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Volume XXXII – Fascicolo I

ANNA ALESSANDRELLO, GIACOMO BRACCHI
& BERNARD RIOU

POLYCHAETE, SIPUNCULAN AND ENTEROPNEUST WORMS FROM THE LOWER CALLOVIAN (MIDDLE JURASSIC) OF LA VOULTE-SUR-RHÔNE (ARDÈCHE, FRANCE)

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Anna Alessandrello, Giacomo Bracchi & Bernard Riou

Museo Civico di Storia Naturale di Milano
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Polychaete, sipunculan and enteropneust worms from the Lower Callovian (Middle Jurassic) of La Voulte-sur-Rhône (Ardèche, France)

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Polychaete, sipunculan and enteropneust worms from the Lower Callovian (Middle Jurassic) of La Voulte-sur-Rhône (Ardèche, France)

Abstract - The worm fauna from the Lower Callovian (Middle Jurassic) of La Voulte-sur-Rhône (Ardèche, France) is described through the recognition of two new genera and five new species of polychaete annelids: the arenicoloidean *Iubarenicola fischeri* n. gen. n. sp. and the aphroditoideans *Paleoaphrodite gallica* n. sp., *Paleoaphrodite briggsiana* n. sp., *Paleoaphrodite adeliae* n. sp. and *Protopholoe rhodanitidis* n. gen. n. sp. Moreover, *Rondeletia scutata* n. gen n. sp. is the third sipunculan species recorded within Mesozoic, *Megaderaion callovianum* n. sp. is the third fossil enteropneust species known. Since the soft tissues of these worms show different degrees of pyritization, some considerations about the La Voulte-sur-Rhône paleoenviroment are proposed.

Key words - Mesozoic, France, polychaetes, sipunculans, enteropneusts, pyritization.

Riassunto - Gli organismi vermiformi del Calloviano inferiore (Giurassico medio) di La Voulte-sur-Rhône (Ardenne, Francia).

Vengono descritti gli organismi vermiformi del giacimento calloviano (Giurassico medio) di La Voulte-sur-Rhône (Ardenne, Francia). Due nuovi generi e cinque nuove specie di annelidi policheti sono riconosciuti: *Iubarenicola fischeri* n. gen. n. sp. (ordine Capitellida), *Paleoaphrodite gallica* n. sp., *Paleoaphrodite briggsiana* n. sp., *Paleoaphrodite adeliae* n. sp. e *Protopholoe rhodanitidis* n. gen. n. sp. (superfamiglia Aphroditoidea). Sono inoltre descritti la terza specie di sipunculide conosciuta per il Mesozoico, *Rondeletia scutata* n. gen n. sp., e il terzo enteropneusto fossile conosciuto, *Megaderaion callovianum* n. gen. n. sp. Essendo i tessuti molli degli esemplari allo studio conservati attraverso vari gradi di piritizzazione, è stato infine possibile proporre alcune considerazioni sull'ambiente di deposizione.

Parole chiave - Mesozoico, Francia, policheti, sipunculidi, enteropneusti, piritizzazione.

INTRODUCTION

Fossil worms are rare in Mesozoic *Lagerstätten*. In addition to the eunicemorph polychaetes from the Kimmeridgian (Upper Jurassic) of Solnhofen, Germany (Ehlers, 1868 and 1869), and from the *Buntsandstein* (Lower Triassic) of Grès a Voltzia, France (Gall & Grauvogel, 1966), fossil polychaetes, nematodes and enteropneusts are known from the Sinemurian (Lower Jurassic) of Osteno, northern Italy (Arduini *et al.*, 1981, 1982 and 1983). Triassic fossil polychaetes have been reported also from the Rhaetian (Lower Triassic) of the Italian Prealps (Alessandrello & Teruzzi, 1986a; Stefani *et al.*, 1992) and from the Olenekian (Lower Triassic) of the Ambilobè region, Madagascar (Alessandrello, 1990), represented by aphroditid species. Triassic worms also include an unrelated species from the Carnian of Slovenia (Kolar-Jurkovšek & Jurkovšek, 1997). However, the most diverse and abundant Mesozic worm fauna has been described recently from the Middle Cenomanian (Upper Cretaceous) of Lebanon, including 6 families, 7 genera and 16 species of polychaete annelids (Alessandrello & Teruzzi, 1986b; Bracchi & Alessandrello, 2004, in press) and a new genus of a tetrameric nematode (Alessandrello & Mattavelli, 2004, in press).

The Callovian outcrop of La Voulte-sur-Rhône is widely known for the exceptional preservation of some invertebrate *taxa* such as bivalves, gastropods, cephalopods, pycnogonids, ophiuroids and asteroids (Fischer, 2003). Thylacocephalan, macruran, cumacean and mysidacean crustaceans have been recorded also (Van Straelen, 1922 and 1923; Secretan & Riou, 1983 and 1986; Carriol & Riou, 1991). Among the vertebrates, a few elasmobranchs, actinopterygians and crossopterygians (Fischer, 2003) have been described together with a crocodilian skull (Kuhn-Schnyder, 1960). Moreover, in the last thirty years, some authors (Dietl & Mundlos, 1972; Briggs & Kear, 1993; Fischer, 2003) have mentioned the existence, in the La Voulte-sur-Rhône outcrop, of worms in generic terms referred to aphroditid and arenicolid polychaetes. In this paper we describe 23 worm specimens from the '*niveau e*' of La Voulte-sur-Rhône (Fischer, 2003), held by the collections of the Laboratoire de Paléontologie (L.P.M.) of the Muséum National d'Histoire Naturelle in Paris.

The rock slabs preserving the La Voulte-sur-Rhône worms have been analyzed through a x-radiographic set (Fig. 1). This method could have been useful to guide preparation of the fossils but did not yield information beyond that directly observable through the microscopical investigation.

The polychaete systematics adopted in this work follows Fauchald (1977).

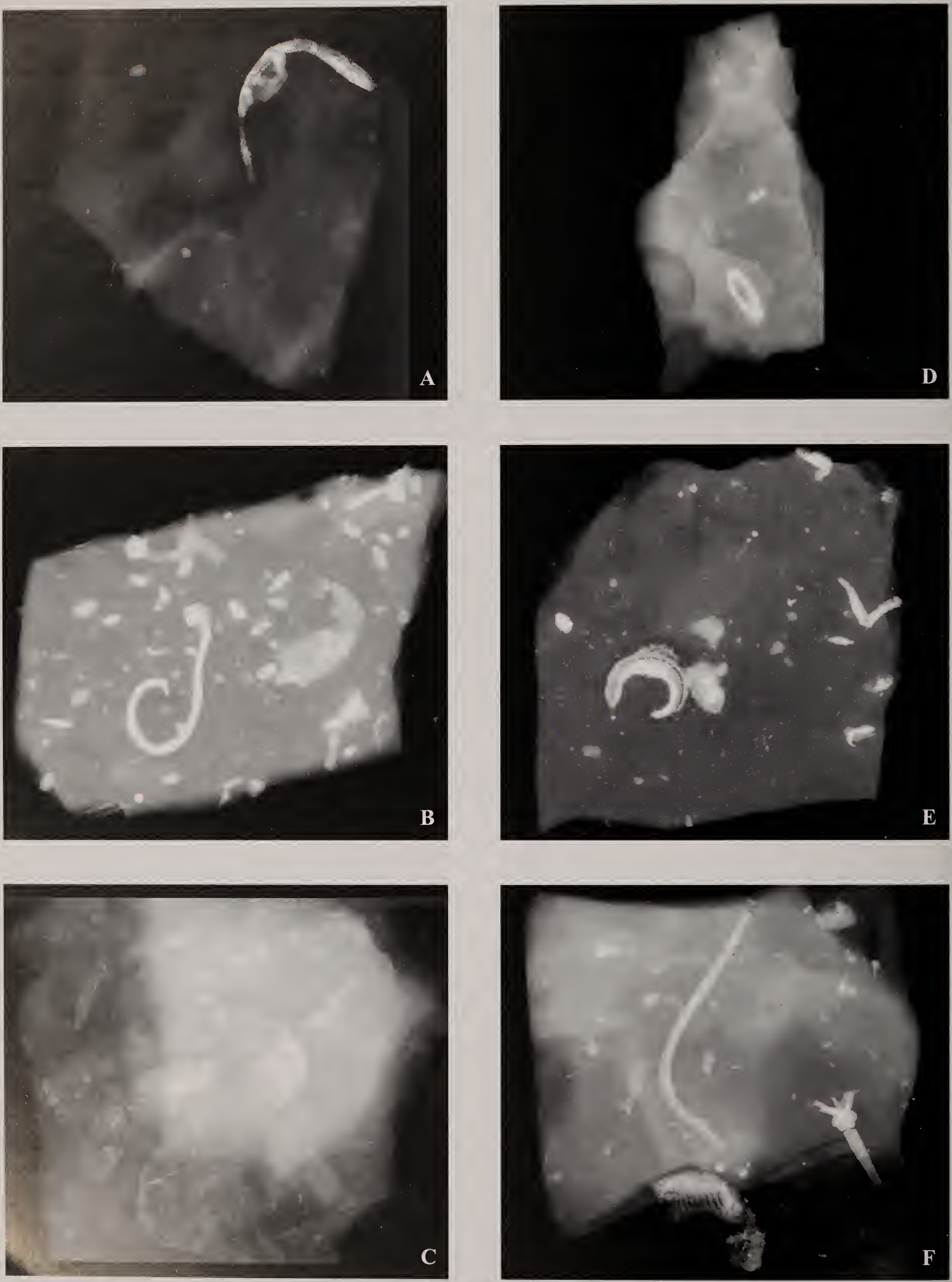

Fig. 1 - X-radiographs of L.P.M.-B.48343 and L.P.M.-B.48353 (A and B, *Iubarenicola fischeri* n. gen. n. sp.), L.P.M.-B.48336 (C, *Paleoaphrodite briggsiana* n. sp.), L.P.M.-B.48340 (D, *Protopholoe rhodanitis* n. gen. n. sp.), L..P.M. B. 48345 (E, *Rondeletia scutata* n. gen. n. sp.) and L.P.M.-B.48347 (F, undetermined worm).

GEOLOGICAL SETTING AND PRESERVATION

The La Voulte-sur-Rhône fossiliferous levels take their name from a small town on the west bank of the Rhone River, in the French southeastern department of Ardèche, and outcrop at La Boissine, a locality along the northern banks of the Gramade stream, slightly west of the La Voulte-sur-Rhône iron mines (Etter, 2002a; Fischer, 2003). The La Voulte-sur-Rhône stratigraphy has been investigated in detail by Elmi (1967), who dated this outcrop to the Lower Callovian on the basis of the ammonite fauna (*gracilis* biozone, *koenigi* sub-biozone). Argillaceous and finely laminated marlstones showing a black, brown, reddish or variegated colour and varying in thickness from 3 m to 7 m, alternate discontinuously with rare calcareous strata. Apart from widespread calcareous, siliceous and pyritic nodules, the marly levels often contain limonite and siderite traces and concretions.

The La Voulte-sur-Rhône fossil worms show different kinds of preservation. That described in some cephalopods (Fischer & Riou, 1982a and 1982b; Etter, 2002a) is surely the most spectacular: soft parts are preserved as pyritized three-dimensional relief. This is also the case for the aphroditoideans and the enteropneust described here. However, as already pointed out for the other fossil remains from La Voulte-sur-Rhône (Etter, 2002a; Fischer, 2003), some specimens are preserved as organic traces in a calcareous or marly-argillaceous matrix, fossilized through substitution by limonite, pyrite or calcite mixed with some argillaceous elements. According to Wilby *et al.* (1995 and 1996) and Wilby (2001), the La Voulte-sur-Rhône soft tissues preserved in the marly-argillaceous matrix and those preserved in early diagenetic concretions underwent a different kind of substitution. In the first case they are flattened on the rock slab and largely made up of apatite, while in the second they are three-dimensional reliefs in which calcite, quartz, gypsum and pyrite are associated in the diagenetic sequence that preserved the organism.

SYSTEMATIC PALEONTOLOGY

Phylum Annelida Lamarck, 1809
Class Polychaeta Grube, 1850
Order Capitellida Fauchald, 1977
Family uncertain
Genus *Iubarenicola* n. gen.

Diagnosis: as for the type species.

Etymology: from the Latin *iuba* (=crest) and from *Arenicola*, a living arenicoloidean genus.

Type species: *Iubarenicola fischeri* n. sp.

Iubarenicola fischeri n. sp.
Fig. 2, Pl. 1A-B

Diagnosis: elongate body comprised of several short metameres of variable length. Two medial, thin, parallel ridges on the dorsal surface delimit a shallow furrow from the first metamere behind the prostomium to the pygidium. Prostomium is small and subconical.

Etymology: dedicated to Jean-Claude Fischer, in recognition of his studies about the La Voulte-sur-Rhône fossils.

Geological age: Lower Callovian (Middle Jurassic).

Type locality: La Boissine, La Voulte-sur-Rhône.

Material: 2 specimens. L.P.M.-B.48343 (holotype, Fig. 2A) and L.P.M.-B.48353 (paratype, Fig. 2B).

Description: both the holotype and paratype are preserved as a three-dimensional pyritized relief. In the holotype, the body width gradually decreases from the prostomium to the pygidium. The paratype body is narrow both at the proximal and distal extremities and it shows a slight widening in the posterior half. Both the holotype and paratype are about 65 mm long and they appear coiled in the posterior part. The holotype is preserved as a dorsoventral compression and the dorsal surface is exposed. The ventral side of the body is flattened and the dorsal is convex: it is difficult to distinguish if this is a preservation artifact or a real feature. The paratype underwent twisting, so that the dorsal and ventral surfaces are evident for different body portions. The body shows a clear metamerical organization, but only in the holotype can all the metameres be counted: there are 65 metameres each about 1 mm long.

The medial ridges developed along the dorsal surface are particularly evident in the anterior part of the body, but they are well preserved in other sections also. It is impossible to establish if the axial furrow reflects a special internal morphology.

The cephalic extremity of the paratype is connected to a sub-circular and slightly flattened structure sensibly wider than the body: we interpret this structure as the globose everted pharynx typical of some Capitellida (Fauvel, 1927; Fauchald, 1977).

Chaetae (setae) are not preserved.

Remarks: the general body morphology together with the little sub-conical prostomium and the presence of a globose everted pharynx suggest to assign the examined specimens to the order Capitellida or to the order Orbinida Fauchald, 1977. The Orbinida can own a prostomium very similar to that of Capitellida, but their eversible pharynx appears as an axial sac or a ventrolateral pad. However, the examined samples lack other characters that would allow us to determine a more precise position within Capitellida.

Capitellida are known from the Triassic to Recent (Howell, 1962). *Archarenicola rhaetica* Horwood, 1912 from the Rhaetian (Lower Triassic) of England is characterized by a frilled prostomium. The genus *Arenicola* Lamarck, 1801 has been recorded from the Cretaceous on the basis of trace fossils (Martinell *et al.*, 2001).

Fig. 2 - *Iubarenicola fischeri* n. gen. n. sp., holotype (L.P.M.-B.48343, A, x 1.5) and paratype (L.P.M.-B.48353, B, x 1.5).

Order Phyllodocida Dales, 1962
Superfamily Aphroditoidea Malmgren, 1867
Family Aphroditidae Malmgren, 1867
Genus *Paleoaphrodite* Alessandrello & Teruzzi, 1986
Paleoaphrodite gallica n. sp.
Fig. 3, Pl. 1C

Diagnosis: small-sized and slightly elongate fusiform aphroditid. Biramous parapodia feature two series of overlapped, crossed and posteriorly oriented setal tufts of variable length and thickness. Each tuft is made up of two setal types.

Etymology: from the Latin *gallicus* (=belonging to the Roman province of Gaul), referring to the geographical origin.

Geological age: Lower Callovian (Middle Jurassic).

Type locality: La Boissine, La Voulte-sur-Rhône.

Material: 5 specimens. L.P.M.-B.48342 Aa (part and counterpart, holotype, Figs. 3A-3B), L.P.M.-B.48341 Aa-g (paratype, Fig. 3C), L.P.M.-B.48337 Ae, L.P.M.-B.48338 Ae (part and counterpart) and L.P.M.-B.48339 Aa-g (part and counterpart).

Description: all the examined specimens are complete and measure from 18 mm (L.P.M. B48337 Ae) to 34 mm (L.P.M. 48342 Aa) in length. The maximum width of the body is 5 mm, excluding chaetae, in all the specimens.

Chaetae are clumped in two series of tufts on each side of the body, clearly indicating biramous parapodia. The tufts of adjacent metameres overlap, as it is clearly evident in L.P.M. 48342 Aa and L.P.M.-B.48341 Aa-g. The maximum length of the chaetae grades from 5 mm to 2 mm. On each side of the body, chaetae form on average 20 pairs of tufts (24 in L.P.M.-B.48341 Aa-g, 18 in L.P.M.-B.48342 Aa) disposed in two overlapping series: the chaetae belonging to the upper series are pressed down on those of the lower series, so as it is impossible to distinguish between the notopodial and neuropodial ones. Each tuft comprises an undetermined number of very thin and subcylindrical chaetae, measuring less than 0.1 mm in thickness, associated with two or three stronger chaetae, maybe aciculae, measuring about 0.1 mm in thickness. The junction between setal tufts and body is only clearly evident in two tufts near the mid-length of L.P.M.-B.48341 Aa-g, because in the other specimens only the medial and distal parts of the chaetae are preserved. However, in these other specimens some attachment points are recognizable as little depressions (in parts) or protuberances (in counterparts) at the proximal extremity of the tufts.

The metamerical subdivision of the body is clearly recognizable in L.P.M.-B.48342 Aa, where 10 segments are preserved near the caudal extremity. Each metamere is 1 mm long and appears to carry two pairs of setal tufts. In the mid-part of the body of L.P.M.-B.48342 Aa, five metameres are distinguished by pronounced constrictions.

Remarks: the general body morphology allows the examined material to be assigned to the superfamily Aphroditoidea

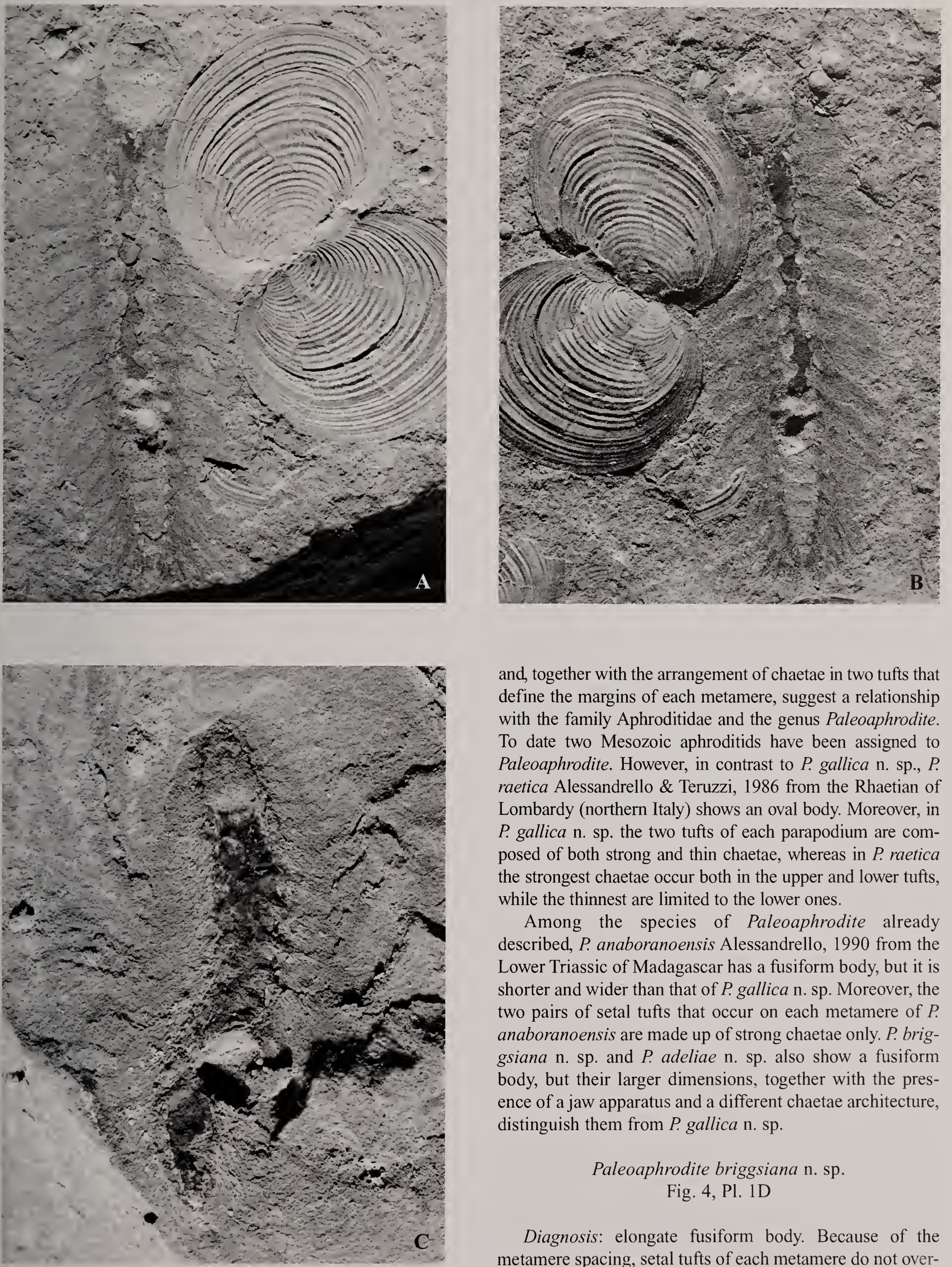

Fig. 3 - *Paleoaphrodite gallica* n. sp., holotype (L.P.M.-B.48342 Aa: A, part, x 4.4; B, counterpart, x 3) and paratype (L.P.M.-B.48341 Aa-g, C; x 2.8).

and, together with the arrangement of chaetae in two tufts that define the margins of each metamere, suggest a relationship with the family Aphroditidae and the genus *Paleoaphrodite*. To date two Mesozoic aphroditids have been assigned to *Paleoaphrodite*. However, in contrast to *P. gallica* n. sp., *P. raetica* Alessandrello & Teruzzi, 1986 from the Rhaetian of Lombardy (northern Italy) shows an oval body. Moreover, in *P. gallica* n. sp. the two tufts of each parapodium are composed of both strong and thin chaetae, whereas in *P. raetica* the strongest chaetae occur both in the upper and lower tufts, while the thinnest are limited to the lower ones.

Among the species of *Paleoaphrodite* already described, *P. anaboranoensis* Alessandrello, 1990 from the Lower Triassic of Madagascar has a fusiform body, but it is shorter and wider than that of *P. gallica* n. sp. Moreover, the two pairs of setal tufts that occur on each metamere of *P. anaboranoensis* are made up of strong chaetae only. *P. briggsiana* n. sp. and *P. adeliae* n. sp. also show a fusiform body, but their larger dimensions, together with the presence of a jaw apparatus and a different chaetae architecture, distinguish them from *P. gallica* n. sp.

Paleoaphrodite briggsiana n. sp.

Fig. 4, Pl. 1D

Diagnosis: elongate fusiform body. Because of the metamere spacing, setal tufts of each metamere do not overlap nor traverse adjacent ones. Each tuft comprises subcylindrical and flattened chaetae. Pharynx armoured with two pairs of jaws. Very large and semicircular prostomium.

Etymology: dedicated to Derek E.G. Briggs, in recognition of his taphonomic studies of the La Voulte-sur-Rhône fossils.

Geological age: Lower Callovian (Middle Jurassic).

Type locality: La Boissine, La Voulte-sur-Rhône.

Material: 1 specimen. L.P.M.-B.48336 (holotype).

Description: the specimen is preserved as a three-dimensional pyritized relief measuring 67 mm in length: only the dorsal side is evident. The maximum width excluding chaetae occurs near the mid-length: 18 mm.

The prostomium is very large and semicircular, measuring at least 10 mm in length and 25 mm in width.

Even if the poor presevation of L.P.M.-B.48336 does not allow a detailed description, at least 14-16 protuberances, that can be interpreted as the attachments of the upper series of setal tufts, are clearly evident on each side of the body. At the mid-length and in the posterior part of the body, the shape and position of the protuberances suggest a real metamerism, evidenced by the presence of 3 segments separated by thin furrows.

The chaetae preserved on each side of the body are organized in tufts, separated from those of the adjacent metameres by 2-3 mm gaps. Neither the original number nor the length of the chaetae can be determined, and the biramous structure of the parapopodia is obscured. However, each tuft appears to consist of two types of strong chaetae: some chaetae, maybe aciculae, show a cylindrical shape, a yellowish or whitish semitransparent colour and a width of 0.1 mm; other chaetae show the same width but are more flattened and darker in colour. It is impossible to establish whether both kinds of chaetae were present in the same tuft of each parapodium or not.

Near the anterior extremity of the body the elements that make up the jaw apparatus are raised slightly above the pyritized relief of the body as little black and shiny structures, but it is very difficult to distinguish their organization and shape; some elements may have been displaced from their former position. Elements here preserved are two scythe-shaped jaws, showing backward oriented tips and converging anteriorly toward a strong semicircular plate, and two smaller and thinner hook-shaped jaws. These last appear to be linked posteriorly, but probably they were formerly separated and arranged on opposite sides of the jaw. The semicircular plate is not in its original position: it does not lie in the same plane as the jaws, but is oriented perpendicular to the bedding plane. There is no evidence that the pharynx is everted, but fossilization of the jaws may be more likely when the pharynx is everted: this is because the La Voulte-sur-Rhône outcrop is characterized by rapid pyritization of the soft tissues after death (Wilby *et al.*, 1996), so that the presence of formerly mineralized tissues, such as polychaete jaws, may be concealed. The hypothesis that the L.P.M.-B.48336 pharynx is everted is supported by the observation that it is the only polychaete specimen from La Boissine in which the jaw apparatus is recognizable near its original position.

Remarks: the general body morphology allows the specimen to be assigned to the family Aphroditidae and to the genus *Paleoaphrodite*. However, the setal architecture, the metamere development and the presence of an armoured pharynx, allow *P. briggsiana* n. sp. to be distinguished from the previously described species in the genus. In addition to *P. briggsiana* n. sp., the other *Paleoaphrodite* species owning a fusiform body are *P. gallica* n. sp. and *P. adeliae* n. sp.. *P. adeliae* n. sp. is very similar in body shape, but it is very different in the development of the prostomium as well as in the jaw apparatus structure. The fusiform body of *P. gallica* n. sp. is sensibly more elongate and narrow if compared with that of *P. briggsiana* n. sp. and *P. adeliae* n. sp., in which is more evident a sensible tapering toward both the cephalic and caudal extremities. With regard to the setal organization *P. adeliae* n. sp. is very similar to *P. briggsiana* n. sp., because of the presence of both subcylindrical and flattened chaetae: however, in *P. briggsiana* n. sp. the setal tufts do not form a continuous coat around the body, but they appear separated by 2-3 mm gaps produced by the major spacing among metameres. Differently from both *P. briggsiana* n. sp. and *P. adeliae* n. sp., *P. gallica* n. sp. owns subcylindrical chaetae only.

Among the fossil aphroditids described to date, the presence of a pharyngeal armature including two pair of jaws has been observed only in the aphroditids of the subfamily Hystriciolinae Thompson, 1979, *Dryptoscolex matthiesae* Thompson, 1979 and *Fastuoscolex gemmatus* Thompson, 1979, both from the Carboniferous of Mazon Creek (Thompson, 1979): this is probably due both to the absence of jaws in some aphroditid species and to artifacts of preservation.

Fig. 4 - *Paleoaphrodite briggsiana* n. sp., holotype (L.P.M.-B.48336, x 0.8).

Paleoaphrodite adeliae n. sp.
Fig. 5, Pl. 1E

Diagnosis: large fusiform body. Two setal types forming a continuous coat around the body and increasing in length from prostomium to pygidium. Jaw apparatus present.

Etymology: dedicated to Adelia Bracchi, for her strong support in recent years.

Geological age: Lower Callovian (Middle Jurassic).

Type locality: La Boissine, La Voulte-sur-Rhône.

Material: 1 specimen. L.P.M.-B.48335 (holotype).

Description: excluding the setal coat, the body of the holotype measures 51 mm in length and 17 mm in width. It is preserved as a three-dimensional pyritized relief revealing the dorsal side of the worm. The subtriangular prostomium measures 4 mm in length and 8 mm in width.

Along each side of the body a single series of aligned protuberances is evident: they probably represent the attachment points of the upper series of setal tufts. At least 20 protuberances are evident along the left side of the body, at least 15 along the right side.

Two kinds of chaetae are present: some chaetae, maybe aciculae, are about 0.1 mm wide and they show a subcylindrical shape and a semitransparent yellowish or whitish colour, while others are slightly thinner, flattened and dark coloured. The chaetae have broken along their length when the slab was split, so it is impossible to determine their exact length or whether they are notopodial or neuropodial, although it is evident that their length increases from the cephalic to the caudal extremity. The poor quality of preservation obscures the biramous nature of the parapodia. The chaetae of the anterior part of the body are turned forward, whereas those of the posterior part are turned backward.

The protuberances clearly indicate the metamerical subdivision of the body. The metameres decrease in length from the mid part of the body (0.3 mm) toward both the anterior and posterior extremity. The first metameres are concave anteriorly, but they become convex toward the caudal extremity of the body. The furrows that separate the metameres are evident only in the last quarter of the body.

The body is covered by several thin, shallow and longitudinally developed furrows: they probably represent the imprint of the felt of capillary fibers that typically covers the dorsal surface of some aphroditids. These fibers are observed here for the first time in *Paleoaphrodite*: they are, however, considered poorly diagnostic because their presence or absence could be the result of differences in preservation.

Near the body center, a small, black, shiny, markedly mineralized and hook-shaped structure bearing a strong tooth near the anterior extremity of its convex side is clearly evident: it is one of the elements comprising the pharyngeal armature and it is slightly displaced from its original position.

Remarks: among described species of *Paleoaphrodite*, that most similar to *P. adeliae* n. sp. is *P. briggsiana* n. sp., particularly in general body morphology, shape and setal organization. Moreover, subcylindrical and semitransparent chaetae identical to those of *P. adeliae* n. sp. are also present in *P. briggsiana* n. sp.. However, the latter has also flattened chaetae. Other differences between these two species are the architecture of the jaws, the shape of the prostomium and the organization of the setal tufts: in *P. adeliae* n. sp. the tufts of adjacent metameres overlap, forming a continuous coat around the whole body, and the prostomium is subtriangular. In *P. briggsiana* n. sp. the tufts of adjacent metameres are clearly separated and the prostomium is larger and semicircular.

Fig. 5 - *Paleoaphrodite adeliae* n. sp., holotype (L.P.M.-B.48335, x 1.7).

Family uncertain

Genus *Protopholoe* n. gen.

Diagnosis: as for the type species.

Etymology: from the Greek πρώτος (=primitive) and from *Pholoe*, living genus.

Type species: *Protopholoe rhodanitis* n. sp.

Protopholoe rhodanitis n. sp.
Fig. 6, Pl. 1F

Diagnosis: dorsally convex, short and subquadrangular body with several metameres and a deep, straight, narrow and slightly concave furrow developed along the median body line. Slightly elongate and oval prostomium. Short and strong aciculae.

Etymology: from the Latin *rhodanitis* (=belonging to *Rhodanus*), referring to the Rhone Valley.

Geological age: Lower Callovian (Middle Jurassic).

Type locality: La Boissine, La Voulte-sur-Rhône.

Material: 1 specimen. L.P.M.-B.48340 (holotype).

Description: holotype preserved as a three-dimensional pyritized relief measuring 13 mm in length: only the dorsal side is evident. The body width varies from 2 mm at the cephalic and caudal extremities to 4 mm in the central part. Twenty metameres separated by shallow furrows are clearly evident. The first seven metameres are concave anteriorly, a condition becoming less pronounced from prostomium to pygidium. The eight longest metameres are those of the central body section: in some cases they are twice the length of those at the cephalic and caudal extremities.

Some posteriorly directed aciculae are preserved as mineralized structures along the left side of the body only, but their parapodial arrangement is not evident.

Remarks: the general body morphology supports an assignment of the specimen examined to the superfamily Aphroditoidea. In particular, the specimen shows strong similarities with the modern genus *Pholoe* Johnston, 1839, which is actually included in Sigalionidae Malmgren, 1867 (Glasby *et al.*, 2000), soft bottom scale-worms that often show a subquadrangular and flattened body (Fauchald, 1977; Fauchald & Rouse, 1997). Moreover, as in the fossil, the body of the living genus *Pholoe* is dorsally convex and shows a deep central furrow separating it into two symmetrical parts from the cephalic to the caudal extremity (Fauvel, 1923). However, because of the absence of soft parts in the fossil specimen, further comparisons are not possible and the systematic position of *P. rhodanitis* n. sp. within the aphroditoideans is uncertain.

Fig. 6 - *Protopholoe rhodanitis* n. gen. n. sp., holotype (L.P.M.-B.48340, x 4.5).

Phylum Sipuncula Stephen, 1935
Class Sipunculidea E.Cutler & Gibbs, 1994
Order and Family uncertain
Genus *Rondeletia* n. gen.

Diagnosis: as the type species.

Etymology: dedicated to Guillame Rondelet, who first described and illustrated sipunculan worms during the sixteenth century.

Type species: *Rondeletia scutata* n. sp.

Rondeletia scutata n. sp.
Fig. 7, Pl. 1G-H-I

Diagnosis: slightly elongate body divided in two distinct regions. A narrow region characterized by few longitudinal ridges is followed by a broader region characterized by several transverse ridges and equipped with a conical shield at its distal extremity. Body wall including some separated and not anostomosing longitudinal muscle bands.

Etymology: from the Latin *scutatus* (=equipped with a shield), referring to the presence of a conical shield covering the caudal extremity.

Geological age: Lower Callovian (Middle Jurassic).

Type locality: La Boissine, La Voulte-sur-Rhône.

Material: 6 specimens. L.P.M.-B.48355 and L.P.M.-B.48356 (holotype, part and counterpart, Figs. 7A-7B), L.P.M.-B.48344 (paratype, Fig. 7C), L.P.M.-B.48345, L.P.M.-B.48354 Aa, L.P.M.-B.48357 Aa and L.P.M.-B.48358 Aa.

Description: the holotype is preserved as a complete external mold, while the paratype is preserved as a three-dimensional pyritized relief, as are L.P.M.-B.48345, L.P.M.-B.48357 Aa and L.P.M.-B.48358 Aa, while L.P.M.-B.48354 Aa is preserved as imprint.

The body is completely preserved in L.P.M.-B.48354 Aa and in the holotype only, where it appears rather coiled up. In both these specimens two distinct regions are evident: in the holotype the narrower region is 30 mm long and characterized by the presence of four longitudinal and parallel ridges. This region decreases slightly in width from its posterior extremity (10 mm in holotype, 8 mm in L.P.M.-B.48354 Aa) toward the anterior extremity. We interpret this region as an everted introvert, the ridges as the longitudinal muscle bands of the body wall. In L.P.M.-B.48354 Aa the diagenetical compression of the early mineralized body resulted in a slight widening of the introvert, so that it appears, in contrast to the other specimens, wider than the rest of the body: it is about 30 mm long.

The introvert is normally followed by a slightly wider region, here interpreted as the trunk, that reaches a maximum width near its mid-length and shows a slight tapering toward both its extremities. In the holotype the trunk measures about 80 mm in length and 18 mm in maximum width, while in the paratype, which only preserves the trunk, the length is 60 mm and the maximum width 8 mm. For L.P.M.-B.48354 Aa the trunk length is 45 mm and the maximum width 10 mm. In L.P.M.-B.48357 Aa and L.P.M.-B.48358 only a fragment of the anterior part of the trunk is preserved, and in L.P.M.-B.48345 the trunk is completely preserved but it cannot be measured precisely, even if similar in dimension to that of the holotype, because it is completely coiled up. Particularly in the paratype, the trunk appears divided into several short but not equally developed segments, evidenced by transverse parallel ridges separated by shallow furrows. These ridges and furrows are probably

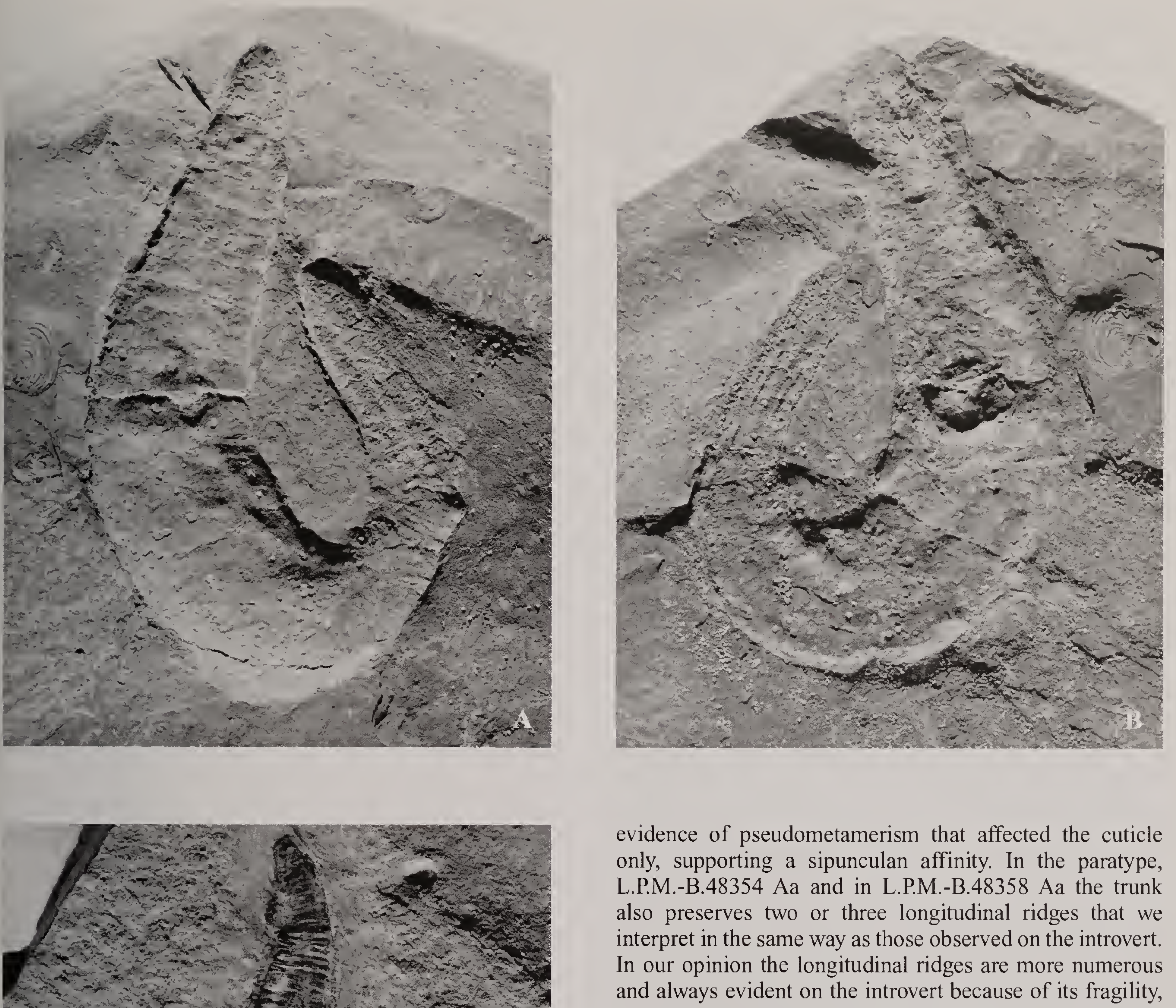

Fig. 7 - *Rondeletia scutata* n. gen. n. sp., holotype (L.P.M.-B.48355, A, part, x 1.6; L.P.M.-B.48356, B, counterpart, x 1.6) and paratype (L.P.M.-B.48344, C, x 1.8).

evidence of pseudometamerism that affected the cuticle only, supporting a sipunculan affinity. In the paratype, L.P.M.-B.48354 Aa and in L.P.M.-B.48358 Aa the trunk also preserves two or three longitudinal ridges that we interpret in the same way as those observed on the introvert. In our opinion the longitudinal ridges are more numerous and always evident on the introvert because of its fragility, which was surely more marked than that of the cuticle covering the trunk. In the examined specimens, apart from the cases described above, the longitudinal ridges are limited to the narrower portion of the body and abruptly terminated where the trunk widens: this allows the introvert-trunk boundary to be identified.

