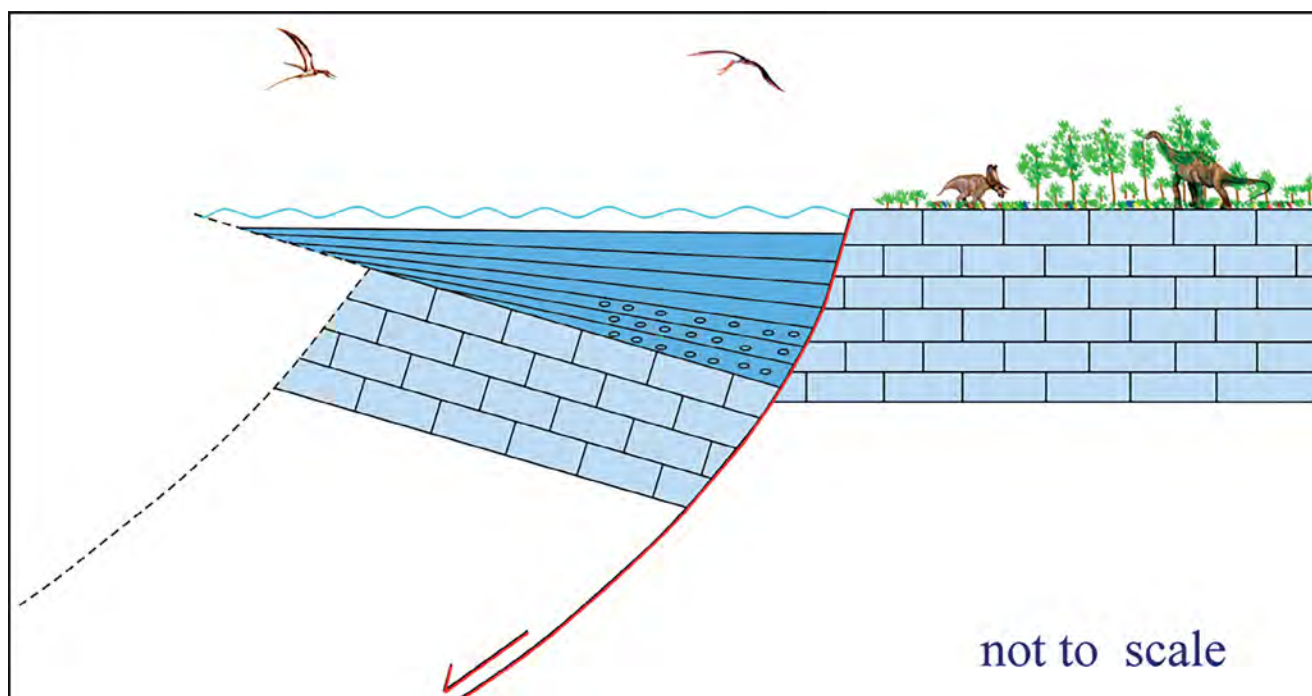


Fig. 10 – Our hypothesis explaining the abrupt tectonic events during the Upper Santonian at Apricena

normal grading may also occur. Chert nodules grey to black in colour, sometimes up to 60-80 cm, also characterise the upper part of the succession (Figure 8). The mudstone-wackestone beds are rich in radiolarians, calcispheres and planktonic foraminifera.

The planktonic foraminifera assemblages are mainly represented by small-size forms (Morsilli *et al.*, 2003), dominated by *Heterobelix* (*H. navarroensis*, *H. reussi*) and *Hedbergella* (*H. delrioensis*, *H. planispira*, *H. flandrini*) with common *Globigerinelloides* (*G. ultramicrus*, *G. caseyi*, *G. prairiehillensis*) and more rare *Archaeoglobigerina* (*A. cretacea*, *A. blowi*) and *Shackoina* sp. Rare and generally poorly preserved keeled specimens also occur. The species *Marginotruncana coronata*, *Globotruncana arca*, *G. bulloides*, *G. linneiana*, *Dicarinella asymetrica* and *D. concavata* were recognized. The occurrence of *D. asymetrica* associated with *D. concavata* and with *Sigalia* sp. allow to refer the assemblages to the Late Santonian *Dicarinella asymetrica* Zone of Robaszynski, Caron, 1995 (see also Morsilli *et al.*, 2002, 2003).

In the last 10 meters of the succession, several leaves and other remains of plants (Conifer, Angiosperm, Fern, *Frenelopsis* sp.) were founded associ-

ated with a few small fishes (Figure 9) (De Cosmo, 2002, De Cosmo, Morsilli, 2002).

INTERPRETATION (FIGURE 10)

The various lithofacies of the Monte Acuto Limestone of the Apricena area could be interpreted as the result of resedimentation episodes alternated and followed by pelagic deposition, in a intraplateform basin setting installed directly above the shallow-water peritidal cycles of the Altamura Limestone. A plausible hypothesis to explain the abrupt contact between these two markedly different deposits is to assume a tectonic event that created the necessary relief for the deposition of breccia and turbidite beds at the base and the overlying pelagic sediments and the next necessary deepening for the deposition of pelagic limestone (Figure 10) (Morsilli *et al.*, 2002, 2003). In this sector such a tectonic event, that created the new basin (Apricena basin), may be connected to the suggested Mesozoic activity of the Mattinata Fault, one of the main structural features of the Gargano Promontory (Chilovi *et al.*, 2000).

Data and interpretation document a drastic change in sedimentation in this sector of the Apulia Carbonate Platform, with at least a partial drowning of the inner platform facies during the Late Santonian. The drowning event recorded in the Apricena area coincides with a general back-stepping of the Apulia platform margin, documented by the deposition, within the Monte Acuto Formation outcropping in the near Gargano Promontory (Unità 3, *sensu* Neri, 1993; see also Neri, Luciani, 1994), of a 50-60 meters thick pelagic wedge during the Late Santonian-Early Campanian in the slope setting of the southwestern part of the Gargano ("Scaglia Tongue"). At least 20 km of back-stepping of the Apulia platform margin is documented also in the southern part of the Apulia (Fasano-Ostuni area) during the Early Campanian. In the same stratigraphic interval a marked marine onlap is observed also in seismic profile in the Adriatic offshore (De Alteriis, Aiello, 1993).

The partial drowning is also suggested by the finding of a diversified terrestrial fossil flora. That suggests the presence of coeval continental environments not too far from this basin (De Cosmo, 2002; De Cosmo, Morsilli, 2002; Morsilli *et al.*, 2003).

The planktonic foraminifera assemblages, dominated by small-sized simple morphotypes of superficial to sub-superficial habitat (Premoli Silva, Sliter, 1999), are probably related to the relatively shallow depth of the basin and to its proximity to the coast (Morsilli *et al.*, 2002, 2003). The abundance of heterohelicids, which are believed to tolerate low-oxygen waters may indicate that the basin was relatively closed and characterised by rich-nutrient waters (abundance of radiolarians, calcispheres and hedbergellids) (Morsilli *et al.*, 2002, 2003).

These data and interpretation change the previous paleogeographic view of the region and suggest to consider both the presence of a basinal setting in the Apricena area, probably connected with the open sea, and the coeval presence of a land area during a general back-stepping and drowning time of the Apulia Platform.

ICHTHYOFAUNA

1. Composition (Figure 11)

The fossil ichthyofauna of the marine Upper Santonian of Apricena comprises the following then species of teleost fishes:

1. *Garganoichthys decosmoi* Taverne, 2009 (Ichthyodectiformes, Ichthyodectidae),
2. *Apricenapiscis depotteri* Taverne, 2013 (Crossognathiformes, Pachyrhizodontidae),
3. *Garganoclupea svetovidovi* Taverne, 2014 (Clupeiformes, Garganoclupeidae),
4. *Apricenaclupea ridewoodi* Taverne, 2014 (Clupeiformes, Clupeidae, Pellonulinae),
5. *Chanoides weberi* Taverne, De Cosmo, 2008 (Ostariophysi, Chanoididae),
6. *Cretargentina chapmani* Taverne, 2013 (Argentiniformes, Pattersonellidae),
7. *Nardodercetis garganoi* Taverne, 2013 (Aulopiformes, Dercetidae),
8. *Diaphus prokofievi* Taverne, 2015 (Myctophiformes, Myctophidae),
9. *Garganomycrophum sorbinii* Taverne, 2021 (Myctophiformes, Myctophidae),
10. *Apricenaichthys italicus* Taverne, 2011 (Polymixiiformes, Polymixiidae).

All those fishes are small and some of them really very small, no more than a few centimetres. This character is probably linked to the proximity of the coast and to the shallow depth of the basin (Morsilli *et al.*, 2002, 2003).

2. Trophic relationships

In such a piscine community, the ichthyodectid *Garganoichthys decosmoi* and the pachyrhizodontid *Apricenapiscis depotteri* undoubtedly were the major predators. They were able to eat all the other fish species present in the area and especially the smaller ones, i. e., the Clupeiformes, the Pattersonellidae, the Myctophidae and the Polymixiidae..

Ichthyodectidae lived from Late Jurassic to Late Cretaceous. They often were big fishes, sometimes reaching several meters in length. Most of them possess strongly toothed jaws, an upturned lower jaw, an elongated and laterally compressed body, dorsal and anal fins rejected close to the tail and a forked caudal fin. That is a typical morphology of a fast swimming fish hunter. They preyed upon all sorts of fishes, small or big, piscivorous or not, including pachyrhizodontids (Maisey, 1991: 191, 1994: fig. 5), enchodontoids (Everhart *et al.*, 2010: fig. 4) and other smaller ichthyodectids (Everhart, 2005: 72-73, fig. 5.1).

Pachyrhizodontidae also are widely distributed from Late Jurassic to Late Cretaceous. They are smaller fishes than ichthyodectids, not exceeding 40 cm long, with a pointed snout, a large horizontally directed mouth, numerous small or large

conical teeth on the jaws, a fusiform body and a forked caudal fin. They surely were also fast swimming predators. They preyed upon crustaceans, smaller fishes and even upon younger specimens of their own species (Maisey, 1994: 7, fig. 4; Cavin, 2008: 2).

Nardodercetis garganoi belongs to the Dercetidae, a family that lived during the Late Cretaceous and the lowermost Paleocene. Generally, they also are smaller predators than ichthyodectids. However, some rare specimens could reach almost a meter long. They exhibit an eel-shaped, laterally compressed body, partially or totally covered by rows of scutes, an elongate narrow head with a long pointed rostrum, small to long conical teeth on the jaws, palatine and pterygoid bones, and a forked caudal fin. With their anguilliform morphology, dercetids surely had an undulatory mode of swimming based on movements of the body and tail (Lindsey, 1978: 14-17). That mode of swimming does not result in high speeds and is generally used by fishes living near the bottom. Dercetids probably preyed on small and rather slow fishes but also on non-armoured invertebrates they turned out from the mud of the bottom with their long rostrum.

Chanoididae are a marine monogeneric family of primitive Ostariophysi with a well developed Weberian apparatus (Patterson, 1984: figs 13-16; Taverne, 2005a: fig. 12; Taverne, De Cosmo, 2008: fig. 4; Mayrinck *et al.*, 2015; Taverne, Capasso, 2021). They are known from Upper Santonian to Middle Eocene in Italy. *Chanoides* Woodward, 1901 comprises three species. It has a carp-like body and can reach 30 to 45 cm in length. The jaw bones are toothless but strongly built. The bones of the palate and of the tongue also are toothless. A kinethmoid and a pair of preethmoids are present in the snout, allowing a slight protrusion of the mouth (Patterson, 1984: figs 6-10; Taverne, 2005a: figs 6, 9) and a possibility of suction. The first branchial arch bears numerous long branchiospines that could serve as a sieve, and there are rather large conical teeth on the fifth ceratobranchial (Patterson, 1984: figs 11, 12; Taverne, 2005a: fig. 10). *Chanoides* probably feeds like many cyprinid fishes, with the mouth moving as a pump to suck in small invertebrates and smaller planktonic particles that the branchial sieve can filter (Uribe-Zamora, 1975).