The cuticle covering the distal extremity of the trunk shows no evidence of segmentation, but seems to form a subconical shield carrying a thin ridge along its median line that is clearly evident in the holotype, paratype and L.P.M.-B.48354 Aa. The maximum dimensions of this shield are those in the holotype, where it measures 7 mm in length and 8 mm in maximum width, while in the paratype it is 4 mm long and 3 mm wide.

There are no traces of appendages.

Remarks: the two distinct regions (introvert and trunk) that comprise the body of the examined specimens, together with the presence of a caudal shield and of the longitudinal muscle bands, justify their assignment to the phylum Sipunculida. This phylum includes the classes Phascolosomatidea E.Cutler & Gibbs, 1995 and Sipunculidea, identified on the basis of several soft part features, usually not recognizable in fossils (Cutler, 1994), such as the arrangement of the tentacles surrounding the mouth at the tip of the introvert (Maxmen *et al.*, 2002). However, the assignment of *R. scutata* n. gen. n. sp. to Sipunculidea is reasonably secure because within Phascolosomatidea only the Aspidosiphonidae Baird, 1868 have a caudal shield but, in contrast to Sipunculidea, generally have an introvert protruding at an angle of 45-90° to the main axis of the trunk and the longitudinal muscle layers of the body wall are separated into anostomosing bands (Cutler, 1994).

Since the Cambrian *Ottoia prolifica*, Walcott 1911 and *Louisella pedunculata* Walcott, 1911 from the Burgess Shale (British Columbia, Canada) were definitively accepted as priapulid worms sharing a common ancestor with sipunculans (Conway Morris, 1977; Cutler, 1994), since *Banffia constricta* Walcott, 1991 from the same outcrop was revised as an arthropod of unknown affinities (Caron, 2001) and since *Schizoproboscina ivanovi* Yakovlev, 1939 from the Carboniferous of Russia and *Stoma hians* Hadding, 1913 from the Ordovician of Sweden were moved to an uncertain order within polychaetes (Sepkoski, 2002), only the Silurian *Lecthaylus gregarius* Weller, 1925 from Blue Island (Illinois) and the Jurassic *Epitrachys* Ehlers, 1869 from the Solnhofen *Plattenkalk* actually preserve evidences supporting a sipunculan affinity (Ehlers, 1869 Weller, 1925; Roy & Croneis, 1931). In comparison with *R. scutata* n. gen. n. sp., *Epitrachys rugosus* Ehlers, 1869, *Epitrachys granulatus* Ehlers, 1869 and *Lecthaylus gregarius* lack the caudal shield but they show a regularly segmented cuticle. Moreover, *Epitrachys* has a granulose cuticle (Ehlers, 1869), not smooth like that of *Rondeletia* n. gen., *Lecthaylus* Weller, 1925 has a smooth cuticle but the relative dimensions of introvert and trunk are very different if compared with those of *Rondeletia* n. gen. (Weller, 1925; Roy & Croneis, 1931). According to Cutler (1994), the remaining sipunculan fossil record includes some ichnogenera from Cambrian to Miocene, such as *Trypanites* Mägdefrau, 1982, *Zoophycos* Massalongo, 1855, *Trichichnus* Frey, 1970 and *Ancorichnus* Heinberg, 1974. Moreover, solitary corals with sipunculan symbionts are known from the Cretaceous of Texas and Tennessee and from the Miocene of Florida (Cutler, 1994), even if Stolarski *et al.* (2001) reported the exsistence of this symbiosis in older outcrops also. Brett & Cottrell (1982) reported the presence, in the Devonian *Pleurodictyum* Goldfuss, 1829 tabulate coral, of overgrown gastropod shells occupied by a secondary resident, probably a sipunculan. Finally, Häntzschel (1975) treated as sipunculan the borings found in some *Cypricardia* Lamarck, 1819 valves from the Pliocene of Italy and described under the ichnogenus *Sabella* Linnè, 1767.

Phylum Hemichordata Bateson, 1885
Class Enteropneusta Gegenbaur, 1870
Family uncertain
Genus *Megaderaion* Arduini, Pinna & Teruzzi, 1981
Megaderaion callovianum n. sp.
Fig. 8, Pl. 1L

Diagnosis: elongate wormlike body clearly divided into three regions: elongate, rounded and ogival proboscis (prosome), short and thick subrectangular collar (mesosome) and vermiform tapering trunk (metasome). Trunk covered by a segmented cuticle.

Etymology: referring to the geological age of the La Voulte-sur-Rhône outcrop.

Geological age: Lower Callovian (Middle Jurassic).

Type locality: La Boissine, La Voulte-sur-Rhône.

Material: 1 specimen. L.P.M.-B. 48352 (holotype).

Description: the examined specimen is mostly preserved as a three-dimensional pyritized relief. The total body length is about 51 mm and the maximum width is 5 mm (in the mesosome). The ogival proboscis is 8 mm long and 2.5 mm wide at the proximal extremity, grading to 4.5 mm toward the base, where it is preserved in more relief. The proboscis and the collar are separated by a deep and 0.1 mm wide furrow. On the left side of the furrow a 0.1 mm long and 1.5 mm wide peduncle connecting the proboscis to the collar is evident: it probably underwent displacement from its original position in the middle of the furrow.

At the proximal extremity the subrectangular and 4 mm long collar is wider (5 mm) than the proboscis, undergoing a slight narrowing distally (4 mm). The lateral and posterior margins of the collar are convex, while the anterior is concave so that it appears slightly folded around the base of the proboscis.

The maximum width of the trunk is at the collar-trunk boundary, where it measures 5 mm, grading to 1 mm distally. The trunk appears divided into two distinct regions separated by a slight narrowing: a subcylindrical and 20 mm long region immediately behind the collar, that decreases in width toward the posterior extremity (5-2.5 mm), and an elongate (17 mm), more flattened and narrower posterior region (1.5-1 mm). The anterior section of the trunk is preserved as an imprint in its posterior half and, as in living enteropneusts, presumably consisted of the branchio-genital, oesophageal and hepatic regions. The boundaries of these regions cannot be distinguished

Fig. 8 - *Megaderaion callovianum* n. sp., holotype (L.P.M.-B. 48352, x 4).

in the fossil. The posterior section may represent the intestinal region. This last appears clearly divided into several thin metameres. The trunk metameres are gradually less evident toward the collar, behind which they are evident only on the right side of the body: this suggests that a segmented cuticle covered the trunk.

Remarks: the three distinct regions (proboscis, collar and trunk) that comprise the body of the specimen justify its assignment to the class Enteropneusta within the phylum Hemichordata, which also includes the Planctosphaeroidea Spengel, 1932 and Pterobranchia Lankester, 1877. Both the Planctosphaeroidea and Pterobranchia have recently been suggested to be included in the Enteropneusta (Harrison & Ruppert, 1997; Cameron *et al.*, 2000). The Enteropneusta are generally subdivided into three families, Spengeliidae Willey, 1899, Ptychoderidae Spengel, 1893 and Harrimannidae Spengel, 1901, on the basis of the stomochord architecture and other anatomical characters, such as liver sacs and nerve roots, structures that have a very low preservation potential (Cameron, 2002). Only two fossil enteropneusts have been described previously: *M. sinemuriense* Arduini, Pinna & Teruzzi, 1981 from the Sinemurian (Upper Jurassic) of Osteno (Lombardy, Italy) and *Mazoglossus ramsdellii* Bardack, 1997 from the Carboniferous of Mazon Creek, Illinois. This poor fossil record is probably due to the very fragile nature of the enteropneust body (Cameron, 2002). The enteropneust fossil record includes some Paleozoic traces referred to the ichnogenus *Nereites* MacLeay in Murchinson, 1839 (Mangano *et al.*, 2000). A Paleozoic enteropneust has been discovered in the Middle Cambrian Burgess Shale (Boulter, 2003), but it is still undescribed.

The assignment of the examined material to the genus *Megaderaion* is supported by the shape and relative dimensions of the prosome, mesosome and metasome. These are very different from those of *Mazoglossus* Bardack, 1997, which has a wider, less elongate proboscis together with a differently shaped collar (Bardack, 1997). A prosome twice as long as the mesosome, together with a rather elongate proboscis, are very similar in their morphology to those of the living *Harrimania planktophilus* Cameron, 2002, supporting the hypothesis (Arduini *et al.*, 1981) that *Megaderaion* is related to the Harrimanidae, the family including the most primitive species of living enteropneusts. The assignment of the *Megaderaion* specimen from La Voulte-sur-Rhône to a different species is justified mainly on the different shape of the collar. Morover, in contrast to that in *M. sinemuriense*, the anterior extremity of the proboscis of *M. callovianum* n. sp. appears not angular but rounded, with a short peduncle at the base.

UNRELATED SPECIMENS

The specimens L.P.M.-B.48346, L.P.M.-B. 48348, L.P.M.-B.48349, L.P.M.-B.48350 (part and counterpart) and L.P.M.-B.48351 represent undetermined *taxa* within the class Polychaeta. Only for L.P.M.-B. 48348 and L.P.M.-B.48351 can an assignment within the order Capitellida be suggested. They are similar to *Iubarenicola fischeri* n. gen. n. sp. in the general body morphology and preservation, since they too have a subconical prostomium and the body is preserved coiled posteriorly, but it is impossible to prove a capitellid affinity. L.P.M.-B. 48348 measures about 20 mm in length and 3 mm in maximum width in the central body section. L.P.M.-B.48351 is about 80 mm long and 4 mm wide along its length.

Noteworthy also is the fact that L.P.M.-B.48346, a 150 mm long and 5 mm wide polychaete largely preserved as an imprint, seems to be preserved with its pharynx everted. The pharynx imprint is about 11 mm long and 7 mm wide. The general body morphology of this specimen, bearing an undetermined number of very elongate chaetae (up to 15 mm) on each metamere, is reminiscent of the eunicemorph polychaetes but as the stomodaeal armature is not preserved, it is impossible to confirm its affinity.

L.P.M.-B.48347 (Fig. 9) remains undetermined, but it does not show any polychaete character. It lacks both the caudal and cephalic extremity and it does not show metamerism or chaetae. The preserved body fragment measures about 70 mm in length and 3 mm in width. The major features of this worm are the dorso-ventrally flattened body with an elliptical section and the presence of four thin longitudinal ridges developed along the preserved body length: these characters are consistent with any group within the phylum Nemertea. In particular the thin ridges may represent the longitudinal muscle bundles that are localized under the epithelium in the nemertines.

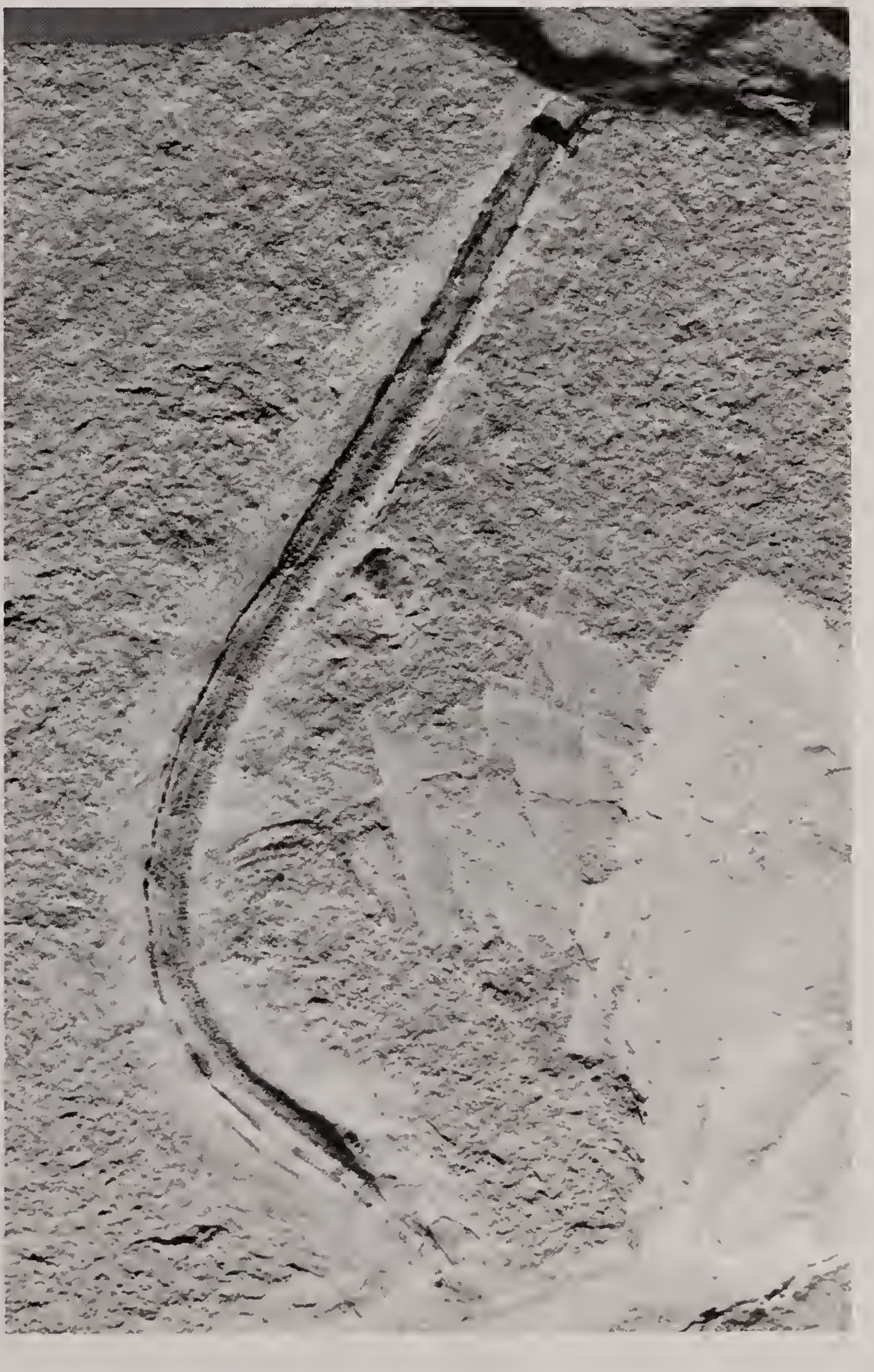
Fig. 9 - L.P.M.-B.48347, undetermined worm (x 1.6).

DISCUSSION AND CONCLUSIONS

The examined material includes 10 polychaetes (2 arenicoloideans and 8 aphroditoideans), 6 sipunculans and 1 enteropneust. Six specimens still remain undetermined: they may be related to polychaetes apart from one specimen which may be a nemertean.

The La Voulte-sur-Rhône biota is noteworthy for the early diagenetic mineralization that results in calcite replacement, phosphatization or pyritization (Wilby & Briggs, 1997; Wilby *et al.*, 1995 and 1996; Wilby, 2001) and thus mostly preventing the collapse or compaction of organic walls (Grimes *et al.*, 2001). Two interpretations of the La Voulte-sur-Rhône paleoenviroment (Dietl & Mundlos, 1972; Fischer & Riou, 1982a; Fischer, 2003) have been offered: the first is a Sargasso sea model where the benthic fauna inhabited carpets of floating algae, while the second involves a hypersaline lagoon. The soft tissues of some of the specimens described here, such as the *Iubarenicola fischeri* n. gen. n. sp. holotype and the *Rondeletia scutata* n. gen. n. sp. paratype, are preserved as pyrite coats in which the internal structures are not evident. These alone allow some considerations of the La Voulte-sur-Rhône paleoenviroment. According to Allison (1990) and Canfield & Raiswell (1991), these mineral coats formed through the pyritization by anaerobic sulphate-reducing bacteria that pseudomorph the soft parts: this process especially occurs in shallow and well-lit enviroments, such as estuaries and delta, even if it is not confined to such settings (Briggs *et al.*, 1996; Grimes *et al.*, 2002). An enviroment located in shallow water has been postulated also for the Devonian Hunsrück Slate, another outcrop known for the widespread three-dimensional pyritization, even if the debate about its origin is still in progress (Etter, 2002b). Moreover, the presence of enteropneusts and sipunculans, the body of which is typically very fragile, the profusion of articulated *Bositra buchi* valves, the presence of well-preserved echinoderms, particularly the ophiuroid *Ophiopinna elegans*, and the lack of evidence of current activity, such as ripple marks, clearly suggest a below storm wave base or a stagnant enviroment (Etter, 2002a; Fischer, 2003), such as a restricted lagoon. The abundance of invertebrates with articulated hard parts, such as ophiuroids (Dietl & Mundlos, 1972) and crustaceans (Secretan & Riou, 1986; Carriol & Riou, 1991), also indicates that the preserved organisms of La Voulte-sur-Rhône probably underwent rapid burial after death, even if this is not a prerequisite for soft tissue pyritization. This kind of fossilization seems to occur in poorly oxygenated (dysaerobic) bottom waters rather than in euxinic enviroments, because in dysaerobic waters the pore fluids circulating in the sediments contain elevated levels of dissolved iron allowing soft part pyritization (Allison, 1990; Allison & Briggs, 1991; Canfield & Raiswell, 1991; Grimes *et al.*, 2002; Briggs, 2003). According to Dietl & Mundlos (1972), the rapid burial of the La Voulte-sur-Rhône fauna was probably the result of mudflows, as evidenced by thin individual layers covering the bedding levels of articulated invertebrates. Moreover, the rapid burial inhibits oxygen diffusion, thereby promoting soft tissue preservation, even if, as previously emphasized, this does not guarantee fossilization. The presence of pelagic and nekto-benthic species at La Voulte-sur-Rhône supports the existence of a poorly-oxygenated enviroment, but the great abundance of benthic *taxa* indicates that the sea bottom was never anoxic for long. According to Etter (2002a), such paleoecological features reflect periodic sediment settling that resulted in periodic oxygen depletion.

Finally, the great spread of both epibenthic (such as the aphroditoideans and reptantian decapods) and endobenthic (such as enteropneusts, sipunculans and arenicoloideans) *taxa*, the presence of several nekto-benthic elements (such as rhynchonellid brachiopods, pycnogonids, ophiuroids, mysidacean, penaeid and cumacean crustaceans), the occurence of relatively few open-water organisms (like actinopterygians, sharks and cephalopods) and the absence of algae remains, is not consistent, in the opinion of the authors, with a Sargasso Sea model (Dietl & Mundlos, 1972; Fischer & Riou, 1982a; Fischer, 2003) for the La Voulte-sur-Rhône outcrop.

It is impossible to establish with reasonable certainty whether La Voulte-sur-Rhône was a deep or a shallow basin. The absence of storm layers seems to indicate that the sediments settled below storm wave base, while the high lateral variability of the Lower Callovian sequence suggests that there was significant relief on the sea bed (Elmi, 1967; Etter, 2002a). However, in the opinion of the authors, this Jurassic *Lagerstätte* can be interpreted as a coastal lagoon, also because of the presence of some continental elements, such as a crocodilian skull, spores and leaves (Fischer, 2003), the great abundance of *Bositra buchi*, which is no longer interpreted as a pseudoplanktonic bivalve (Etter & Tang, 2002), the presence of pyritization, which can imply shallow water, and the presence of terrigenous clastics that were deposited in the epicontinental sea of the La Voulte area following erosion from the eastern margin of the Massif Central (Etter, 2002a).

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The opinions expressed in the paper remain our own.

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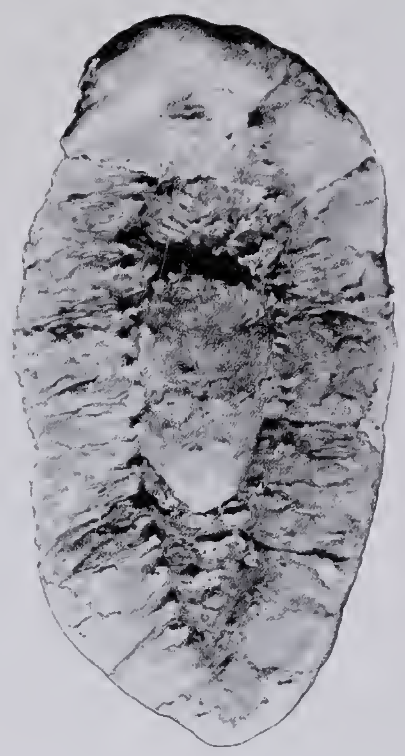

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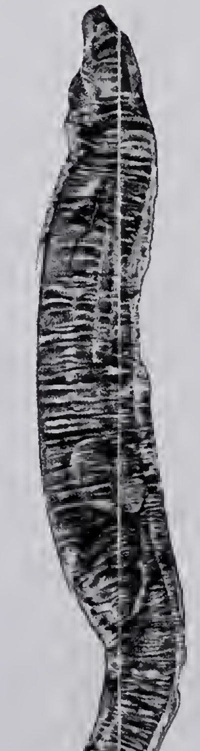

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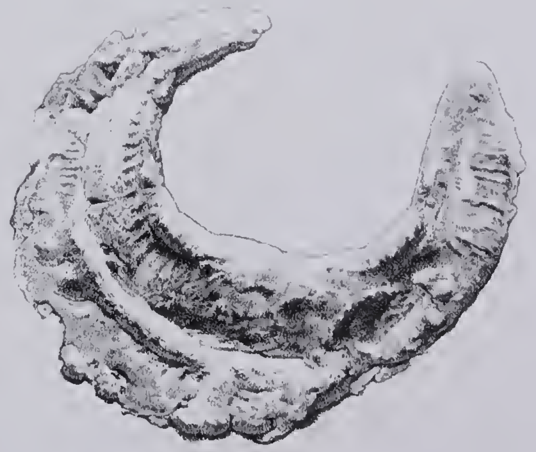

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Volume XXXII – Fascicolo II

OLIVER RIEPPEL & JASON J. HEAD

NEW SPECIMENS OF THE FOSSIL SNAKE GENUS *EUPODOPHIS* RAGE & ESCUILLIÉ, FROM CENOMANIAN (LATE CRETACEOUS) OF LEBANON

MILANO DICEMBRE 2004

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In copertina: *Eupodophis descouensi*. Fotografia di Luciano Spezia.

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Olivier Rieppel & Jason J. Head

New specimens of the fossil snake genus *Eupodophis* Rage & Escuillié, from Cenomanian (Late Cretaceous) of Lebanon

Abstract - Three new specimens of the mid-Cretaceous marine snake, *Eupodophis descouensi* Rage & Escuillié, from Lebanon are described in detail, and the phylogenetic affinities of this taxon are discussed. Two of the three specimens represent nearly complete, articulated skeletons of immature individuals. *Eupodophis* shares the presence of well-developed hind limbs with *Pachyrhachis* and *Haasiophis*, both marine mid-Cretaceous snakes from the Middle East. *Eupodophis* is unique amongst the Cenomanian snakes with well-developed hind limbs in having distally fused, but proximally bifurcating chevrons in its relatively very short tail. The type of articulation of these chevrons with the vertebral centra is autapomorphic for *Eupodophis*, and cannot be compared to varanoid or any other non-ophidian squamate ('lizard') condition. The skull of *Eupodophis* most closely resembles that of *Pachyrhachis*, whereas its vertebral morphology most closely approaches that of *Simoliophis* and *Mesophis*. The *status* of these mid-Cretaceous basal macrostomatans, and their interrelationships are discussed.

Key-words - Reptilia, Lepidosauria, Serpentes, fossil snakes, Cretaceous, Cenomanian, phylogeny.

Riassunto - Nuovi esemplari del serpente fossile *Eupodophis* Rage & Escuillié (Cenomaniano, Cretacico superiore, Libano).

Vengono descritti in dettaglio tre nuovi esemplari del serpente marino *Eupodophis descouensi* Rage & Escuillié provenienti dal Libano e vengono discusse le affinità filogenetiche del taxon. Due dei tre esemplari sono scheletri articolati quasi completi appartenenti a individui immaturi. *Eupodophis* condivide con *Pachyrhachis* e *Haasiophis*, serpenti marini del Cretacico superiore del Medio Oriente, la presenza di arti posteriori ben sviluppati. Caso unico tra i serpenti cenomaniani con arti posteriori ben sviluppati, nella breve coda *Eupodophis* possiede chevrons fusi distalmente, ma biforcati in prossimità dei corpi vertebrali. La modalità di articolazione di tali chevrons con i centra vertebrali rappresenta un'autapomorfia di *Eupodophis*, e non può essere comparata alla condizione che si osserva nei varanoidi o in qualsiasi altro squamato non-ofidiano ("lucertole"). Il cranio di *Eupodophis* è molto simile a quello di *Pachyrachis*, mentre le vertebre sono morfologicamente molto simili a quelle di *Simoliophis* e *Mesophis*. Vengono infine discussi lo *status* di questi macrostomati basali del Cretacico superiore, nonché le loro relazioni filogenetiche.

Parole chiave - Reptilia, Lepidosauria, Serpentes, serpenti fossili, Cretacico, Cenomaniano, filogenesi.

INTRODUCTION

The origin of snakes is a longstanding problem in herpetology (Bellairs & Underwood, 1951; Rieppel, 1988), a problem that has recently taken center stage again in the form of an intensive debate about the bearing of mid-Cretaceous snakes with well-developed hind limbs on snake origins (for a detailed review of this debate see Rieppel *et al.*, 2003). The genera relevant to this debate are: (i) *Pachyrhachis* Haas (1979; see also Haas, 1980a, b) from the Cenomanian of 'Ein Yabrud (Westbank, Middle East), re-described as the most basal snake and as sister-group to all other, extant, snakes by Caldwell and Lee (1997; see also Lee & Caldwell, 1998, Caldwell, 2000; Zaher, 1998; Zaher & Rieppel, 2002); (ii) *Eupodophis* Rage & Escuillié (2000; see also Rage & Escuillié, 2001, 2003), from the Cenomanian of Al Namoura (Lebanon), described as a basal snake with a skull anatomy that is convergent on macrostomatans; and (iii) *Haasiophis* Tchernov *et al.* (2000; see also Rieppel *et al.*, 2003) from the Cenomanian of 'Ein Yabrud (Westbank, Middle East), described as a basal macrostomatan with well-developed hind limbs. All these snake taxa combine the presence of well-developed hind limbs with a macrostomatan skull structure (Coates & Ruta, 2000; Greene & Cundall, 2000), a combination of characters that is difficult to reconcile with the current understanding of snake phylogeny as based on morphology (Fig. 1). Among extant snakes, the highly autapomorphic scolecophidians (blind snakes and thread snakes) are considered to be the sister-group of Alethinophidia; within Alethinophidia, the (probably paraphyletic) 'anilioids' (pipe snakes and shield tails) are the (possibly successive) sister-group(s) of Macrostomata (Cundall *et al.*, 1993; Cundall & Greene, 2000). *Loxocemus*, *Xenopeltis*, and the 'booids' (boas, pythons, and their relatives) constitute basal macrostomatans, whereas colubroids (colubrid snakes, cobras, sea snakes, and vipers) represent derived macrostomatan clades. Most scolecophidians, 'anilioids,' and basal macrostomatans retain either some pelvic girdle rudiments and/or hind limb rudiments (Kley *et al.*, 2002), but these elements are not nearly as well-developed as they are in the three fossil snake genera listed above. By contrast, these fossil snakes show a skull structure resem-

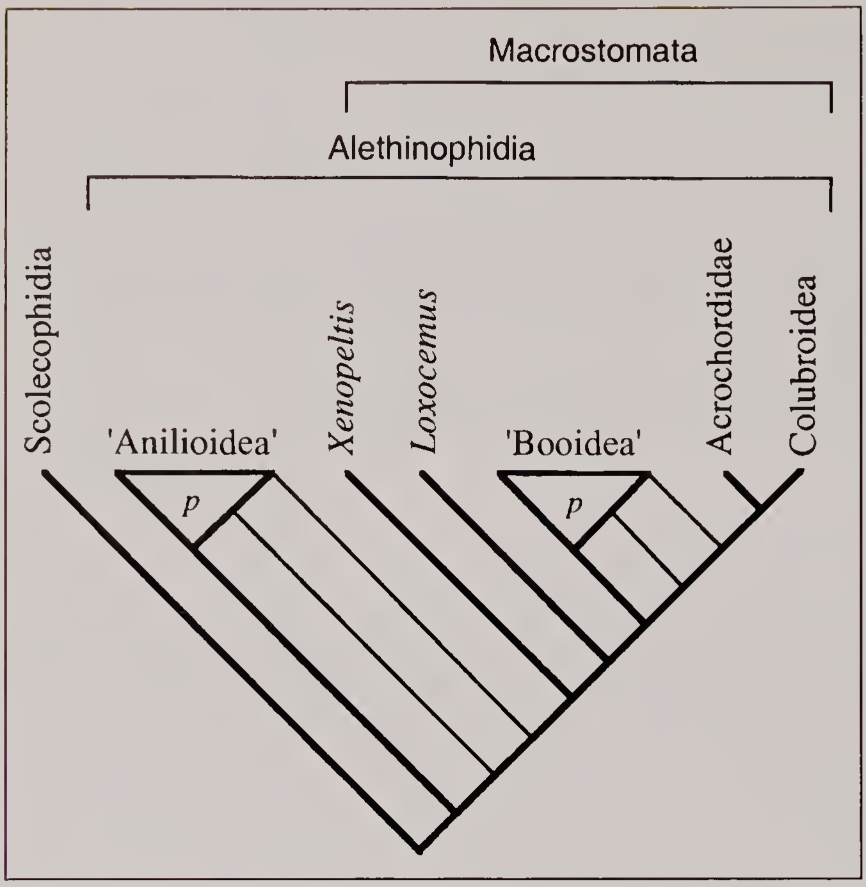


Fig. 1 - The phylogenetic interrelationships of extant snakes based on morphology. Anilioidea and 'Booidea' are putatively paraphyletic groups. Cundall & Greene (2000) exclude *Xenopeltis* and *Loxocemus* from Macrostomata.

bling that of macrostomatan snakes, allowing for a greater degree of jaw kinesis than is characteristic of 'anilioids' (Cundall, 1995; jaw kinesis in scolecophidians is highly autapomorphic: Kley, 2001; Kley & Brainerd, 1999). The enigma created by this character combination was aptly summarized by Rage & Escuillié (2000: 515): "If bipedal snakes are really basal Ophidia, then the distribution of the macrostomatan structure of the skull within Ophidia is problematic." Note that Ophidia was used by Rage & Escuillié (2000) in the sense of Lee & Caldwell (1998), who grouped the bipedal fossil snakes as sister-taxa of extant snakes, referring to the whole assemblage as Ophidia, and to the extant snakes – nested within Ophidia – as Serpentes. Given the morphology based topology of snake phylogeny for extant taxa (Greene & Cundall, 2000; see also Scanlon & Lee, 2000; Lee & Scanlon, 2002), the skull anatomy of the fossil snakes with well-developed hind limbs optimizes unequivocally as convergent upon the skull anatomy of basal macrostomatans if these fossil snakes are positioned basal to all extant snakes.

The description of *Eupodophis* by Rage & Escuillié (2000) introduced two characters that had not previously been discussed in arguments on the phylogenetic relationships of the fossil snakes with well-developed hind limbs, viz. medial frontal pillars, and articulated chevrons. All alethinophidian snakes are characterized by medial downgrowths of the frontals, separating the two olfactory tracts from one another at the anterior end of these elements (e.g., Rieppel, 1988). Similar medial frontal flanges are absent in scolecophidians, and they were (tentatively) claimed to be absent in *Eupodophis* by Rage & Escuillié (2000). The absence of such medial frontal flanges would lend important support to a basal position of that taxon relative to alethinophidians. A basal position of *Eupodophis* relative to all extant snakes was furthermore claimed by Rage & Escuillié (2000) to be supported by the presence of distally fused, but proximally bifurcated chevrons that articulate (i.e., are not fused) with the caudal vertebrae. Such lizard-like articulated chevrons were also claimed to be present in the snake genus *Wonambi* from the Pleistocene of South Australia by Scanlon & Lee (2000), who referred that taxon to the Madtsoiidae, a putative family of fossil snakes that they considered basal to all extant snakes. A review of the skeletal anatomy of *Wonambi* by Rieppel *et al.* (2002) confirmed the "booid" status of the latter genus (Barrie, 1990), and the coding of distally fused yet proximally articulating chevrons for both *Wonambi* and *Eupodophis* in a new phylogenetic analysis did not cause these two snake genera to group outside basal extant snakes (Rieppel *et al.*, 2002). Instead, they grouped with *Pachyrhachis* and *Haasiophis* as basal macrostomatans again.

In this paper we describe the skeletal anatomy of three additional specimens of *Eupodophis* from the middle Cenomanian of Lebanon, kept at the Museo Civico di Storia Naturale di Milano, and discuss their phylogenetic significance.

ABBREVIATIONS USED IN THE FIGURES

ang	angular
avt.p	anteroventral process
bo	basioccipital
bs	basisphenoid
c	coronoid
chv	chevron
cn	vertebral centrum
com	compound bone (of lower jaw)
d	dentary
ec	ectopterygoid
eo	exoccipital
f	frontal
f.c	facet on compound bone for coronoid
fe	femur
fi	fibula
fp.prf	foot process of prefrontal
hy	hypapophysis
il	ilium
is	ischium
izr	interzygapophyseal ridge
lf.f	lateral frontal flange
ls	laterosphenoid
m	maxilla
Mc	Meckel's canal

mf.f	medial frontal flange
mp.m	medial (palatine) process of maxilla
mp.pl	medial (choanal) process of palatine
n	nasal
nc	neural canal
ns	neural spine
p	parietal
pcl	pedicel for chevron articulation
pev.f	pelvic fragments
pl	palatine
pm	premaxilla
pmf	posterior mylohyoid foramen
po	postorbital
poz	postzygapophysis
prf	prefrontal
pro	prootic
prz	prezygapophysis
pt	pterygoid
q	quadrate
rb	rib
r.prl	recess for paralymphatic system
sc.f	subcentral foramen
sm	septomaxilla
so	supraoccipital
sp	splenial
st	supratemporal
stp	stapes
syn	synapophysis
ti	tibia
zyg	zygantrum
zys	zygosphene
v	vomer
v19	19th precloacal vertebra
v22	22nd precloacal vertebra
v37	37th precloacal vertebra (as preserved)
v40	40th precloacal vertebra (as preserved)
v76	76th precloacal vertebra (as preserved)
v78	78th precloacal vertebra (as preserved)
v115	115th precloacal vertebra
v117	117th precloacal vertebra
v141	141st precloacal vertebra
v143	143rd precloacal vertebra
v146	146th precloacal vertebra
v150	150th precloacal vertebra
v151	151st precloacal vertebra
v155	155th precloacal vertebra

MATERIAL

MSNM V 3660: a series of anterior, middle, and posterior precloacal vertebrae, measuring 590 mm in length (620 mm in Dal Sasso & Renesto, 1999; three measurements of the specimen yielded values between 587 mm and 591 mm as measured from the anterior end of the first preserved vertebra to the posterior end of the posterior precloacal vertebral column as it re-emerges from the mid-precloacal vertebral column for the second time). Middle Cenomanian, Haqel outcrop, Lebanon.

MSNM V 3661: a nearly complete, articulated specimen measuring 330 mm in length (300 mm in Dal Sasso & Renesto, 1999). Middle Cenomanian, Namoura outcrop, Lebanon.

MSNM V 4014: a nearly complete, articulated specimen measuring 388 mm in length. Middle Cenomanian, Namoura outcrop, Lebanon.

THE GEOLOGICAL PROVENIENCE OF *EUPODOPHIS*

The specimen of *Eupodophis* described by Rage & Escuillié (2000, 2003) came from the quarries near the village of Al Namoura (also written as 'en Nammoûra', or 'Nammoura') located in the mountains on the south side of the valley of Nahr Ibrahim, northern Lebanon (Forey *et al.*, 2003: 230). The same locality yielded two of the specimens described here (MSNM V 3661, MSNM V 4014). The third specimen described here comes from the famous outcrop near Haqel (also written as 'Hakel') in Ouadi Haqel in northern Lebanon (Hückel, 1970; Hemleben, 1977). The geological and depositional characteristics of these *Lagerstätten* were last commented upon by Dalla Vecchia *et al.* (2002), and Forey *et al.* (2003). Both localities produced fossil land plants, various invertebrates (including an indisputably marine echinoid from Namoura: Forey *et al.*, 2003: 231), fishes, *Eupodophis*, and – in the case of Namoura – a dolichosaur and a theropod dinosaur (Dalla Vecchia *et al.*, 2002). Fossil fishes, including those that document mass mortality events, are more common at the Haqel than at the Namoura locality. According to Hückel (1970), the *Plattenkalke* of Haqel were deposited in small basins (with diameters of up to 250 meters) that formed at the outer margin of the continental shelf. In contrast, the exposure of the *Plattenkalk* deposits is much more extensive at Namoura, there is no evidence of mass mortality events at that locality. The more abundant remains of land plants suggest that Namoura was closer to nearby land than Haqel (Forey *et al.*, 2003: 231), although this was probably "manifest as emergent islands since the main continental coastline was several hundred kilometers to the south" (Forey *et al.*, 2003: 232; approximately 400 kilometers in the case of the Haqel locality according to Hückel, 1970). Forey *et al.* (2003: 232) reconstructed the paleoenvironment at Namoura as "a shallow marine, gently sloping platform abutting islands in the Tethys". Hückel (1970) determined the age of the fossiliferous Haqel deposits as later Lower Cenomanian, while Forey *et al.* (2003: 232), based on Dalla Vecchia *et al.* (2002), conservatively dated the fossiliferous deposits at Namoura as the middle portion of the Middle Cenomanian, mid-Createaceous (Late Cretaceous).

Fig. 2 - Specimen MSNM V 3660 (approx. x 1.18). Photo: Luciano Spezia.

DESCRIPTION OF THE MATERIAL

Specimen MSNM V 3660
(Figs. 2 - 4)

The specimen consists of a series of more than 111 vertebrae (of which the last six are partially concealed) that is approximately 590 mm long (Fig. 2). In its size, this specimen matches the specimen described by Rage & Escuillié (2000). The specimen comprises anterior, and mid- to posterior precloacal vertebrae. Elongated ribs are associated with the posteriormost preserved vertebrae, indicating that these still belong to the precloacal series. There are no preserved elements of the skull, of the cloacal, or of the caudal region, nor are there preserved elements of the pelvis or hind limb. In part, the vertebrae and ribs split in two when the part and counterpart slabs were separated, rendering preservation rather poor. Those vertebrae that were not split are exposed in either lateral (anteriorly) or ventral view.

The first 13 (preserved) precloacal vertebrae are characterized by an elongated, slender, blade-like (i.e., laterally compressed) and posterodorsally slanting neural spine that rises from the posterior part of the neural arch (Fig. 3A). This neural spine caused the vertebrae to tilt during deposition on the sediment surface, such that the vertebrae are preserved in right lateral view. Their morphology matches closely the anterior precloacal ('cervical') vertebrae of *Pachyophis*, which also tilted during the embedding process because of the presence of a tall, slender and blade-like neural spine and hence are exposed in lateral view in the prepared fossil (Nopcsa, 1923a). The morphology of these vertebrae also closely resembles that of the "posterior precloacal vertebra" of *Simoliophis libycus* described and figured by Nessov *et al.* (1998). These latter vertebrae closely match the morphology of the anterior precloacal vertebrae as seen in the articulated specimens of *Pachyophis* (Nopcsa, 1923a) and *Pachyrhachis* (Lee & Caldwell, 1998), which confirms their nature as anterior, rather than posterior, precloacal vertebrae. A similar neural spine, thin and slender at its broken base, was inferred to have been present in *Simoliophis* (*S. rochebrunei* sensu Rage, 1984) by Nopcsa (1925).

The anterior precloacal vertebrae rapidly increase in size posteriorly, as was also recognized to be the case in *Pachyophis* (Nopcsa, 1923a), *Mesophis* (Bolkay, 1925), *Simoliophis* (Nopcsa, 1925), and *Pachyrhachis* (Lee & Caldwell, 1998). The centrum length of the well-preserved eighth element in the series is 3.3 mm. The ventral margin of the centrum of these anterior precloacal vertebrae is concave in lateral view. Towards its anterior end, the centrum carries a weakly developed and confluent dia-parapophysis (synapophysis), which only weakly protrudes from the centrum, and which faces in a lateroventral direction.

As is also the case in *Simoliophis* (Nopcsa, 1925), the anterior precloacal vertebrae carry no distinct hypapophyses. Nopcsa (1925) described short, 'knob-like' hypapophyses projecting from the posteroventral margin of the centrum of larger anterior precloacal vertebrae. A similarly short and knobby hypapophysis is absent in specimen MSNM V 3660, or only very weakly developed as in the eighth element preserved in the series (Fig. 3A). A hypapophysis also appears to be absent on the anterior precloacal vertebra figured for *Simoliophis libycus* (Nessov *et al.*, 1998), but in the text Nessov *et al.* (1998: 269) describe a "small tubercle-like hypapophysis" for their "posterior trunk" (anterior precloacal) vertebrae. In contrast, a short yet distinct hypapophysis was described for the anterior precloacal vertebrae of *Pachyrhachis* (Lee & Caldwell, 1998). In general, the hypapophyses of the pachyostotic fossil snakes, if distinct, are smaller, more posteriorly oriented, and more ovoid in cross-section, than in other snakes. These hypapophyses must not be confused with the knob-like posterior termination of a low midventral ridge at the posterior margin of the ventral surface of the centrum that was described for *Mesophis* (Bolkay, 1925: 129; "*Knoten*", and fig. 3. See below for the description of the same feature in the posterior precloacal vertebrae of specimen MSNM V 3660).

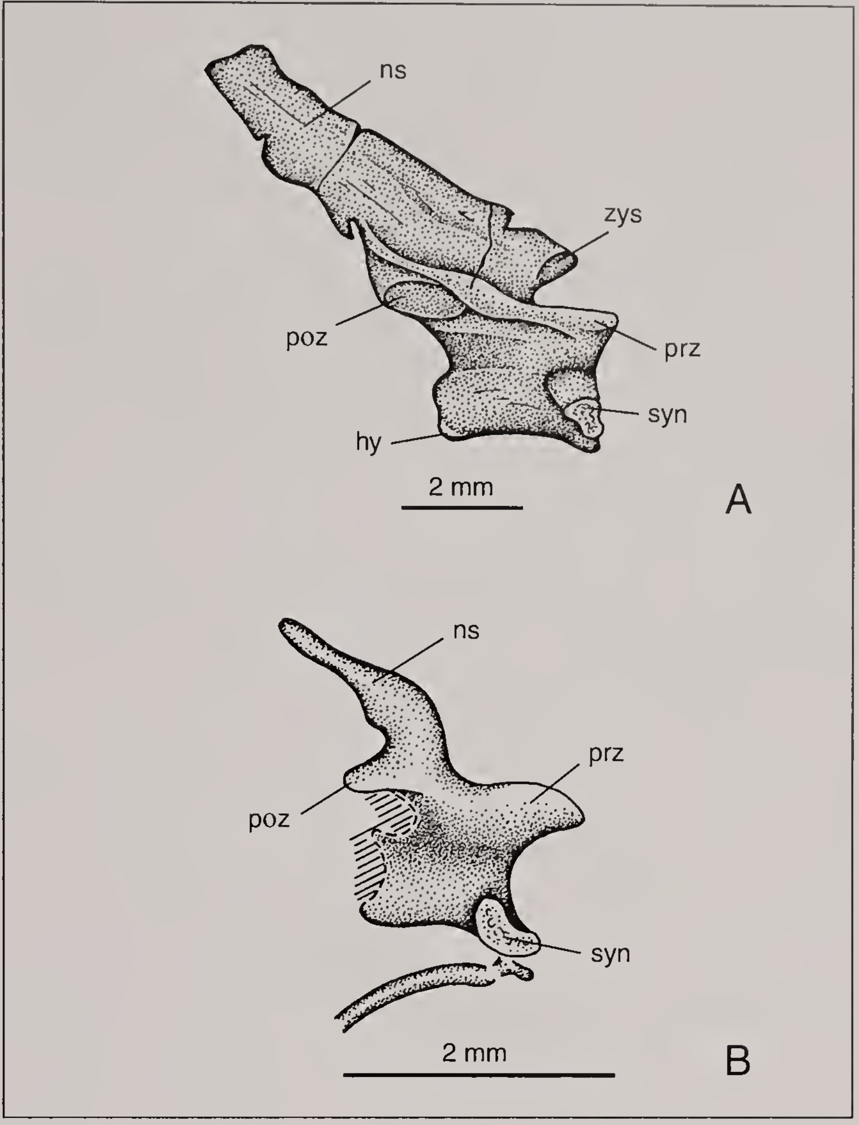


Fig. 3 - A) Anterior precloacal vertebra (8th preserved element) of specimen MSNM V 3660; B) Anterior precloacal vertebra (8th element) of specimen MSNM V 4014.

As in *Pachyophis* (Nopcsa, 1923a) and *Simoliophis* (Nopcsa, 1925), the pre- and postzygapophyses are connected by a distinct, laterally projecting keel in the anterior precloacal vertebrae in specimen MSNM V 3660. This keel (Fig. 4) has been previously named 'interzygapophyseal ridge' by Johnson (1955). The articular surface of the prezygapophysis is mildly inclined dorsomedially, matching the weakly ventrolaterally facing articular surface of the postzygapophysis. As in *Pachyophis* (Nopcsa, 1923a), *Simoliophis* (Nopcsa, 1925), *Haasiophis* (Rieppel *et al.*, 2003) and *Pachyrhachis* (Lee & Caldwell, 1998), a prezygapophyseal process is absent. The zygosphene is well exposed at the base of the neural arch above the neural canal, with its laterally facing articular surface oriented almost vertically. Rage & Escuillié (2000) report an anteriorly notched (concave) zygosphenal lamina (zygosphenal tectum) for *Eupodophis*, a putatively plesiomorphic character (but see Rieppel *et al.*, 2002 for a discussion), which cannot be assessed in the anterior precloacal vertebrae of specimen MSNM V 3660 due to their exposure in lateral view.

More posterior vertebrae are all exposed in ventral view (some segments of the string of vertebrae being split horizontally). As in *Pachyophis* (Nopcsa, 1923a), *Simoliophis* (Nopcsa, 1925; Nessov *et al.*, 1998) and *Pachyrhachis* (Lee & Caldwell, 1998), these vertebrae are subject to pachyostosis that is most distinctly developed in the middle of the precloacal skeleton (Fig. 4). From their exposure in ventral view the presence of a relatively low neural spine can be inferred. This is because the presence of a tall neural spine would have caused the orientation of the vertebrae in lateral view, as is the case in the anterior precloacal elements. The transition from the anterior precloacal vertebrae with a relatively tall neural spine exposed in lateral view, and the more posterior vertebrae exposed in ventral view occurs relatively abruptly in the region between the 21st and 23rd element preserved in the series. Pachyostosis starts to become apparent in the region around the 30th element in the series, and it is prominent in the 36th and the following vertebrae through approximately the 69th vertebra, after which it becomes progressively less expressed. The vertebrae posterior to the 85th element are no longer pachyostotic.

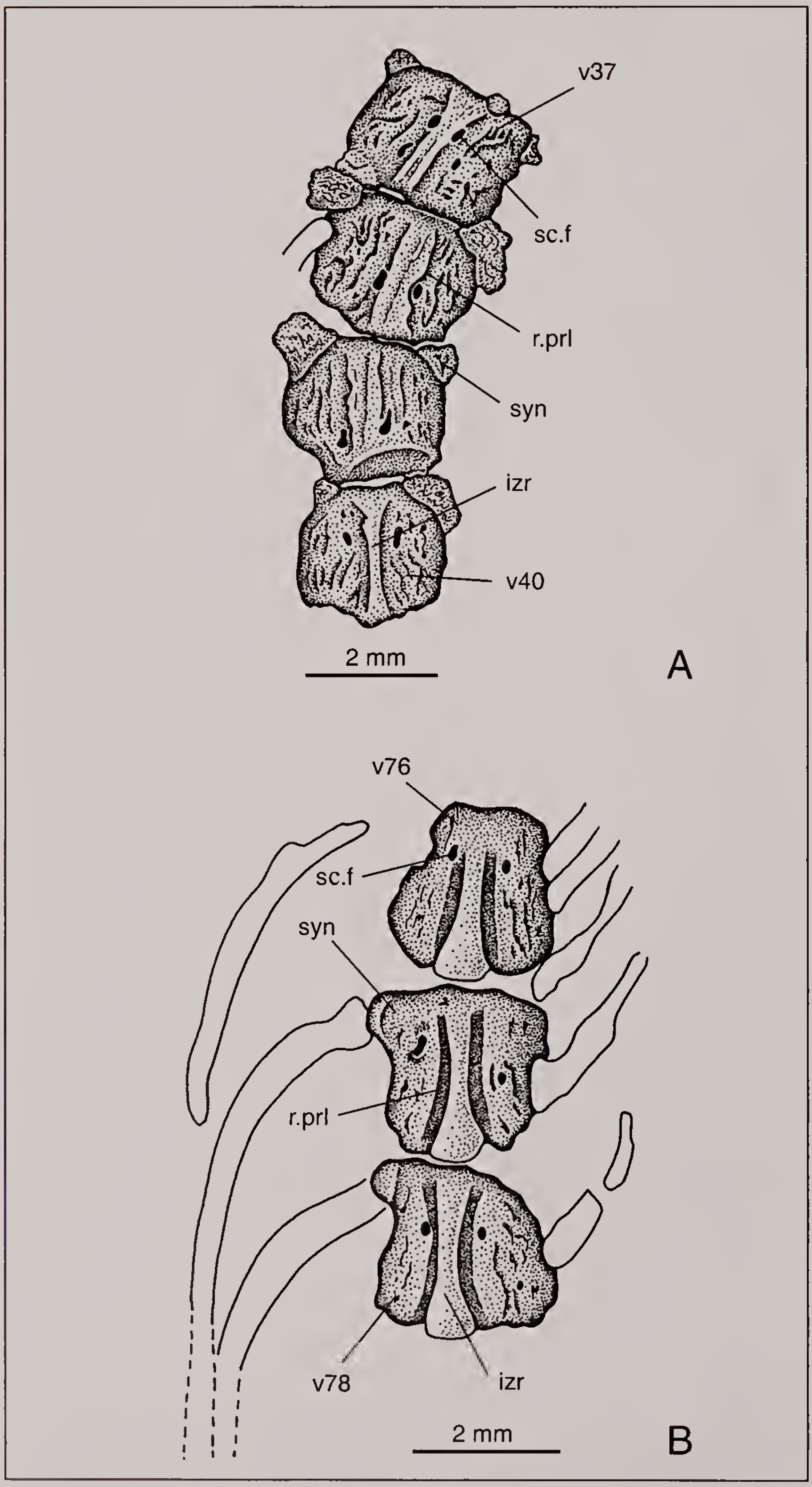


Fig. 4 - A) Anterior precloacal vertebrae of specimen MSNM V 3660 in ventral view; B) Posterior precloacal vertebrae of specimen MSNM V 3660 in ventral view.

Bolkay (1925) has emphasized that the vertebrae as exposed in ventral view are always wider than long in *Mesophis*. In specimen MSNM V 3660, the first well-preserved vertebra exposed in ventral view is the 30th element preserved in the series. Measurements for it and well-preserved succeeding vertebrae are listed in Table 1.

Table 1 - Measurements of the best-preserved vertebrae (exposed in ventral view) of specimen MSNM V 3660. Length of the centrum is measured as the maximum length of the exposed centrum from its anterior to its posterior margin. Width of the centrum is again measured as the maximum width of the exposed centrum across the synapophyses.

Well preserved vertebrae exposed in ventral view	length	width	$\frac{\text{width}}{\text{length}}$
30th	5.08	5.67	1.12
35th	4.93	7.28	1.48
41st	5.65	7.56	1.34
52nd	5.15	8.49	1.65
62nd	5.73	7.78	1.36
66th	5.18	7.65	1.48
70th	5.22	7.05	1.35
75th	5.52	~6.33	1.15
79th	5.24	6.21	1.19
85th	4.84	6.18	1.28
93rd	4.77	4.85	1.02

Given the articulated nature of the material, and its sometimes incomplete exposure, these measurements must be considered somewhat approximate. They nevertheless confirm that the vertebral centra are wider than long in *Eupodophis*, and that the relation of width to length increases with an increasing degree of pachyostosis in the mid-precloacal region. The same appears to obtain for *Pachyophis* with the vertebrae exposed in dorsal view (Lee *et al.*, 1999, fig. 1).

Pachyostosis affects not only the centrum, but also the parapophyseal part of the synapophysis, which is located on the lateroventral aspect of the anterior end of the centrum in specimen MSNM V 3660. In the pachyostotic vertebrae of *Haasiophis*, the smaller diapophyseal part of the synapophysis is separated from the hypertrophied parapophyseal part by a distinct groove (Rieppel *et al.*, 2003). MSNM V 3660 is not preserved well enough to allow the assessment as to whether there is a distinct groove that separates the hypertrophied parapophyseal from a smaller diapophyseal component of the synapophysis (Fig. 4). The difference in size between the parapophyseal and diapophyseal components of the synapophysis is no greater in *Pachyrhachis* (Lee & Caldwell, 1998) than in the majority of alethinophidians (Hoffstetter & Gasc, 1969). A groove separating the parapophyseal and diapophyseal components of the synapophysis is absent in *Pachyophis* and in the Egyptian material of *Simoliophis* (Nopcsa, 1925), unlike in *Simoliophis rochebrunei* (Buffrénil & Rage, 1993; Rage, 1984).

The pachyostotic vertebrae, exposed in ventral view show what Nopcsa (1925: 21) described as a "longitudinal tripartition of the ventral surface of the centrum … that characterizes the anterior pachyostotic vertebrae of the Egyptian species …" of *Simoliophis*. The same morphology is observed in *Mesophis* (Bolkay, 1925, fig. 3). In fact, specimen MSNM V 3660 shows that this tripartition can be recognized to a variable degree throughout the series of pachyostotic mid-precloacal vertebrae (Fig. 4). The tripartition results from a pair of shallow longitudinal grooves that demarcate a relatively broad, shallow and blunt medioventral (hemal) 'keel' (rather: ridge) from the collateral parts of the flat ventral surface of the centrum. Within those shallow longitudinal grooves (Fig. 4A), or along their lateral margins (Fig. 4B), lie the subcentral foramina which, as in *Simoliophis* (Nopcsa, 1925), are irregularly shaped and distributed, i.e. not strictly bilaterally symmetrically arranged. The posterior end of the midventral keel expands into a rounded, knob-like structure ("*Knoten*" of Bolkay, 1925) at the posterior margin of the ventral surface of the centrum, a feature that is most distinctly expressed behind the 70th vertebra preserved in the series in specimen MSNM V 3660 (Fig. 4B). The shallow grooves of Nopcsa's (1925) 'tripartition' are recesses for the paralymphatic system that are present in all alethinophidians and some scolecophidians (Head, personal observation). Similar grooves are also present in *Pachyrhachis* and *Haasiophis*, although the general appearance of the subcentral grooves in MSNM V 3660 is more similar to *Mesophis* and *Simoliophis* than to the previous taxa.

Numerous ribs are preserved, some of them (most notably the left rib associated with the 42nd vertebra preserved in the series) switched so as to expose the posterodorsally directed and rather weakly developed tuberculum. A similar rib morphology was described for *Simoliophis* by Nopcsa (1925). As in the latter genus, as well as in *Pachyrhachis* (Lee & Caldwell, 1998), the ribs are curved in their proximal 'shoulder' region, but straight distally (see also Rage, 1984). Although somewhat thickened in the proximal shoulder region within the pachyostotic precloacal section, the ribs are subject to a lesser degree of pachyostosis in *Eupodophis* than is characteristic of *Pachyophis* (Nopcsa, 1923a; Lee *et al.*, 1999), *Pachyrhachis* (Lee & Caldwell, 1998), or *Haasiophis* (Rieppel *et al.*, 2003). In that respect, *Eupodophis* more closely resembles *Mesophis* (Bolkay, 1925). Nopcsa (1925) mentions distinct pachyostosis proximally in some ribs of *Simoliophis*.

Bolkay (1925: 130) noticed a marked difference in the length of the longest ribs in *Pachyophis* and *Mesophis*. He lists the average length for the longest ribs as 23.2 – 25.5 mm for *Mesophis*, but ~40 mm for *Pachyophis*. But to judge from Nopcsa's (1923a) plate VII (assumed to render the specimen at approximately natural size), the longest ribs do not seem to exceed 26 mm in length. The slightly longer ribs of *Pachyophis* may well reflect the somewhat larger overall size of the latter specimen as compared to *Mesophis*. Almost none of the ribs are fully exposed in specimen MSNM V 3660, and their distal part is often represented only by an impression in the matrix, which creates some inexactness of measurements. However, both the proximal and distal parts of the left rib associated with the 81st vertebra (as preserved) are present, connected with each other by an impression in the matrix that represents the missing middle section of that rib. The length of that rib is 27.8 mm, which is just a bit longer than the longest ribs in *Pachyophis*. This may reflect the fact the specimen MSNM V 3660 is of slightly larger overall size than *Pachyophis*.

In summary, and as noted by Rage & Escuillié (2000), the vertebrae of *Eupodophis* are very closely similar to those of *Simoliophis*, differing from the latter only in the presence of anterior protuberances on the dorsal surface of the neural arch, a character which is not exposed in specimen MSNM V 3660 (but see below for the description of specimen MSNM V 4014). The anterior vertebrae of *Eupodophis* share with those of *Pachyophis* (Nopcsa, 1923a) and *Pachyrhachis* (Lee & Caldwell, 1998) the tall neural spine, and the ventrally exposed vertebrae of specimen MSNM V 3660 closely match those of *Mesophis* (Bolkay, 1925) in details of surface structure and in the general tendency of being wider than long.

Specimen MSNM V 3661

(Figs. 5 - 8)

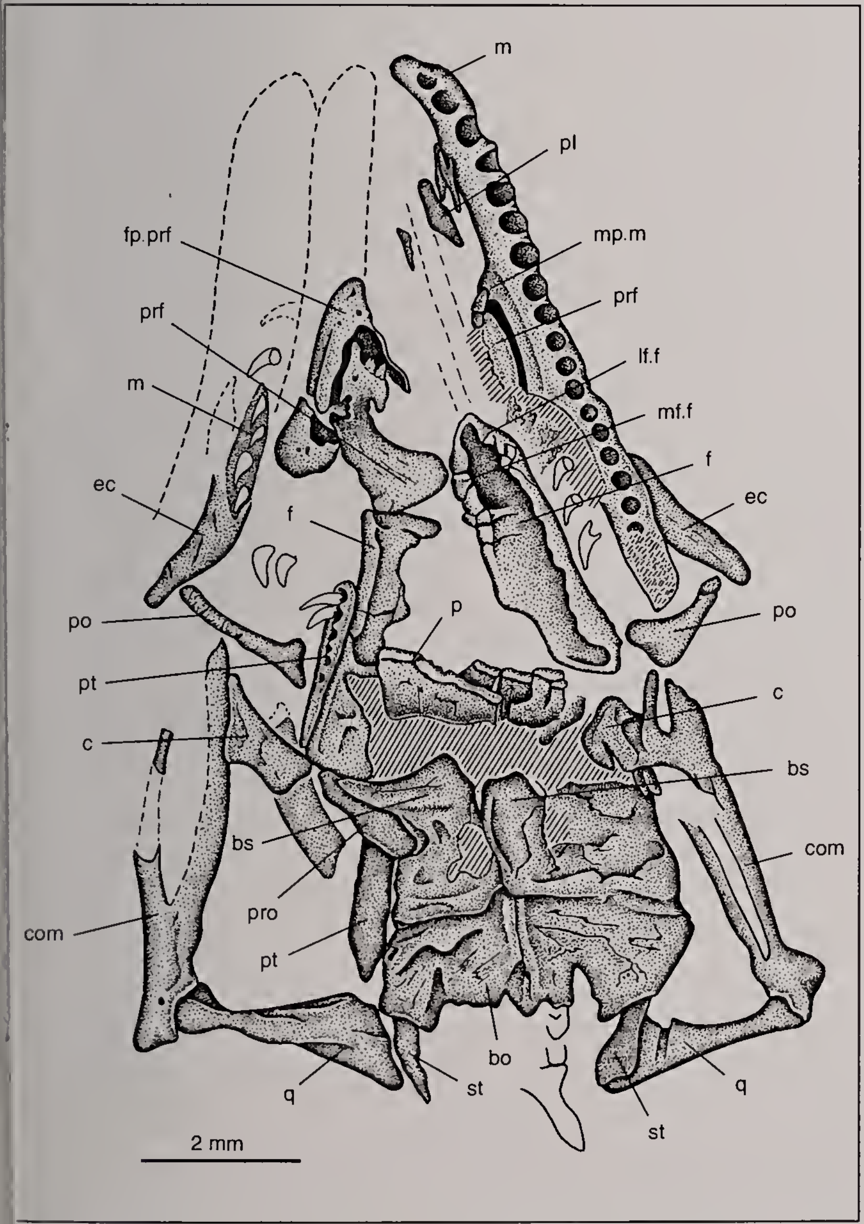
This is a nearly complete, articulated specimen (Fig. 5) that is much smaller than either the specimen described by Rage and Escuillié (2000), or MSNM V 3660. The total length of MSNM V 3661 measures 314 mm from the anterior tip of the skull to the posterior tip of the preserved portion of the tail. The skull measures 13.2 mm from the posterior tip of the left supratemporal to the anterior tip of the left maxilla, and 12.3 mm from the posterior end of the basicranium (as preserved) to the anterior tip of the left maxilla.

The skull is exposed in ventral view (Fig. 6). Preservation of the skull is incomplete due to the separation of the part and counterpart slabs, and some of the elements (right dentary, right maxilla) are vaguely indicated as natural molds only. However, some of the elements are

Fig. 5 - Specimen MSNM V 3661 (approx. x 1.36). Photo: Luciano Spezia.

well preserved and offer important anatomical detail. The left maxilla is well preserved except for its posteriormost tip, and it shows a total of 18 preserved tooth positions; accounting for the poorly preserved posterior end, the entire maxilla may have carried as many as 21 teeth. The anterior end of the maxilla is weakly curved medially, and its anterior tip is smooth and blunt, indicating the absence of a sutural contact with the premaxilla. No trace of a premaxilla can be identified, but the anterior tip of the left maxilla approaches the anterior end of the natural mold of the right maxilla closely enough to allow the inference that the premaxilla must have been small and narrow, as is also the case in *Pachyrhachis* (Lee & Caldwell, 1998) and *Haasiophis* (Rieppel *et al.*, 2003). As in macrostomatan snakes such as *Python*, the maxilla carries a broad-based and shelf-like medial (palatine) process, which is broken due to the underlying (morphologically: overlying) apex of the elongate prefrontal (Frazzetta, 1966, Fig. 16). Only a tooth-bearing fragment of the posterior part of the right maxilla is preserved.

Of the left prefrontal, only the apex that has been pushed through the medial (palatine) process of the maxilla is preserved. Crushed bone behind the medial (palatine) process of the left maxilla, and between the latter and the left frontal, may also represent the prefrontal. On the right side of the skull, the prefrontal is also crushed, but its outlines and its contact with the anterior margin of the frontal are preserved (Fig. 6). The prefrontal is elongate and slender, more closely resembling that of the anilioid *Cylindrophis* than that of *Python*. The posterolateral corner of the prefrontal appears to be somewhat thickened, forming an articular knob (Frazzetta, 1966, fig. 18), which appears to be received by a shallow facet on the anterolateral edge of the frontal. The identification of this articulation is somewhat tenuous, as it depends on a variable angle of illumination of the specimen, but if indeed present, it would indicate that the skull of *Eupodophis* might have been prokinetic.



ig. 6 - The skull of specimen MSNM V 3661 as preserved in ventral iew.

Both frontals are preserved in ventral view, although in a crushed condition. They have been forced apart during the fossilization process. Two features of the frontal are observable and important. First, both frontals are of equal length, and their length relative to the rest of the skull is unusually elongate compared to extant snakes such as 'anilioids' or basal macrostomatans. Indeed, due to their shape and proportions, the frontals are more similar to those of non-ophidian squamates than to those of extant snakes. Such frontals are so far known to occur only in specimen MSNM V 3661 and in *Pachyrhachis* (Lee & Caldwell, 1998) among snakes. Secondly, the left frontal shows what appear to be remnants of a crushed anterior medial pillar that is characteristic of alethinophidian snakes (Fig. 6). Although preservation is not entirely satisfactory, it seems that a gap might have persisted between the medial and lateral frontal flanges, as is the case in 'anilioids' (Rieppel, 1978); in macrostomatans, the medial and lateral frontal flanges establish contact medioventral to the olfactory tract (Frazzetta, 1966). It should be noted, however, that the ventral margins of both the lateral and medial frontal flanges are subject to breakage, such that the exact nature of their configuration cannot be established.

At the back end of the left maxilla, and close to the posterior tip of the left ectopterygoid, the left postorbital is exposed (Fig. 6). Its ventral tip is incomplete. The dorsal head of the postorbital is expanded at its articulation with the lateral wing of the parietal (which itself is not preserved) in a manner closely comparable to the postorbital in *Pachyrhachis* (Rieppel & Zaher, 2000, fig. 15B). The right postorbital is also preserved, but less completely so than the left one. Given the similarity of the left postorbital with that of *Pachyrhachis*, a nearly complete postorbital margin can be reconstructed for *Eupodophis*, a macrostomatan feature.

Behind the frontals, transversely oriented and vertically positioned shards of bone project from the sediment (Fig. 6). It is difficult, if not impossible, to unequivocally identify these bone fragments, but they may belong to the parietal. The only but rather unlikely other alternative would be to interpret these bone fragments as parts of the basipterygoid processes, which would then be ventrally projecting and transversely oriented structures resembling the basipterygoid processes in *Python*.

The supratemporal in *Eupodophis* projects from below (morphologically: from above) the preserved basicranium on both sides of the skull, forming a free-ending posterior process for the suspension of the quadrate (Fig.

6). The left supratemporal is better preserved than the right, and it shows a slight expansion of the posterior end of the free-ending process. A similar expansion of the posterior end of the supratemporal is present in *Haasiophis* (Rieppel *et al.*, 2003), where it is more distinctly developed than in *Eupodophis*.

Both quadrates are preserved, splayed outwards due to the dorsoventral compression of the skull during fossilization. As preserved, the quadrates slant slightly anteroventrally, an orientation that is also observed in *Haasiophis* with a dorsoventrally crushed skull, and that is attributed to postmortem dislocation. Given the overall proportions of the skull (see below for a discussion), the quadrate was positioned vertically, or slanted slightly posteroventrally, as is characteristic of basal alethinophidians, including basal macrostomatans. The dorsal ends of the quadrates are broadly expanded, but the shaft of the quadarates narrows progressively towards the mandibular condyles (Fig. 6). In having what appear to be a ventrally slender quadrate, specimen MSNM V 3661 resembles *Haasiophis* more closely than *Pachyrhachis*, and it also resembles the specimen of *Eupodophis* described by Rage & Escuillié (2000). However, another specimen (MSNM V 4014) described below exhibits a broad quadrate, such that the question arises whether the quadrates of MSNM V 3661 are incompletely ossified. The anterior and posterior margins of both quadrates appear to be complete in specimen MSNM V 3661. The posterior margin of the left quadrate in particular is perfectly preserved and documents the absence of a stylohyal in MSNM V 3661.

Little morphological detail can be offered for the dermal palate. Bone fragments medial to the anterior part of the left maxilla may represent parts of the palatine and vomer respectively. Nothing is preserved of the left pterygoid, whereas a tooth-bearing fragment of the palatine ramus of the right pterygoid is positioned alongside the lateral margin of the right frontal. What might be the posterior end of the quadrate ramus of the right pterygoid is located alongside the basicranium. As preserved, it terminates in a blunt tip just in front of the dorsal end of the quadrate. The problem with this interpretation is that the quadrate ramus of the pterygoid would be much more massively developed in specimen MSNM V 3661 than in specimen MSNM V 4014. The questionable strip of bone might therefore also be interpreted as parts of the crushed basicranium that were originally facing laterally (the 'lateral wings' of the para-basisphenoid and adjacent areas). Both ectopterygoids are preserved, the left one more completely so than the right one. The ectopterygoid of specimen MSNM V 3661 closely resembles that of *Pachyrhachis* (Rieppel & Zaher, 2000, fig. 15B). It is a horizontally positioned lamina of bone that slightly expands towards its anterior end (Fig. 6). The anterior end is not exposed as it underlaps (morphologically: overlaps) the posterior end of the maxilla. The somewhat narrower posterior end has a complete, rounded margin, and underlies the ventral tip of the postorbital. The complete preservation of the ectopterygoid in specimen MSNM V 3661 refutes the claim made by Rieppel & Zaher (2000) that the ectopterygoid is broken across the posterior end of the maxilla in *Pachyrhachis*. This claim was made to account for the shortness of the ectopterygoid, and for its position almost entirely in front of the ventral tip of the postorbital. These are characteristics which specimen MSNM V 3661 shares with *Pachyrhachis*, and which led to the identification of the ectopterygoid as a jugal in *Pachyrhachis* (Lee & Caldwell, 1998; Lee & Scanlon, 2002). However, as will be discussed in more detail below, the position of the ectopterygoid almost entirely in front of the postorbital results from the unusually elongate frontals that carry the postorbital backwards.

Of the braincase, only the crushed ventral surface of the posterior part of the basicranium is preserved (other than possible fragments of basipterygoid processes: see the discussion of the parietal above). However, the ventral surface of the basioccipital is macrostomatan in nature (Tchernov *et al.*, 2000), as it shows distinct ventrally projecting crests (Fig. 6). A longitudinal crest served as the site of origin of the protractor pterygoidei (Frazzetta, 1966, fig. 30), while laterally positioned and posteriorly concave crests delineate facets on the ventral surface of the basioccipital for the insertion of hypaxial neck muscles.

Posterior parts of both mandibular rami are preserved on either side of the skull. The anterior end of the right dentary is preserved as a natural mold only; no tooth counts are therefore available for the lower jaw. The right mandibular ramus shows the well-preserved coronoid process formed by the coronoid (crushed in the left mandibular ramus). The coronoid of specimen MSNM V 3661 is closely similar to that of *Pachyrhachis* (Lee & Caldwell, 1998), and very different from that of *Haasiophis* and all extant snakes, in that it forms a broad, high coronoid process of almost rectangular outlines (Fig. 6). Different from *Pachyrhachis*, the dorsal margin of the broad coronoid process slants posteroventrally in specimen MSNM V 3661. The coronoid is weakly expanded at its base in an anteroventral direction, and it is applied to the medial surface of the compound bone (i.e., not bracing the dorsal aspect of the surangular as it does in nonophidian squamates: Rieppel & Zaher, 2000). The compound bone is broken on both sides, but preserved in articulation with the quadrate. The right mandibular ramus preserves the rounded and "stubby" retroarticular process that is characteristic of alethinophidian snakes (Rieppel & Zaher, 2000).

The teeth in specimen MSNM V 3661 are slender, needle-shaped and recurved, much like small replicas of the teeth seen in boas and pythons. The small size of the teeth makes it difficult to identify anterior, posterior, or lateral (as in *Pachyrhachis*: Lee & Caldwell, 1998) cutting edges, but in general the enamel surface is smooth and lacks the ridges or fluting seen in *Haasiophis* (Rieppel *et al.*, 2003).

A total of 163 vertebrae are preserved in specimen MSNM V 3661. Of those, the first 41 vertebrae are characterized by a tall, slender and blade-like neural spine that is located towards the posterior end of the neural arch and that projects in a posterodorsal direction (Fig. 7A; no neural spine is developed on the atlantal neural arch). The height of the neural spine diminishes gradually in the last

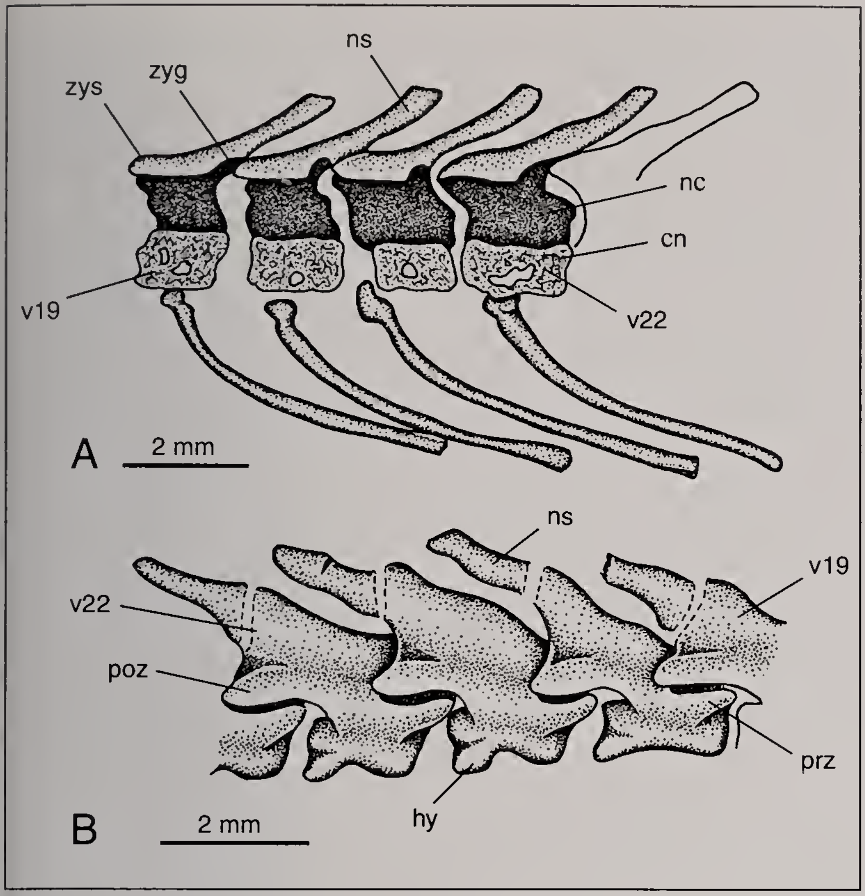


Fig. 7 - A) Anterior precloacal vertebrae of specimen MSNM V 3661, as preserved in lateral view; B) Anterior precloacal vertebrae of specimen MSNM V 4014, as preserved in lateral view.

few elements of that series. As in *Pachyophis* (Nopcsa, 1923a), *Pachyrhachis* (Lee & Caldwell, 1998), and specimen MSNM V 3660, the neural spines have caused the vertebrae to tilt relative to the bedding plane, so that they are exposed in lateral view. Separation of the part and counterpart slabs caused a sagittal splitting of the vertebral centra, but not of the blade-like neural spines. The sagittally split vertebrae expose the right half of the zygosphene in medial view underlapped (as preserved and exposed) by the zygantrum of the preceding neural arch (Fig. 7A). The zygosphene is prominently developed in *Eupodophis*, as was also noted to be the case in *Pachyophis* by Nopcsa (1923a). As in specimen MSNM V 3660, there is no indication of the presence of hypapophyses in the anterior precloacal region, not even as a slight posteroventral protuberance of the (split) vertebral centra as it is known from *Simoliophis* (Nopcsa, 1925; but see the description of specimen MSNM V 4014 below).

Vertebrae posterior to the first 41 elements continue to be embedded with their lateral side parallel to the bedding plane. Again, the vertebrae are sagittally split, exposing the spongy bone inside the vertebral centrum. The neural canal is relatively very wide (with a vertical diameter that exceeds the height of the centrum; see also Fig. 7A), and the well-developed zygosphenes continue to be exposed in medial view in these sagittally split vertebrae. There is no indication of even low neural spines, which suggests that the better part of the vertebrae adhered to the counterpart slab (not available). A small neural spine is apparent again in the tail region. It starts to become noticeable on the 154th vertebra, and increases in height towards the mid-section of the tail. It is of a peculiar morphology, in that it is a curved structure (concave anteriorly, convex posteriorly) that rises from the posterior end of the neural arch and terminates dorsally in a straight, horizontally oriented margin (see Fig. 12 showing the same morphology for specimen MSNM V 4014).

The ribs in specimen MSNM V 3661 are not subject to pachyostosis. This may be related to the small size of the specimen (see the discussion of pachyostosis as related to ontogeny in Lee *et al.*, 1999). Along the entire precloacal body, the ribs are curved in their proximal 'shoulder' region, but straight for most of their length, and they show a slight distal expansion. Rib morphology thus suggests a lateral compression of the body (Rage & Escuillié, 2000). As far as can be ascertained, there is no indication of a well-developed tuberculum, as is present in *Simoliophis* (Nopcsa, 1925), and there is no evidence that ribs were developed beyond the 142nd vertebra.