The other species in the ichthyofauna of Apricena are very small edentulous fishes that certainly were micro-planktonic feeders.

3. *Comparisons with other Senonian (Late Cretaceous) actinopterygian faunas from the eurafrican Mesogean realm*

3. 1. THE MARINE UPPER SANTONIAN

ACTINOPTERYGIANS OF SAHEL ALMA, LEBANON

The marine Upper Santonian beds of Sahel Alma, Lebanon, has produced one of the most famous and various fossil fish fauna of Late Cretaceous times, a fauna studied by many scientists (Agassiz, 1833-1844; Heckel, 1849; Pictet, 1850; Costa, 1857; Pictet, Humbert, 1866; Davis, 1887; Woodward, 1942; Patterson, 1967; Goody, 1969; Forey, 1973; Gaudant, 1969; Gayet, 1993; Taverne, Filleul, 2003; Taverne, 2005b). There are about 40 species ranged in almost 30 genera and 20 families.

Only three families are common with the fauna of Apricena, the Dercetidae, the Myctophidae and the Polymixiidae but all genera and species are different. At Sahel Alma, Dercetidae are represented by *Dercetis* Agassiz, 1834 and *Benthesikyma* White, Moy-Thomas, 1940, Myctophidae by *Acrognathus* Agassiz, 1844 and *Opisthopteryx* Pictet, Humbert, 1966, and Polymixiidae by *Pycnosterinx* Heckel, 1849 and *Omosoma* Costa, 1857. On the other hand, the families Ichthyodectidae, Pachyrhizodontidae, Clupeidae and Chanoididae and the order Argentiniformes, present at Apricena, are missing at Sahel Alma.

3. 2. THE MARINE UPPER CRETACEOUS (SANTONIAN TO MAASTRICHTIAN) ACTINOPTERYGIANS OF NORTHERN FRANCE, BELGIUM AND DUTCH LIMBURG

Many authors have reported Upper Cretaceous actinopterygian fishes from northern France, Belgium and Dutch Limburg during the 19th century and the beginning of the 20th. Leriche (1906, 1929) gives all the references and summarizes the data. He mentions about 20 species and 15 genera and families.

Three of these families are also present at Apricena, the Ichthyodectidae, the Pachyrhizodontidae and the Polymixiidae. However, the genera and species are different. Isolated teeth of the ichthyodectid *Xiphactinus* Leidy, 1870 (= *Portheus* Cope, 1871) and fragments of the pachyrhizodontid *Pachyrhizodus* Dixon, 1850 have been reported in Belgium by Dollo (1892: 3). Fragments of ichthyodectids and

the polymixiid *Berycopsis* Dixon, 1850 are known in northern France.

3. 3. THE MARINE CAMPANIAN ACTINOPTERYGIANS OF WESTPHALIA, GERMANY

The marine Campanian ichthyofauna of Baumberge and Sedenhorst in Westphalia, Germany, is as rich as that of Sahel Alma and was also studied by numerous authors (see a complete list of references in Dietze, 2009). This fauna comprises about 40 species, 25 genera and 15 families.

Here also, Ichthyodectidae, Pachyrhizodontidae, Clupeidae and Chanoididae are not present, and only the three families Dercetidae, Myctophidae and Polymixiidae are common to faunas of Westphalia and Apricena. But, once again, the species and genera are different. At Baumberge and Sedenhorst, the Dercetidae are represented by *Dercetis* and *Pelargorhynchus* Von Der Marck, 1858, the Myctophidae by *Sardinius* Von Der Marck, 1858 and *Tachynectes* Von Der Marck, 1863, and the Polymixiidae by *Berycopsis* and *Omosoma*.

3. 4. THE UPPER CHALK ACTINOPTERYGIANS OF ENGLAND

The upper part of the English Chalk is of Senonian (uppermost Late Cretaceous) age. The fishes have been studied principally by Woodward (1902-1912) and Patterson (1964, 1968). The Upper Chalk actinopterygians comprise about 15 species, and a dozen of genera and families.

Once again, only the three families Ichthyodectidae, Dercetidae and Myctophidae are present both in the Upper Chalk and in the Santonian of Apricena. But neither the genera nor the species are common to the two beds. In England, *Xiphactinus* is the only ichthyodectid, *Dercetis* the only dercetid and *Acrognathus* the only myctophid.

3. 5. THE MARINE MAASTRICHTIAN ACTINOPTERYGIANS OF THE PHOSPHATE FORMATION OF MOROCCO

Those fishes were studied by Arambourg (1962). He describes 7 species, 5 genera and 5 families in the Maastrichtian part of the Phosphate Formation of Morocco. All of them are missing in the Santonian of Apricena.

Arambourg (1962: 238) mentions the Dercetidae in that ichthyofauna, based on the presence of *Stratodus apicalis* Cope, 1872. However, Taverner (2006: 36, 37, fig. 9) proved that *S. apicalis* did not belong to the Dercetidae but to the Cimolichthyidae.

3. 6. THE MARINE CAMPANIAN-MAASTRICHTIAN

ACTINOPTERYGIANS OF NARDÒ, SOUTHERN ITALY

Like Apricena, Nardò is a city located in Apulia (southern Italy). The abundant marine Campanian-Maastrichtian ichthyofauna of Nardò and a few bordering cities (Altamura Formation, Salento) has been studied in a great number of papers since 1981 (see the complete references in Taverner, Capasso, 2018) but is not yet completely known. The already described fishes represent 38 species, one skate and 37 actinopterygians distributed in 37 genera and almost 25 families.

Five families, the Ichthyodectidae, Pachyrhizodontidae, Clupeidae, Chanoididae and Dercetidae, are common to the fish communities of Nardò and Apricena. Concerning the first three families, the genera are different in the two faunas. At Nardò, Ichthyodectidae are represented by *Saurodon* Hays, 1830, *Capassoichthys* Taverner, 2015 and *Altamuraichthys* Taverner, 2016, Pachyrhizodontidae by *Nardopiscis* Taverner, 2008 and Clupeidae by *Nardoclupea* Taverner, 2002, *Pugliaclupea* Taverner, 2004, *Italoclupea* Taverner, 2007, *Portoselvaggioclupea* Taverner, 2007 and *Lecceclupea* Taverner, 2011. However, one of the two clupeiform fishes from Apricena belongs to the subfamily Pellonulinae and the tribe Ehiravini as *Lecceclupea*. Chanoididae are a monogeneric family, thus the genus *Chanoides* Woodward, 1901 is present in both localities but the species are different. Dercetidae are numerous at Nardò, being represented by five genera, *Ophidercetis* Taverner, 2005, *Nardodercetis* Taverner, 2005, *Apuliadercetis* Taverner, 2006, *Caudadercetis* Taverner, 2006 and *Leccedercetis* Taverner, 2008. The genus *Nardodercetis* is common to both formations but, once again, the species are different.

From all the actinopterygian faunas from the Senonian Eurafrian realm of the Tethys Ocean, it is clearly that of Nardò which exhibits the closest affinities with the one of Apricena, despite the 10 MY separating those two fish communities.

4. Taphonomic conditions

Most samples are disarticulated skeletal portions or isolated scattered bones. This indicates a rather slow burial process allowing scavengers and other bioturbators to break up the skeletons (Elder, Smith, 1988). Some samples seem to be dissociated remains grouped in pellets, a probable consequence of ingestion and partial digestion by predators (Dodson, 1973). Mostly, specimens are greatly incomplete and the broken body parts are not preserved

close to one another. This denotes that the skeletal disarticulation is not the result of a separation during the bloating and the normal body decomposition (Weigelt, 1989).

ACKNOWLEDGMENTS

We greatly thank Dr. Alexandra Aspes, former director of the Museo Civico di Storia Naturale di Verona, and Dr. Roberto Zorzin, head of the Department of Geology and Paleontology of the same museum, for the kindly reception they gave to us during all our visits in Verona. We also thank the anonymous colleagues who have reviewed our paper.

REFERENCES

- AGASSIZ L., 1833-1844. Recherches sur les poissons fossiles. Imprimerie de Petitpierre, Genève, texte: 5 tomes: 1420 p., atlas: 5 volumes: 396 pl.
- ARAMBOURG C., 1962. Les vertébrés fossiles des gisements de Phosphates (Maroc – Algérie – Tunisie). *Service Géologique du Maroc, Notes et Mémoires*, 92: 1-372.
- BERNOULLI D., 1972. North Atlantic and Mediterranean Mesozoic facies: a comparison. In: Hollister C. D., Ewing J.L. *et al.* (editors). Initial Reports of the Deep Sea Drilling Project, 11, Government Printing Office, Washington: 801-871.
- BERNOULLI D., 2001. Mesozoic-Tertiary carbonate platforms, slopes and basins of the external Apennines and Sicily. In: Vai G.B., Martini I.P. (editors). *Anatomy of an Orogen: the Apennines and Adjacent Mediterranean Basins*, Kluwer Academic Publishers, Great Britain: 307-326.
- BERTOTTI G., CASOLARI E., PICOTTI V., 1999. The Gargano Promontory: a Neogene contractional belt within the Adriatic plate. *Terra Nova*, 11: 168-173.
- BILLI A., SALVINI F., 2000. Sistemi di fratture associate a faglie in rocce carbonatiche: nuovi dati sull'evoluzione tettonica del Promontorio del Gargano. *Bollettino della Società Geologica Italiana*, 119: 237-250.
- BOSELLINI A., 2002. Dinosaurs "re-write" the geodynamics of the eastern Mediterranean and the paleogeography of the Apulia Platform. *Earth-Science Review*, 59: 211-234.
- BOSELLINI A., MORSILLI M., NERI C., 1999. Long term event stratigraphy of the Apulia Platform Margin (Upper Jurassic to Eocene, Gargano, Southern Italy). *Journal of Sedimentary Research*, 69: 1241-1252.
- BOSELLINI A., NERI C., LUCIANI V., 1993. Platform margin collapses and sequence stratigraphic organization of carbonate slopes: Cretaceous-Eocene, Gargano Promontory. *Terra Nova*, 5: 282-297.
- BRANKMAN C.M., AYDIN A., 2004. Uplift and contractional deformation along a segmented strike-slip fault system: the Gargano Promontory, southern Italy. *Journal of Structural Geology*, 26: 807-824.
- CAVIN L., 2008. Supposed and direct evidence of trophic relationships within the marine community from the Lower Turonian of Goulmima, Morocco. *Dansk Geologisk Forening, On Line Series 1*: 1-3.
- CHILOVI C., DE FEYTER A.J., POMPUCCI A., 2000. Wrench zone reactivation in the Adriatic Block: the example of the Mattinata Fault System (SE Italy). *Bollettino della Società Geologica Italiana*, 119: 3-8.
- COSTA O.G., 1857. Descrizione di alcuni pesci fossili del Libano. *Memorie della Reale Accademia delle Scienze di Napoli, Matematiche, Scienze Naturali, e Scienze Morali*, 2: 97-112.
- D'ARGENIO B., 1976. Le piattaforme periadriatiche: una rassegna di problemi nel quadro geodinamico mesozoico dell'area mediterranea. *Memorie della Società Geologica Italiana*, 13 (1974): 137-159.
- DAVIS J.W., 1887. The fossil fishes of the Chalk of Mount Lebanon, in Syria. *The Scientific Transactions of the Royal Dublin Society*, series 2, 3: 457-636.
- DE ALTERIIS G., AIELLO G., 1993. Stratigraphy and tectonics offshore of Puglia (Italy, southern Adriatic Sea). *Marine Geology*, 113: 233-253.
- DE COSMO P.D., 2002. Rilevamento geologico e stratigrafia dell'area di Apricina (Provincia di Foggia). Tesi di Laurea, Università di Ferrara: 165 pp.
- DE COSMO P.D., MORSILLI M., 2002. Segnalazione di resti di flora ed ittiofauna fossile del Santoniano superiore nell'area di Apricina (Puglia, Gargano). Gruppo informale di Sedimentologia, IX Riunione annuale, Pescara 21-22 ottobre: 39-40.
- DIETZE K., 2009. Morphology and phylogenetic relationships of certain neoteleostean fishes from the late Cretaceous of Sendenhorst, Germany. *Cretaceous Research*, 30 (3): 559-574.
- DODSON P., 1973. The significance of small bones in paleoecological interpretation. *Contributions to Geology, University of Wyoming*, 12: 15-19.
- DOLLO L., 1892. Première note sur les téléostéens du Crétacé supérieur de la Belgique. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie*, 6: 1-9.
- EBERLI G.P., BERNOULLI D., SANDERS D., VECSEI A., 1993. From aggradation to progradation: the Maiella Platform, Abruzzi, Italy. In: Simo J.A.T., Scott, R.W., Masse J.P. (editors). *Cretaceous Carbonate Platform. A.A.P.G. Memoir*, 56: 213-232.
- ELDER R.L., SMITH G.R., 1988. Fish taphonomy and environmental inference in palaeolimnology. *Palaeogeography Palaeoclimatology Palaeoecology*, 62: 577-592.
- EVERHART M.J., 2005. Oceans of Kansas. A natural history of the Western Interior Sea. Indiana University Press: XIV + 322 pp.
- EVERHART M.J., HAGEMAN S.A., HOFFMAN B.L., 2010. Another Sternberg "fish-within-a-fish" discovery: First report of *Ichthyodectes ctenodon* (Teleostei; Ichthyodecti-