In specimen MSNM V 3661, the longest ribs (occurring between the 80th and 100th vertebrae) are 16 mm long. As in *Pachyrhachis*, the ribs remain relatively long up to a level shortly in front of the femur. The last distinctly elongated rib is associated with the 140th vertebra. Its length, as indicated by an impression left in the matrix, is 6.1 mm, which equals the length of the 5 following vertebrae (140th to 145th). The ribs associated with the 141st and 142nd vertebrae are poorly preserved (poorly ossified?), but they are abruptly much shorter. No ribs are unequivocally identifiable beyond the 142nd vertebra. Next to the ventral edge of the 142nd vertebra lie two small splints of bone that appear to represent either 2 short ribs lying parallel to one another, or a broken bifurcating element. Preservation is poor and structural detail difficult to

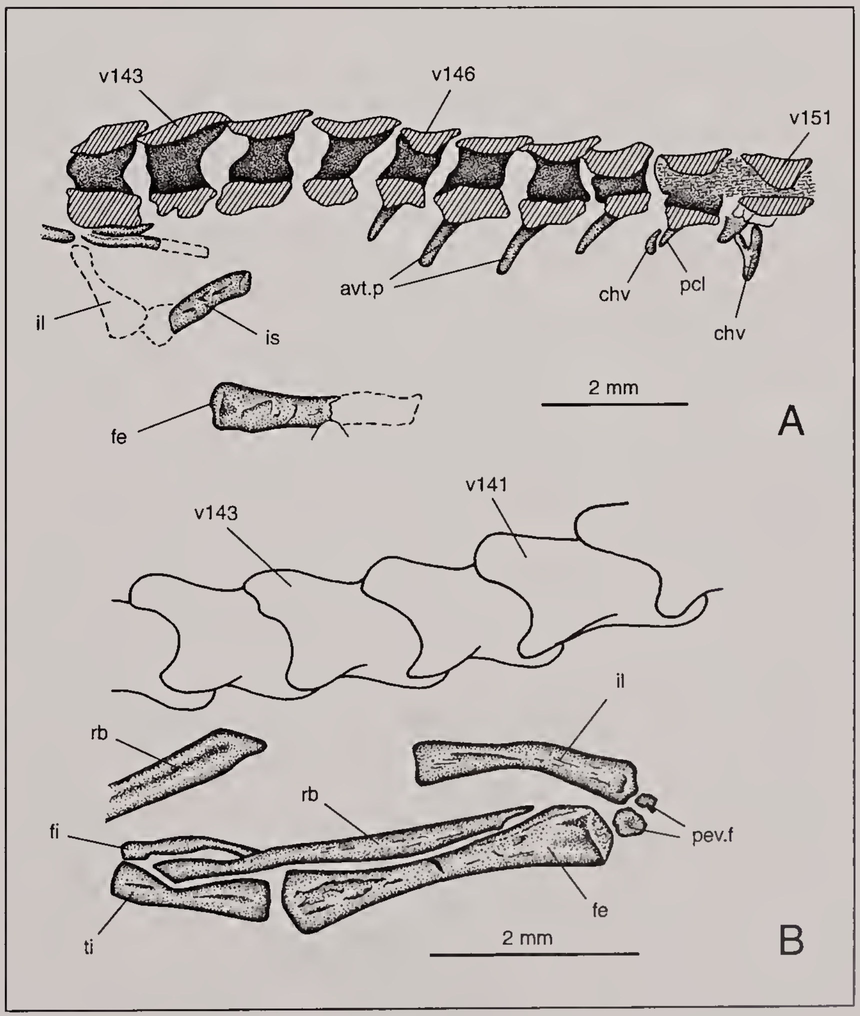


Fig. 8 - A) The cloacal region of the vertebral column and the hind limb as preserved in specimen MSNM V 3661; B) The pelvic rudiments and hind limb as preserved in specimen MSNM V 4014.

ascertain (Fig. 8A), but given the absence of lymphapophyses behind the 142nd vertebra (lymphapophyses are also absent in specimen MSNM V 4014), the structures mentioned above are interpreted as ribs. This interpretation leaves *Eupodophis* without lymphapophyses (note that the putative 'sacral rib' of *Pachyrhachis* is the first [articulated] lymphapophysis: Lee, 1998). As preserved in specimen MSNM V 3661, the dorsal end of the ilium lies at the same level as the non-bifurcating short rib associated with the 141st vertebra, i.e., behind the seemingly bifurcating structure that is associated with the 142nd vertebra. It is also impossible to identify any element in specimen MSNM V 3661 as a putative sacral vertebra (see Lee & Caldwell [1998] for the identification of a sacral vertebra in *Pachyrhachis*, and the comments in Rieppel & Zaher [2000] and Rieppel *et al.* [2003] on this issue), which argues for the use of 'precloacal' rather than 'presacral' vertebrae in the description of *Eupodophis*.

In the absence of lymphapophyses it is difficult to demarcate precloacal from cloacal vertebrae. Additionally, *Eupodophis* appears to lack caudal pleurapophyses, a potential autapomorphy of the taxon. However, Rage & Escuillié (2000) noted the relatively very short tail of *Eupodophis*, as well as the presence of distally fused, but proximally bifurcated chevrons. They considered these an important plesiomorphy of *Eupodophis* (Rage & Escuillié, 2000: 518). In specimen MSNM V 3661, the 146th through 149th vertebrae are peculiar in that they develop a distinct, ventrally projecting sagittal keel on the ventral surface of the centrum (Fig. 8A). At the anterior end of the centrum, this keel is developed into a medioventrally located, anteroventrally projecting, curved (convex anteriorly, concave posteriorly) and blade-like process that terminates in a blunt (not pointed) tip. On the 150th and 151st vertebrae, this same process is reduced to a small but distinct (unpaired) blade-like pedicel (Figs. 8, 12) located medioventrally at the anteroventral margin of the centrum. It is with these pedicels that the first two chevrons articulate, each 'embracing' the pedicel of its associated vertebra with the proximally bifurcating 'arms' (Fig. 8A). In specimen MSNM V 3661, these two anteriormost chevrons are much shorter than more posterior ones. In fact, these two anteriormost chevrons form little more than a minute V-shaped structure with little distal extension. Although frequently broken, the length of the chevrons that articulate with the 152nd and more posterior vertebrae is indicated by natural molds. The chevrons form distinctly elongate, flattened, blade-like structures with a relatively short, proximally bifurcating part. The chevrons slope posteroventrally relative to the long axis of the vertebral column. At the posterior end of the preserved part of the tail, the chevrons are only represented by weak impressions in the matrix.

Two small rod-shaped elements are apparent next to the femur (one as a distinct natural mold only), which are interpreted as remnants of the rudimentary pelvis (Fig. 8A). The anterior one of these elements is tentatively identified as the ilium (represented by a natural mold), the other as ischium (preserved in bone). The ilium shows a slight basal expansion.

Of the hind limbs, only one femur is (partially) preserved on the right side of the 144th to 146th vertebral elements. The posterior part of the femur is represented by a distinct natural mold. The length of the femur is 2.98 mm (average of three measurements), and it equals almost exactly the length of the three consecutive vertebrae lying next to it (as measured through their split centra). The femur is a straight, slender and essentially featureless element with a slightly constricted diaphysis and slightly expanded proximal and distal ends. No other parts of the limb are preserved.

Specimen MSNM V 4014
(Figs. 3, 7 - 12)

The total length of the complete and articulated specimen (Fig. 9) is approximately 388 mm (the very tip of the tail is concealed by a loop of the body). The specimen therefore matches MSNM V 3661 in size, both being much smaller in size than MSNM V 3660 and the specimen described by Rage & Escuillié (2000). The head length is best assessed by the length of the well-preserved right mandibular ramus, which measures 14.9 mm from its symphyseal tip to the posterior tip of the retroarticular process.

The skull is again exposed in ventral view, but with only a very limited assortment of bones preserved (Fig. 10). At the anterior end of the skull is located the small and narrow premaxilla with what appears to be a single, medially located (and presumably internally subdivided) premaxillary channel, and short and pointed posterior vomerine processes. The premaxilla of specimen MSNM V 4014 is edentulous, and in its size and proportions closely resembles the edentulous premaxilla of *Haasiophis* (Rieppel *et al.*, 2003; contra Tchernov *et al.*, 2000). The premaxilla is not known for *Pachyrhachis* (Lee & Caldwell, 1998), *Pachyophis* (Nopcsa, 1923a) or *Mesophis* (Bolkay, 1925).

Along the midline of the skull, in front of the right palatine (Fig. 10), paired crests of bone represent the ventral exposure of the medially descending flanges of the nasals. At a deeper (morphologically more dorsal) level, the left nasal preserves a triangular part of its dorsal lamina. Not enough bone is preserved, however, to allow the assessment of the outlines of the entire dorsal lamina of the nasal.

Between the left nasal and the anterior tip of the left mandibular ramus, the septomaxillary – vomer complex housing Jacobson's organ is exposed in articulation in ventral view. The septomaxilla protrudes narrowly from below (morphologically: above) the anterior dentigerous process of the left palatine (itself pressed against the left half of the mandible), but it can be identified clearly as it forms the lateral margin of the opening of Jacobson's organ. The left vomer is almost completely preserved, and it forms the medial margin of the opening of Jacobson's organ, meeting the septomaxilla in a straight longitudinal suture in front of and behind that opening. The slender and elongate vomer has a rounded anterior end, a slightly

Fig. 9 - Specimen MSNM V 4014 (approx. x 2.28). Photo: Luciano Spezia.

damaged lateral margin, and a tapering posterior part that is broken off from the main body of the vomer and that ends in a pointed posterior tip.

The anterior dentigerous process of the palatine, an alethinophidian feature, is preserved on both sides of the skull, although the left one is only poorly exposed, being pressed against the left mandibular ramus (Fig. 10). The right palatine is almost completely preserved, although broken in its anterior part. The anterior dentigerous process carries eight tooth positions. The posterior end of the palatine forms a notch that engaged in a tongue-and-groove articulation with the anterior end of the palatine ramus of the pterygoid in a configuration that recalls the 'booid' condition. Also resembling the macrostomatan condition is the medial (choanal) process of the palatine that is narrow and located towards the posterior end of the palatine (Fig. 10). It tapers medially as it provides a passage for the choanal tube, ending in a blunt tip. There was no well-defined contact between the choanal process of the palatine and the vomer in specimen MSNM V 4014.

The quadrate ramus of the right pterygoid is preserved and well exposed (Fig. 10). The bone shows a weak lateral expansion just in front of a laterally facing facet that would have received the posterior end of the ectopterygoid. More anteriorly, the teeth of the palatine ramus of the pterygoid are aligned along a strip of bone that represents the incompletely preserved anterior part of the pterygoid, which itself lies alongside the basisphenoid. Superficial inspection might create the impression that the pterygoid in specimen MSNM V 4014 carried a massively developed, laterally projecting transverse process, as indicated by bilaterally symmetrically arranged globular fragments of bone, the right one situated next to the weak lateral expansion of the pterygoid. These fragments of bone represent parts of the prootic, however, as will be discussed in more detail below.

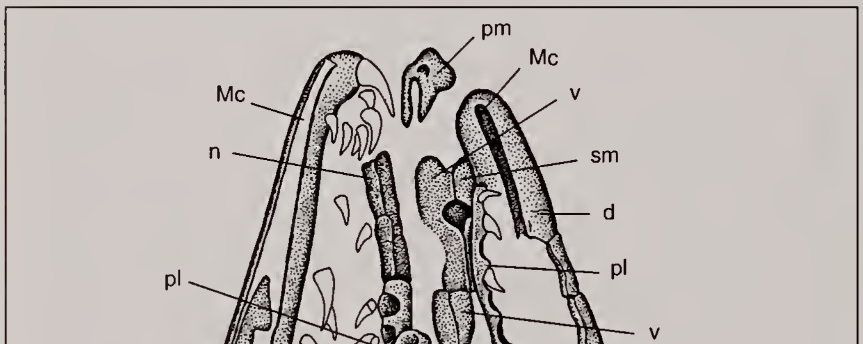


Fig. 10 - The skull of specimen MSNM V 4014 as preserved in ventral view.

The posterior end of the quadrate ramus of the right pterygoid overlaps the internal surface of the broad quadrate. The right quadrate is disarticulated and rotated posterolaterally, which renders the assessment of its orientation and original shape difficult. It also appears that the broken distal part of the shaft of the stapes adheres to its (topological) anterior margin (Fig. 10). But whatever the details of the structure of the quadrate, specimen MSNM V 4014 resembles *Pachyrhachis* more closely than MSNM V 3661 or the specimen described by Rage & Escuillié (2000) in having an unusually broad quadrate. Only the ventral half of the right quadrate is preserved, but again it is broader than is seen in specimen MSNM V 3661. Its orientation indicates that the quadrate was positioned vertically, or slanted slightly posteroventrally. In front of the left quadrate, the posterior tips of two rod-shaped elements are exposed. The lateral one of these is relatively broad anteriorly, but tapering to a blunt tip posteriorly. It represents the posterior part of the quadrate ramus of the pterygoid. The medial element is somewhat more delicate, and represents the distal end of the shaft of the stapes.

Of the basicranium, part of the crested ventral surface of the basisphenoid rostrum is exposed, behind which the ventral surface of another disarticulated and rotated part of the basicranium (?) emerges (Fig. 10). The cresting on the ventral surface of the basisphenoid is again a macrostomatan feature of specimen MSNM V 4014. The part of the basisphenoid that is preserved indicates the presence of a broad, anteriorly tapering para-basisphenoidal rostrum in MSNM V 4014. Little detail can be offered with respect to more posterior parts of the basicranium, except that a weakly demarcated knob-like projection is present at what presumably constitutes its posterior margin. This projection is too small to represent the occipital condyle located at the posterior margin of the basioccipital. In *Haasiophis* (Rieppel *et al.*, 2003), a knob-like projection marks out the posterior end of the midventral longitudinal crest on the basicranium (basioccipital). In specimen MSNM V 4014, there is no distinct crest, however, that leads up to this small posterior knob-like projection.

On the other hand, a small foramen is seen to pierce the element which, if interpreted as a foramen for a root of the hypoglossal nerve, would identify the element as part of the exoccipital. On that interpretation, the hypoglossal foramen would be located slightly in front of and above the posterior knob-like projection. The projection itself could be the contribution of the exoccipital to the formation of the tripartite occipital condyle that is characteristic of squamates (with the exception of uropeltines). But the general shape and structure of the bone fragment is such that no unequivocal and satisfactory interpretation can be offered.

Lateral to the weak lateral extension of the right pterygoid sits a globular fragment of bone that has a counterpart on the left side of the skull and that could easily be mistaken for a massively developed lateral (transverse) process of the pterygoid. However, these bone fragments are here interpreted as part of the prootic. The description will focus on the right element which is more fully exposed (Fig. 10). The fragment has an irregular appearance. As preserved, the 'left' side of the fragment is of a bulbous structure, with a strongly convex surface and a moderate posterior projection that terminates in a blunt tip. This part of the fragment formed a lappet that projected laterally from the base of the laterosphenoid-region of the braincase and extended backwards to underlap the posterior trigeminal (mandibular branch) foramen. Such a laterally projecting prootic (laterosphenoid) lappet is known from several basal macrostomatans such as boas and pythons (Rieppel *et al.*, 2002), and it is also prominently developed in *Haasiophis* (Rieppel *et al.*, 2003). Its presence, in fact, indicates the presence of a laterosphenoid, which is an alethinophidian feature (e.g., Rieppel, 1988). The part of the fragment which lies topologically medial (morphologically dorsal) to the bulbous projection exposes a distinctly concave surface that is deeper anteriorly than posteriorly. The anterior margin is also evenly curved (concave). This part of the fragment formed the posterior margin of the medial entry foramen into the trigemino-facialis chamber (Rieppel, 1979). The concave surface behind the entry foramen into the trigemino-facialis chamber is the part of the prootic lying deep to the exiting mandibular branch of the trigeminal nerve: this is why it is more deeply concave anteriorly than posteriorly. There is one caveat with this interpretation, however. In basal macrostomatans such as *Boa* or *Python*, the hyomandibular branch of the facialis nerve typically pierces the prootic within the recess for the exit of the mandibular branch of the trigeminal nerve, but a corresponding foramen cannot be located in the same position in the prootic fragment of specimen MSNM V 4014. However, the facialis nerve pierces the prootic in a more posterior position in anilioid snakes such as *Anilius* and *Cylindrophis* (Rieppel, 1977).

Both mandibular rami are preserved, but in spite of their superficially rather complete appearance, they offer only limited anatomical detail. The anterior tips of the dentaries are smooth and rounded, indicating the absence of a lower jaw symphysis. Meckel's canal opens in front of the splenial along the medioventral edge of the dentary (Fig. 10). The splenial is identifiable at the ventral margin of the medial aspect of the right mandibular ramus. A notch in its posterior part may indicate the posterior mylohyoid foramen (Fig. 10). If a bone fragment on the medial side of the right mandibular ramus is correctly interpreted as the anterior part of the splenial, it suggests that the splenial extended relatively far anteriorly. This is a macrostomatan feature that is also observed in *Haasiophis* (Rieppel *et al.*, 2003). The exact configuration and posterior extent of the posterior dentigerous process of the dentary cannot be established. The exact configuration of the coronoid process is again impossible to establish. As described above, specimen MSNM V 3661 shares with *Pachyrhachis* a very prominent coronoid process of more or less rectangular outlines. Specimen MSNM V 4014 shows a weak elevation with a smoothly rounded dorsal margin in the region behind the posterior dentigerous process of the right dentary. This elevation is recognized as a dorsal projection of the right compound bone, which on its medial side carries a facet for the reception of the coronoid. The latter must have separated from the mandibular ramus when the slab and counterslab were split apart. An element on the left side of the skull, located at the posterolateral margin of the preserved part of the basisphenoid and narrowly overlapping the latter, could well represent the detached and dislocated left coronoid (Fig. 10). If correctly identified, it would indicate that specimen MSNM V 4014 shares the same tall coronoid as specimen MSNM V 3661. Both mandibular rami show the compound bone in articulation with the quadrates, and both display the short, 'knobby' retroarticular process that is also observed in specimen MSNM V 3661.

The teeth are of similar structure in both specimens, a distinct ridging or fluting of the enamel surface also being absent in MSNM V 4014.

A total of 162 vertebrae are preserved in specimen MSNM V 4014, with the posterior tip of the tail concealed by a coil of the body. The anterior precloacal vertebrae again carry the slender, bladelike neural spines that ascend in a posterodorsal direction from the posterior part of the neural arch (Figs. 3B, 7B). The first 30 vertebrae are preserved and exposed in lateral view, presumably again because of tilting caused by the tall neural spines. Behind the 30th vertebra, the neural spines are seen to decrease in height; a neural spine is present but relatively short in the 37th preserved vertebra. Behind that element, the vertebrae are split horizontally due to the separation of the part and counterpart slabs. Nevertheless, it can be stated that as in specimen MSNM V 3661, there are more than 37 anterior vertebrae that carry a distinct neural spine in specimen MSNM V 4014.

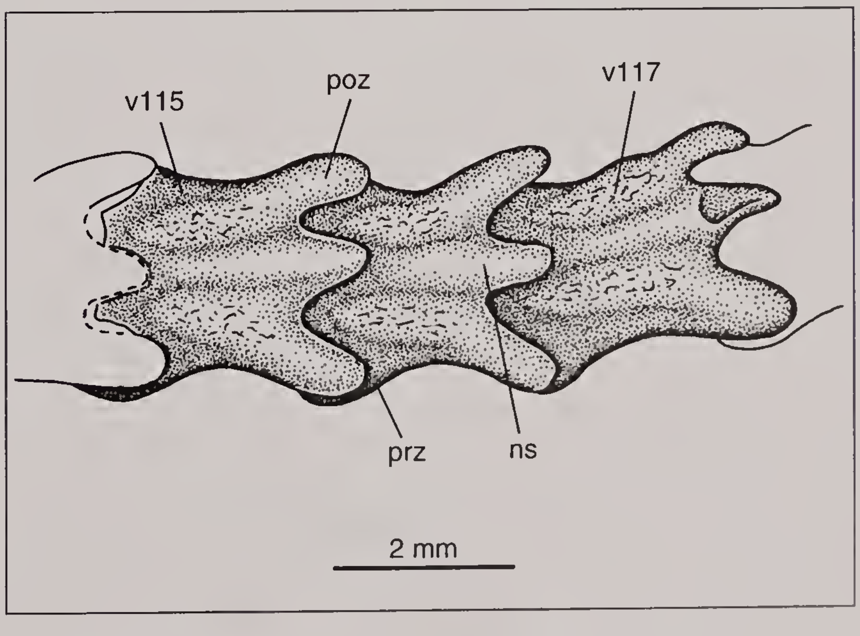


Fig. 11 - Precloacal vertebrae of specimen MSNM V 4014 as preserved in dorsal view.

Some of the anterior precloacal vertebrae of specimen MSNM V 4014, preserved in lateral view, show a short and blunt yet distinct protuberance at the posteroventral margin of the centrum (Fig. 7B), resembling the rudimentary hypapophyses that were described for *Simoliophis* by Nopcsa (1925). Such rudimentary hypapophyses are absent on the first 16 vertebrae. If present on the 17th vertebra, it would be concealed by a body coil. The 18th vertebra is poorly preserved, but a small protuberance is present on the posteroventral margin of the centrum of the 19th through the 23rd vertebrae. Behind the 23rd vertebra, preservation becomes poor again, and behind the 30th vertebra, torsion of the vertebral column begins. But the rudimentary hypapophyses can be identified up to the 30th, perhaps even 34th, vertebra. The para-diapophysis (synapophysis) is situated very low on the centrum towards its anterior end, facing lateroventrally (Fig. 3B). The subcentral foramen is located lateroventrally between the synapophysis and the rudimentary hypapophysis (where present). Finally, the accessory prezygapophyseal process is absent in specimen MSNM V 4014.

Behind the 37th vertebra, most of the vertebrae are split horizontally, some above, and some below the level of the pre- and postzygapophyseal articulations. However, in the posterior third of the precloacal skeleton the vertebrae are well preserved again and exposed in dorsal view. In the posterior precloacal region, the neural spine forms but a low ridge at the anterior margin of the neural arch. It increases slightly in height towards the posterior margin of the neural arch, from where it projects in a posterodorsal direction, forming a short stubby process that overlaps the anterior margin of the neural arch of the succeeding vertebra. In cases where this short, posteriorly projecting neural spine is broken off (e.g., in the 114th and 116th preserved vertebra) the zygosphenal lamina (zygosphenal tectum: Rieppel *et al.*, 2002) of the succeeding vertebra (the 115th and 117th preserved element) is exposed in dorsal view. The zygosphenal tectum has a straight (117th vertebra) or only very slightly notched (115th vertebra, Fig. 11) anterior margin, unlike the vertebra described and illustrated by Rage & Escuillié (2000), which shows an anteriorly notched zygosphenal lamina. The 115th vertebra displays nicely the zygosphene – zygantrum articulation, especially on the left side. The zygosphene faces laterally, the zygantrum medially, in a more or less vertically oriented plane of articulation. The zygantrum is formed by a pedicel that is set off from the medial side of the prezygapophysis of the preceding vertebra. The well-preserved vertebrae of the posterior precloacal region also show the 'swelling' or protuberances on the dorsal surface of the neural arch on both sides of the neural crest / spine (Fig. 11), which Rage & Escuillié (2000) found to be diagnostic of their new taxon, and which is the only difference by which its vertebrae could be distinguished from those of *Simoliophis*. However, the neural arch morphology as described for specimen MSNM V 4014 is also closely similar to that described for *Pachyophis* (Nopcsa, 1923a; Lee *et al.*, 1999: 515, and fig. 1).

Nopcsa (1923a) described an interesting pattern of variation of the plane of articulation between the pre- and postzygapophyses within the precloacal vertebral column of *Pachyophis*. In the anterior precloacal region, the plane of articulation is weakly inclined (20° to 25° according to Lee *et al.*, 1999; given its preservation, it seems doubtful that the zygapophyseal angle can be estimated to an accurate degree in *Pachyophis*). In the mid-precloacal region, the articular surfaces on the pre- and postzygapophyses are almost horizontally oriented. But in the posterior precloacal region, the plane of articulation becomes progressively inclined again, the prezygapophysis facing upwards and inwards, the postzygapophysis facing downwards and outwards. The swelling on the dorsal surface of the neural arch that is prominently expressed in the mid-precloacal region recedes as the vertebrae become relatively narrower in the posterior precloacal region, until only deep grooves persist on either side of the low and posteriorly projecting neural spine. This shows that the swelling on the dorsal surface of the neural arch, which Rage & Escuillié (2000) took to be diagnostic for *Eupodophis*, is correlated with pachyostosis, as it is in specimen MSNM V 4014.

In specimen MSNM V 4014, the first 16 vertebrae are well exposed in lateral view. A slight disarticulation between the 7th and 8th vertebrae shows the plane of articulation between the prezygapophysis (facing upwards and inwards) and the postzygapophysis (facing downwards and outwards) to be slightly inclined by about 20° to 25°, i.e., to a degree comparable to *Pachyophis* (Lee *et al.*, 1999). The 19th through the 24th vertebrae are tightly articulated, making it difficult to assess the orientation of the intervertebral articulation. The vertebrae following the 24th element are crushed, and those behind the 38th element are split horizontally, which renders it impossible to assess the exact orientation of the plane of articulation between the pre- and postzygapophyses. However, within the series of horizontally split vertebrae, the 48th and 49th elements preserve their neural arch, and show the plane of articulation between the pre- and postzygapophyses to be only weakly inclined, perhaps by 15° to 20°. However, the tight articulation between the vertebrae renders that assessment somewhat tentative. Between the 75th and 90th vertebrae, the articulation between pre- and postzygapophysis is nearly horizontally oriented, inclined by no more than 5°. Behind the 95th vertebra, the inclination of the articular surfaces of the pre- and postzygapophyses rapidly increases again, as the vertebrae become relatively narrower, and the swelling on the dorsal surface of the neural arch recedes (due to a diminishing degree of pachyostosis) leaving deep grooves on either side of the low neural spine. Around the 125th vertebra, the inclination of the articular plane has increased to about 60°, the prezygapophysis facing upwards and inwards, the postzygapophysis facing downwards and outwards. Towards the 145th vertebra, this inclination of the articular plane becomes even more accentuated, as does the narrowing of the vertebrae in general. Specimen MSNM V 4014 thus documents a closely similar pattern of variation of the intervertebral articulation between *Eupodophis* and *Pachyophis*.

The relation of the length to the width of the centrum, which is an indicator of the degree of pachyostosis, is hard to determine in specimen MSNM V 4014 given its preservation in dorsal view. The extent of pachyostosis along the precloacal vertebral column is therefore difficult to assess, but approximate measurements indicate that some degree of pachyostosis is expressed between the 40th and 155th vertebrae, and that pachyostosis is most distinctly expressed between the 65th and 95th vertebrae.

Throughout the precloacal region, the para-diapophysis (synapophysis) is set low on the vertebral centrum and hence is not exposed in dorsal view. It is exposed in a few vertebrae that have been split horizontally at a relatively low level, and these vertebrae, as well as the position of the proximal ends of the ribs, indicate that the synapophysis is again located towards the anterior end of the centrum. The proximal articular ends of the ribs are generally buried under the exposed dorsal part (neural arch) of the vertebrae, in which case it is impossible to assess the presence or absence of a tuberculum. Some posteriormost dorsal ribs are fully exposed, however, but no tuberculiform process can be identified on them. The ribs are curved in their proximal shoulder region but straight distally, indicating a lateral compression of the body in *Eupodophis*.

The longest ribs in specimen MSNM V 4014 reach a length of 17 mm in the middle precloacal region (75th vertebra; 16.5 mm for the rib associated with the 95th vertebra). Specimen MSNM V 4014 resembles specimen MSNM V 3661 and *Pachyrhachis*, but not *Pachyophis* (or *Haasiophis*) in that elongated ribs extend further backwards towards the cloacal (i.e., hind limb) region, followed by two to four abruptly shortened ribs. The rib that articulates with the 137th vertebra in specimen MSNM V 4014 equals the length of 3.5 adjacent centra (approx. 5 mm). Abruptly much shortened ribs are associated with the vertebrae 138 through 140. No rib is associated with the 141st vertebra. The left ilium, along with two tiny and rounded specks of bone, lies to the left side of the 141st and 142nd vertebrae. Two slender strips of bone are emerging from below the 145th and 146th vertebrae on their left side, but their identity cannot be unequivocally assessed. They do not appear to be ribs (no ribs are preserved on the right side of the vertebral column behind the 140th vertebra), nor are they bifurcated as lymphapophyses would be.

The limb of specimen MSNM V 4014 is located in the area of the 141st to 144th (145th) preserved vertebrae (Fig. 8B). The vertebrae adjacent to the limb and the pelvic girdle rudiments show no trace of transverse processes or lymphapophyses. Indeed, none of the specimens of *Eupodophis* show any indication of the presence of transverse processes or lymphapophyses in the cloacal region, and none of them allows the identification of one or several putative 'sacral' vertebra(e).

In specimen MSNM V 4014, the orientation of the articular surfaces of the pre- and postzygapophyses becomes almost vertical in the tail region (Fig. 12). Beginning with the 148th vertebra, a distinct neural spine with rectangular outlines is developed, which rises from the posterior part of the neural arch and slightly slants in a posterodorsal direction. This results in an increasing height of the short, laterally compressed tail.

The 145th through 148th vertebrae again develop a distinct, ventrally projecting sagittal keel on the ventral sur-

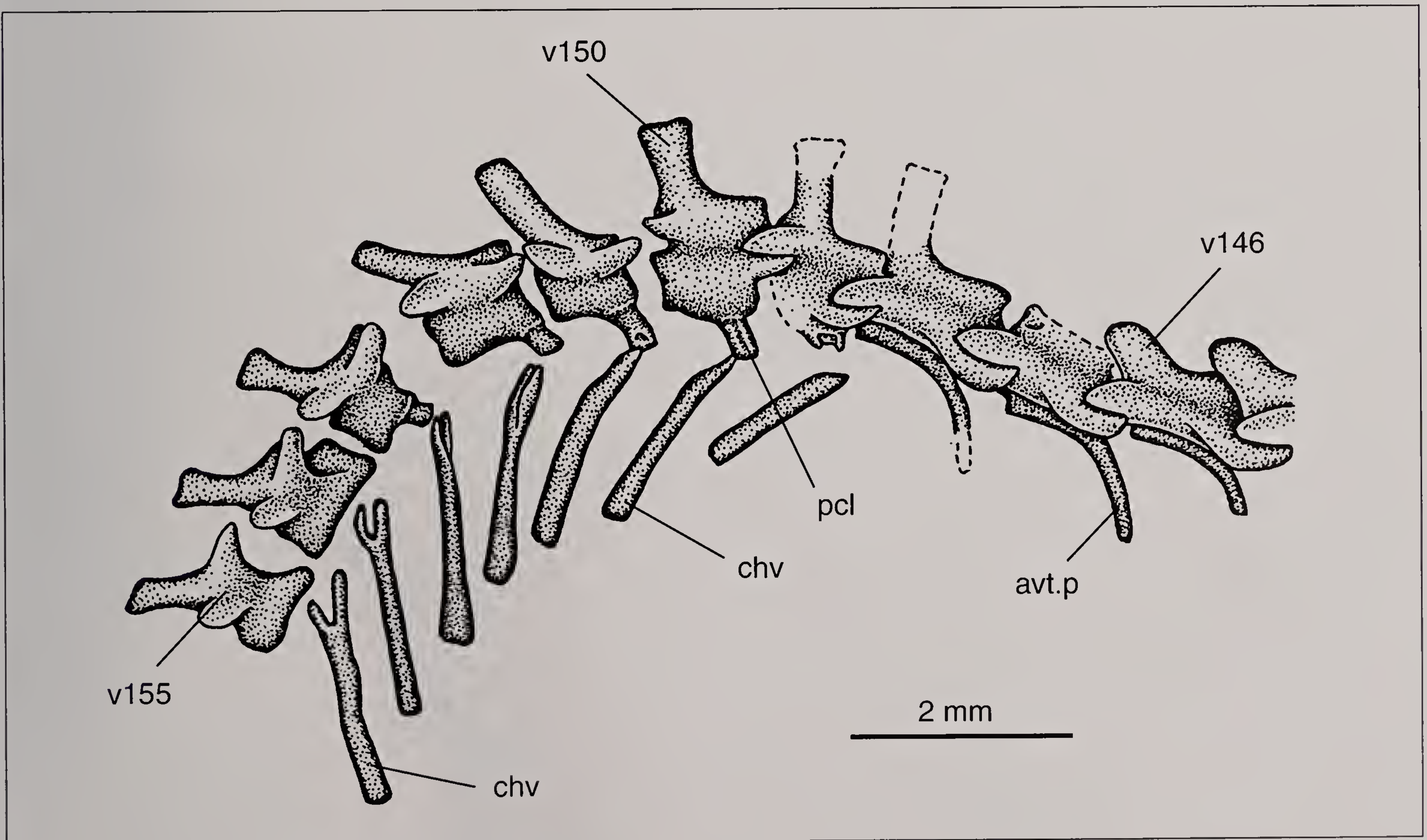


Fig. 12 - The cloacal and proximal tail region of the vertebral column as preserved in specimen MSNM V 4014.

face of the centrum. At the anterior end of the centrum of these four vertebrae, this keel is developed into a slender, blade-like and curved (anteriorly convex, posteriorly concave) process that projects in an anteroventral direction. More posteriorly (identifiable on the 149th through the 154th vertebra), this anteroventral process is reduced to form a short, medioventral (sagittal, unpaired) pedicel at the anteroventral margin of the centrum for the articulation of the chevrons. The chevrons 'embrace' this antero-medio-ventral pedicel with their short, proximally bifurcating 'arms'. The first vertebra to carry the curved, anteroventrally projecting process is the 146th preserved element in specimen MSNM V 3661, but the 145th vertebra in specimen MSNM V 4014. This may very well be due to individual variation. However, it also should be noted that the atlas is not unequivocally identifiable behind the skull of specimen MSNM V 4014, and a body coil conceals the vertebrae following the 16th preserved element. Conservatively, a single vertebra has been assumed to fill a gap in the exposure of the vertebral column in this region. Considering these caveats, the vertebral counts given for specimen MSNM V 4014 throughout this description might be too low by one or perhaps even two elements.

The anteriormost chevron is associated with the 149th vertebra (Fig. 12); it is somewhat shorter (though not much, as compared to specimen MSNM V 3661) than the succeeding chevrons. The chevrons reach their maximum length at the 153rd vertebra, and then decrease again in length towards the tip of the tail. The latter is concealed by a coil of the body. The chevrons are tilted in a posteroventral direction relative to the long axis of the vertebral column.

A rod-shaped, somewhat curved element lies between the femur and the vertebral column, its distal end slightly anterior but in close proximity to the proximal end of the femur. This element is interpreted as the ilium (Fig. 8B). Its length is 2.4 mm. Between the ilium and the proximal end of the femur there are two flakes of bone which might represent remnants of other pelvic girdle elements not preserved in their entirety. Two similar specks of bone are also preserved near the left ilium, which itself lies in close proximity to the vertebral column. There is no well-defined contact between the ilium and any vertebrae in the cloacal region.

The length of the femur of specimen MSNM V 4014 equals the length of 2.5 adjacent vertebral centra (Fig. 8B). The length of the femur equals the length of three adjacent vertebral centra in MSNM V 3661, and of 2.5 centra again in the much larger specimen described by Rage & Escuillié (2000). The absolute length of the femur is 3.46 mm in specimen MSNM V 4014 (average of three measurements). As in specimen MSNM V 3661 it is a straight, rather featureless bone with slightly expanded proximal and distal ends and a slightly constricted diaphysis. The tibia appears to be of a distinctly more robust structure than the fibula, but a rib that lies between tibia and fibula may conceal some parts of the latter (Fig. 8B). The length of the tibia is 1.8 mm, and it again is a straight element with slightly expanded ends and a slightly constricted diaphysis. The exact length of the fibula cannot be measured, but the element seems to be weakly curved, which would result in a spatium interosseum between tibia and fibula. No autopodal elements are preserved or present.

DISCUSSION

Specimens MSNM V 3661 and 4014 lend additional support to the earlier finding that *Eupodophis* shares macrostomatan affinities (Rieppel *et al.*, 2002). The poorly expressed articulation of the right prefrontal with the right frontal, as well as the indication of the presence of medial frontal flanges on the left frontal of specimen MSNM V 3661 (Fig. 6) suggest the presence of a prokinetic joint. The supratemporal terminates in a slightly expanded, free ending posterior process. The vomer is slender and pointed posteriorly. The palatine carries a well-developed anterior dentigerous process, and the slender medial (choanal) process is located towards the posterior end of the bone. The pterygoid meets the palatine in a characteristic tongue-and-groove articulation. The prootic flange underlapping the posterior (mandibular branch) trigeminal foramen indicates the presence of a laterosphenoid. The basicranium is distinctly crested, suggesting the presence of a well-developed constrictor internus dorsalis musculature. The splenial reaches far forwards on the medial aspect of the lower jaw. All of the above are characters that diagnose alethinophidian or macrostomatan snakes (Tchernov *et al.*, 2000).

A character that has figured prominently in discussions of the phylogenetic relationships of all Cenomanian snakes with well-developed hind limbs is the identification of a jugal in *Pachyrhachis* by Caldwell & Lee (1997; Lee & Caldwell, 1998; see also Lee, 1998). That identification was based on the shape and relative shortness of the element, and its position at the ventral margin of the orbit almost entirely in front of the ventral tip of the postorbital. Rieppel & Zaher (2000; see also Zaher & Rieppel, 2002) disputed this identification, and identified the element in question as an incomplete ectopterygoid, broken across the posterior end of the maxilla in *Pachyrhachis*. However, specimen MSNM V 3661 of *Eupodophis* shows the same element of same relative size and proportions and in an equivalent position, i.e., mostly in front of the ventral tip of the postorbital as is observed in *Pachyrhachis*. Careful preparation of the left element in the skull of specimen MSNM V 3661 (by C. Dal Sasso) revealed complete natural edges around the exposed parts of the bone, thus refuting the claim made by Rieppel & Zaher (2000) that the equivalent element in *Pachyrhachis* was subject to breakage. However, *Pachyrhachis* shares with *Eupodophis* unusually elongated frontals. If such elongated frontals are properly accounted for in a reconstruction of the skull of *Eupodophis* (Fig. 13), it becomes apparent that the elongated frontals carry the postorbital (articulating with the anterolateral wings of the parietal, and perhaps the poste-

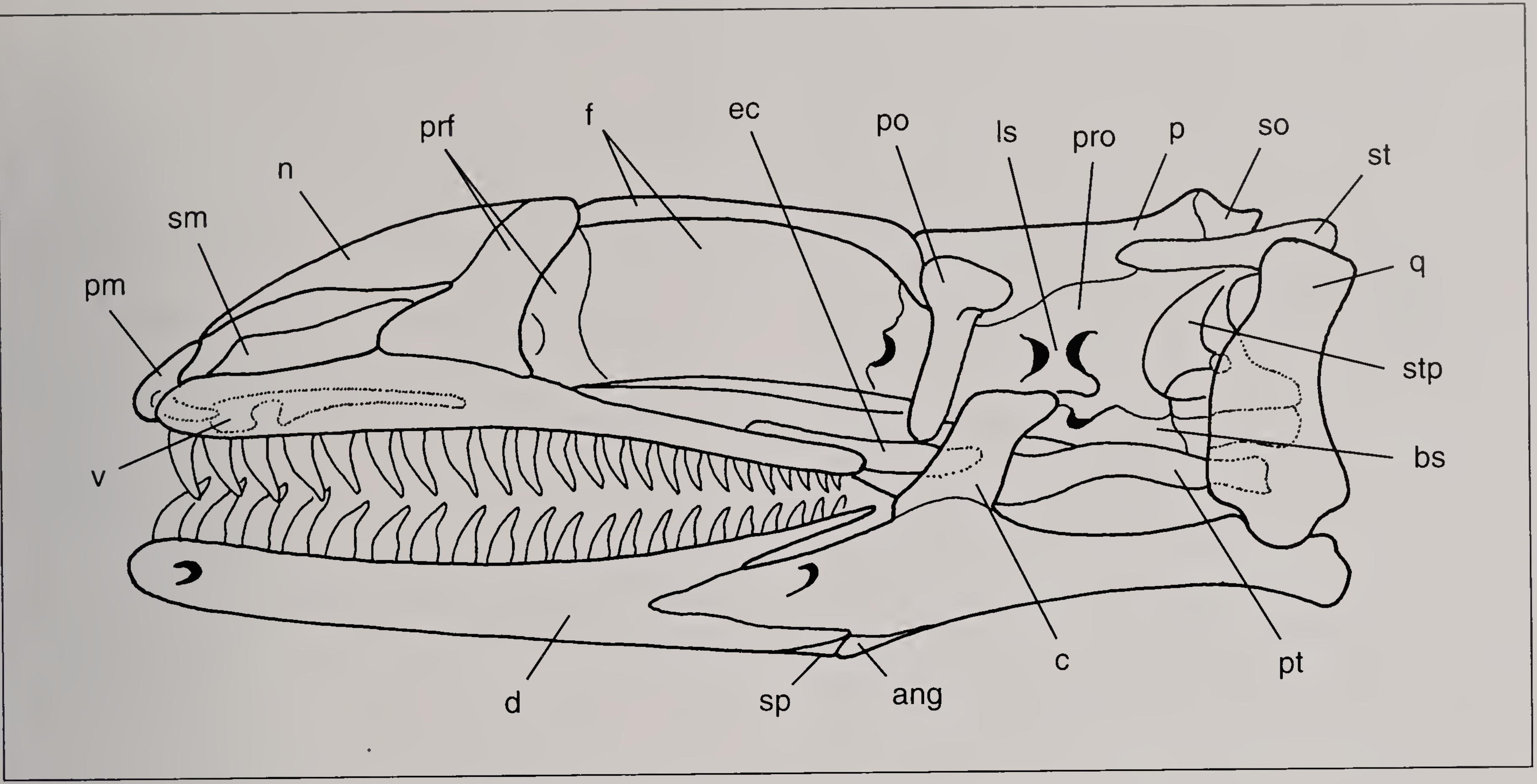


Fig. 13 - The reconstruction of the skull of *Eupodophis*, based on specimens MSNM V 3661 and 4014.

riormost aspect of the frontal) backwards. The elongated frontals are thus seen to be responsible for the position of the ectopterygoid mostly in front of the ventral tip of the postorbital, which explains the reason why these elements had initially been identified as jugals (Lee & Caldwell, 1998). Indeed, specimen MSNM V 3661 shows that if the corresponding elements were identified as jugals, ectopterygoids would have to be absent.