formes) with stomach contents. *Transactions of the Kansas Academy of Science*, 113 (3-4): 197-205.

FOREY P.L., 1973. A revision of elopiform fishes, fossil and recent. *Bulletin of the British Museum (Natural History)*, *Geology*, supplement 10: 222 pp.

GAUDANT M., 1969. Sur quelques nouveaux poissons bérycoïdes crétacés du Mont Liban. *Notes et Mémoires sur le Moyen-Orient*, 10: 273-283.

GAYET M., 1993. Gonorhynchoidei du Crétacé supérieur marin du Liban et relations phylogénétiques des Charitosomidae nov. fam. *Documents du Laboratoire de Géologie de l'Université de Lyon*, 126: 131 pp.

GOODY P., 1969. The relationships of certain Upper Cretaceous teleosts with special reference to the myctophoids. *Bulletin of the British Museum (Natural History)*, *Geology*, supplement 7: 255 pp.

GRANDE L., 1985. Recent and fossil clupeomorph fishes with material for revision of the subgroups of clupeoids. *Bulletin of the American Museum of Natural History*, 181 (2): 231-372.

HECKEL J.J., 1849. Die fossilen Fische des Libanon. In: von Russegger J. (editor). *Reisen in Europa, Asien und Afrika*, 2 (3), print. E. Schweizerbart, Stuttgart: 336-346.

LAVIANO A., MARINO M., 1996. Biostratigraphy and paleoecology of Upper Cretaceous carbonate successions in the Gargano Promontory. *Memorie della Società Geologica Italiana*, 51: 685-701.

LERICHE M., 1906. Contribution à l'étude des poissons fossiles du Nord de la France et des régions voisines. *Annales de la Société géologique du Nord*, 35: 338-356.

LERICHE M., 1929. Les poissons du Crétacé marin de la Belgique et du Limbourg hollandais. *Annales de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 37 (3): 199-299.

LINDSEY C.C., 1978. Form, function, and locomotory habits in fish. In: Hoar W.S., Randall D.J. (editors). *Fish physiology*. Volume 7, Academic Press: 1-100.

LUPERTO SINNI E., 1996. Schema stratigrafico del Cretacico del Gargano basato su risultati di recenti ricerche. *Memorie della Società Geologica Italiana*, 51: 1019-1036.

LUPERTO SINNI E., MASSE J.P., 1986. Données nouvelles sur la stratigraphie des calcaires de plate-forme du Crétacé inférieur du Gargano (Italie méridionale). *Rivista Italiana di Paleontologia e Stratigrafia*, 92: 33-66.

MAISEY J.G., 1991. *Cladocyclus* Agassiz, 1841. In: Maisey J.G. (editor). *Santana Fossils. An Illustrated Atlas*. T.H.F. Publications, Inc., Neptune City, New Jersey, USA: 190-207.

MAISEY J.G., 1994. Predatory-prey relationships and trophic level reconstruction in a fossil fish community. *Environmental Biology of Fishes*, 40: 1-22.

MAYRINCK D., BRITO P.M., OTERO O., 2015. Review of the osteology of the fossil fish formerly attributed to the genus *Chanoides* and implications for the definition of otophysan bony characters. *Journal of Systematic Palaeontology*, 13 (5): 397-420.

MORSILLI M., BOSELLINI A., 1997. Carbonate facies zonation of the Upper Jurassic-Lower Cretaceous Apulia Platform margin (Gargano Promontory, southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 103: 193-206.

MORSILLI M., DE COSMO P.D., BOSELLINI A., LUCIANI V., 2002. L'annegamento Santoniano della piattaforma Apula nell'area di Apricena (Gargano, Puglia): nuovi dati per la paleogeografia del Cretaceo superiore. Gruppo informale di Sedimentologia, IX Riunione annuale, Pescara 21-22 ottobre: 65-66.

MORSILLI M., DE COSMO P.D., BOSELLINI A., LUCIANI V., 2003. Late Santonian partial drowning of the Apulia Carbonate Platform (Gargano promontory, southern Italy): new data for paleogeographic reconstructions. 22nd IAS Meeting of Sedimentology – Opatija 2003.

NERI C., 1993. Stratigraphy and sedimentology of the Monte Acuto Formation (Upper Cretaceous-Lower Paleocene, Gargano Promontory, Southern Italy). *Annali dell'Università di Ferrara*, (Nuova Serie), Sezione XI, *Scienze geologiche e paleontologiche*, 4: 13-44.