The vertebral column of *Eupodophis* is very closely similar to that of *Simoliophis*, *Pachyophis* and *Mesophis* (see systematic discussion below). The configuration of the ribs indicates a lateral compression of the body. Specimens MSNM V 3661 and 4014 show a very wide neural canal with a diameter that exceeds the diameter of the vertebral centrum. In contrast, the specimen described by Rage & Escuillié (2000) is much larger than these specimens, and presents a 'normal' neural canal diameter where it is preserved. For that reason, we interpret the wide neural canal in specimens MSNM V 3661 and 4014 as ontogenetic variation.

Eupodophis is unique among snakes in lacking lymphapophyses in the cloacal region. There are also no transverse processes present that would allow the identification of a 'sacral' region. Small and rod-shaped pelvic girdle rudiments are present, but there is no evidence for a contact of the ilium with the axial skeleton. The most complete hind limb among all MSNM specimens of *Eupodophis* is preserved in MSNM V 4014 (Fig. 8B), where it consists of a femur, a tibia and a fibula (indications of more distal elements are preserved in the specimen described by Rage & Escuillié, 2000). As is also the case in *Pachyrhachis* and *Haasiophis*, the femur in *Eupodophis* is a rather featureless, slender and straight element that lacks the complex morphology which characterizes the femur of adult males of extant snakes that retain hind-limb rudiments (Kley *et al.*, 2002). It is possible that the simple femur morphology in these marine snakes is a result of skeletal paedomorphosis, or that the femur morphology of males of extant snakes is highly derived.

The character of *Eupodophis* that has attracted the greatest attention is the presence of elements that resemble chevrons in the short tail (Figs. 8A, 12). It is evident, however, that the structure of the caudal vertebrae and 'chevrons' of *Eupodophis* do not correspond to a non-ophidian or, in particular, varanoid morphology. In varanoids, the caudal centra bear paired ventral pedicels, located at the posterior margin of the vertebral centrum, with which the chevrons articulate. These are Y-shaped elements with a short distal stem. In *Eupodophis*, the chevrons (with the possible exception of the first two in the series) have a comparatively much longer distal stem. Their proximal bifurcation results in the formation of two short proximal 'arms' that embrace an unpaired, blade-like pedicel that is located at the anterior end of the centrum on the midline of its lower surface. The four vertebrae that precede the first one associated with chevrons show a midventral crest which, at the anterior end of the centrum, extends into an anteroventrally curving, blade-like process. The formation of the pedicels that articulate with the chevrons result from the reduction of this anteroventral process. This morphology is unique for *Eupodophis* among all known squamates, and it creates problems of homology for the interpretation of the caudal vertebrae in other snakes.

The chevrons in non-ophidian squamates are considered to represent intercentra, and they are located in an intercentral position in the plesiomorphic condition. In varanoids, the chevrons become associated with the posterior end of the preceding vertebrae. These develop paired pedicels from the posterior end of the ventral surface of the centra, which articulate with the chevrons and which are considered genuine parts of the centrum.

In snakes other than *Eupodophis*, the anterior precloacal vertebrae develop unpaired ventral processes or hypapophyses from the posterior part of the centrum. On the basis of some embryological evidence (Männer, 1899: 65; Hoffstetter & Gasc, 1969: 284), these hypapophyses are considered to be homologous to intercentra that have become associated with the posterior end of the preceding vertebra. The extent to which hypapophyses are developed posteriorly is variable among snakes (Hoffstetter & Gasc, 1969). In some taxa, a more or less distinctly developed medioventral hemal crest or ridge may be present on the middle and/or posterior precloacal vertebrae. In the caudal region, snakes develop paired ventral processes (hemapophyses, unpaired in the Uropeltinae), which fuse with the centrum (Männer, 1899: 66; Brünauer, 1910: 15; Hoffstetter & Gasc, 1969: 285), and which are again considered homologous to intercentra (presumably to the proximal 'arms' of the chevron).

In *Eupodophis* there is at best a very weakly developed indication of a hypapophysis in the anterior precloacal vertebrae. The ventral surface of the trunk vertebrae is characteristically tripartite (Nopcsa, 1925) due to the presence of subcentral grooves that extend along a medial prominence, a structural feature that is shared by *Mesophis* (Bolkay, 1925) and that is variably present in alethinophidians. In the cloacal region, four vertebral centra develop a low medioventral keel from the anterior end of which projects a curved and blade-like medioventral process. This keel and process could be considered an elaboration of the hemal keel, or a peculiar transformation of an unpaired hemapophysis. Again, hemapophyses are described as undergoing ontogenetic fusion with the centrum, which is why they are homologized with intercentra associated with the posterior end of the preceding centrum. In the fossil taxon *Eupodophis*, there is naturally no evidence for the ontogenetic fusion of these processes that project anteroventrally from the anterior margin of the centrum. Given their location at the anterior end of the centrum, it seems therefore more likely that these anteroventral processes present in four vertebrae of the cloacal region represent genuine neomorphic formations of the centrum. More posteriorly, within the tail itself, these processes become reduced to small, blade-like and unpaired pedicels located on the midline of the anterior margin of the ventral surface of the centra. With these articulate the chevrons, which, if interpreted as intercentra, would therefore have become associated with the anterior end of the posteriorly following centrum (rather than with the posterior end of the preceding centrum as in varanoids). Such an association of the chevrons is unknown among non-ophidian squamates. Only some members of Agamidae show a slight posterior dislocation of the chevrons "to a position under the following vertebra" (Hoffstetter & Gasc, 1969: 267). Otherwise, chevrons retain an intervertebral position or undergo an anterior dislocation amongst non-ophidian squamates.

Rieppel *et al.* (2002) showed that coding *Eupodophis* (and *Wonambi*) for the presence of chevrons did not alter their phylogenetic relationships with basal macrostomatans. The presence of chevrons is, after all, a plesiomorphic feature. And whereas *Eupodophis* is currently the only snake known, fossil or extant, that shows the presence of chevrons, these certainly do not correspond to a plesiomorphic condition as indicated by out-group comparison with non-ophidian squamates such as varanoids, and the correlation of chevrons with the apomorphic anterior pedicel in caudal vertebrae.

SYSTEMATIC CONCLUSIONS

In his original description of *Pachyrhachis problematicus*, Haas (1979) noted the similarity between the vertebrae of this taxon and those of *Simoliophis*, and therefore included *Pachyrhachis* in Simoliophidae (he attributed the family name to Nopcsa, 1924 [for 1925], who used Symoliophidae). Since he did not believe in the ophidian status of *Pachyrhachis*, he removed the simoliophids from the "snakes proper," and referred the family to snake-like "varanids" instead (Haas, 1979: 64). Similarly, Rage & Escuillié (2000) noted the close resemblance of the precloacal vertebrae of *Eupodophis* with those of *Simoliophis* (see also Rage & Escuillié, 2003). Lee *et al.* (1999: 517) referred both *Pachyophis* and *Pachyrhachis* to Pachyophiidae (an emendation of Pachyophidae Nopcsa, 1923a; Pachyophinae in Nopcsa, 1923b; Pachyophiidae first appears in Bolkay, 1925: 130), noting that other fossil snakes such as *Simoliophis* may have to be referred to that family as well. Bolkay (1925) had already included *Mesophis* in Pachyophiidae.

Nopcsa (1923a: 139) first erected the family Pachyophidae to include *Pachyophis* (Nopcsa, 1923b: 124, used Pachyophinae as a subfamily of Cholophidae). Following Cannatella's (1990) orthographic analysis, Lee *et al.* (1999: 510) "more correctly" applied the "taxon name Pachyophiidae to *Pachyophis*, *Pachyrhachis*, and all taxa more closely related to these genera than to modern snakes" (Lee *et al.*, 1999: 517). In the case of *Pachyophis* the question is what the proper stem of 'ophis' would be? The problem is that 'ophis' has a peculiar genitive in Attic Greek. According to some sources, 'opheos' would be the correct genitive, while in other dialects the genitive of 'ophis' is straightforwardly 'ophios', which gives the stem 'ophi-'. According to the Code of Nomenclature, this latter genitive translates into the family name Ophiidae. On the other hand, Ophidia is the neuter plural of a genuine Greek diminutive ophidion ('little snake'). This derived noun is built on the stem oph- plus the diminutive suffix -idion. This argues for Ophidae. So, it is arguable that Pachyophidae is not 'incorrect Greek,' but it is also arguable that Pachyophiidae follows the rules of the Code more straightforwardly (Howard Don Cameron, personal communication; see also Cannatella, 1990).

In his description of the *Simoliophis* material from Egypt, Nopcsa (1925) recognized a close affinity of *Pachyophis* and *Simoliophis*, raising the question whether the two taxa should be treated as representatives of two families (Pachyophidae and Symoliophidae [*sic*] respectively), or as two separate subfamilies within one family. He later (Nopcsa, 1928) formally accepted the latter solution, listing Pachyophinae and Symoliophinae as subfamilies of his Cholophidae. Hoffstetter (1955) lists Pachyophidae and Simoliophidae as two separate families within Cholophidia. Romer (1956: 563) includes *Pachyophis* and *Simoliophis* in the subfamily "*Simoliophinae (Pachyophinae)*" that is included in his family Palaeophidae (which he equates with Cholophidae and Cholophidia). Kuhn (1967) finally considered as valid names Simoliophidae Hoffstetter (1955: 464), and Pachyophinae Nopcsa (1923b: 124).

In his discussion of the material attributed to *Simoliopohis*, Nopcsa (1925) found the vertebrae to be variable to a degree that only one species name could be justified, which by priority is *Simoliophis rochebrunei* Sauvage, 1880 (see also Rage, 1984). Since that time, another species, *Simoliophis libycus* was described by Nessov *et al.* (1998), but they misidentified the anterior precloacal vertebrae for posterior precloacal elements, which removes their main reason for the recognition of a second species. Rage & Escuillié (2003: 7) consider the validity of *Simoliophis libycus* questionable on the grounds that the characters that differentiate this taxon from *Simoliophis rochebrunei* might be due to ontogenetic variation or variation along the vertebral column. Rage & Escuillié (2003: 7) furthermore consider the material described by Nopcsa (1925) to comprise two different taxa, one of which is a separate species of *Simoliophis* that remains to be named. Caldwell & Lee (1997; see also Lee & Caldwell, 1998) correctly recognized *Ophiomorphus colberti* Haas, 1980b [*Estesius*, Wallach, 1984], as a subjective junior synonym of *Pachyrhachis problematicus*, and Head (J. Head, in preparation) recognizes the synonymy of *Pachyrhachis* with *Simoliophis*, a conclusion that was also suggested by Rage & Escuillié (2003: 7). Closely similar forms are *Pachyophis* (Nopcsa, 1923a) and *Mesophis* (Bolkay, 1925). However, given the many characters of skull structure, as well as differences in postcranial anatomy (lack of tall neural spines in the anterior precloacal region, configuration of the rib cage, differentiation of mid-precloacal pachyostosis), there can be no doubt that *Haasiophis* (Tchernov *et al.*, 2000; Rieppel *et al.*, 2003) represents a separate genus, yet related to the above mentioned taxa and again included in Pachyophiidae (see also Rieppel *et al.*, 2002). The same case is not quite as easily made for *Eupodophis*.

Rage & Escuillié (2000) recognized the close similarity of the vertebrae of *Eupodophis* to those of *Simoliophis*, and cited the protuberances on the dorsal surface of the neural arch as the only difference from the latter genus (these protuberances are correlated with pachyostosis as described above; see also Fig. 11). At the same time, Rage & Escuillié (2003: 7) find the dorsal tubercles on the vertebrae of *Eupodophis* to preclude the latter genus from being a subjective junior synonym of *Simoliophis*, a synonymy which they consider possible for *Pachyrhachis* and *Haasiophis* (but see above). Specimen MSNM V 3660 is preserved in ventral view, and both in size and structure matches the specimen described by Rage & Escuillié (2000) as well as the material referred to *Simoliophis* (Nopcsa, 1925; Nessov *et al.*, 1998). Specimens MSNM V 3661 and 4014 are much smaller than the known material referred to *Pachyrhachis* and *Simoliophis*, and the material referred to *Eupodophis* just mentioned, but they share characters both with *Pachyrhachis* (in the skull) and *Eupodophis* (in the postcranial skeleton), and therefore they also share similarities, *impliciter*, with *Simoliophis*.

We are here taking a conservative approach to specimens MSNM V 3661 and 4014 in considering them juveniles of *Eupodophis descouensi* Rage & Escuillié (2000), rather than a separate taxon of small snakes (see the discussion of the unusually wide neural canal in these specimens above). One of the problems here is that the skull of the holotype of *Eupodophis descouensi* is very poorly and incompletely preserved, and no skull is preserved in specimen MSNM V 3660. This leaves for comparison the postcranial skeleton only. It is not inconceivable, however, that future finds of larger specimens with a skull referable to *Eupodophis descouensi* may show that the small individuals here described belong to a different species.

The skull characters which the specimens MSNM V 3661 and 4014 collectively share with *Pachyrhachis* (but not with *Haasiophis*) include the relatively long frontals, the shape of the postorbital, the shape and proportions of the ectopterygoid, and the high coronoid of rectangular outlines (the quadrate is broad in MSNM V 4014, but narrow in MSNM V 3661; this character must therefore be considered polymorphic unless it is due to a preservational artifact). The postcranial characters which the specimens MSNM V 3661 and 4014 share with *Eupodophis* are the absence of lymphapophyses in the cloacal region (present in *Pachyrhachis*: see the re-interpretation of the putative sacral rib described by Lee & Caldwell [1998] as a lymphapophysis [Lee, 1998; Scanlon & Lee, 2000]), and the presence of elongated, proximally bifurcated chevrons (possibly absent in *Pachyrhachis*, but only the very proximal part of the tail is known for that genus). The specimens MSNM V 3661 and 4014 also share characters with *Haasiophis*, such as the posteriorly weakly expanded free ending process of the supratemporal. Given this character distribution, there can be little doubt that specimens MSNM V 3661 and 4014 may represent juvenile specimens of *Eupodophis*, that *Eupodophis* may be more closely related to *Pachyrhachis* than *Haasiophis* on the basis of skull structure, and that the three taxa represent three different species. However, no part of the skull is preserved in the material that has so far been referred to *Simoliophis*, nor is it known whether *Simoliophis* did have lymphapophyses in the cloacal region, or chevrons in the tail. Since *Pachyrhachis problematicus* cannot be recognized as different from *Simoliophis*, *Pachyrhachis* can be considered a junior synonym of *Simoliophis*. In contrast, *Eupodophis* can be recognized as distinct, such that it is kept separate from *Simoliophis*. *Haasiophis* would then be a third, monotypic genus in the family Pachyophiidae Nopcsa 1923 (1923a).

Amongst the marine Cenomanian snakes here discussed, mid-trunk pachyostosis is expressed to a lesser degree in *Eupodophis* and *Mesophis* than in *Haasiophis*, *Pachyrhachis*, *Pachyophis*, *Simoliophis*. However, there is a possibility of ontogenetic differences in the extent of pachyostosis. *Pachyrhachis* shares with *Eupodophis* the abrupt shortening of the last few dorsal ribs (not preserved in *Mesophis* and *Simoliophis*), the elongated frontals, the broad quadrate (conservatively considered polymorphic in *Eupodophis*) and the tall and rectangular coronoid process (the skull is not preserved in *Mesophis* and *Simoliophis*). *Pachyophis* shares with *Pachyrhachis*, *Eupodophis* and *Simoliophis* the tall neural spines on the anterior precloacal vertebrae, and the laterally strongly compressed body, the latter a character that is also present in *Mesophis*. In summary, the genera *Eupodophis*, *Mesophis*, *Pachyophis*, *Pachyrhachis and Simoliophis* appear more closely related to each other and to *Simoliophis* than either is to *Haasiophis*. This, indeed, is also strongly reflected in terms of skull morphology (as described and discussed above), which is known for *Eupodophis*, *Haasiophis*, and *Pachyrhachis*, but not for the other three taxa of pachyostotic Cenomanian marine snakes. At the bottom line, however, some of the taxa (*Mesophis*, *Pachyophis*, and *Simoliophis*) are just too incompletely preserved to warrant a more complete phylogenetic analysis.

GENERAL CONCLUSIONS

The genus *Eupodophis* from the Cenomanian of Lebanon is part of a mid-Cretaceous radiation of marine snakes in the western Tethyan (Neotethys) faunal realm, which also includes the genera *Haasiophis*, *Mesophis*, *Pachyophis*, *Pachyrhachis*, and *Simoliophis* (Rage & Escuillié, 2003). Amongst those taxa, well-developed hind limbs are known to occur in *Eupodophis*, *Haasiophis*, and *Pachyrhachis*, but recognizing their close interrelationships, Rage & Escuillié (2003) hypothesized that such hind limbs may also have been present in the other genera known from that radiation. As noted by Rage & Escuillié (2003: 7; see also Rage & Escuillié, 2000), the combination in these snakes of a macrostomatan skull with the presence of well-developed hind limbs "poses a serious problem," because "two diametrically opposite" phylogenetic conclusions may obtain. The hypothesis that the fossil snakes with well-developed hind limbs are basal to all extant snake lineages (Lee & Caldwell, 1998; Lee & Scanlon, 2002) implies that the macrostomatan skull is primitive for snakes (Rage & Escuillié, 2000, 2003). Alternatively, and on the basis of the current morphology-based phylogeny for extant snake lineages (which places scolecophidians and 'anilioids' basal to macrostomatans: e.g., Cundall *et al.*, 1993; Cundall & Greene, 2000; Tchernov *et al.*, 2000; Lee & Scanlon, 2002), the hypothesis that the fossil snakes are basal macrostomatans (Rieppel *et al.*, 2002) implies that the well-developed hind limbs either redeveloped in the fossil snakes, or that hind limbs were subject to repeated reduction and loss within snakes (Rieppel *et al.*, 2003; see also the discussion in Coates & Ruta, 2000).

However, recent molecular studies of snake interrelationships (Wilcox *et al.*, 2002; Slowinski and Lawson, 2002; Vidal & David, 2004; Vidal & Hedges, 2004) have called into question the current understanding of the phylogeny of extant snakes as based on morphology in several respects. Most importantly, there is a recurrent signal for a basal position of the macrostomate genera *Tropidophis* and *Tachyboa* outside the conventional macrostomatan clade (Wilcox *et al.*, 2002), possibly close to *Anilius* (Vidal & David, 2004; Vidal & Hedges, 2004). Conversely, the non-macrostomate genus *Cylindrophis* and the related uropeltines may nest inside the conventional macrostomatan clade (Wilcox *et al.*, 2002; Vidal & David, 2004; Vidal & Hedges, 2004). These molecular findings, if confirmed by future studies, may well result in a novel understanding of snake interrelationships that may cast new light on the interpretation of the Cenomanian snakes with well-developed hind limbs.

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MEMORIE

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PALEODIVERSITY OF THE FREE-LIVING POLYCHAETES (ANNELIDA, POLYCHAETA) AND DESCRIPTION OF NEW *TAXA* FROM THE UPPER CRETACEOUS *LAGERSTÄTTEN* OF HAQEL, HADJULA AND AL-NAMOURA (LEBANON)

MILANO FEBBRAIO 2005

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Giacomo Bracchi & Anna Alessandrello

Sezione di Paleontologia degli Invertebrati, Museo Civico di Storia Naturale di Milano

Paleodiversity of the free-living polychaetes (Annelida, Polychaeta) and description of new *taxa* from the Upper Cretaceous *Lagerstätten* of Haqel, Hadjula and Al-Namoura (Lebanon)

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In copertina: olotipo di *Eunicites diopatroides* n. sp. Foto di Roberto Appiani.

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Giacomo Bracchi & Anna Alessandrello

Paleodiversity of the free-living polychaetes (Annelida, Polychaeta) and description of new *taxa* from the Upper Cretaceous *Lagerstätten* of Haqel, Hadjula and Al-Namoura (Lebanon)

Abstract - The present work reports the results of a morphologic and taxonomic study of 377 specimens of free-living fossil polychates hold in the collections of the Museo Civico di Storia Naturale di Milano. The examined specimens come from the Cenomanian (Upper Cretaceous) *Lagerstätten* of Haqel (361), Hadjula (15) and Al-Namoura (1) (Lebanon). A systematic definition at species level has been possible for 110 specimens from Haqel and 2 from Hadjula so as 6 families (Aphroditidae, Didonidae n. fam., Eunicidae, Goniadidae, Lumbrineridae and Oenonidae), 7 genera (*Didone* n. gen., *Eunicites*, *Ferragutia* n. gen., *Lumbriconerites*, *Paleoaphrodite*, *Phoeniciarabella* n. gen. and *Teruzzia* n. gen.) and 17 species (*Didone pulcherrima* n. gen. n. sp., *Eunicites diopatroides* n. sp., *Eunicites falcatus* n. sp., *Eunicites joinvillei* n. sp., *Eunicites mariacristinae* n. sp., *Ferragutia cenomaniana* n. gen. n. sp., *Lumbriconereites garassinoi* n. sp., *Lumbriconereites hadjulae* n. sp., *Paleoaphrodite libanotica* n. sp., *Phoeniciarabella caesaris* n. gen. n. sp., *Phoeniciarabella orensanzi* n. gen. n. sp., *Phoeniciarabella pinnulata* n. gen. n. sp., *Teruzzia gryphoeides* n. gen. n. sp., *Teruzzia pezzolii* n. gen. n. sp., *Teruzzia pusilla* n. gen. n. sp. and *Teruzzia sagittifera* n. gen. n. sp.) of polychaetous annelids have been recorded from the Cenomanian fossiliferous levels of Lebanon.

In addition to the results of the study of the examined material is reported a systematic appraisal of the fossil polychaetes where the *taxa* described from Cambrian to Eocene are listed with regard to the free-living forms.

Key words - Lebanon, Cenomanian, Polychaeta.

Riassunto - Paleodiversità dei policheti a vita libera (Annelida, Polychaeta) e descrizione di nuovi *taxa* dai giacimenti a conservazione eccezionale del Cretacico superiore di Haqel, Hadjula e Al-Namoura (Libano).

Sono riportati i risultati di un'indagine volta allo studio morfologico e tassonomico di 377 esemplari di policheti fossili conservati nelle collezioni del Museo Civico di Storia Naturale di Milano. I fossili esaminati sono riferibili a organismi a vita libera e provengono dai giacimenti a conservazione eccezionale di Haqel (361), Hadjula (15) e Al-Namoura (1) (Libano settentrionale), tutti di età cenomaniana (Cretacico superiore). Gli esemplari per cui è stato possibile proporre una classificazione a livello di specie (112) provengono per la quasi totalità da Haqel (110), in minima parte da Hadjula (2). Tali esemplari sono stati attribuiti a 6 famiglie (Aphroditidae, Didonidae n. fam., Eunicidae, Goniadidae, Lumbrineridae e Oenonidae), 7 generi (*Didone* n. gen., *Eunicites*, *Ferragutia* n. gen., *Lumbriconerites*, *Paleoaphrodite*, *Phoeniciarabella* n. gen. and *Teruzzia* n. gen.) e 17 specie (*Didone pulcherrima* n. gen. n. sp., *Eunicites diopatroides* n. sp., *Eunicites falcatus* n. sp., *Eunicites joinvillei* n. sp., *Eunicites mariacristinae* n. sp., *Ferragutia cenomaniana* n. gen. n. sp., *Lumbriconereites garassinoi* n. sp., *Lumbriconereites hadjulae* n. sp., *Paleoaphrodite libanotica* n. sp., *Phoeniciarabella caesaris* n. gen. n. sp., *Phoeniciarabella orensanzi* n. gen. n. sp., *Phoeniciarabella pinnulata* n. gen. n. sp., *Teruzzia gryphoeides* n. gen. n. sp., *Teruzzia pezzolii* n. gen. n. sp., *Teruzzia pusilla* n. gen. n. sp. and *Teruzzia sagittifera* n. gen. n. sp.) eleggendo il giacimento di Haqel quale *Lagerstätten* mesozoico per cui è nota la più ampia e varia fauna di organismi vermiformi.

Accanto all'esposizione dei risultati ottenuti dallo studio del materiale considerato viene riportata una *check-list* di famiglie, generi e specie di policheti fossili noti dal Cambiano all'Eocene, con riferimento alle sole forme a vita libera.

Parole chiave - Libano, Cenomaniano, Polychaeta.

INTRODUCTION

The first scientific treatise on the fossil fauna from the Upper Cretaceous *Lagerstätten* of Lebanon was edited during the first half of the XIX century. The first paleontological note regarding the Lebanese ichthyolithic limestones consists of a description of two new species of clupeomorph fish by De Blainville (1816) in "Nouveau Dictionnaire d'Histoire Naturelle". The fossil fish from Lebanon had previously been cited by Herodotus (450 B.C.) and later by Sir Jean de Joinville (1248, 1309) in his memoirs about the crusades of King Louis IX. The fossil ichthyofauna from the Cretaceous *Lagerstätten* in Lebanon were also mentioned in various volumes published during the XVIII century, such as the following editions of the "Voyage au Levant" (Le Brun, 1714; Banjer, 1725), "Travels or observations" (Shaw, 1738) and "Traité des Pétrifications" (Bourguet, 1742). The presence of both land plants and marine molluscs within the same outcrops was first reported by Volney (1787). The toponym "Haqel" (also written as "Hakel" or "Haql") first appears as "Heckel" in the new edition of the fifth volume of "Voyage au Levant" (Le Brun, 1725): nowadays this toponym reminds one of the richest fossiliferous locality within the Mesozoic.

There were many contributions on land plants, vertebrates and invertebrates from the Lebanese Cretaceous *Lagerstätten* in the years following the publication by De Blainville (1816). Agassiz (1833-1844), Egerton (1844), Heckel (1849), Pictet (1850), Pictet & Humbert (1866), Lewis (1878) and Sauvage (1878) all increased the knowledge about the ichthyofauna from the localities of Haqel and Sahel-Alma, describing several new genera and species of bony and cartilaginous fish. In the following decades new *taxa* of teleosts, sharks and rays were described by Dawis (1895), Woodward A.S. (1892, 1895a, 1895b, 1898, 1899a, 1899b, 1901, 1942), Hay (1903a, 1903b, 1903c), Roger (1946), Patterson (1967, 1970), Forey (1973, 1997), Capetta (1980), Goody (1969a, 1969b), Gaudant (1975, 1976, 1978a, 1978b), Gayet (1980a, 1980b, 1984, 1988), Tyler & Sorbini (1996), Bannikov & Bacchia (2000), Belouze & Gayet (2001), Brito & Dutheil (2001), Nursall & Capasso (2001), Zaragueta Bagils (2001), Poyato-Ariza & Wenz (2002), Capasso (2003) and Forey *et al.* (2003). Terrestrial vertebrates were first recorded by Lartet (1869) who referred to a fossil lizard from Sahel-Alma: the actual systematic relationships of this reptile should be revised because Sahel-Alma is characterized by a particularly open sea facies (Dalla Vecchia, pers. comm.). More recently, Krassilov & Bacchia (2000) and Dalla Vecchia *et al.* (2002) mentioned the exsistence of articulated phalanges assignable to a theropod dinosaur in a small store in Jbail, locality near Al-Namoura (also written as "en Nammoûra", "Nammoura" or "Namoura"). The first avian skeletons from the northern Gondwana has been also discovered in Al-Namoura together with some small feathers (Dalla Vecchia & Chiappe, 2002; Dalla Vecchia *et al.*, 2002). Four tiny amber inclusions are exceptionally preserved in the latter and are the first record of fossil resin from Al-Namoura. However, the presence of amber in fossiliferous outcrops in Lebanon had already been recorded from the Lower Cretaceous localities of Hammana, Kdeirji, Mdeyrji and others, so as several nematodes, snails, mites, opilionids, spiders, insects, the oldest reptile (lizard) in amber and the first complete feather preseerved in a fossil resin have been described (Hennig, 1972; Schlee, 1973; Szadwieski, 1995, 1996; Prentice *et al.*, 1996; Azar *et al.*, 1999a, 1999b, 2000, 2003; Borkent, 2000; Grimaldi, 2001, 2004; Poinar & Milki, 2001; Podenas *et al.*, 2001; Arnold *et al.*, 2002; Azar & Nel, 2003; Penney & Selden, 2002; Lukaschevich & Mostovski, 2003; Penney, 2003; Perrichot *et al.*, 2003; Nel *et al.*, 2004). Moreover, Al Namoura has yielded new genera and species of semiaquatic (Dal Sasso & Pinna, 1997; Dal Sasso & Renesto, 1999) and flying reptiles (Dalla Vecchia *et al.*, 2001) together with an hindlimbed snake (Rage & Escuillié, 2000, 2001, 2003; Rieppel & Head, 2004) and at least six specimens of chelonians (Dalla Vecchia *et al.*, 2002). The notes by Russegger (1836), Roger (1946), Dilcher & Basson (1990), Dalla Vecchia & Venturini (1999), Krassilov & Bacchia (2000) and Dalla Vecchia *et al.*, (2002) concerning the algae and land plants (cycadophytes, auraucarias and angiospermae) from Hadjula (also written as "Hadjoula" or "Hjoula") and Al-Namoura are also worth mentioning.

The first reference to Cretaceous invertebrates from the Lebanese *Lagerstätten* was by König (1825) who illustrated two ophiuras from Haqel. Botta (1833) was the first to mention the crustacean fauna from Sahel-Alma while Brocchi (1875) gave the first scientific description of a fossil invertebrate from Haqel, the decapod crustacean *Penaeus libanensis*. Fraas (1878) and Dames (1866) described and revised decapod crustaceans and cephalopods.

The decapod crustaceans from the Upper Cretaceous *Lagerstätten* in Lebanon represent the most well-known aspect of the invertebrate fauna discovered here to date. Thanks to the works by Fraas (1878), Dames (1886), Van Straelen (1930, 1940), Glaessner (1945), Roger (1946), Förster (1984) and Garassino (1994, 2000, 2001), several specimens of macruran decapods have been assigned to the Aegeridae, Benthesicymidae, Callianassidae, Erymidae, Glypheidae, Nephropidae, Oplophoridae, Palinuridae, Penaeidae, Scyllaridae and Stenopodidae. In addition to the above, Garassino (1994) also described a new family, the Carpopenaeidae. Withers (1928), Roger (1946) and Förster (1968) contributed to the knowledge of the brachyuran decapods from the same *Lagerstätten*: Förster (1968) assigned the material he examined to the Calappidae, whereas the specimen formerly assigned to a living genus of Xanthiidae by Roger (1946) has been recently revised as a new genus of the Necrocarcinidae (Larghi, 2004). Other Cretaceous brachyurans from Lebanon have been assigned to a new species of Raninidae (Dames, 1866; Glaessner, 1945; Roger, 1946), even if the type material needs revision (Garassino, pers. comm.), and to a new subfamily and a new genus of Dorippidae (Larghi & Garassino, 2000; Larghi, 2004). Dames (1886), Van Straelen (1938), Roger (1946), Teruzzi (1983), Schram *et al.* (1999) and Lange *et al.* (2000) have also reported the presence of cirriped, mysidacean, stomatopod and thylacocephalan crustaceans.

Apart from the crustacean studies, few investigations of the other invertebrates preserved in the Upper Cretaceous *Lagerstätten* of Lebanon have been carried out and the fauna is mainly still unrecorded. Some data have been reported by Fraas (1878), Woodward H. (1879, 1883), Kolbe (1888), A.S. Woodward (1896), Naef (1922), Roger (1946), Engeser & Reitner (1986), Forey *et al.* (2003), Novati (2003) and Fuchs (in press) regarding foramminifers, molluscs, horseshoe crabs, insects, opilionids and echinoderms. This is probably a reflection of the methods applied in the collection of the fossils: the Lebanese limestones have been and are often excavated by the local population that disregard small fossils of no aesthetic interest, because of their limited economical value. Consequently, very little data about Lebanese fossil polychaetes have been collected to date by Roger (1946) and Kozur (1971). The former author studied some mouth apparata, scolecodonts and incomplete specimens from Haqel and Hadjula. He assigned a maxillary apparatus and an incomplete specimen to the fossil eunicid *Eunicites* Ehlers, 1868 and an incomplete specimen to the living phyllodocid *Phyllodoce* Savigny, 1818. Two poorly preserved specimens were described by Roger (1946) as indeterminable "worms" or "annelids?". In the same way, Kozur (1971) described two polychaete specimens from Haqel as indeterminate eunicids. However, in recent years, due to an increasing interest in some previously neglected invertebrate *taxa*, several specimens of cephalopods, nematodes, polychaetes and echiurans from the Lebanese *Lagerstätten* are now housed within the collections of some scientific institutions, such as the

Museo Civico di Storia Naturale di Milano (Alessandrello *et al.*, 1995). To date this has resulted in two publications regarding descriptions of a new polychaete species, *Eunicites phoenicius* Alessandrello & Teruzzi, 1986, and a new tetrameric nematode (Alessandrello & Mattavelli, in press), both from Haqel.

Aims of the present study are the description of approximately 400 specimens of free-living polychaetes from the Cenomanian of Lebanon as well as a systematic appraisal, with regard to the free-living forms, of the fossil polychaetes where the *taxa* described from Cambrian to Eocene are listed.

STUDY AREA AND GEOLOGICAL SETTING

The examined specimens come from the sub-lithographical limestones of Haqel, Hadjula and Al-Namoura, the most celebrated fossiliferous localities of Lebanon, renowned world-wide for the variety and the excellent conservation of the preserved fauna. These localities are located in north-west Lebanon, some kilometres north-east of Beirut, together with the other paleontological sites of Sahel-Alma, Maifouk and Dahr-el-Kelb. The sites of Haqel and Hadjula are positioned 12 km from the Lebanese coast, at an altitude of approximately 700 m above sea level. They are about 4 km distant from each other and 45 km from Beirut. Maifouk and Dahr-el-Kelb are located a few kilometres north of Hadjula, whereas the 15 m to 30 m thick limestones of Al-Namoura outcrop closer to the coast, 25 km south of Haqel and 20 km north of Beirut.

Geological studies on the Cretaceous outcrops of Lebanon were started in the second half of the XIX century by Botta (1833), who investigated the lithology of the Haqel and Sahel-Alma areas. Some years later, Heckel (1849) assigned an Upper Cretaceous age to Sahel-Alma, while Pictet & Humbert (1866) suggested a slightly older age for Haqel. The first geological data concerning the locality of Hadjula was published by Lewis (1878) and Fraas (1878), who considered both Haqel and Hadjula as Turonian in age. However, the Cenomanian age of Haqel, Hadjula and Maifouk was later recognized by Douvillé (1910), Zumoffen (1926) and Patterson (1967). Blankehorn (1926), Dubertert & Vautrin (1937) and Ejel & Dubertret (1966) dated Sahel-Alma back to the Senonian. The biostratigraphical studies of Dubertret (1959, 1966), Hückel (1969, 1970, 1974a, 1974b) and Saint Marc (1974) placed the sequences at Haqel, Hadjula and Maifouk at the Lower-Middle Cenomanian boundary. According to Hemleben (1977) Haqel and Hadjula are younger: he dated back these sites to the late Cenomanian. Hückel (1970) also attested the younger age of the Haqel strata that actually occur twenty metres higher stratigraphically than those of Hadjula. At the same time, the strata at Sahel-Alma and Al-Namoura have been dated back, through the investigation of the foraminifera fauna, to the late Senonian (Ejel & Dubertret, 1966) and to the middle Cenomanian (Dalla Vecchia & Venturini, 1999; Dalla Vecchia *et al.*, 2002; Forey *et al.*, 2003) respectively.

According to Hückel (1969, 1970, 1974a, 1974b), Hemleben (1977) and Capetta (1980), the sub-lithographical limestones from Haqel and Maifouk are hard, fine grained, well-bedded and laminated, often characterized by a rich fossiliferous content, a yellowish colour that sometimes may become greyish. Some levels of the Haqel outcrop are particularly rich in flint nodules. The same authors describe the limestone from Hadjula as a more compact, soft and laminated rock, characterized by a lighter yellow or grey-yellow colour and without flint nodules. In comparison with the rocks from the other Lebanese sites, the limestone from Sahel-Alma is lighter coloured (Capetta, 1980). The limestone from Al-Namoura is very thinly laminated, green to grey-blue in colour and is rich in flint nodules (Dalla Vecchia & Venturini, 1999).

PRESERVATION

The favourable conditions present for fossilization during the late Cretaceous in Lebanon are expressed in the state of preservation of the polychaetes and other soft-bodied metazoans. Compared with those from other *Lagerstätten* the polychaetes from Haqel are among the best preserved fossil worms known (Briggs & Kear, 1993). With regard to the lightly skeletized tissues, the fossil polychaetes from Lebanon show preservation of the cuticle (samples MSNM i26329 (Fig. 1), MSNM i26335 and MSNM i26338), resistant against degradation thanks to its structure of collagen fibers arranged in crossed strata and enriched with biopolymers (Storch, 1988; Stankiewicz *et al.*, 1997), the chaetae, in living polychaetes formed of sclerotinized chitin and inorganic material (Specht, 1988; Butterfield, 1990a), and the pharyngeal apparatus. The latter varies greatly in composition in the modern polychaetes (Olive, 1980) but it is generally formed of sclerotinized collagen mineralized with calcite or aragonite (Voss-Foucart *et al.*, 1973; Fauchald & Rouse, 1997). In some *taxa*, such as the oenonids and certain glyceroideans, the jaws and maxillae are strenghtened with metal-ions, such as iron, copper or zinc (Colbath, 1986, 1988; Colbath & Larson, 1987; Purschke, 1988; Eriksson & Elfman, 2000), and with organic compounds, such as tanned proteins, aromatic aminoacids, glycerine and hystidine (Bergman, 1989). In the material examined here, the chaetae and pharyngeal apparata are preserved both as molds and mineralized structures but the latter is more common than the former. In some specimens the mineralized elements that comprise the pharyngeal apparatus are black and shiny, in others they are whitish and pearly. The former type of fossilization often involves also the three-dimensionally preserved chaetae. In the examined specimens the lighter coloured material is resulted typical of the mouth apparatus of the labidognath eunicidans, such as the eunicids and lumbrinerids, while the darker material is resulted typical of the prionognath eunicidans, such as the oenonids (Colbath, 1986; Fauchald & Rouse, 1997). Some of the specimens examined (MSNM i9355 for example) possess a pharyngeal apparatus impregnated by a very flaky and whitish mineral. With regard to soft-tissue preservation, the fossil polychaetes from Lebanon generally show traces of the alimentary canal and body outline only, although two anal cirri have been recognized by the authors in a lumbrinerid specimen (MSNM i13301) and in an undetermined specimen (MSNM i23414). Some longitudinal muscle bundles are evident in two goniadid samples (MSNM i12423 and MSNM i24961). Worthy of note are the traces of pigmentation in the undetermined specimen MSNM i26326 (Fig. 2), a feature already observed by Arduini *et al.* (1982) in a fossil lumbrinerid from the prealpine *Lagerstätte* at Osteno (Lower Jurassic), northern Italy. Most of the samples examined in the present study have usually been found flattened along the bedding plane and they show a dorso-ventral compression, even if in a few cases a lateral compression is evident.