NERI C., LUCIANI V., 1994. The Monte S. Angelo Sequence (late Cretaceous-Paleocene, Gargano Promontory, southern Italy): physical stratigraphy and biostratigraphy. *Giornale di Geologia*, 56: 149-165.

PATTERSON C., 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Society of London*, series B, *Biological Sciences*, 247 (739): 213-482.

PATTERSON C., 1967. New Cretaceous berycoid fishes from the Lebanon. *Bulletin of the British Museum (Natural History)*, *Geology*, 14 (3): 69-109.

PATTERSON C., 1968. The caudal skeleton in Mesozoic acanthopterygian fishes. *Bulletin of the British Museum (Natural History)*, *Geology*, 17 (2): 47-102.

PATTERSON C., 1984. *Chanoides*, a marine Eocene otophysan fish (Teleostei: Ostariophysi). *Journal of Vertebrate Paleontology*, 4 (3): 430-456.

PICTET F.J., 1850. Description de quelques poissons fossiles du Mont Liban. Imprimerie J.G. Fick, Genève: 59 pp.

PICTET F.J., HUMBERT A., 1866. Nouvelles recherches sur les poissons fossiles du Mont Liban. Georg (editor), Genève, Imprimerie J.-B. Baillièrre et fils – F. Savy, Paris: 115 pp.

PREMOLI SILVA I., SLITER W.V., 1999. Cretaceous paleoceanography: evidence from planktonic foraminiferal evolution. *Geological Society of America*, Special Paper, 332: 301-328.

ROBASZYNSKI F., CARON M., 1995. Foraminifères planctoniques du Crétacé: commentaire de la zonation Europe-Méditerranée. *Bulletin de la Société Géologique de France*, 166: 691-692.

TAVERNE L., 2005a. Les poissons crétacés de Nardò. 20°. *Chanoides chardonii* sp. nov. (Teleostei, Ostariophysi, Otophysi). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 29: 39-54.

TAVERNE L., 2005b. Les poissons crétacés de Nardò. 21°. *Ophidercetes italiensis* gen. et sp. nov. (Teleostei, Aulopi-

formes, Dercetidae). Une solution ostéologique au problème des genres *Dercetis* et *Benthesikyme* (= *Leptotrachelus*). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 29: 55-79.

TAVERNE L., 2006. Les poissons crétacés de Nardò. 24°. *Caudadercetis bannikovi* gen. et sp. nov. (Teleostei, Aulopiformes, Dercetidae). Considérations sur la phylogénie des Dercetidae. *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 30: 27-48.

TAVERNE L., 2009. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 2°. *Garaganoichthys decosmoi* gen. et sp. nov. (Teleostei, Ichthyodectiformes, Ichthyodectidae). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 33: 27-39.

TAVERNE L., 2011. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 3°. *Apricenaichthys italicus* gen. et sp. nov. (Teleostei, Polymixiiformes). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 35: 19-31.

TAVERNE L., 2013a. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 4°. *Apricenapiscis depoteri* gen. et sp. nov. (Teleostei, Crossognathiformes, Pachyrhizodontidae). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 37: 57-66.

TAVERNE L., 2013b. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 5°. *Nardodercetis garganoi* sp. nov. (Teleostei, Aulopiformes, Dercetidae). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 37: 67-72.

TAVERNE L., 2013c. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 6°. *Cretargentina chapmani* gen. et sp. nov. (Teleostei, Argentiniformes). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 37: 73-80.

TAVERNE L., 2014. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 7°. *Garganoclupea svetovidovi* gen. et sp. nov. et *Apricenaclupea ridewoodi* (Teleostei, Clupeiformes). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 38: 27-49.

TAVERNE L., 2015. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 8°. *Diaphus prokofievi* sp. nov. (Teleostei, Myctophiformes, Myctophidae). *Bolletti-*

no del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria, 39: 35-46.

TAVERNE L., 2021. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 9°. *Garganomycetophum sorbinii* gen. et sp. nov. (Teleostei, Myctophiformes, Myctophidae). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 45: 65-75.

TAVERNE L., CAPASSO L., 2018. Les poissons crétacés de Nardò. 40°. *Nardoglossus sanctibernardini* gen. et sp. nov. (Teleostei, Gonorynchiformes, Gonorynchoidei). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 42: 3-19.

TAVERNE L., CAPASSO L., 2021. The Cretaceous fishes of Nardò. 41°. New data on the teleosts *Capassoichthys alfonsoi* (Ichthyodectidae) and *Chanoides chardonii* (Ostariophysi, Otophysi). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 45: 55-64.

TAVERNE L., DE COSMO P.D., 2008. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 1°. *Chanoides weberi* sp. nov. (Teleostei, Ostariophysi, Otophysi, Chanoididae). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 32: 29-38.

TAVERNE L., FILLEUL A., 2003. Osteology and relationships of the genus *Spaniodon* (Teleostei, Salmoniformes) from the Santonian (Upper Cretaceous) of Lebanon. *Palaeontology*, 46 (5): 927-944.

TONDI E., PICCARDI L., CACON S., KONTNY B., CELLO G., 2005. Structural and time constraints for dextral shear along the seismogenic Mattinata Fault (Gargano, southern Italy). *Journal of Geodynamics*, 40: 134-152.

URIBE-ZAMORA M., 1975. Sélection des proies par le filtre branchial de la carpe miroir, *Cyprinus carpio*. Thèse de l'Université de Lyon: 127 pp.

WEIGELT J., 1989. Recent vertebrate carcasses and their paleobiological implications. University of Chicago Press: XVI + 188 (English translation of "Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung", Leipzig, 1927).

WOODWARD A.S., 1902-1912. The fossil fishes of the English Chalk. Printed by the Palaeontographical Society, London: 264 pp.

WOODWARD A.S., 1942. Some new and little known Upper Cretaceous fishes from Mount Lebanon. *Annals and Magazine of Natural History*, series 11, 9: 537-568.