Fig. 1 - MSNM i26329, undetermined specimen preserving the cuticle.

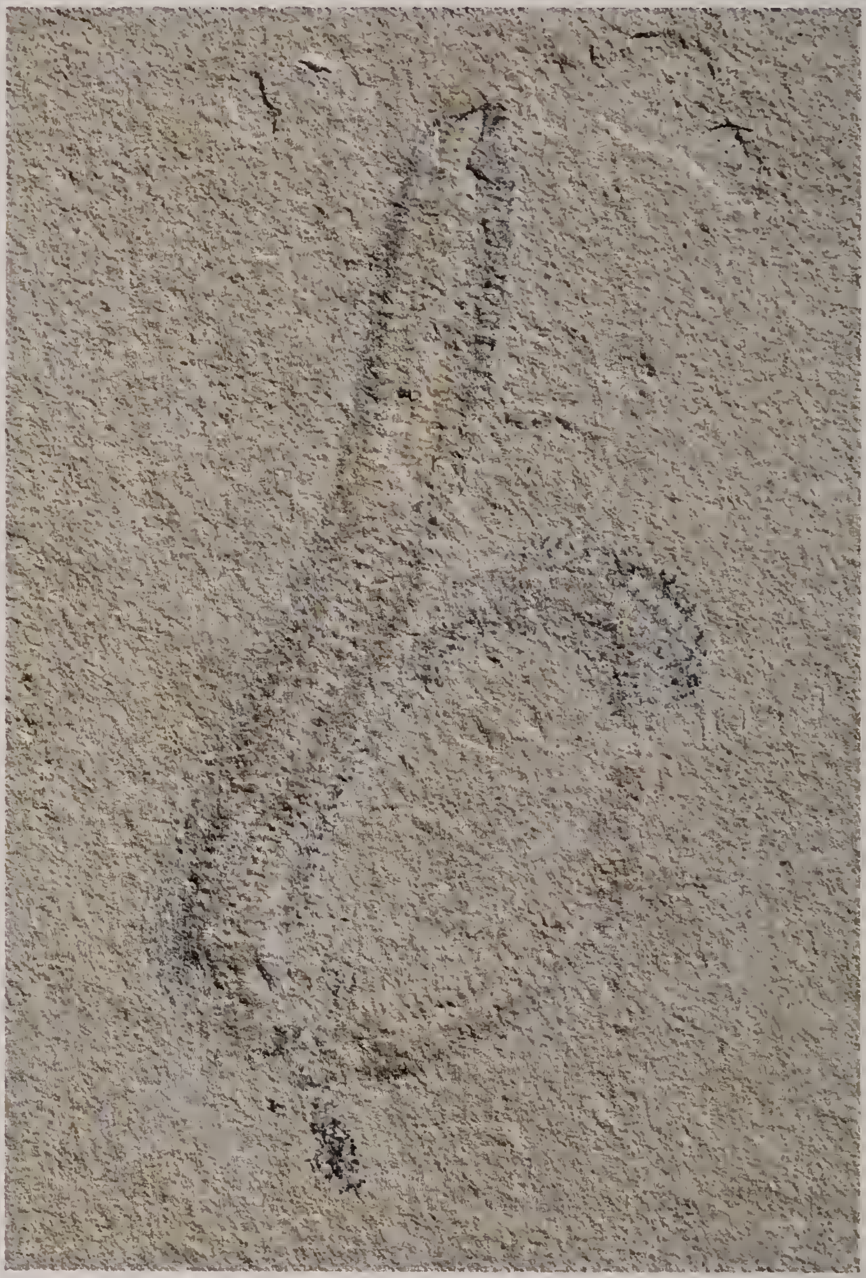

Fig. 2 - MSNM i26326, undetermined specimen preserving traces of pigmentation.

MATERIALS AND METHODS

There are 379 polychaete specimens (see Appendix) from the Upper Cretaceous of Lebanon housed in the paleontological collections of the Museo Civico di Storia Naturale di Milano (MSNM). Two specimens from Haqel have already been described by Alessandrello & Teruzzi (1986) as *Eunicites phoenicius*. Among the samples examined here, 362 are from Haqel, 15 from Hadjula (MSNM 25107, MSNM i25108, MSNM i25109, MSNM i25110, MSNM i25113, MSNM i25115, MSNM i25116, MSNM i25119, MSNM i25120, MSNM i25125, MSNM i25443, MSNM i26332, MSNM i26335, MSNM i26336 and MSNM i26338) and 1 (MSNM i9363) from Al-Namoura.

The systematic relationships of the examined specimens have been recognized, where possible, through comparisons with both fossil and living species.

The polychaete taxonomy adopted in this work essentially follows Fauchald (1977).

POLYCHAETE FOSSIL RECORD

The polychaete fossil record includes traces, articulated pharyngeal apparata, isolated elements of the jaw apparatus and, more rarely, fully preserved specimens (Howell, 1962; Häntzschel, 1975; Wills, 1993). The isolated elements of the pharyngeal apparata of the euniceans and glyceroideans are particularly common in Paleozoic deposits: they have been defined by Croneis & Scott (1933) as "scolecodonts". Since the erection of a taxonomic scheme based on fragmentary specimens does not comply with the rules of the International Code of Zoological Nomenclature (Aldridge, 1990) and in consideration of the the difficulty of comparing articulated apparata, whole-preserved specimens and scolecodonts, it follows that the latter should have, in the same way as the conodonts, a biostratigraphical and paleoecological value but not a useful systematical significance (Zawidzka, 1975; Bergman, 1989, 1995, 1998; Hints, 1999a; Eriksson, 1998; Eriksson & Bergman, 2003; Eriksson & Leslie, 2003). This is for example the case of the arabellid genus *Synclinophora* Eisenack, 1975 from the Silurian of Sweden and Poland, recently re-described by Mierzejewski (1984) based on an articulated maxillary apparatus. This apparatus is difficult to compare with those of the arabellid specimens from Lebanon that we have described here. Even though the Lebanese arabellids also have the jaw apparatus and part of the body preserved, however, in most cases, the maxillae are lacking. Thus, for a long time, most of those studying the polychaetes have argued that parataxonomical investigations of the scolecodonts should be kept separate from the orthotaxonomical studies on full-preserved specimens (Eller, 1964; Bengston, 1985a; Tasch & Stude, 1965). A *parataxon* has been defined by Melville (1959) as "a *taxon* based on a fragment [...] which can be classified at the genus-group and species-group levels [...] but cannot be assigned to the same *(ortho)taxa* at those levels as the whole animal to which they belong". However, some authors, such as Snajdr (1951), Kielan-Jaworovska (1961, 1968) and Kozur (1970, 1971), have tried to combine the orthotaxonomical and parataxonomical investigations of the fossil polychaetes. Consequently, over the last 40-50 years, some authors have used the scolecodonts to reconstruct articulated apparata (Lange, 1949; Kozlowski, 1956; Sylvester, 1959; Kielan-Jaworovska, 1962, 1966; Szaniawski, 1968, 1970, 1974; Kozur, 1971; Szaniawski & Wrona, 1973; Corradini & Olivieri, 1974; Jansonius & Craig, 1974, 1975; Mierzejewski & Mierzejewska, 1975; Mierzejewski, 1978; Szaniawski & Gadzicki, 1978; Bergman, 1979, 1981; Männil & Zaslavskaya, 1985a, 1985b; Colbath, 1987; Szaniawski & Imajima, 1996; Hints, 1999a, 1999b; Eriksson & Bergman, 1998; Eriksson, 2003a). This method has been criticized by Jansonius & Craig (1971), Szaniawski & Wrona (1973) and Thompson & Johnson (1977), although according to Bergman (1989, 1991) some Paleozoic scolecodonts should be orthotaxonomically investigated and compared both at the genus and species level. On the one hand, the application of this method has resulted in the resolution of some problems within polychaete systematics, thanks to the recognition of several "form genera" (Edgar, 1984), or rather in the recognition of some scolecodonts as belonging to later discovered jaw apparata or whole-preserved specimens (Eriksson & Bergman, 1998; Nakrem *et al.*, 2001). On the other hand, the same method has contributed to confusion within polychaete systematics, both because a high number of synonyms have been yielded when scolecodonts occur in more than one form genus and as some *parataxa* have been absorbed by some *orthotaxa*. In even worse cases, some scolecodonts have been assigned to previously described *orthotaxa*, thus generating serious problems in the use of the same *orthotaxa* during the description of newly discovered fully preserved specimens. This is, for instance, the case of *Eunicites* Ehlers, 1868 and *Lumbriconereites* Ehlers, 1869, both based on full-preserved specimens but later adopted in order to classify several scolecodonts.

As pointed out by Howell (1962) and Wills (1993) polychaete traces, scolecodonts, jaw apparata and full-preserved specimens have been recorded in Paleozoic, Mesozoic and Cenozoic rocks, ranging from the Cambrian to the Pleistocene. The presence of polychaete annelids within the Precambrian still requires definitive confirmation (Xiao *et al.*, 2001; Sepkoski, 2002). Several Ediacaran fossils have been assigned to the Polychaeta (Glaessner, 1976a, 1976b, 1979) however, even if in some cases they appear to actually possess some polychaete characters, their systematic relationships remain unsubstantiated. Only *Spriggina* Glaessner, 1958 has been definitively accepted as an arthropod-like metazoan. The genera *Parmia* Gnilovskaya, 1998, *Pararenicola*, Wang, 1983 *Ruedemannella* Howell, 1969 and *Protoarenicola* Wang, 1983 from the Upper Riphean (Lower Algonkian) of Russia (Timan biota) and China (Huainan biota) are considered to be non-free-living "annelidomorphs" (Gnilovskaya *et al.*, 2000), enigmatic polychaetes (Howell, 1965) or enigmatic metazoans (Sun *et al.*, 1986; Chen, 1988). However, some authors (Qian *et al.*, 1999) have recently re-interpreted *Protoarenicola* and *Ruedemannella*, the latter found also in the Pridolian (Upper Silurian) of New York State (Howell, 1959), as a megascopic alga, while other researchers (Sun *et al.*, 1986; Chen, 1988; Xiao *et al.* 2001) suspect that *Pararenicola* and *Protoarenicola* are sponges.

In the following paragraphs an annotated check-list has been compiled for the free-living forms of the fossil polychaetes ranging in age from Cambrian to Eocene. Only those with a description based on full-preserved specimens have been included. Families and genera are ordered alphabetically. The fact that the fossil free-living polychaetes need a general systematic revision clearly emerges from the check-list, in particular with regard to the Mesozoic euniceans as well as the *taxa* described in the first half of the XX century or earlier. Moreover, the check-list underlines that the fossil record of the whole-preserved free-living polychaetes is rather poor due to the essentially soft-bodied nature of these invertebrates: taking into account also the *taxa* of essentially uncertain affinities, approximately only 15-20% of the extant families have been recognized within the fossil fauna. Full-preserved polychaetes are more abundant where exceptional conditions of fossilization prevail: in addition to that of Haqel, some famous *Lagerstätten* such as the Burgess Shale (Cambrian, British Columbia), Bear Gulch (Carboniferous, Montana), Mazon Creek (Carboniferous, Illinois), Grès à Voltzia (Triassic, France), Osteno (Jurassic, Italy), La Voulte sur-Rhône (Jurassic, France), Solnhofen (Jurassic, Bavaria), Ponte Giurino (Triassic, Italy) and Bolca (Eocene, Italy), have yielded several examples of exceptionally preserved specimens (Briggs & Clarkson, 1987; Alessandrello, 1990a; Briggs & Kear, 1991; Etter, 2002a, 2002b; Hagadorn, 2002a, 2002b; Schellenberg, 2002; Tang, 2002; Alessandrello & Bracchi, 2004; Alessandrello *et al.*, 2004).

An updated polychaete fossil record including both *parataxa* and sedentary forms is given in Sepkoski (2002).

Family Amphinomidae Savigny in Lamarck, 1818

(Carboniferous-Recent)

Full-preserved amphinomids have been recorded from the Upper Carboniferous of Europe and North America, more precisely from the Kasimovian-Gzelian (Upper Carboniferous) of Montceau-les-Mines (Pacaud *et al.*, 1982; Rolfe *et al.*, 1982; Heyler, 1986; Heyler & Poplin, 1988), France, and from Mazon Creek (Meek & Worthen, 1865; Thompson, 1979). The only Mesozoic full-preserved amphinomids have been described by Ehlers (1869) from the Solnhofen *Plattenkalk*. The specimens described by Ehlers (1869) and Thompson (1979) retain imprints of the soft body as well as bunches of bristly spines. In the living organism, these bristles were probably filled with poison. Some modern amphinomids possess nearly identical poisonous spines which justify the nickname "fireworms" used for these polychaetes.

***Meringosoma* Ehlers, 1869** (Jurassic; Germany) - This genus includes only the type species *M. curtum* Ehlers, 1869, characterized by a short (2-3 cm), oval and flattened body equipped with bristles at the mid-length. However, in the opinion of the authors and in consideration of what can be deduced from the available plates and photos, the systematic relationships of *Meringosoma* should be revised in respect of the recent discovery of several aphroditids in some Mesozoic *Lagerstätten*.

***Paleocampa* Meek & Worthen, 1865** (Carboniferous; Illinois and France) - Meek & Worthen (1865) described a full-preserved worm-like organism from the Coal Measures of Illinois as *P. anthrax* Meek & Worthen, 1865. Thompson (1979) later described about thirty amphinomid specimens from the famous "Pit 11" mine of Mazon Creek as *Raphidiophorus hystrix* Thompson, 1979. In the following years several authors (Pacaud *et al.*, 1982; Rolfe *et al.*, 1982; Heyler, 1986; Heyler & Poplin, 1988; Briggs & Kear, 1993) reported full-preserved polychaetes referable to *Paleocampa* from the Carboniferous of Montceau-les-Mines, suggesting that *Paleocampa* and *Rhaphidiophorus* are synonyms. According to Schellenberg (2002), the taxonomic relationships of *Paleocampa* within the polychaetes is uncertain: a further revision of the fossil amphinomids is needed in order to resolve this issue and to verify the relationships between *Paleocampa* and *Raphidiophorus*. The latter was described by Thompson (1979) as an epifaunal or pelagic, probably carnivorous amphinomid bearing tentacular cirri, an unarmed pharynx and biramous parapodia with heavy and protective chaetae. The body of *R. hystrix* is short (20-25 mm) and includes few segments.

Superfamily Aphroditacea Fauchald, 1977

(Devonian?-Recent)

In the most recent linnean treatment of the polychaete taxonomy (Fauchald, 1977), the superfamily Aphroditacea includes six families often indicated as "scale-worms": Acoetidae Kingberg, 1856, Aphroditidae Malmgren, 1867, Eulephetidae Chamberlin, 1919, Polynoidae Malmgren, 1867, Pholoidae Kingberg, 1858 and Sigalionidae Malmgren, 1867. In the aphroditacean fossils the recognition of the characters that can be useful to hypothesize affinities with one of these families is rather problematic, particularly in the distinction among aphroditids, pholoids, polynoids and sigalionids. Since only a few species have been assigned doubtfully to the Pholoidae, Polynoidae and Sigalionidae in the aphroditacean fossil record, the definition of the scale-worms as a superfamily is considered by the authors of the present work as being more suitable to the usual situations observed for the fossils, in which real affinities with the aphroditacean families are, in most cases, only suspect.

Fossils which could be tentatively assigned to Sigalionidae have been recorded in the Ordovician of Minnesota (U.S.A.) by Stauffer (1933), who described the *parataxon Thalenessites* Stauffer, 1933, on the basis of some polygonous scales and jaws. More recently Alessandrello *et al.* (2004) have described the enigmatic aphroditacean *Protopholoe* Alessandrello, Bracchi & Riou, 2004 from La Voulte-sur-Rhône and pointed out some similarities between this Jurassic genus and the modern sigalionid *Pholoe* Johnston, 1839.

Some affinities with the Polynoidae have been pointed out for both Paleozoic and Mesozoic aphroditaceans: these are the Carboniferous scale-worms from Mazon Creek (Thompson, 1979) and the Triassic scale-worms from Grès a Voltzia (Gall & Grauvogel, 1966).

The fossil record of full-preserved specimens which could be assigned to Aphroditidae includes both Paleozoic (Clarke, 1903; Thompson, 1979) and Mesozoic (Alessandrello & Teruzzi, 1986b; Alessandrello, 1990b; Alessandrello *et al.*, 2004) genera. The Cenozoic genus *Sthenelaites* Rovereto, 1904 was proposed in order to absorbe (Rovereto, 1904) the Eocenic species *Nereites dasiaeformis* Massalongo, 1855 and it has been included among the aphroditids (Howell, 1962; Sepkoski, 2002). However, Alessandrello (1990a) recently revised *Sthenelaites* and identified it as a seaweed of the family Dasycladaceae. Thompson (1979) included the Carboniferous aphroditids from Mazon Creek within the new subfamily Hystriciolinae Thompson, 1979. The hystricioline aphroditids seem to be the most common polychaetes from Mazon Creek: they are jawed aphroditids that possess an eversible proboscis and biramous parapodia equipped with at least five types of chaetae that are however, lacking the elytrae. Other whole-preserved aphroditids have been recorded from both Gondwanan and Laurasian *Lagerstätten* of Mesozoic age (Alessandrello & Teruzzi, 1986b; Alessandrello *et al.*, 2004). These Triassic and Jurassic aphroditids show evidence of both jaws and elytrae occurring together with biramous parapodia and a variety of setal types. The fossil aphroditids are in need of systematic revision, in particular regarding the Mesozoic *taxa*.

***Dryptoscolex* Thompson, 1979** (Carboniferous; Illinois) - Hystricioline aphroditid known only on the basis of the type species *D. matthiesae* Thompson, 1979 from Mazon Creek. *Dryptoscolex* was probably an epifaunal polychaete, in life habits very similar to the non-commensal species of the modern family Polynoidae Malmgren, 1867 (Thompson, 1979). *D. matthiesae* is one of the few fossil aphroditids to possess an elongate worm-like body and a pharynx armoured with some jaw pieces.

***Fastuoscolex* Thompson, 1979** (Carboniferous; Illinois) - Predaceous aphroditids assigned by Thompson (1979) to the subfamily Hystriciolinae but strictly related to the epifaunal aphroditids. The genus includes only the type species *F. gemmatus* Thompson, 1979 from Mazon Creek: it is one of the few fossil aphroditids to possess a pharyngeal armature (Thompson, 1979).

***Homaphrodite* Gall & Grauvogel, 1966** (Triassic; France) - The type species *Homaphrodite speciosa* Gall & Grauvogel, 1966 from Grès à Voltzia is the only species recognized within this genus. The actual systematic relationship of *Homaphrodite* within the polychaetes should be revised through comparisons with the other Mesozoic aphroditids. This is particularly necessary as Thompson (1979) argued that *H. speciosa* should probably be moved to the Polynoidae Malmgren, 1867 because it possesses a pair of dorsoventral maxillae whose structure is quite similar to that of the modern representatives of the family (Gal & Grauvogel, 1966). However, a similar pattern of the pharyngeal armature has already been observed in both living (Fauchald & Rouse, 1997) and fossil aphroditids (Alessandrello *et al.*, 2004). In the opinion of Gall & Grauvogel (1966) *Homaphrodite* possesses elytrae.

***Hystriciola* Thompson, 1979** (Carboniferous; Illinois) - Epifaunal and free-living aphroditid known only on the basis of the type species *H. delicatula* Thompson, 1979 from Mazon Creek. It is the most common aphroditid in the Coal Measures of Illinois (Thompson, 1979).

***Paleoaphrodite* Alessandrello & Teruzzi, 1986** (Triassic-Cretaceous; Italy, France, Madagascar and Lebanon) - Most of the Mesozoic aphroditids found to date are included within this genus, which seems strictly related to the extant genus *Aphrodita* Linnaeus, 1758. This is especially true with regard to the general morphology and shape of the body, which is typically similar to that of the sea-mice, as well as for the architecture of the parapodial chaetae. In addition to the type species *P. raetica* Alessandrello & Teruzzi, 1986 from the Triassic of the Italian Prealps, the only species of the group that seems to preserve the elytrae (Alessandrello & Teruzzi, 1986b), the following have been recorded to date: *P. anaboranoensis* Alessandrello, 1990 from the Olenekian (Lower Triassic) of Madagascar, *P. adeliae* Alessandrello, Bracchi & Riou, 2004, *P. briggsiana* Alessandrello, Bracchi & Riou, 2004 and *P. gallica* Alessandrello, Bracchi & Riou, 2004 from La Voulte sur-Rhône, France. *P. briggsiana* and *P. adeliae* are the largest fossil aphroditids known (10-15 cm) and they are very similar to each other in the general morphology of the body. However, these two Jurassic species can be distinguished on the basis of the architecture of the jaw pieces that armour the pharynx: they are the only species of the genus that preserve these structures (Alessandrello *et al.*, 2004). *P. briggsiana* also shows evidence of the existence of an eversible pahrynx within the genus, while *P. adeliae* preserves a felt of capillary fibers on the dorsum. As they are naturally unlikely to be fossilized, capillary fibers must be considered, in the same way as the elytrae, as a poor diagnostic feature in systematic studies of *Paleoaphrodite* (Alessandrello & Teruzzi, 1986a; Alessandrello *et al.*, 2004). A new species *P. libanotica* n. sp. from Haqel is described in the present study. The gut content retained by one specimen of *P. libanotica* suggests a predatory habit for this genus, since it includes some fish vertebrae. The six species included within *Paleoaphrodite* to date should be revised by comparison with the other Mesozoic aphroditids.

***Protonympha* Clarke, 1903** (Devonian; Canada) - The type species *P. salicifolia* Clarke, 1903 is the oldest aphroditid known. This poorly known *taxon* has been found in the Devonian shales of Ontario County, Naples, Canada.

Family Burgessochaetidae Conway Morris, 1979
(Cambrian)

Monospecific family established by Conway Morris (1979) subsequent to the revision of some specimens from the Burgess Shale formerly assigned to *Canadia* Walcott, 1911. The relationships of the family Burgessochaetidae within the class Polychaeta are uncertain (Wills, 1993). However, among the modern polychaetes, Amphinomidae and Nephtyidae seem to show close similarities with the notosetae and neurosetae of the bugessochaetids (Conway Morris, 1979). According to Fauchald & Rouse (1997) only some phyllodocid traits can be inferred from the fossils of *Burgessochaeta*.

***Burgessochaeta* Conway Morris, 1979** (Cambrian; Canada) - The only species known within this genus is the type species *B. setigera* (Walcott, 1911). *Burgessochaeta* is interpreted as a burrower that propelled itself on chaetae (Conway Morris, 1979).

Family Canadiidae Walcott, 1911
(Cambrian)

This monospecific family seems to share some similarities with the modern chrysopetalids (Conway Morris, 1979; Butterfield, 1990a) but its relationship within the class Polychaeta are considered uncertain (Wills, 1993). Together with the wiwaxiids, the canadiids have been included into the fossil superfamily Canadiacea Butterfield, 1990 within Phyllodocida. According to Fauchald & Rouse (1997) only some phyllodocid traits can be inferred from the fossils of *Canadia*. *Selkirkia* Walcott, 1911 from the Burgess Shale had also been previously assigned to the canadiid polychaetes (Howell, 1962) but it is now assumed to be a priapulid (Wills & Sepkoski, 1993).

***Canadia* Walcott, 1911** (Cambrian; Canada) - The type species *C. spinosa* Walcott, 1911 is the only species that is still included within this genus after Conway Morris (1979) revised the Burgess Shale polychaetes. The other *taxa* referred to *Canadia* by Walcott (1911) have been split between the burgessochaetids and peronochaetids by Conway Morris (1979). The same author interpreted *Canadia* as a benthic and free-living polychaete. According to Butterfield (1990a) *C. spinosa* must probably be affiliated to the chrysopetalids.

Family Chrysopetalidae Ehlers, 1864
(Carboniferous?- Recent)

While investigating the polychaete fauna from Mazon Creek, Thompson (1979) referred to the presence of undescribed polychaetes of the family Palmyridae Kingberg, 1858. Palmyrids are nowadays included among the chrysopetalids, with the exception of *Palmyra* Savigny, 1818, which has been moved to the aphroditids (Fauchald & Rouse, 1997). The Mazon Creek "palmyrids" represent the only fossils known within the Chrysopetalidae, even if Conway Morris (1979, 1985) and Butterfield (1990a) have pointed out that *Canadia spinosa* and *Wiwaxia corrugata* from the Burgess Shale show some modern chrysopetalid-like traits.

Family Didonidae n. fam.
(Cretaceous)

The institution of this family is based on the description, proposed in this paper, of five specimens of large-bodied eunicemorph polychaetes from Haqel. The didonids show intermediate characters between the labidognath eunicidans and the dorvilleids. Furthermore, the most significant feature of the didonids is the maxillary apparatus equipped with an unpaired carrier. Among the modern and free-living eunicidans such a carrier can be found in some dorvilleids. However, since the carrier of the five specimens from Haqel is not strongly linked to the forceps, we prefer to relate them to a new group of the oenonid-dorvilleid line.

***Didone* n. gen.** (Cretaceous; Lebanon) - The type species *D. pulcherrima* n. gen. n. sp. from Haqel is newly described in the present study.

Family Eunicidae Berthold, 1827
(Ordovician-Recent)

The oldest full-preserved fossil eunicids are Carboniferous in age, but the family also includes some Paleozoic scolecodonts from Europe and North America (Howell, 1962).

***Esconites* Thompson & Johnson, 1977** (Carboniferous; Illinois) - This genus includes only the type species *E. zelus* Thompson & Johnson, 1977 from Mazon Creek. The systematic relationships of *Esconites* within the Eunicidae need to be revised. According to Thompson & Johnson (1977) these full-preserved eunicids from Mazon Creek cannot be assigned to *Eunicites*, even if their morphology appears to be strictly related with it, as numerous scolecodonts have previously been assigned to this *taxon*. However, the original description of *Eunicites* edited by Ehlers (1868) was based on a whole-preserved specimen and not on isolated jaws or maxillae. Thus, the full-preserved specimens from Mazon Creek could eventually be related to the *orthotaxon Eunicites*, while the scolecodonts should eventually be assigned to other *parataxa*. In the same way as *Eunicites*, also *Esconites* appears to be strictly related to the extant genus *Eunice* Cuvier, 1817.

***Eunicites* Ehlers, 1868** (Jurassic-Eocene; Germany, Italy and Lebanon) - Some full-preserved specimens assigned to *Eunicites* have been found within the Mesozoic: *E. triasicus* Gall & Grauvogel, 1966 from Grès à Voltzia and *E. orobicus* Alessandrello & Bracchi, 2004 from the Italian Prealps are Triassic in age, *E. proavus* (Germar, 1842) from Solnhofen is Jurassic in age while *E. phoenicius* Alessandrello & Teruzzi, 1986 from Haqel is Cretaceous in age. Ehlers (1868) described the type species *E. avitus* Ehlers, 1868 based on the description of the genus *Eunicites* for some eunicid polychaetes from Solnhofen. Ehlers (1869) later described *E. atavus* Ehlers, 1869 and *E. dentatus* Ehlers, 1869 from the same outcrop and proposed the binomial *E. proavus* as a new combination for *Geophilus proavus* Germar, 1842. Some years later Kozur (1971) stated that *E. avitus, E. atavus, E. dentatus* and *E. proavus* are synonyms of *E. avitus*: following the rules of the International Code of Zoological Nomenclature, *E. proavus* has priority. However, it is considered here that by closely studying the plates of the manuscripts on the worms from the Solnhofen *Plattenkalk* (Ehlers, 1868, 1869) it can be clearly deduced that the synonymity proposed by Kozur (1971) is rather doubtful: further studies are required to confirm this issue. While revising the polychaetes from Monte Bolca (Massalongo, 1850, 1855), Alessandrello (1990a) also described *E. affinis* (Massalongo, 1855), *E. gazolae* (Massalongo, 1855), *E. intermedia* (Massalongo, 1855) and *E. pinnai* Alessandrello, 1990. All the other species described under *Eunicites* (Hinde, 1879, 1880, 1882, 1896; Foerste, 1888; Patte, 1921; Eller, 1934a, 1934b, 1938, 1940, 1941, 1942, 1944, 1945, 1955, 1963a, 1964; Seidel, 1959; Sylvester, 1959; Taugourdeau, 1968, 1970) were not based on full-preserved specimens but on scolecodonts. These scolecodonts are hardly comparable with the full-preserved species of the same genus or with the genus description furnished by Ehlers (1868) in particular. Consequently, according to the rules of the I.C.Z.N., the classification of these scolecodonts should be kept separated from the *orthotaxon Eunicites* by the institution of a different *parataxon* or *parataxa*. In this paper new specimens of full-preserved *Eunicites* from Haqel are described as *E. joinvillei* n. sp., *E. falcatus* n. sp., *E. diopatroides* n. sp. and *E. mariacristinae* n. sp. The most significant features for distinguishing the full-preserved species assigned to date to the *Eunicites* reside in the pharyngeal armature. The shape of the jaws (subtriangular, scythe-shaped or subelliptical), the pattern of the anterior borders (smooth or denticulate) and the shape of the carriers, which are usually paired, triangular, joined along a median line or sometimes equipped with small lateral and rounded paddles (*E. diopatroides* n. sp.), seem to be particularly diagnostic.

Family Fossundecimidae Thompson, 1979
(Carboniferous)

Thompson (1979) instituted this family to include the second most common polychaete species from Mazon Creek. According to Thompson (1979), the fossundecimids seems phyllodocids that show intermediate characters between the hystricioline aphroditids and nereidids. They have a similar paleoecology, external morphology and architecture of jaws and chaetae as the former and the number and architecture of the jaws is the same as in the latter.

***Fossundecima* Thompson, 1979** (Carboniferous; Illinois) - Epifaunal and probably omnivorous polychaetes known on the basis of the type species *F. konecniorum* Thompson, 1979 only. Thompson (1979) hypothesized that *F. konecniorum* could be a primitive ancestor of the nereidid polychaetes.

Family Goniadidae Kingberg, 1865
(Carboniferous-Recent)

The goniadids have been included within Glyceridae for a long time (Fauchald & Rouse, 1997). Full-preserved goniadids have been found to date within the Paleozoic, more precisely in the Carboniferous strata of North America (Schram, 1979; Thompson, 1979). In the present paper the Mesozoic *Ferragutia* n. gen. from Haqel is described. Moreover, the goniadid fossil record includes several Triassic scolecodonts (macrognaths) formerly assigned to the *parataxon Alienites* Kozur, 1970 but later moved to the extant genus *Goniada* Adouin & Milne Edwards, 1833. However, Szaniawski (1974) and Zawidzka (1975) believe that the assigment of these isolated macrognaths to a living genus is rather dubious as the architecture of the macrognaths among the goniadids is very similar. Therefore, these structures do not represent a diagnostic character in the systematic definition of these polychaetes. Moreover, *Goniada* is not a *parataxon*: this implies that it cannot be adopted in order to classify isolated macrognaths or other isolated and disjunct glyceroidean jaws.

***Carboserostris* Schram, 1979** (Carboniferous; Montana) - The type species *C. megaliphagon* Schram, 1979 is the only one known within this genus. It is the most abundant species among the polychaetes from Bear Gulch. The stomodaeum of *Carboserostris* is equipped with micrognaths and macrognaths. The latter have not been observed in *Ferragutia* n. gen. and *Pieckonia* (see below).

***Ferragutia* n. gen.** (Cretaceous; Lebanon) - The genus is established here based on the description of the type species *F. cenomaniana* n. gen. n. sp., the second most common polychaete among those from Haqel. The stomodaeum of *Ferragutia* n. gen. is equipped with both micrognaths and chevrons. The latter have not been observed in *Carboserostris* and *Pieckonia* (see above and below).

***Pieckonia* Thompson, 1979** (Carboniferous; Illinois) - This genus includes only the type species *P. helenae* Thompson, 1979. It is considered to be a rapid burrower, in the same way as the modern goniadids. The stomodaeum of *Pieckonia* is equipped with micrognaths however, differently from *Carboserostris* and *Ferragutia* n. gen. (see above), it lacks both macrognaths and chevrons. *Ferragutia* n. gen. is lacking the macrognaths as does *Pieckonia*, a condition that Thompson (1979) explains by hypothesizing a primitive condition.

Family Hesionidae Grube, 1850
(Carboniferous-Recent)

Only a dozen polychaete specimens from Europe and North America have been assigned to the hesionids to date: two specimens from Monte Bolca (Alessandrello, 1990b), ten specimens from Mazon Creek (Thompson, 1979).

***Rutellifrons* Thompson, 1979** (Carboniferous; Illinois) – At present this genus includes only the type species *R. wolfforum* Thompson, 1979 from Mazon Creek. The specimens described by Thompson (1979) are worthy of note due to the preservation of various soft parts, such as the eversible muscular proboscis together with the tentacular and parapodial cirri. *R. wolfforum* was probably an epifaunal polychaete.

***Siphonostomites* Rovereto, 1904** (Eocene; Italy) - Rovereto (1904) described under this genus the material reported by Massalongo (1855) as *Nereites hesionoides* Massalongo, 1855. Alessandrello (1990b) confirmed the revision of Rovereto (1904) and pointed out a strong similarity between *Siphonostomites* and the extant genus *Hesione* Savigny, 1818.

Family Insolicoryphidae Conway Morris, 1979
(Cambrian)

Monospecific family set up by Conway Morris (1979), who pointed out that insolicoryphids do not show characters that could suggest close similarities with any modern polychaete or with the other monospecific families from the Burgess Shale.

***Insolicorypha* Conway Morris, 1979** (Cambrian; Canada) - The type species *I. psygma* Conway Morris, 1979 has been interpreted as a pelagic swimmer.

Family Lumbrineridae Schmarda, 1861
(Ordovician-Recent)

To date full-preserved lumbrinerids have been recorded from both Mesozoic (Ehlers, 1869; Arduini *et al.*, 1982) and Paleozoic (Schram, 1979) strata and have been assigned to three genera. Moreover, Howell (1962) has documented the presence of the living genus *Lumbrineris* Grube, 1840 from the Pliocene to recent times. The new Cretaceous genus *Teruzzia* n. gen. is newly described in this study. According to Szaniawski & Imajima (1996) the lumbrinerids originated from some representatives of the family Hartmaniellidae Imajima, 1977, such as *Lysaretides* Kozur, 1970, during the Upper Cretaceous. Infact, the hartmaniellids now include both *Lysaretides* and *Delosites*? Kozur, 1967, genera formerly included within the family Lysaretidae Kingberg, 1865 emend. Kozur, 1970 but later included within the Lumbrineridae and Oenonidae respectively (Colbath; 1989; Orensanz, 1990; Fauchald & Rouse, 1997). However, the Cretaceous specimens described in the present work and the Carboniferous *Phiops* are very similar to the modern representatives of the family and do not show any kind of primitive character. Thus, it is considered here that the origin of the lumbrinerids can probably be dated back to the Middle-Upper Paleozoic by the systematic revision of various scolecodonts erroneously assigned to the *orthotaxon Lumbriconereites* (Hinde, 1879, 1882; Foerste, 1888; Stauffer, 1933, 1939; Eller, 1938, 1941, 1942, 1945, 1946, 1963a, 1964, 1969; Taugourdeau, 1968; Seidel, 1959; Sylvester, 1959; Jansonius & Craig, 1971; Tasch & Stude, 1966). The *"Lumbriconereites* scolecodonts" should therefore be revised systematically with the eventual institution of new *parataxa*.

Lumbriconereites **Ehlers, 1869** (Ordovician?-Cretaceous; Germany) - Genus described on the basis of full-preserved specimens assigned to the type species *L. deperditus* Ehlers, 1869, that must consequently be considered an *orthotaxon*. However, as mentioned above, some polychaete researchers assigned several scolecodonts from Paleozoic and Mesozoic rocks to *Lumbriconereites* and thus adopted the genus like a *parataxon*. Since the original description of *Lumbriconereites* proposed by Ehlers (1869) is not based on scolecodonts but on whole-preserved specimens, it follows that the scolecodonts formerly assigned to this genus should probably be moved to one or more new *parataxa*. However, the real systematic value of *Lumbriconereites* has been questioned by Kozur (1971), who argued that *L. deperditus* is a synonym of *Eunicites proavus*, another eunicemorph polychaete from Solnhofen. It is considered in the present study, that by observing the plates of the manuscript on the worms from the Solnhofen *Plattenkalk* (Ehlers, 1869), one can clearly deduce that there are differences in the architecture of the jaws of *E. proavus* and *L. deperditus*: further studies are required to confirm this issue. In the present work the new species *L. hadjulae* n. sp. and *L. garassinoi* n. sp. from the Haqel and Hadjula localities are described.

Melanoraphia **Arduini, Pinna & Teruzzi 1982** (Jurassic; Italy) - Genus known only on the basis of the type species *M. maculata* Arduini, Pinna & Teruzzi 1982, from the Italian Prealps. The most interesting feature of *M. maculata* is the presence of pigmentation traces on the parapodia (Arduini *et al.*, 1982). In the opinion of the authors the relationships of *Melanoraphia* within the Eunicida need to be revised as the absence of the antennae in the available specimens, used as a decisive character in the recognition of the systematic affinities of the genus, could be an artifact of fossilization. Furthermore, the pharyngeal armature of *M. maculata* is that of a typical labidognath eunicidan and its general architecture together with the presence of little semicircular paddles on the sides of the carriers as well as the absence of antennae seem to suggest eunicid-like traits.

Phiops **Schram, 1979** (Carboniferous; Montana) - The specimens from the Carboniferous of Bear Gulch described under the binomial *P. aciculorum* Schram, 1979 are noteworthy for the good state of preservation of the lobate parapodia. The genus can be clearly distinguished from the other fossil lumbrinerids simply on the basis of the subtriangular shape of the jaws which, differently from that of *Lumbriconereites* and *Teruzzia* n. gen., shows no similarity with the species included in the living *Lumbrineris*.

Teruzzia **n. gen.** (Cretaceous; Lebanon) - In the same way as *Lumbriconereites*, *Teruzzia* n. gen. appears to be strictly related to the living genus *Lumbrineris*. *Teruzzia* n. gen. includes, in addition to the type species *T. pezzolii* n. gen. n. sp., *T. gryphoeides* n. gen. n. sp., *T. sagittifera* n. gen. n. sp. and *T. pusilla* n. gen. n. sp., and represents the most common polychaete *taxon* in the Haqel outcrop.

Family Nephtyidae Grube, 1850
(Carboniferous-Recent)

Full-preserved polychaetes of this family are known only from the Paleozoic of North America and they have been assigned to two genera (Thompson, 1979; Schram, 1979). With approximately one thousand specimens discovered to date, the nephtyids seem to be the most common free-living polychaetes from Mazon Creek, even if in some cases their systematic affinities are questioned.