INDICE

GIOVANNI ADAMI, MASSIMO SARACINO

Cronistoria delle ricerche sull'età del Ferro nel territorio veronese (parte 1):

tra il collezionismo antiquario e la nascita della paleontologia veronese pag. 5

LUIGI CAPASSO

Palaeophysiology of reproduction in fossil fishes:

an overview and new insights, with the description of four new ichnotaxa pag. 23

LOUIS TAVERNE, PIETRO DOMENICO DE COSMO, MICHELLE MORSILLI, VALERIA LUCIANI

The marine Upper Santonian (Late Cretaceous) of Apricena

(Gargano Promontory, southern Italy) and its fossil fish fauna pag. 75

Il Bollettino del Museo Civico di Storia Naturale di Verona esce annualmente in due distinte sezioni: 1. Botanica e Zoologia; 2. Geologia, Paleontologia e Preistoria, e pubblica sia estesi contributi sia brevi note riguardanti gli aspetti naturalistici di tali discipline.

PRESENTAZIONE DEI LAVORI

I lavori devono essere indirizzati alla Redazione Editoriale - Museo Civico di Storia Naturale di Verona Lungadige Porta Vittoria, 9 37129 Verona, accompagnati da indirizzo, recapito telefonico ed eventuali fax e casella di posta elettronica dell'autore o, in caso di più autori, di un autore di riferimento. I contributi ricevuti dalla Redazione saranno inviati per una valutazione a revisori scientifici e quindi, se accettati, verranno rinviati agli autori con richiesta di eventuali modifiche. L'accettazione o il rifiuto dei lavori è in ogni caso di competenza della Redazione.

NORME DA SEGUIRE NELLA STESURA DEI TESTI

I contributi devono essere presentati su supporto informatico e in due copie stampate, con tavole e illustrazioni anche in fotocopia. Il lavoro dovrà essere accompagnato da un Abstract in inglese (comprensivo del titolo e di Key Words in numero non inferiore a 3) e da un Riassunto in italiano (comprensivo di Parole Chiave in numero non inferiore a 3). Abstract e Riassunto dovranno essere di almeno tre righe.

Intestazione: Titolo del lavoro in grassetto, nome e cognome (per esteso) dell'autore o degli autori in maiuscolo, Ente o Istituto di appartenenza oppure città di residenza degli autori in corsivo e tra parentesi, esempio: **Indagini idrogeologiche nell'area del Corno d'Aquilio (Monti Lessini nordoccidentali - Verona)** ROBERTO ZORZIN

(Museo Civico di Storia Naturale di Verona)

Testo: riportare i nomi scientifici di genere e di specie in corsivo; utilizzare le unità di misura ammesse dal Sistema Internazionale con relativa simbologia; non inserire alcuna nota a piè di pagina. I riferimenti bibliografici nel testo devono essere indicati tra parentesi come nei seguenti esempi: (Failla e Messina, 1978: 362); (Disconzi, 1865: 98-103); (Failla et al., 1994); (Ruffo, 1999: Fig 1a); se vengono citati più lavori dello stesso autore, pubblicati nello stesso anno, il numero indicante l'anno sarà seguito da lettere alfabetiche minuscole (es. 1969a; 1969b e così via). I testi che l'autore intende stampare in corpo più piccolo (ad esempio le sinonimie) devono essere evidenziati a matita a margine della copia stampata inviata alla Redazione. Per il simbolo di maschio utilizzare \$, per il simbolo di femmina utilizzare #.

Illustrazioni: Ogni illustrazione deve essere accompagnata da una breve ed esauriente didascalia in due lingue (la lingua originale del lavoro e la lingua inglese). Predisporre le figure, tenendo conto anche dello spazio occupato dalle didascalie, in un formato tale da supportare la riduzione alle dimensioni definitive della stampa (cm 17,5 x 23,5 o, per figure che occupino una sola colonna, 8,75 x 11,75). Nella copia stampata inviata alla Redazione dovrà essere indicato a matita dove inserire le figure nel testo. Il costo della stampa di eventuali figure a colori è a carico dell'autore. Le figure fornite in formato digitale devono essere ad alta risoluzione (300 dpi) e salvate in uno dei seguenti formati: .jpg; .tiff.

Bibliografia: Indicare gli autori citati nel testo in ordine alfabetico e cronologico come nei seguenti esempi:

BONNIER J., 1896. Edriophthalmes (Résultats scientifiques de la campagne du "Caudan" dans le Golfe de Gascogne, août-septembre 1895). *Annales de l'Université de Lyon*, 26: 527-689.

CARTES J.E., SORBE J.C., 1993. Les communautés suprabenthiques de la Mer Catalane (Méditerranée occidentale): Données préliminaires sur la répartition bathymétrique et l'abondance des crustacés pécarides, *Crustaceana*, 64 (2): 155-171.

MYERS A.A., 1982. Family Aoridae. In: Ruffo S. (Editor). The Amphipoda of the Mediterranean. Part 1. *Mémoires de l'Institut Océanographique*, 13: 111-158.

STEARNS S.C., 1992. The evolution of life history. Oxford University Press, New York: 249 pp.

TAVERNE L., 1997a. Les Poissons Crétacés de Nardò. 3°. L'ordre des Ichthyodectiformes (Pisces, Teleostei). *Bollettino del Museo Civico di Storia Naturale di Verona*, 21: 383-400.

TAVERNE L., 1997b. Les Poissons Crétacés de Nardò. 4°. *Apulichthys gayeti* gen. nov., sp. nov. (Teleostei, Ostariophysi, Goniorhynchiformes). *Bollettino del Museo Civico di Storia Naturale di Verona*, 21: 401-436.

INDIRIZZO DELL'AUTORE O DEGLI AUTORI

Deve essere indicato dopo la bibliografia come nel seguente esempio: SANDRO RUFFO - Museo Civico di Storia Naturale di Verona, Lungadige Porta Vittoria, 9 - 37129 Verona; e-mail: sandro.ruffo@comune.verona.it

BOZZE

L'autore riceverà una sola bozza in formato pdf. Per i lavori a più nomi la bozza verrà inviata all'autore di riferimento. La bozza, corretta con indicazioni chiare e leggibili, deve essere inviata per e-mail alla Redazione entro 10 giorni dalla data di ricevimento. La ritardata restituzione potrà comportare il passaggio del lavoro al volume successivo. Nella correzione non sono ammesse aggiunte, riduzioni o modifiche al testo, se non a spese dell'autore.

ESTRATTI

A ogni autore o gruppo di autori verrà inviata una copia elettronica dell'articolo in formato.pdf ad alta risoluzione. Eventuali estratti stampati potranno essere richiesti, a spese degli autori, direttamente alla tipografia.

The Bollettino del Museo Civico di Storia Naturale di Verona is issued annually in two distinct parts: 1. Botany and Zoology; 2. Geology, Paleontology and Archaeology. Both extended contributions and brief notes regarding the naturalistic aspects of these disciplines are published.

SUBMISSION OF MANUSCRIPTS

Manuscripts should be addressed to: Redazione Editoriale - Museo Civico di Storia Naturale di Verona, Lungadige Porta Vittoria, 9 37129 Verona, and should be accompanied by the address, telephone number and, if possible, the fax number and email address of the author or in the case of multiple authors, that of the corresponding author. The manuscripts received by the editors will be sent for evaluation to scientific referees and, if accepted, will then be returned to the authors for eventual requested modifications. The final decision for acceptance or refusal of manuscripts is always taken by the editors.

INSTRUCTIONS FOR MANUSCRIPT PREPARATION

The contributions must be presented on computer disc and in two printed copies with photocopies also of the plates and illustrations. The work should be accompanied by an Abstract in English (including the title and the Key Words which should not be less than three in number) and by an Abstract (Riassunto) in Italian (including the Key Words which should not be less than three in number). Both the Abstract and Riassunto should consist of at least three lines of text.

Headings: Title of the article in bold, name and surname (in full) of the author or authors in capitals, institution or city of residence of the authors in italics and between brackets, for example: **Indagini idrogeologiche nell'area del Corno d'Aquilio (Monti Lessini nordoccidentali - Verona)**

ROBERTO ZORZIN

(Museo Civico di Storia Naturale di Verona)

Text: Scientific names of genera and species should be in italics; utilize the standard units of measurement allowed by the International System with the relative symbols; do not insert footnotes. The bibliographic references in the text should be indicated between brackets as shown by the following examples: (Failla and Messina, 1978: 362); (Disconzi, 1865: 98-103); (Failla et al., 1994); (Ruffo, 1999: Fig 1a); if more than one publication by the same author is cited, published in the same year, then the number indicating the year should be followed by small letters in alphabetical order (ex. 1969a; 1969b etc.). The text that the author intends to print in smaller characters (for example the synonymy) should be highlighted in pencil in the margin of the printed copy sent to the editors. The symbol to be used for male is \$, the symbol for female #.

Illustrations: each illustration should be accompanied by a brief and comprehensive caption in two languages (the original language of the article and in English). The figures should be arranged, keeping in mind the space required for the caption, in a format which may be reduced to the final printing dimensions (cm 17.5 x 23.5 or, for single column figures, 8.75 x 11.75). The position of the figure within the text should be indicated in pencil on the printed copy sent to the editor. The cost of colour figures will be charged to the author. Figures submitted in digital form should be at high resolution (300 dpi) and saved in one of the following formats: .jpg; .tiff.

References: Indicate the authors cited in the text in alphabetical and chronological order as is shown in the following examples:

BONNIER J., 1896. Edriophthalmes (Résultats scientifiques de la campagne du "Caudan" dans le Golfe de Gascogne, août-septembre 1895). *Annales de l'Université de Lyon*, 26: 527-689.

CARTES J.E., SORBE J.C., 1993. Les communautés suprabenthiques de la Mer Catalane (Méditerranée occidentale): Données préliminaires sur la répartition bathymétrique et l'abondance des crustacés pécarides, *Crustaceana*, 64 (2): 155-171.

MYERS A.A., 1982. Family Aoridae. In: Ruffo S. (Editor). The Amphipoda of the Mediterranean. Part 1. *Mémoires de l'Institut Océanographique*, 13: 111-158.

STEARNS S.C., 1992. The evolution of life history. Oxford University Press, New York: 249 pp.

TAVERNE L., 1997a. Les Poissons Crétacés de Nardò. 3°. L'ordre des Ichthyodectiformes (Pisces, Teleostei). *Bollettino del Museo Civico di Storia Naturale di Verona*, 21: 383-400.

TAVERNE L., 1997b. Les Poissons Crétacés de Nardò. 4°. *Apulichthys gayeti* gen. nov., sp. nov. (Teleostei, Ostariophysi, Goniorhynchiformes). *Bollettino del Museo Civico di Storia Naturale di Verona*, 21: 401-436.

ADDRESS OF THE AUTHOR OR AUTHORS

This/these should be given after the bibliography as in the following example: SANDRO RUFFO - Museo Civico di Storia Naturale di Verona, Lungadige Porta Vittoria, 9 - 37129 Verona; e-mail: sandro.ruffo@comune.verona.it

PROOFS

The author will receive only one set of proofs in pdf format. In the case of more than one author the proofs will be sent to the author nominated to receive correspondence regarding the manuscript. The proofs, corrected with clear and legible indications, should be sent by e-mail to the editors within 10 days of the date of receipt. The late return of the proofs may lead to the manuscript being held over for the successive volume. Additions, reductions or modifications to the text will not be accepted in the corrections unless at the expense of the author.

OFFPRINTS

Each author or group of authors will be sent an electronic copy of the article in pdf format at high resolution.

Printed offprints at the author's expense may be requested directly from the printers.

GIOVANNI ADAMI, MASSIMO SARACINO

Cronistoria delle ricerche sull'età del Ferro nel territorio veronese (parte 1):
tra il collezionismo antiquario e la nascita della paleontologia veronese

LUIGI CAPASSO

Palaeophysiology of reproduction in fossil fishes:
an overview and new insights, with the description of four new ichnotaxa

LOUIS TAVERNE, PIETRO DOMENICO DE COSMO, MICHELLE MORSILLI, VALERIA LUCIANI

The marine Upper Santonian (Late Cretaceous) of Apricena
(Gargano Promontory, southern Italy) and its fossil fish fauna