Astreptoscolex **Thompson, 1979** (Carboniferous; Illinois and Montana) - The type species *A. anasillosus* Thompson, 1979, from the Coal Measures of Mazon Creek (Thompson, 1979) and from Bear Gulch (Schram, 1979) was probably gregarious. Thompson (1979) interpreted *Astreptoscolex* as an epifaunal creeper.

Didontogaster **Thompson, 1979** (Carboniferous; Illinois) - The type species *D. cordylina* Thompson, 1979, with approximately 650 specimens found to date, is the second most common polychaete from Mazon Creek. Recently Sutton *et al.* (2001a) have considered the relationships of *Didontogaster* with the nephtyids as doubtful, even if the characters pointed out by Thompson (1979) seem to confirm these affinities with reasonable certainty.

Family Nereididae Johnston, 1865
(Ordovician-Recent)

Since the Eocenic species described by Massalongo (1855) under the living genus *Nereis* Linnaeus, 1758 have been included within the eunicid genus *Eunicites* (Alessandrello, 1990a), full-preserved fossil nereidids are recorded only from Mesozoic and Paleozoic strata. However, the nereidid affinities of the three fossil genera listed below have to be newly demonstrated as they are recognized on the basis of old notes. Thus, the data available regarding the full-preserved fossil nereidids should be updated by an adequate revision that takes into account the current scientific developments in fossil polychaete research: meanwhile, their inclusion among the nereidids is considered provisional. With regard to the Paleozoic, several *parataxa* have been related to this family (Hinde, 1879, 1880; Stauffer, 1933, 1939; Žebera, 1935; Eisenack, 1939; Eller, 1940, 1941, 1942, 1945, 1955, 1963a, 1963b, 1964, 1969; Sylvester, 1959; Tasch & Stude, 1966; Kozur, 1967; Taugoudeau, 1968, 1970; Jansonius & Craig, 1971). The Lower Cambrian *Fauciveremis yunnanicus* Hou & Chen, 1989 has been tentatively assigned to the nereidid polychaetes (Hou & Chen, 1989; Chen & Erdtmann, 1991; Delle Cave & Simonetta, 1991) although, in the opinion of Fauchald & Rouse (1997), the presence of polychaetes in the Lower Cambrian cannot be confirmed to date. This is due to the fact that the Lower Cambrian worm-like fossils from China seem to not show any characters that can definitively demonstrate a nereidid or polychaete affinity.

Ctenoscolex **Ehlers, 1869** (Jurassic; Germany) - This genus includes only the type species *C. procerus* Ehlers, 1869 from Solnhofen. The specimens described by Ehlers (1869) as polychaetes of doubtful but probable nereidid affinities, were re-examined by Kozur (1970) who argued that *Ctenoscolex* is not a polychaete as it lacks the chaetae in spite of an excellent preservation. The same author (Kozur, 1971) later suggested that *Ctenoscolex* be considered as related to an uncertain family within the Phyllodocida.

Nawnites **Roy, 1929** (Devonian; New York) - Poorly known *taxon* from the Devonian of North America. It has been described on the basis of the type species *N. gilboensis* Roy, 1929 only. Roy (1929) furnished few morphological characters of this polychaete and limited his description to the segmented body.

Triadonereis **Mayer, 1954** (Triassic; Germany) - Genus strictly related to the living genus *Nereis* and described on the basis of the type species *T. eckertii* Mayer, 1954 from the *Trochitenkalk* (Middle Triassic) of Germany. The suggested relationships of *Triadonereis* link it to the neridids (Mayer, 1954) but its actual affinities within the polychaetes must be demonstrated.

Family Oenonidae Kingberg 1865
(Silurian?-Recent)

This family presently includes all the genera previously included within Arabellidae Hartman, 1944 and some genera formerly assigned to Lysaretidae (Colbath, 1989; Orensanz, 1990; Fauchald & Rouse, 1997). To date the fossil record of the oenonid polychaetes comprises some Paleozoic scolecodonts and articulated apparata from the Silurian of the Baltic area and North America that have been assigned to *Synclinophora* Eisenack, 1975 (Mierzejewski, 1984; Eriksson, 2003b) as well as several Mesozoic scolecodonts from central Europe that have been described by Kozur (1970, 1971) under the modern genera *Arabella* Grube, 1850, *Halla* Costa, 1844, *Drilonereis* Clarapède, 1870, *Notocirrus* Schmarda, 1861 and *Oenone* Savigny, 1818. However, Szaniawski (1974) and Zawidzka (1975) have already expressed doubts regarding the assignment of these Mesozoic scolecodonts to modern oenonid genera with any reasonable certainty. Moreover, the genera mentioned by Kozur (1970, 1971) are *orthotaxa* that cannot be considered within the parataxonomical investigation of the scolecodonts. In the present study the first full-preserved oenonid genus within the Mesozoic has been described: it includes three species. In the opinion of Kielan-Jaworovska (1966), Szaniawski (1970) and Szaniawski & Gadzicki (1978), the oenonids arose from the parataxonomical family Atraktoprionidae during the Middle-Upper Paleozoic, even if Mierzejewski (1984) argued that oenonids and atraktoprionids are sister *taxa* that share a common ancestor.

Phoeniciarabella **n. gen.** (Cretaceous; Lebanon) - Large-bodied oenonids strictly related to the living genus *Arabella*. Among the examined material, apart from the type species *P. pinnulata* n. gen. n. sp., *P. caesaris* n. gen. n. sp. and *P. orensanzi* n. gen. n. sp. were also recognized. *Phoeniciarabella* n. gen. represents the only oenonid genus known within the Mesozoic. All the species of the genus possess elongate and slender carriers in the same way as the modern oenonids, but they seem to lack the unpaired piece that is usually associated to the maxillary carriers of the latter.

Family Peronochaetidae Conway Morris, 1979
(Cambrian)

Monospecific family established by Conway Morris (1979) after revison of specimens from the Burgess Shale formerly assigned (Walcott, 1911) to *Canadia*. The relationships of the family Insolicoryphidae within the Polychaeta are uncertain (Wills, 1993). However, in the opinion of Conway Morris (1979) the uniramous parapodia of the peronochaetids recall the posterior neuropodia of the modern Paraonidae Cerruti, 1909.

Peronochaeta **Conway Morris, 1979** (Cambrian; Canada) - Conway Morris (1979) interpreted the type species *P. dubia* Walcott, 1911 as a burrower and a scavenger.

Family Phyllodocidae Örsted, 1843
(Devonian-Recent)

Together with those of the nereidids and sigalionids, the phyllodocid fossil record is one of the most reduced among the full-preserved free-living polychaetes. To date whole-preserved phyllodocids have not been recorded within the Mesozoic (Howell, 1962), apart from one specimen from the Upper Cretaceous of Sahel-Alma, Lebanon, doubtfully assigned by Roger (1946) to the living genus *Phyllodoce* Savigny, 1818. The earliest records of the fossil phyllodocids are from the Middle-Late Paleozoic of North America where the majority of the specimens assigned to the family have been found.

Levisettius **Thompson, 1979** (Carboniferous; Illinois) - Genus tentatively assigned to the phyllodocids based on the description of the only known species *L. campylonectus* Thompson, 1979, interpreted as a free-living and carnivorous polychaete (Thompson, 1979). However, in the opinion of the authors, the inclusion of *Levisettius* within the phyllodocids should be considered provisional and as doubtful as the specimens described by Thompson (1979) lack the decisive traits that could demonstrate a phyllodocid affinity.

Palaeochaeta **Clarke, 1903** (Devonian; New York) - Clarke (1903) assigned this genus to the aphroditids and described only the type species *P. devonica* Clarke, 1903. However, the same author indicated the resemblance between *Paleochaeta* and the modern representatives of *Phyllodoce* and *Nereis*, intrinsically anticipating its assignment to the phyllodocids (Howell, 1962; Sepkoski, 2002).

Family Stephenoscolecidae Conway Morris, 1979
(Cambrian)

Monospecific family established by Conway Morris (1979), who pointed out only a superficial similarity with the modern Iospiliidae Bergström, 1914.

Stephenoscolex **Conway Morris, 1979** (Cambrian; Canada and Utah) - The type species *S. argutus* Conway Morris, 1979 is the worst preserved polychaete among those from the Burgess Shale. Conway Morris tentatively suggested that this species was benthic. According to Briggs & Kear (1991) also some specimens from the Middle Cambrian Spence Shale of Utah can be doubtfully assigned to *Stephenoscolex*.

Family Tomopteridae Johnston, 1865
(Carboniferous-Recent)

Probably due to the pelagic mode of life and the absence of jaws typical of these polychaetes, their fossil record is reduced to a few Paleozoic specimens (Briggs & Clarkson, 1987). However, according to Glaessner (1976a), also *Spriggina floundersi* Glaessner, 1958 from the Vendian of the Ediacara Hills, Australia, can be considered a tomopterid polychaete. Wills & Sepkoski (1993) included *Spriggina* within the enigmatic class Paratrilobita Fedonkin, 1985 which comprises some problematic Precambrian *taxa* that have been variously assigned to the Arthropoda and Annelida. More recently McMenamin (2003) defined *Spriggina* as a trilobitoid ecdysozoan and underlined its arthropod affinites.

***Eotomopteris* Briggs & Clarkson, 1987** - (Carboniferous; Scotland) - Genus based on the description of the type species *E. aldrigei* Briggs & Clarkson, 1987, from the Lower Carboniferous of the Granton Shrimp Bed, near Edinburgh (Scotland). The exceptional preservation of these Paleozoic tomopterids allows evidence of tentacular cirri and parapodia to be observed.

Family Wiwaxiidae Walcott, 1911
(Cambrian)

The systematic relationships of this monospecific family from the Burgess Shale have been discussed for a long time. Even if Wills & Sepkoski (1993) treat the wiwaxiids as problematic metazoans, according to Butterfield (1990a) they show some affinities with the Phyllodocida. However, together with *Canadia*, they should be included in the fossil superfamily Canadiacea Butterfield, 1990 which shares some characters with both the Chrysopetalidae and Aphroditidae. More recently, Conway Morris & Peel (1995) and Conway Morris & Gould (1998) underlined that the wiwaxiids are closely related to the halkieriids, problematic invertebrates from the Lower Cambrian (Bengston & Missarzhevsky, 1981; Jell, 1981; Bengston & Conway Morris, 1984; Bengston, 1985b; Conway Morris & Peel, 1990), because both groups have very similar sclerites. The same authors pointed out that the halkieriids show some primitive characters that link them to the polychaetes and brachiopods and that the wiwaxiids might be a sister *taxon* to the Polychaeta. This view seem to be accepted also by Dzik (2003) who put the halkieriids along the same lineage of the brachiopods, molluscs and polychaetes even if the transitional stages among these groups have not yet been found in the fossil record. According to Butterfield (1990a) *Wiwaxia* and *Canadia* are more closely related to each other than either are to any other fossil organism and that sclerites such as theirs have been widely adopted by disparate groups of organisms.

***Wiwaxia* Walcott, 1911** (Cambrian; Canada and Utah) - The type species *W. corrugata* (Matthew, 1899) was first described by Matthew (1899), thanks to a single spine found across the valley of the Burgess Shale, where full-preserved specimens were later discovered (Walcott, 1911). *Wiwaxia* was interpreted as a primitive mollusc or an elytigerous scale-worm for a long time (Walcott, 1911; Butterfield, 1990a). However, Conway Morris (1985) and Butterfield (1990a) investigated the microstuctural details of some sclerites and noticed that they are very similar to the paleae (flattened chaetae) of some modern chrysopetalids and aphroditids. According to Briggs & Kear (1991) also some specimens from the Middle Cambrian Spence Shale of Utah can be tentatively assigned to *Wiwaxia*. In the opinion of Conway Morris & Gould (1998) *Wiwaxia* might be a member of the annelid stem group, or rather a creature still in the process of becoming an annelid. In the opinion of Fauchald & Rouse (1997) the systematic position of *Wiwaxia* has yet to be clarified even if it clearly shows some chrysopetalid-like traits.

Unrelated and problematic genera

***Acaenoplax* Sutton, Briggs, Siveter & Siveter, 2001** (Silurian; England) – Vermiform organism from the Herefordshire *Lagerstätte* of England, originally described as an aplacophoran mollusc (Sutton *et al.*, 2001b, 2001c, 2004). However, this systematic interpretation has been argued by Steiner & Salvini-Plawen (2001) who proposed to consider *A. hayae* Sutton, Briggs, Siveter & Siveter, 2001 as an highly specialized polychaete that shares some characters with the modern Aphroditidae, Chaetopteridae, Cirratulidae and Sternaspidae.

***Eopolychaetus* Ruedemann, 1901** (Ordovician; New York) - Only the type species *E. albaniensis* Ruedemann, 1901, from the Canajoharie Shale of New York State, has been assigned to this genus. According to Wills (1993) and Sepkoski (2002), *Eopolychaetus* belongs to an unnamed family within an uncertain order.

***Kenostrychus* Sutton, Briggs, Siveter & Siveter, 2001** (Silurian; England) – On the basis of a cladistic analysis, *K. clementsi* Sutton, Briggs, Siveter & Siveter, 2001, from the Silurian volcanoclastic deposit of Herefordshire, has been interpreted as a member of a stem group from which both the Phyllodocida and Eunicida originate (Briggs *et al.*, 1996; Sutton *et al.*, 2001a).

***Myoscolex* Glaessner, 1979** (Cambrian; Australia) – The systematic relationships of *M. ateles* Glaessner, 1979 from the Lower Cambrian of Kangaroo Island (South Australia) have been discussed for a long time (Conway Morris, 1979; Glaessner, 1979; Wills, 1993; Briggs & Nedin, 1997; Dzik, 2003). In the opinion of Glaessner (1979) the anatomy of *Myoscolex* link it to the echiurids but according to Conway Morris (1979) and Briggs & Nedin (1997) both echiurid and polychaete affinities are questionable. Recently Dzik (2003) re-discussed the anatomical features of *Myoscolex* and proposed to consider it as one of the oldest polychaete annelid known, superficially similar to the modern opheliids. Moreover, Dzik (2003) pointed out the resemblance between *Mysocolex* and the Cambrian *Pikaia gracilens* Walcott, 1911 from the Burgess Shale which has been originally described as an annelid (Walcott, 1911) but later interpreted as a chordate (Conway Morris, 1979).

***Pontobdellopsis* Ruedemann, 1901** (Ordovician; New York) - This genus includes only the type species *P. cometa* Ruedemann, 1901, a poorly known *taxon* from the Ordovician of the Canajoharie Shale, New York State. According to Wills (1993), this genus belongs to an unnamed family within an uncertain order.

***Protopholoe* Alessandrello, Bracchi & Riou, 2004** (Jurassic; France) - Enigmatic aphroditacean recently described from La Voulte sur-Rhône on the basis of a single pyritized specimen. Alessandrello *et al.* (2004) pointed out that *Protopholoe* shares some characters with the living *Pholoe*, a genus actually included among the sigalionid aphroditaceans.

***Ramesses* Schram, 1979** (Carboniferous: Montana) - The type species *R. magnus* Schram, 1979 is characterized by parapodia similar in some respects (Schram, 1979) to those of the modern Orbiniidae Hartman, 1942. According to Wills (1993) and Sepkoski (2002) this genus belongs to an unnamed family within an uncertain order. However, the modern orbiniids are not free-living forms as *Ramesses* seems to be.

***Soris* Schram, 1979** (Carboniferous: Montana) - Schram (1979) indicated the type species *S. labiosus* Schram, 1979 as belonging to an undetermined polychaete order. The same author pointed out, through the investigation of the pharyngeal armature of the only two available specimens, a superficial similarity with some Paleozoic *parataxa* such as *Glycerites* Hinde, 1879 and *Paranereites* Eisenack, 1939. According to Wills (1993) and Sepkoski (2002) this genus belongs to an unnamed family within an uncertain order.

***Trentonia* Pickerill & Forbes, 1978** (Ordovician; Canada) - The type species is *T. shegiriana* Pickerill & Forbes, 1978 from the Ordovician of the Quebec City area (Trenton Series). To date *Trentonia* has been doubtfully considered an enigmatic eunicemorph polychaete (Pickerill & Forbes, 1978; Wills, 1993; Sepkoski, 2002).

SYSTEMATIC PALEONTOLOGY

As clearly emerges from the check-list compiled above and as already pointed out by Fauchald & Rouse (1997), the systematic paleontology of the free-living polychaetes can be very confusing, even to those studying the polychaetes. This is essentially due to the soft-bodied nature of these invertebrates. Thus, several diagnostic characters related to soft parts and adopted in the systematic neontology of the polychaetes, such as the cirri, the antennae, the gills, the parapodia or the elytrae, are usually not evident in the fossils. This is also the case even when the latter are represented by whole-preserved specimens.

Most of the characters adopted in the systematic paleontology of the polychaetes derive from the jaw pieces that armour the pharynx in some groups such as the eunicidans, glyceroideans, some aphroditaceans, the nephtyids and others, and from other structures resistant to degradation, such as the chaetae, even if the latter usually do not preserve their diagnostic ultrastructure. This situation implies that the fossil *taxa* can hardly be incorporated within the linnean schemes of the polychaete taxonomy. Such a problem is, for example, evident in the paleontological investigation of the labidognath eunicidans and aphroditaceans. Among the former the preservation of the lateral and median antennae can be useful in distinguishing the eunicids from the lumbrinerids, despite a very similar pharyngeal armature (George & Hartman-Schröder, 1985; Fauchald & Rouse, 1997). In the fossil eunicids that show full-preservation, the preservation of the antennae has, for example, only been documented in one specimen of the Cretaceous species *Eunicites phoenicius* from Lebanon (Alessandrello & Teruzzi, 1986a). However, in the other species of the same genus these soft structures have never been observed, even if all the eunicids should possess them by definition. On the contrary, the living lumbrinerids are lacking antennae (George & Hartman-Schröder, 1985; Fauchald & Rouse, 1997) while in the Jurassic eunicidan species *Melanoraphia maculata*, the absence of antennae has been considered a decisive factor in the assignment of this *taxon* to the lumbrinerids (Arduini *et al.*, 1982), despite the fact that the species has a very similar pharyngeal armature, especially in the architecture of the jaws and carriers, to that of certain Mesozoic eunicids. However, the soft-bodied nature of the antennae make the possible preservation of these prostomial structures very unlikely in fossils: according to this overview the absence of antennae in *Melanoraphia* and in most of the species assigned to the *Eunicites* could therefore be an artifact of fossilization. Consequently, the affinities of these *taxa* cannot be considered as proven at all if the rules of the systematic neontology of the polychaetes are followed. With regard to the aphroditaceans, the elytrae and the dorsal felt of capillary fibers are diagnostic soft-bodied features which are very rarely preserved in the fossil forms: for example, the Triassic species *Paleopahrodite raetica* and the Jurassic species *Paleoaphrodite adeliae* respectively have the elytrae and the dorsal felt preserved. However, these structures have not been observed in the other species of the same genus. Thus, the elytrae and dorsal felt of the aphroditaceans are, differently from what is outlined in the systematic neontology of the group (Day, 1967; Fauchald & Rouse, 1997), not useful as diagnostic features for their definition within systematic paleontology.

With the exception of those from the Middle Cambrian of the Burgess Shale, mostly represented by carbonaceous remains (Butterfield, 1990b), most of the fossil polychaetes are too poorly preserved to be characterized using the rules of systematic neontology. The information that can be deduced from these fossils is limited and an actual systematic, taxonomic and phylogenetic analysis is substantially not possible even if some authors (Orensanz, 1990) have tried to include some fossil *taxa* within their systematic treatment of the modern polychaetes. Thus, the systematic paleontology of the free-living polychaetes must be based on characters that are often evident in the fossil forms but that have little significance in a systematic review of the modern polychaetes. A similar situation is found with regard to the systematic paleontology of other worm-like invertebrates, such as the sipunculans and enteropneusts (Cutler, 1994; Alessandrello *et al.*, 2004).

Phylum Annelida Lamarck, 1809
Class Polychaeta Grube, 1850
Order Eunicida Dales, 1962
Family Eunicidae Savigny, 1818
Genus *Eunicites* Ehlers, 1868

Eunicites joinvillei n. sp.
Pl. I

Diagnosis: subelliptical jaws not protruding beyond the lateral borders of the forceps, closely positioned side by side along a central junction line and disposed at an angle of almost 180°. Jaws with denticulate front borders equipped with 4 teeth, strongly rounded lateral borders and slightly convex back margins. Separated, triangular, elongate and longitudinally grooved mandibular processes. Short, triangular and symmetrical carriers joined along a central junction line.

Derivatio nominis: dedicated to Sir Jean de Joinville, a crusader of King Louis IX, who first mentioned (1305-1308) the existence of the Lebanese fossils.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 5 specimens. MSNM i12420 (holotype), MSNM i12414 and MSNM i13304 (paratypes), MSNM i20612, MSNM i25456.

Description: elongate and thin body measuring from 140 mm (MSNM i12420) to 290 mm (MSNM i20612) in length and from 2.5 mm (MSNM i12414) to 9 mm (MSNM i12420) in width. The body width is constant with the exceptions of MSNM i20612, in which it decreases from the cephalic to the caudal extremity, and of MSNM i25456, in which it slightly increases at the level of the pharyngeal region. The measurements of the examined specimens are typical of a large bodied polychaete.

Only the stomodaeal apparatus and a short (30 mm) part of the cephalic extremity are preserved in MSNM i13304 and MSNM i25456, while MSNM i12414 (220 mm) lacks the caudal extremity. The other specimens are full-preserved.

In MSNM i13304 the jaw apparatus is preserved as an imprint, while mineralized jaws and molds of the maxillary apparatus are present in the other specimens. However, small, mineralized fragments of the anterior part of the latter are evident in MSNM i12420, MSNM i20612 and MSNM i25456. The pharyngeal armature measures from 4.2 mm (MSNM i25456) to 13 mm (MSNM i12420) in length. In the holotype the jaws measure 3 mm in length and 1.2 mm in width.

The anterior ends of arcuate and hooked forceps are always preserved but only in MSNM i12414 (3.8 mm) and MSNM i25456 (1.7 mm) is the distance between them measurable. Excluding MSNM i12414, in which a small fragment of the left forcep is mineralized, the forceps are always preserved as imprints.

The carriers are always poorly preserved as imprints with the exception of MSNM i20612, in which two small, mineralized fragments (15-20 mm) are evident along the central junction line.

The forceps and carriers are only not preserved in MSNM i13304.

The poor quality of preservation of the examined specimens does not allow the total number of metameres to be counted even if, on the basis of the aciculae arrangement, at least 300 metameres (0.8 mm in thickness) can be counted in MSNM i20612, 170 (0.5 mm in thickness) in MSNM i12414, 100 (1 mm in thickness) in MSNM i12420 and 50 in MSNM i25456.

Three aciculae equip each parapodium. Each parapodium bears two elongate (0.8 mm in MSNM i25456, 3 mm in MSNM i12414) and thickened aciculae toward the prostomium and a third shorter and thinner acicula that appear to be divaricated from the longer ones and turned backwards. So as in the living *Eunice*, the slenderest acicula could be interpreted as notopodial, the thickest as neuropodial (Fauchald, 1992). In MSNM i12414 the length of the two longest aciculae decreases from the cephalic extremity (3 mm) to the caudal one (2 mm) and in MSNM i25456 the parapodia bear tufts of two parallel and thick aciculae that show the same length. However, in consideration of the stomodaeal apparatus architecture of MSNM i12414 and MSNM i25456, which is very similar to that of the other specimens that are assigned here to *E. joinvillei* n. sp., the aciculae arrangement must be considered as being poorly diagnostic due to the intraspecific variability and the fossilization artifacts. The position in which the notopodial and neuropodial aciculae of MSNM i25456 and MSNM i12414 are preserved suggests that the ventral surface is being observed in these specimens. Probably the same specimens were subjected to compression during diagenesis so that, in the fossils, the notopodial acicula appear to be located behind the neuropodial acicula. Morover, in the same specimens, the jaw apparatus seems to be superimposed on the maxillary apparatus: since in the eunicemorph polychaetes the jaws are located along the ventral side of the pharynx, this kind of preservation confirms that it is the ventral surface of these specimens that is being observed. On the contrary, the position in which the elements of the pharyngeal apparatus of MSNM i12420 are preserved suggests that the dorsal surface is being observed.

Traces of the digestive tube are preserved as dark-brown traces in MSNM i12414, MSNM i12420 and MSNM i25456.

Remarks: the complex architecture of the pharyngeal armature of the examined specimens clearly marks them as eunicidan polychaetes. Moreover, the pattern of the jaws, the shape of the paired carriers and the kind of preservation of the pharyngeal apparatus, sometimes consisting of a white and pearly material quite similar to the original one, suggest that they belong to the labidognath eunicids or lumbrinerids (Fauchald, 1992; Fauchald & Rouse, 1997). It is preferred here to assign the material examined to *Eunicites*, especially due to the strong similarity of the stomodaeal armature (Ehlers, 1868, 1869), even if the eunicids should possess, in contrast to the lumbrinerids, prostomial antennae that were, however, not observed in the specimens (George & Hartman-Schröder, 1985). Among the full-preserved *Eunicites* described to date, grooved mandibular processes very similar to those of *E. joinvillei* n. sp. have already been recorded (Ehlers, 1868; Kozur, 1970; Alessandrello, 1990) in *E. proavus* and *E. affinis*. Furthermore, the jaws of *E. proavus* are subelliptical like those of *E. joinvillei* n. sp., but they are not denticulate or sharpened at the lateral ends. Moreover, in *E. proavus* the jaws are separated by an angle of about 120-140°, as well as having totally joined and smooth surfaced mandibular processes: on the contrary in *E. joinvillei* n. sp. the same angle measures almost 180° and the mandibular processes show a grooved surface. The jaws of *E. affinis* have denticulate front borders like those of *E. joinvillei* n. sp. but they show a regular oval shape and slightly sharpened lateral ends. Moreover, the mandibular processes of *E. affinis* are grooved like those of *E. joinvillei* n. sp., but they are joined for 2/3 of their length, differently from the completely separated mandibular processes of *E. joinvillei* n. sp.

In addition to *E. joinvillei* n. sp., jaws with denticulate front borders can also be found in the Triassic species *E. orobicus* and *E. triasicus* from the Italian Prealps and Grès à Voltzia respectively, as well as in the Jurassic species *E.*

dentatus, the latter considered by Kozur (1971) as a synonym of *E. proavus*. However, in contrast to *E. joinvillei* n. sp., all these *Eunicites* possess smooth surfaced mandibular processes (Ehlers, 1869; Gall & Grauvogel, 1966; Alessandrello & Bracchi, 2004). Moreover, even if the subelliptical jaws of *E. joinvillei* n. sp., *E. orobicus* and *E. triasicus* are quite similar in shape, the jaws of *E. joinvillei* n. sp. bear 4 teeth, whereas the same structures in *E. orobicus* are equipped with 5-6 teeth (Alessandrello & Bracchi, 2004) and those of *E. triasicus* with 8-9 teeth (Gall & Grauvogel, 1966). Finally, the jaws of *E. dentatus* are scythe shaped and equipped with 6 teeth (Ehlers, 1868).

Eunicites falcatus n. sp.
Pl. II (Figs. A, B)

Diagnosis: scythe shaped jaws positioned side by side along a central junction line and protruding beyond the lateral borders of the forceps. Jaws inclined at an angle of almost 180°, with concave and smooth front borders, markedly sharpened lateral ends, straight and turned forward posterior borders. Short and triangular mandibular processes joined for about 1/5 of their length. Very short triangular and symmetrical carriers.

Derivatio nominis: from the Latin *falcatus* (= scythe shaped), referring to the shape of the jaws.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 1 specimen. MSNM i8488 (holotype).

Description: the examined specimen is whole-preserved (120 mm in length) and it has a constant body width, apart from a slight broadening at the level of the pharyngeal region.

The stomodaeal apparatus is 8 mm in length and is mostly preserved as an imprint.

Only the left jaw is full-preserved, while the right one is rather damaged and lacks the anterior part. The left jaw is 0.7 mm long and 2 mm wide.

The basal parts of the mandibular processes are quite mineralized while the other sectors are preserved as weak imprints.

Elongate, arcuate and hooked forceps are articulated to very short triangular carriers. The articulation hinge between carriers and forceps shows a concave pattern. The hooked shape of the left forcep may be clearly distinguished and the imprint of the external margin of the right forcep is also evident.

At the mid-length of the pharyngeal apparatus the left maxilla II is preserved as a faint subrectangular trace.

The posterior tip of the left mandibular process of the holotype is superimposed on the left maxilla II: this suggests a dorsal preservation as in the eunicidans the jaw apparatus occupies a ventral position inside the pharynx, while the maxillae are dorsally placed (Fauchald, 1992; Fauchald & Rouse, 1997).

Only a few metameres preserve the aciculae: they appear grouped in bundles of two equally thicknened elements for each parapodium however, it is impossible to establish for certain if they are notopodial or neuropodial. Although in consideration of the dorsal preservation of the specimen, they should be interpreted as notopodial. The poor quality of preservation did not allow the exact number of metameres to be counted.

Remarks: the complex architecture of the pharyngeal armature of the examined specimen clearly marks it as an eunicidan polychaete. Moreover, the pattern of the jaws, the shape of the paired carriers and the kind of preservation of the pharyngeal apparatus, formed of a white and pearly material quite similar to the original one, suggest that it is a labidognath eunicid or lumbrinerid (Fauchald, 1992; Fauchald & Rouse, 1997). Even if the eunicids possess, differently from the lumbrinerids, prostomial antennae that are not evident in the material examined (George & Hartman-Schröder, 1985), it is preferred here to assign the specimen to *Eunicites*, especially due to the strong similarity of the stomodaeal armature (Ehlers, 1868, 1869). The jaws of the examined material are very similar in shape to those of *E. affinis* and *E. dentatus*, especially regarding the sharpened lateral ends (Ehlers, 1868; Alessandrello, 1990) that produce a scythe shape. However, when compared with *E. falcatus* n. sp., the mandibular processes of both *E. affinis* and *E. dentatus* are longer and stronger. The mandibular processes of both *E. affinis* and *E. dentatus* are joined for almost their whole length: in *E. falcatus* n. sp. the same structures are joined for about 1/5 of their length. Moreover, the anterior borders of the jaws are denticulate in both *E. affinis* and *E. dentatus*, not smooth like those of *E. falcatus* n. sp. Jaws with sharpened lateral ends that produce a scythe-shape structure can also be found in *E. atavus* and in *E. proavus*. However, the anterior borders of the jaws of *E. atavus* are not simply concave like those of *E. joinvillei* n. sp., they are undulate, concave externally and convex internally. Finally, the jaws of *E. proavus* are quite similar to those of *E. joinvillei* n. sp. with regard both to the shape and to the pattern of the anterior borders, but the angle they form has a reduced magnitude and the mandibular processes are triangular, thin, elongate and completely separated.

Eunicites diopatroides n. sp.
Pl. II (Figs. C, D); Pl. III (Figs. A, B); Pl. XV

Diagnosis: subelliptical jaws totally joined along a central junction line, inclined at an angle of almost 180° and projecting beyond the lateral borders of the mandibular processes but not protruding more than the forceps. Jaws anterior and posterior borders smooth and slightly concave, lateral borders markly rounded. Triangular, elongate and grooved mandibular processes, positioned side by side along a median line for about 2/3 of their length. Triangular, short, broad and symmetric carriers completely joined along a median line. Each carrier laterally provided with a strong and semicircular paddle.

Derivatio nominis: referring to the resemblance between the maxillary apparatus of the examined material and that of the modern onuphid genus *Diopatra*.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 3 specimens. MSNM i23084 (holotype), MSNM i13288 (part and counterpart) and MSNM i20613 (paratypes).

Description: each specimen lacks the terminal part of the body however, the pharyngeal apparatus is always preserved. It measures 7.8 mm in MSNM13288, 7 mm in MSNM 20613 and 9 mm in MSNM i23084. In MSNM 23084 (132 mm in length) jaws, forceps, fragments of mandibular processes and carriers are clearly mineralized, while in MSNM 20613 (140 mm in length) only the paddles of the carriers and the basal parts of the mandibular processes are three-dimensionally preserved. Regarding MSNM i13288 (18 mm in length) both the part and counterpart of the specimen are available: the jaws are not preserved in the part, while the other components of the stomodaeal apparatus appear disjuncted and fragmented both in the part and counterpart. The body shows a constant width in MSNM i13288 (8.7 mm) and MSNM 23084 (2.8 mm), while MSNM 20613 (2.8 mm) shows a slight widening at the level of the pharyngeal region (3.6 mm).

In MSNM i13288 the jaws are slightly distorted, in MSNM 20613 they are also disarticulated. The grooves of the mandibular processes are evident in the holotype, the only specimen showing full-preserved forceps. The forceps of the holotype are thick, notably projecting beyond the lateral borders of the jaws and measure 5 mm in length: the maximum distance between the external margins is 3.7 mm. In MSNM i20613 the imprints of the forceps are 4.4 mm apart in the point of maximum separation.

The maxillary apparatus is also represented by well-preserved carriers, a small fragment of the right maxilla II (MNSNM i23084) and a weak imprint of the left maxilla II (MSNM i13288). Both the carriers are laterally provided with a rounded and semicircular device (paddle).

In MSNM i13288 each parapodium is provided with two strong aciculae turned toward the cephalic extremity and one shorter intercalary acicula, divaricating from the others but similarly oriented. In MSNM i23084 the first half of the body bears tufts of two equally developed aciculae, while the other tufts consist of three elements arranged as in MSNM i13288. The longest aciculae measure between 2 mm (MSNM i23084) and 3 mm (MSNM i13288). In MSNM i20613 the aciculae are not preserved. Therefore, as in the living genus *Eunice*, the slender acicula could be interpreted as notopodial, the thick ones as neuropodial (Fauchald, 1992). The interpretation of the parapodial position of the aciculae of MSNM i13288 and MSNM i23084 is confirmed by the position in which these specimens are preserved: considering the superimposition of the jaw apparatus upon the maxillary apparatus the ventral surface is evidently being observed.

Some metameres are evident in the holotype (140: each 1.7 mm in thickness) and MSNM i13288 (27: each 0.4 mm in thickness).

Apart from short lengths of the alimentary canal and body outline, the soft parts are not preserved.

Remarks: the complex architecture of the pharyngeal armature of the examined specimens clearly indicates that they are eunicidan polychaetes. Moreover, the pattern of the jaws, the shape and architecture of the paired carriers and the kind of preservation of the pharyngeal apparatus, sometimes formed of a white and pearly material quite similar to the original one, suggest that they are labidognath eunicids or lumbrinerids (Fauchald, 1992; Fauchald & Rouse, 1997). Even if the eunicids possess, in contrast to the lumbrinerids, prostomial antennae that are not evident in the material examined (George & Hartman-Schröder, 1985), it is preferred here to assign the latter to *Eunicites*, especially due to the strong similarity of the stomodaeal armature (Ehlers, 1868, 1869). Subelliptical jaws and grooved mandibular processes such as those of *E. diopatroides* n. sp. are typical of *E. proavus*, *E. joinvillei* n. sp. and *E. affinis*. However, the jaws of both the latter *taxa* do not have smooth borders but have a denticulate anterior margin. Moreover, all these species lack carriers laterally equipped with semicircular paddles like those of *E. diopatroides* n. sp. (Ehlers, 1868; Kozur, 1970; Alessandrello, 1990). Such carriers have already been observed in both modern and fossil eunicemorph polychaetes, such as the Carboniferous eunicid *Esconites zelus,* whose jaws have a denticulate anterior border (Thompson & Johnson, 1977), and the Jurassic species *Melanoraphia maculata*. The latter was assigned to the lumbrinerids even if its affinities within the eunicidans must still be demonstrated (Arduini *et al.*, 1982).

Among the modern eunicids carriers equipped with such paddles can be found, for instance, in some species of *Eunice* and *Marphysa* Quatrefages, 1865 (Fauvel, 1923; Lange, 1950; Fauchald, 1970, 1992). Moreover, a pharyngeal apparatus very similar in the shape and arrangement of the jaws, mandibular processes and carriers to that seen in *E. diopatroides* n. sp. can also be found in some species of the onuphid genus *Diopatra* Audouin & Milne-Edwards, 1833 (Hartman, 1944; Kozlowski, 1956; Fauchald, 1977). Even if the onuphids are phylogenetically and morphologically related to the eunicids, they are tubicolous polychaetes (Paxton, 1986; Orensanz, 1990) that should have left traces of their tubes in the Haqel limestones. Since tubicolous polychaetes or their tubes have not been found to date in the fossiliferous outcrops of Lebanon, it is preferred here to assign the examined specimens to *Eunicites*.

Eunicites mariacristinae n. sp.
Pl. III (Figs. C, D)

Diagnosis: smooth bordered and half-ellipse shaped jaws, closely positioned side by side along a central junction line and forming a V-shaped complex. Elongate, triangular, thin and completely disjuncted mandibular processes.

Derivatio nominis: dedicated to Maria Cristina Gambi, an Italian marine biologist, in recognition of her studies on the modern polychaetes.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 1 specimen. MSNM i8490 (holotype).

Description: the body of the examined specimen is preserved as a dark, coiled and 110 mm long trace. No morphological features were observed because of the poor quality of preservation. The body has a constant width of about 2.5 mm, with the exception of the pharyngeal region which broadens slightly (3.5 mm). The chaetae are not preserved.

With regard to the stomodaeal apparatus, only the jaws and mandibular processes are preserved: they are evident as imprints at a distance of about 10 mm from the base where the pharyngeal region widens. The jaws show straight anterior and posterior borders, while the lateral ones are noticeably rounded. The lateral borders are quite turned anteriorly so that the jaws are inclined at an angle of about 60-70° and they form a V-shaped complex. The internal border of each jaw is straight and 0.15 mm long: it completely coincides with the internal border of the other jaw.

Due to the absence of both the chaetae and maxillary apparatus it is impossible to recognize the position in which the specimen is preserved.

Remarks: the architecture of the pharyngeal armature of the examined specimen clearly indicates that it is an eunicidan polychaete. Even if the eunicids possess, in contrast to the lumbrinerids, prostomial antennae that are not evident in the material examined (George & Hartman-Schröder, 1985), it is preferred here to assign the latter to *Eunicites*, especially due to the strong similarity in the pattern of the jaws (Ehlers, 1868, 1869). Among the species assigned to the genus *Eunicites* to date, three show some similarities with *E. mariacristinae* n. sp. with regard to the architecture of the jaws. They are the Eocenic species *E. gazolae* and *E. pinnai* from Monte Bolca (Alessandrello, 1990b) together with the Cretaceous species *E. phoenicius* from Haqel (Alessandrello & Teruzzi, 1986). However, in all these species the complex formed by the jaws does not show the same combination of characters as described for *E. mariacristinae* n. sp. In *E. gazoale* and *E. phoenicius* the jaws are not half-ellipse shaped and closely positioned side by side, they are instead triangular and joined for a short distance along a central junction line. Moreover, in *E. gazolae* the lateral extremities of the jaws are turned laterally, so that the jaws form an angle of greater magnitude when compared with that formed by the same structures in *E. mariacristinae* n. sp. In conclusion, even if the mandibular processes of *E. pinnai* are quite similar to those of *E. mariacristinae* n. sp., the jaws of the former are subtriangular, laterally elongate, slightly arcuate at the posterior end and, as in *E. phoenicius*, they form an angle of almost 180°.

Family Lumbrineridae Savigny, 1818

Genus *Teruzzia* n. gen.

Diagnosis: thread-like and small-bodied worms. Body sometimes tapering both anteriorly and posteriorly. Three patterns recognized in the morphology of the jaw apparatus: small, oval and separated jaws provided with long and triangular mandibular processes joined for about 3/4 of their length; subelliptical jaws fused in a V-shaped complex equipped with long and triangular mandibular processes joined for about 3/4 of their length; jaws and mandibular processes fused in a Y-shaped complex. Maxillae consisting of 5 paired plates as maximum. Short and symmetrical carriers heavily linked to strong and arcuate forceps and sometimes provided with a support, which articulates them to the maxillae I.

Derivatio nominis: dedicated to Giorgio Teruzzi, for his useful advice and support during this work.

Type species: *Teruzzia pezzolii* n. sp.

Teruzzia pezzolii n. sp.
Pl. IV; Pl. XVI

Diagnosis: small and oval jaws, smooth bordered, concentrically grooved on their surfaces, not joined along a median line. Sub-triangular mandibular processes, longitudinally grooved and joined for about 4/5 of their length but rather divaricate at the posterior end. Semicircular carriers equipped with a rounded support, which articulates them to the forceps.

Derivatio nominis: dedicated to Luigi Pezzoli for his support during this study.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 52 specimens. MSNM i13290 (holotype), MSNM i20611 and MSNM i24943 (paratypes), MSNM i8342, MSNM i8344, MSNM i8346, MSNM i8382, MSNM i8384, MSNM i8385, MSNM 8479, MSNM i8487, MSNM i9178, MSNM i9184, MSNM i9193, MSNM i9362, MSNM i12401, MSNM i12407, MSNM i12408 (part) and MSNM i12412 (counterpart), MSNM i12415 (part) and MSNM i13305 (counterpart), MSNM i12419, MSNM i13284, MSNM i13297, MSNM i13298, MSNM i13299, MSNM i13301, MSNM i13302, MSNM i16282, MSNM i20600, MSNM i20608, MSNM i20628, MSNM i20640, MSNM i20651, MSNM i20653, MSNM i20654, MSNM i20659, MSNM i22836, MSNM i23046, MSNM i23417 I, MSNM i23417 II, MSNM i23419 I, MSNM i23419 II, MSNM i23457, MSNM i24926 (part and counterpart), MSNM i24930, MSNM i24933, MSNM i24936 I (part and counterpart), MSNM i24977, MSNM i25000, MSNM i25001, MSNM i25004 and MSNM i25438.

Description: thread-like worms, measuring from 20 mm (MSNM i23419 I) to 85 mm (MSNM i12408 and MSNM i12412) in length, from 0.2 mm (MSNM i13284, MSNM i23419 I, MSNM i23419 II and MSNM i24977) to 1.2 mm (MSNM i13299) in width. The metameres are between 0.1 mm (MSNM i20651) and 0.5 mm (MSNM i12408 and i12412) long. In most of the examined specimens the pharyngeal region is not preserved, probably due to the cuticle slenderness in this body sector.

The complex formed of the jaws and their processes, which are often the only preserved elements of the stomodaeal apparatus. It is between 0.8 mm (MSNM i8342, MSNM i13290 and MSNM i13299) and 1.5 mm (MSNM i12407) in length. In most of the examined samples the jaws are three-dimensionally preserved: they show smooth anterior borders and they protrude slightly beyond the lateral borders of the mandibular processes but they are less jutted than the forceps.

The mandibular processes are longitudinally grooved, elongate, thin and quite expanded behind the jaws.

The forceps are rather shorter than the mandibular processes: they measure from 0.4 mm (MSNM i25004) to 0.7 mm (MSNM i20611 and MSNM i23457) in length and their apical hooks extend to about 3/4 of the length of the mandibular processes. The external margins of the forceps are between 0.2 mm (MSNM i25004) and 0.6 mm (MSNM i23419 I) apart.

Some specimens (MSNM i8342, MSNM i8384, MSNM i8479, MSNM i12401, MSNM i12407, MSNM i13284, MSNM i13290, MSNM i13298, MSNM i13301, MSNM i20611, MSNM i20628, MSNM i20640, MSNM i23419 II, MSNM 24943, MSNM 25000, MSNM i25001 and MSNM i25438) preserve fragments of the maxillae II. These structures show a denticulate inner margin provided with 4 teeth. Only MSNM i20640 preserves fragments of a maxillary plate which may be a maxilla III, IV or V.

Short (about 0.3 mm), semicircular and symmetrical carriers completely joined along a median line are preserved in most of the examined specimens. Each carrier is linked on a support, which articulates it to the forcep. These supports are joined along a median line and have the shape of a circumference quarter, with a rounded external border and a straight inner margin. In some specimens

(MSNM i8479, MSNM i13290 and MSNM i25001 for example) the carriers appear heavily linked to the forceps.

Only a few aciculae were observed but they are poorly preserved and it was not therefore possible to investigate how they relate to each parapodium. The aciculae measure from 0.3 mm (MSNM i20653) to 0.7 mm (MSNM i8385) in length.

With regard to the soft parts, the body outline is often preserved. Moreover, the dark traces of the alimentary canal are evident in a few specimens. MSNM i13301 has two anal cirri preserved as thin and faint imprints that measure 1 mm in length.

The dorsal surface is exposed in most of the specimens examined (for example MSNM i8479, MSNM i13290, MSNM i24943 and MSNM i25001): this can be clearly deduced from the position in which the jaw and maxillary apparata are preserved (Fauchald & Rouse, 1997).

Remarks: the general body morphology together with the architecture of the jaw apparatus clearly indicate that *Teruzzia* n. gen. belongs to the eunicidans. Furthermore, the presence of carriers which are heavily linked to the forceps suggest a labidognath architecture for the pharyngeal apparatus of *Teruzzia* n. gen. The labidognath eunicidans include Onuphidae, Dorvilleidae, Eunicidae and Lumbrineridae. The assignment of *Teruzzia* n. gen. to Onuphidae and Dorvilleidae is excluded here. In the first place, because the onuphids are tubicolous polychaetes, not free-living forms like *Teruzzia* n. gen., in the second because the maxillary apparatus of the dorvilleids consists of 2-4 longitudinal rows of small toothed plates and not of 5 paired plates as maximum such as is present in the Eunicidae, Lumbrineridae and, as it seems, also in *Teruzzia* n. gen. The distinction between the lumbrinerids and eunicids is especially based on the presence of prostomial antennae, non-mineralized structures which are difficult to observe in fossils. However, the jaw apparatus of *Teruzzia* n. gen. is quite similar to that of some species of the living lumbrinerid *Lumbrineris* Blainville, 1828 and that of the Jurassic *Lumbriconereites* (Ehlers, 1868; Hartman, 1944; Imajima & Higuchi, 1975; Orensanz, 1990). Differently from *Teruzzia* n. gen., the jaws of *Lumbriconereites* (430 mm) are subrectangular and have slightly rounded anterior borders. They are joined along a central junction line so that they form an heart-shaped complex.

When *Teruzzia* n. gen is compared with the Jurassic species *Melanoraphia* many differences may be noted. In contrast to the small and oval jaws of *Teruzzia* n. gen, the jaws of *Melanoraphia* are triangular and wing shaped. Moreover, the jaws of *Melanoraphia* bear short, subtriangular, rounded and separated mandibular processes (Arduini *et al.*, 1982), rather different from the complex the same structures form in *Teruzzia* n. gen. Finally, the carriers of *Melanoraphia* are laterally provided with two semicircular paddles that are not present in *Teruzzia* n. gen.

There are also significant differences between the lumbrinerid *Phiops* of Mississipian age and *Teruzzia* n. gen., especially with regard to the shape of the jaws (Schram, 1979). The jaws of *Phiops* are not oval like those of *Teruzzia* n. gen., but are subtriangular, laterally expanded and completely joined along a central junction line, with rather concave lateral borders, convex front borders and quite sharpened lateral ends. Moreover, the carriers of *Phiops aciculorum* are subrectangular and not semiciurcular like those of *T. pezzolii* n. gen. n. sp.

T. pezzolii n. gen. n. sp. and *T. sagittifera* n. gen. n. sp. may be distinguished on the basis of the shape and development of the carriers: in the former they are semicircular and articulated to the forceps by a rounded support, in the latter they form an arrow head shaped complex and lack any kind of support. The distinction between *T. pezzolii* n. gen. n. sp. and *T. pusilla* n. gen. n. sp. can be limited to the shape of the jaws: oval and separated in the former, subelliptical and fused in a V-shaped complex in the latter. Finally, *T. pezzolii* n. gen. n. sp. and *T. gryphoeides* n. gen. n. sp. may also be easily distinguished on the basis of the morphology of the jaw apparatus. This consists of two strong subtrapezoidal jaws forming a Y-shaped complex in the latter and two small oval jaws bearing triangular, elongate and joined mandibular processes in the former.

Teruzzia sagittifera n. sp.

Pl. V

Diagnosis: small, oval and smooth-bordered jaws, completely separated and laterally elongate beyond the external borders of the forceps. Slightly elongate carriers, joined for 1/2 of their length and forming an arrow head shaped complex.

Derivatio nominis: from the Latin *sagittiferus* (= bearing an arrow), referring to the shape of the complex formed by the maxillary carriers.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 2 specimens. MSNM i23436 (holotype) and MSNM i8476 (paratype).

Description: the holotype is flattened on the surface of a small and thin limestone slab where two fish are also preserved. In both the holotype and paratype the body is completely preserved as a rust coloured trace and it is quite coiled: however, a length of 50 mm and a width of 0.5 mm is reasonably valuable. The metameres and aciculae are not preserved.

The stomodaeal apparatus is 1.3 mm in length and is equipped with two elongate, triangular and symmetrical carriers (0.6 mm). Only the jaws and carriers are completely preserved, the former three-dimensionally, the latter as imprints. The basal parts of the forceps are strongly fragmented. Only the posterior extremities of the smooth surfaced mandibular processes are preserved as imprints: even if the mandibular processes are fragmentary, the pattern seems to be very similar to that of the other species described here under *Teruzzia* n. gen. In the holotype, the superimposition of the maxillary apparatus on the mandibular processes allow its dorsal preservation to be recognized.

The carriers are heavily linked to two strong and 0.25 mm thick forceps: the anterior extremities of the forceps are preserved as arcuate and hooked imprints. The tips of the forceps do not extend as far as the posterior borders of the jaws.

In the paratype only the jaws, mandibular processes, carriers are preserved as well as a long reddish trace of the body at the posterior end of the pharyngeal region: the superimposition of the forceps on the mandibular processes allow to recognize the ventral preservation of this specimen.

Remarks: the shape of the jaws and their processes suggest that the examined specimen should be assigned to

Teruzzia n. gen. Even if the jaw apparatus of *T. sagittifera* n. gen. n. sp. is very similar to that of *T. pezzolii* n. gen. n. sp., they may be distinguished on the basis of the shape of the carriers. In *T. sagittifera* n. gen. n. sp. the carriers are arrow head shaped and are directly articulated to the forceps, while in *T. pezzolii* n. gen. n. sp. there are two semicircular supports that articulate the triangular carriers to the forceps. In the only specimen examined of *T. gryphoeides* n. gen n. sp. the carriers are not preserved but the large, subtrapezoidal jaws are very different from the small oval ones of *T. sagittifera* n. gen. n. sp. The distinction between *T. sagittifera* n. gen. n. sp. and *T. pusilla* n. gen. n. sp. can be limited to the shape of the jaws: oval and disjuncted in the former, subellitptical and fused in a V-shaped complex in the latter.

Teruzzia pusilla n. sp.
Pl. VI (Figs. A, B)

Diagnosis: mandibular processes thick, triangular, elongate, longitudinally grooved, joined for about 4/5 of their length and slightly divaricate posteriorly. Completely fused, slightly elongate and subelliptical jaws forming a V-shaped and smooth bordered complex. Jaws embedded with grooves running parallel to their lateral and posterior borders.

Derivatio nominis: from the Latin *pusillus* (= tiny), referring to the dimensions of the examined specimen in comparison with the other species of the same genus.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 1 specimen. MSNM i8379 (holotype).

Description: thread-like worm that preserves the cephalic extremity and the pharyngeal apparatus but lacks the caudal extremity. At the level of the pharyngeal region a length of approximately 3.5 mm of the body is not preserved. The examined specimen measures 2.5 mm in length, 0.6 mm in width. The latter is constant. Both sides of the body are provided with aciculae however, due to the poor quality of preservation it was not possible to determine the relationship to each parapodium.

The pharyngeal apparatus appears formed of a pair of joined jaws (0.4 mm in length and 0.25 mm in width) with a smooth anterior border. The junction line between the jaws is not present so that they seem to form a single V-shaped complex. Two thick mandibular processes are articulated on the posterior end of the jaws: they are 0.7 mm in length.

The other elements that comprise the buccal apparatus are not preserved: thus it was not possible to recognize with certainty the position in which the specimen examined is preserved.

Discussion: the mandibular processes of the examined specimen are very similar in shape and development to those of *T. pezzolii* n. gen. n. sp. and *T. sagittifera* n. gen. n. sp. Moreover, the mandibular processes of *T. pusilla* n. gen. n. sp. are grooved like those *T. pezzolii* n. gen. n. sp., even if in *T. pusilla* n. gen. n. sp. these structures seem more prominent. However, the subelliptical jaws of the examined material show a difference in shape when compared with those of *T. pezzolii* n. gen. n. sp and *T. sagittifera* n. gen. n. sp.. These possess small, oval and completely separated jaws which do not form a V-shaped complex like that of *T. pusilla* n. gen. n. sp. Finally, in *T. gryphoeides* n. gen. n. sp. the jaw apparatus consists only of two subtrapezoidal and elongate jaws that form a Y-shaped complex. Furthermore, the species included in the living *Lumbrineris* can also have, in the same way as the strictly related *Teruzzia* n. gen., a jaw apparatus either with the pattern of *T. pezzolii* n. gen. n. sp and *T. sagittifera* n. gen. n. sp., of *T. pusilla* n. gen. n. sp. or of *T. gryphoeides* n. gen. n. sp. (George & Hartman-Schröder, 1985).

Teruzzia gryphoeides n. sp.
Pl. VI (Figs. C, D)

Diagnosis: subtrapezoidal and smooth surfaced jaws with denticulate anterior borders, joined along a median line and quite divaricate both anteriorly and posteriorly.

Derivatio nominis: from the Greek γριφοειδες (= enigmatical), referring to the vicissitudes during the systematic definition of the examined specimens (see the remarks).

Geological period: Cenomanian.

Type locality: Haqel.

Material: 1 specimen. MSNM i24967 (holotype).

Description: the studied specimen is 35 mm in length and the body is thread-like. The jaw apparatus and the caudal extremity are preserved but not the maxillary apparatus, except for a short length of the left maxillae I and II. At the level of the pharyngeal region the body is not preserved for a length of about 3.5 mm. The body measures 0.7 mm in width at the mid-length, but this decreases toward both the cephalic and caudal extremities. Alongside the body some imprints of poorly preserved aciculae are evident. The observed elements of the stomodaeal apparatus are preserved in three-dimensions with the exception of the left forcep, which is seen as an imprint.

The jaws measure 1.5 mm in length and are subtrapezoidal in shape. These subtrapezoidal jaws are joined along their straight and shorter flanks and have concave lateral borders. The anterior and posterior extremities of the jaws are sharpened and quite divaricate so that the jaw apparatus appears Y-shaped. On the side of the left jaw a 0.5 mm a long imprint of a hooked forcep is preserved together with a longitudinally elongate and subrectangular plate that probably represents a fragment of the left maxilla II. The latter is partially superimposed on the underlying jaws that in the eunicidan polychaetes are typically ventral: a dorsal preservation of the examined specimen may thus be inferred.

The carriers and chaetae are not preserved.

Remarks: the morphological pattern of the jaw apparatus of *T. gryphoeides* n. gen. n. sp. is very different from all the other species described here under *Teruzzia* n. gen. The jaw apparatus of *T. gryphoeides* n. gen. n. sp. actually lacks the distinction between jaws and mandibular processes that can be so clearly observed in the other species of the genus: these structures seem completely fused in a single Y-shaped complex so that the latter appears formed of two subtrapezoidal jaws only. The pharyngeal armature of the examined specimen is worthy of note due also to the absence of carriers.

Among the eunicemorph polychaetes, a jaw apparatus like that described for *T. gryphoeides* n. gen. n. sp., or rather a jaw apparatus formed of two large ventral plates that form a Y-shaped complex, can also be found in the oenonids and dorvilleids. Moreover, several dorvilleids possess a ctenognath maxillary apparatus, among the modern eunicidans this is the only one that can be characterized by the absence of carriers, a structure not present in the examined specimen. However, the assignment of the examined material to these families may reasonably be excluded. In the oenonids the pharynx is armoured with a prionognath maxillary apparatus which typically has paired, slender and elongate carriers and is formed of a heavily sclerotinized, shiny and black material strenghtened with metals. In the examined material the carriers are not present but the jaw apparatus consists of a very different lighter material. This material is whitish in colour, pearly, calcified and very similar to that of the labidognath eunicidans, such as the lumbrinerids. It also resembles that of the other specimens assigned here to *Teruzzia* n. gen. Moreover, both in the prionognath oenonids and dorvilleids the maxillary apparatus consists of longitudinal rows (2-4) of small, subrectangular and denticulate maxillae (Fauchald, 1970, 1977; Fauchald & Rouse, 1997). *T. gryphoeides* n. gen. n. sp. possesses large, ventral and Y-shaped jaws however, it lacks carriers like those observed in some dorvilleids. A longitudinally elongate and subrectangular fragment of the left maxilla II is also preserved. It may be inferred from a study of the morphology of this fragment that the maxillary apparatus of *T. gryphoeides* n. gen. n. sp. shows a very different pattern when compared with those typical of both the oenonids and dorvilleids. On the contrary, the pattern of this fragment seems to fit better with the maxillae typical of the labidognath eunicidans, among which only the lumbrinerids possess a jaw apparatus that consists of a large, ventral and Y-shaped complex like that of *T. grypheoides* n. gen. n. sp. With regard to the examined material it is preferred here, for the reasons outlined, to consider the absence of the carriers an artifact of fossilization: thus the studied specimen is tentatively assigned to the lumbrinerids and to the genus *Teruzzia* n. gen. Moreover, the general morphology of the body and the kind of preservation that characterize the specimen assigned to *T. gryphoeides* n. gen. n. sp. are the same as for the specimens assigned to the other species of the genus. Furthermore, also the species included in the living *Lumbrineris* may show, in the same way as the closely related *Teruzzia* n. gen., a jaw apparatus either with the pattern of *T. pezzolii* n. gen. n. sp and *T. sagittifera* n. gen. n. sp., the pattern of *T. pusilla* n. gen. n. sp. or with the pattern of *T. gryphoeides* n. gen. n. sp. (George & Hartman-Schröder, 1985).

The distinction between *T. gryphoeides* n. gen. n. sp. and the other species of *Teruzzia* n. gen. may be limited to the jaw apparatus, which in *T. gryphoeides* n. gen. n. sp. is only formed of two large subtrapezoidal pieces fused in a Y-shaped complex. In *T. pezzolii* n. gen. n. sp. and *T. sagittifera* n. gen. n. sp. the jaws are small, oval and clearly distinct from the triangular and elongate mandibular processes that they carry posteriorly. Finally, in *T. pusilla* n. gen. n. sp. the jaws are fused in a V-shaped complex but are nevertheless, clearly distinct from the mandibular processes. The latter are quite similar in shape and development to those of *T. pezzolii* n. gen. n. sp. and *T. sagittifera* n. gen. n. sp.

Genus *Lumbriconereites* Ehlers, 1869

Lumbriconereites hadjulae n. sp.
Pl. VII, Pl. VIII

Diagnosis: subrectangular and smooth bordered jaws, spatulate, grooved, anteriorly elongate, positioned side by side for about 3/4 of their length and slightly divaricate anteriorly. Short, slender, triangular and medially joined mandibular processes. Subtriangular and symmetrical carriers forming a arrow head shaped complex, medially joined for approximately 3/4 of their length and posteriorly divaricate at the back. Presence of a semicircular support, which links the carriers to the forceps.

Derivatio nominis: referring to Hadjula, site of finding of two specimens assigned to this new species.

Geological period: Cenomanian.

Type locality: Haqel.

Material: 16 specimens. MSNM i12424 (holotype, part and counterpart), MSNM i10402, MSNM 12632 (part and counterpart) and MSNM i20614 (paratypes), MSNM i8489, MSNM 9359 (part and counterpart), MSNM i20623, MSNM i22831, MSNM i23441, MSNM i25091, MSNM i25092, MSNM i25115 (part and counterpart), MSNM i25120 (Hadjula), MSNM i25125 (Hadjula), MSNM i25445 and MSNM i25446.

Description: only a few specimens (MSNM i9359, MSNM i20614, MSNM i25092, MSNM i25115, MSNM i25120, MSNM i25445) are full-preserved. The body measures from 40 mm (MSNM i9359) to 240 mm (MSNM i25120) in length, from 0.8 mm (MSNM i25445) to 4.5 mm (MSNM i252120) in width. The segmentation of the body is clearly evident only in MSNM i25091 (94 metameres: 0.3 mm in thickness), MSNM i252120 (150 metameres: 0.7 mm in thickness) and MSNM i25446 (118 metameres: 0.5 mm in thickness), but the full number of the metameres is never preserved.

The pharyngeal armature measures from 4 mm (MSNM i8489) to 4.5 mm (MSNM i12424) in length and has very elongate jaws. The jaws measure from 0.8 mm (MSNM i254746) to 1.8 mm (MSNM i9539, MSNM i10402 and MSNM i25120) in length and they protrude slightly beyond the lateral borders of the forceps. The lateral borders of the jaws are concave, whereas both the posterior and the anterior borders are convex. The surfaces of the jaws are characterized by straight growth lines running parallel to the lateral and posterior borders.

The small mandibular processes are preserved only in two specimens (MSNM i12632 and MSNM i20614), where they appear to be shorter than the jaws, they show slightly rounded borders and are divaricate at the posterior extremity.

In most of the examined specimens the forceps are also evident but their anterior extremity is never preserved. Nevertheless, the arcuate and hooked shape of the forceps may often be desumed by the investigation of their fragments or partial imprints. The presence of two elongate (almost from 1.5 mm in MSNM i8489 to 2.7 mm in MSNM i25120) and slightly distant (0.6 mm in MSNM i25445 and MSNM i25446, 1.1 mm in MSNM i12424) structures is observed. The anterior ends of the forceps seem to extend as far as the posterior borders of the jaws.

In most of the examined specimens some disjuncted remains of the maxillary apparatus are preserved. For example, between the forceps of MSNM i10402, a small fragment of the maxilla II is preserved: it is armoured with four small teeth on the inner border. A small plate with three longer teeth which may be attributed to the maxilla III is preserved in the same specimen. A similar situation characterizes the maxillary apparatus of MSNM i9539. Some fragments of the maxillary apparatus are evident also in the counterpart of MSNM i12424, in both part and counterpart of MSNM i12632 as well as in MSNM i22831 and MSNM 25092.

The carriers measure from 1 mm (MSNM i25446) to 2.6 mm (MSNM i10402) in length. They are joined for almost their whole length but are divaricate at the posterior extremity where their tips are 1 mm apart. Each carrier is linked to a support that articulates it to the forcep. These supports are well preserved only in the paratype, where they form a semicircular complex slightly narrower than the carriers.

In many specimens the aciculae appear as faint, scattered imprints or they are not preserved. However, at least two aciculae seem to be present in each parapodium. The parapodia have three aciculae only in MSNM i25092. The aciculae are always the same length and thickness and they measure from 1.1 mm (MSNM i25445 and MSNM i25446) to 1.8 mm (MSNM i25120) in length. Due to the absence of morphological differences in the preserved aciculae of each specimen it was not possible to establish whether these structures were notopodial or neuropodial.

The superimposition of the maxillary apparatus on the jaw apparatus suggests a dorsal preservation both for the holotype and paratype.

The preserved soft parts include the body outline and dark traces of the alimentary canal.

Remarks: the complex architecture of the pharyngeal armature of the examined specimens clearly indicates that they are eunicidan polychaetes. Moreover, the pattern of the jaws, the shape and architecture of the paired carriers and the kind of preservation of the pharyngeal apparatus, sometimes formed of a white and pearly material quite similar to the original one, suggest that they are labidognath eunicids or lumbrinerids (Fauchald, 1992; Fauchald & Rouse, 1997). However, the eunicids possess, in contrast to the lumbrinerids, prostomial antennae that are not evident in the material examined (George & Hartman-Schröder, 1985). Even if the absence of antennae in the fossil polychaetes could be an artifact of fossilization, the similarity between the pharyngeal armature of the examined specimens and those of the species included in the living genus *Lumbrineris* is remarkable. Thus, it is preferred here to assign the specimens examined to *Lumbriconereites*, especially due to the strong similarity of the stomodaeal armature (Ehlers, 1869). Only one full-preserved specimen has been assigned to *Lumbriconereites* to date. It is the Jurassic species *L. deperditus* from Solnhofen (Ehlers, 1869). Although the shape of the jaws of *L. hadjulae* n. sp. is very similar to that of the jaws of *L. deperditus* and *L. garassinoi* n. sp., the latter described below, these three species can be easily distinguished on the basis of the structure of the carriers. The triangular shape of the carriers of *L. deperditus* is not as regular as that of *L. hadjulae* n. sp. This is due to the fact that in *L. depertidtus* the carriers have rounded lateral borders, while the anterior and inner margins are straight. Consequently the complex formed by the carriers of *L. deperditus* is elongate, thicker and stronger than that of *L. hadjulae* n. sp. However, the semicircular support, which links the carriers to the forceps, is the more significant feature for distinguishing between the carriers of *L. hadjulae* n. sp. and *L. deperditus*: it is clearly evident in all the specimens assigned here to *L. hadjulae* n. sp. but is absent in both *L. deperditus* and *L. garassinoi* n. sp.

Lumbriconereites garassinoi n. sp.
Pl. IX (Figs. A, B)

Diagnosis: subrectangular and smooth bordered jaws, spatulate, grooved, anteriorly elongate, positioned side by side for about 3/4 of their length and anteriorly divaricate. Very short, slender, subtriangular and medially joined mandibular processes. Sub-triangular and short carriers with concave lateral borders and sharpened posterior ends.

Derivatio nominis: dedicated to Alessandro Garassino, in recognition of his studies on fossil invertebrates from Lebanon.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 1 specimen (holotype). MSNM i9355 (part) and MSNM i20618 (counterpart).

Description: the examined specimen lacks the posterior part of the body. The preserved fragment measures of 180 mm in length and 3.7 mm in width. Along the anterior extremity of the body some faint traces of the metameres may be observed. In some cases also the aciculae are preserved along the two flanks of the body, however, due to the poor quality of preservation of the specimen it was not possible to evaluate the number of metameres which form the trunk or the number of aciculae related to each parapodium.

The stomodaeal apparatus is approximately 6.2 mm long and the jaws measure 2 mm in length. Some parallel growth lines are preserved as thin ridges on the surface of the jaws: these ridges run from the anterior to the posterior border of each jaw.

Two short, triangular mandibular processes are preserved at the back of the jaws. The part also has arcuate forceps preserved: the left forcep is integrally preserved apart from the anterior hook, but the hook and the basal part of the right forcep are evident. The external margins of the forceps are 1.6 mm apart.

The short, triangular and medially joined carriers show a slight broadening at the articulation hinge with the forceps.

Fragments of the dorsal maxillae are present both in the part and counterpart, however due to the poor quality of preservation it is not possible to determine whether they belong to maxilla II, III or IV.

The relative positions of the jaw and maxillary apparata suggest a dorsal preservation for the holotype.

Remarks: the complex architecture of the pharyngeal armature of the examined specimen clearly indicates that it is an eunicidan polychaete. Moreover, the pattern of the jaws, the shape and architecture of the paired carriers and the kind of preservation of the pharyngeal apparatus, formed of a white and pearly material, suggest that they are labidognath eunicids or lumbrinerids (Fauchald, 1992; Fauchald & Rouse, 1997). However, the eunicids possess, in contrast to the lumbrinerids, prostomial antennae that are not evident in the material examined (George & Hartman-Schröder, 1985). Even if the absence of antennae in the fossil polychaetes could be an artifact of fossilization, the similarity between the pharyngeal armature of the examined specimens and those of the species included in the living genus *Lumbrineris* is remarkable. Thus, it is preferred here to assign the studied specimen to *Lumbriconereites*, especially due to the strong similarity of the stomodaeal armature (Ehlers, 1869). The morphology of the jaw apparatus of *L. garassinoi* n. sp. is very similar to that of *L. hadjulae* n. sp., except in the shape of the carriers which justifies the assignment of the examined specimen to a different species. Moreover, in contrast to *L. hadjulae* n. sp., the maxillary apparatus of *L. garassinoi* n. sp. lacks, as does that of *L. deperditus*, any kind of support linking the carriers to the forceps. Finally, the carriers of *L. deperditus* are subtriangular the same as those of *L. garassinoi* n. sp., although in the latter they are rather less elongate. However, their lateral borders are convex, not concave.

Family Oenonidae Kingberg, 1965

Genus *Phoeniciarabella* n. gen.

Diagnosis: elongate and thin worms. Jaws from subtriangular to subelliptical, sometimes fused in a single subtrapezoidal or heart-shaped complex, sometimes separated. Smooth surfaced or grooved mandibular processes, from subtriangular to subrectangular. Very long, slender and paired carriers, apparently not associated to a median unpaired piece, linked to the forceps for a short distance, more or less joined along a central junction line, often more elongate than the remaining pharyngeal apparatus and sometimes laterally provided with a small pinnula. Forceps with denticulate inner borders. Five pair of maxillae at least.

Derivatio nominis: from the Latin *phoenicius* (= native of *Phoenicia*, the latin name for modern Lebanon) and from *Arabella*, a living oenonid genus.

Type species: *Phoeniciarabella pinnulata* n. sp.

Phoeniciarabella pinnulata n. sp.
Pl. IX (Figs. C, D)

Diagnosis: subtriangular and elongate jaws, medially joined for about 3/4 of their length, slightly divaricate anteriorly and forming a trapezoidal complex. Triangular, elongate, thick and smooth surfaced mandibular processes. Long and slender carriers laterally equipped with a small pinnula and joined along a central junction line for about 1/3 of their length.

Derivatio nominis: from the Latin *pinnulatus* (= equipped with a paddle), referring to the presence of a small pinnula on each carrier.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 1 specimen. MSNM i12411 (holotype).

Decription: the holotype measures 20 mm in length and 2 mm in width. The aciculae and the segmentation of the body are not preserved.

The pharyngeal apparatus is 3.7 mm long and is preserved partly in three-dimensions, partly as an imprint. The maxillary apparatus and the external borders of the jaws are mineralized by a black, shiny material that is quite similar to the original material and which gives evidence of a heavily sclerotinized pharyngeal apparatus (Fauchald & Rouse, 1997). The jaws are 0.8 mm long and 0.4 mm wide and form a subtrapezoidal complex in which the shorter side coincides with the articulation hinge between jaws and mandibular processes. The smooth borders of the jaws exhibit a straight pattern apart from the anterior ends, where a convex pattern is exposed.

Beside the left jaw, two small, thick, hooked and slightly arcuate structures are evident: they represent the left maxilla III and the left maxilla II respectively. Their tips are oriented backward. Other small plates preserved between the basal parts of the forceps can be interpreted as fragments of the maxillary apparatus.

The right mandibular process is fragmented but clearly evident behind the jaws. It is short, subtriangular and slightly tapering at the back extremity. The right mandibular process partially hides the tip of the underlying right forcep: this is evidence of ventral preservation. The left forcep is three-dimensionally preserved at the mid-length only: along its inner margins two small teeth may be distinguished. The forceps are linked to the carriers for a short distance and are separated with a maximum distance apart of 0.8 mm. Their tips extend as far as the posterior borders of the jaws.

The carriers are quite elongate (1.9 mm) and laterally bear an anteriorly directed, small and rounded pinnula, at a point 1/4 of the distance along their length. These pinnulae have rounded tips and show a slight opening from the principal axis of the carriers. The carriers are slightly divaricate at the posterior extremity and are quite expanded at the articulation hinge with the forceps, where they form a semicircular complex with convex lateral borders and a concave anterior borders.

The superimposition of the jaw apparatus on the maxillary apparatus suggests a ventral preservation for the specimen examined.

Remarks: the complex jaw apparatus of the examined specimen clearly indicates that *Phoeniciarabella* n. gen. is an eunicidan polychaete. The long, slender morphology of the maxillary carriers, the forceps linked for a short distance to the carriers as well as the heavily sclerotinized jaws and maxillae are all evidence of the prionognath architecture which characterizes the pharyngeal apparatus of *Phoeniciarabella* n. gen. The same characteristics allow *Phoeniciarabella* n. gen. to be assigned to the oenonids (Colbath, 1986; Fauchald & Rouse, 1997). Among the modern eunicemorph polychaetes a prionognath stomodaeal apparatus can be found in the Histriobdellidae Vaillant, 1980 and the Oenonidae. However, the former are highly modified, achaetous and tiny polychaetes (< 2 mm) that live as parasites in the gills of crustaceans. They possess a single unpaired carrier (George & Hartmann-Schröder, 1985). Moreover, the carriers of *Phoeniciarabella* n. gen. are very similar to those of the living genera *Aglaurides* Ehlers, 1868, *Arabella*, *Drilonereis*, *Notocirrus* and *Oenone* (Hartman, 1944; Fauchald, 1970, 1977; George & Hartmann-Schröder, 1985; Orensanz, 1990). The maxillary carriers of these modern genera are usually provided with a third unpaired median piece that is not present in *Phoeniciarabella* n. gen.: it is possible that the absence of this structure in the examined specimen is a fossilization artifact. However, among the oenonids, this unpaired median piece can be absent in both parasitic (Martin & Britayev, 1998) and free-living *taxa* (Orensanz, 1990): if the absence of this structure in *Phoeniciarabella* n. gen. is real, this character could suggest a primitive condition.

Among the modern free-living oenonids the number of maxillae varies within both genera and species (Colbath, 1989) but the large-bodied forms, such as *Arabella* and *Oenone*, usually possess five or more pairs of maxillae, while the small-bodied forms, such as *Drilonereis*, have a smaller number of maxillae (Fauchald & Rouse, 1997). The dimensions as well as the five pairs of maxillae of the examined specimens suggest that *Phoeniciarabella* n. gen. is related with the large-bodied oenonids.

Moreover, *P. pinnulata* n. gen. n. sp. seems to share some similarity with the Silurian *Synclinophora synclinalis*, recently re-described on the basis of an articulated apparatus as the oldest arabellid known (Mierzejewski, 1984): the arabellids have been recently moved to the oenonids (Colbath, 1989; Orensanz, 1990). Although *S. synclinalis* lacks the pinnulae that provide the lateral borders of the carriers of *P. pinnulata* n. gen. n. sp. and even if it shows maxillae and carriers very similar to those of *P. pinnulata* n. gen. n. sp., these two species are hardly comparable as in *S. synclinalis* the jaws are not preserved. Furthermore, maxillae and carriers have a very similar pattern among the oenonids so that their general features are not diagnostic for distinguishing *Synclinophora* from *Phoeniciarabella* n. gen.

P. pinnulata n. gen. n. sp. differs from *P. caesaris* n. gen. n. sp. and *P. orensanzi* n. gen. n. sp. on the basis of the shape of the jaws and the pinnulae that occur laterally on each carrier. Neither *P. caesaris* n. gen. n. sp. nor *P. orensanzi* n. gen. n. sp. possess these pinnulae. Moreover, in contrast to *P. pinnulata* n. gen. n. sp., the jaws of *P. orensanzi* n. gen. n. sp. are subelliptical and separated, are not subtriangular and are fused in a subtrapezoidal complex, while the same structures of *P. caesaris* n. gen. n. sp. are subelliptical and form an heart-shaped complex.

Phoeniciarabella orensanzi n. sp.
Pl. X (Figs. A, B)

Diagnosis: stomodaeal apparatus with subelliptical, laterally elongate and separated jaws. Smooth surfaced, thick and subrectangular mandibular processes with rounded posterior borders. Long and slender carriers joined along a central junction line for about 4/5 of their length.

Derivatio nominis: dedicated to José-Maria Orensanz, for his contribution to the knowledge of oenonid systematics.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 1 specimen. MSNM i13283 (holotype).

Description: the preserved body measures 150 mm in length and 5 mm in width at the mid-length. It lacks the caudal extremity.

On both sides of the body a few poorly preserved aciculae are evident as imprints but it is not possible to distinguish their parapodial organization and exact length. The dark trace of the digestive tube is preserved along the central sector of the body.

The stomodaeal apparatus is comprised of two smooth bordered jaws that measure 0.2 mm in length and 0.3 mm in width. The jaws are positioned side by side along a medial line and their rounded lateral ends protrude significantly beyond the lateral borders of the mandibular processes. Behind the jaws the 0.6 mm long mandibular processes are preserved. The left jaw and its process are well preserved while the right ones are quite shattered.

Some fragments of the medial and posterior sectors of long and slender carriers are three-dimensionally preserved and appear as shiny, black pieces while the remaining parts are evident as imprints or, as in the case of the anterior extremities, are not preserved at all. The carriers are joined along a central junction line for about 4/5 of their length and are slightly divaricate at the posterior extremities. The complex formed by the carriers is very long (1.5 mm) when compared with the whole pharyngeal apparatus (about 2.7 mm).

The lack of the forceps and maxillae did not allow further information to be acquired.

The superimposition of the mandibular processes on the maxillary carriers over a short distance suggests a ventral preservation for the specimen examined.

Remarks: the assignment of the specimens examined to *Phoeniciarabella* n. gen. is mostly justified on the basis of the shape of the carriers and the kind of preservation of the pharyngeal armature. In the same way as the other species of the genus, the carriers of *P. orensanzi* n. gen. n. sp. are long, slender and are not equipped with a third unpaired piece. The pharyngeal armature shows mineralization by a black, shiny material. Differently from *P. pinnulata* n. gen. n. sp., *P. orensanzi* n. gen. n. sp. has significantly larger dimensions and differently shaped jaws and carriers. In particular the jaws of *P. orensanzi* n. gen. n. sp. are subelliptical, not subtriangular, whereas the carriers do not possess the pinnulae that characterize those of *P. pinnulata* n. gen. n. sp. As in *P. orensanzi* n. gen. n. sp., the carriers in *P. caesaris* n. gen. n. sp. are also not provided laterally with a pinnula, however, the jaws of *P. caesaris* n. gen. n. sp. are fused forming an heart-shaped complex. Its mandibular processes are triangular, thick, short and sharpened at the posterior extremities and longitudinally grooved, in contrast to the triangular, thinner, longer, smooth-surfaced and posteriorly rounded mandibular processes of *P. orensanzi* n. gen. n. sp.

Phoeniciarabella caesaris n. sp.
Pl. X (Figs. C, D); Pl. XI (Figs. A, B)

Diagnosis: stomodaeal apparatus with subelliptical jaws forming an heart-shaped complex. Triangular, thick, short, smooth-surfaced mandibular processes trimed with longitudinal grooves and sharpened at the posterior extremities. Long and slender carriers, completely joined along a central junction line.

Derivatio nominis: in memory of Cesare Alessandrello.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 2 specimens. MSNM i20610 (holotype, part and counterpart) and MSNM i23421 (paratype).

Description: instead of the holotype, it is the paratype which is completely preserved, however, the jaw apparatus of MSNM i20610 is better preserved. The fragmented body of the holotype is 270 mm in length and 10 mm in width, while the full-preserved paratype measures 60 mm in length and 0.7 mm in width. The body measurements of both the holotype and paratype are typical, in the same way as the other species of the genus, of a large-bodied oenonid.

The pharyngeal armature of the paratype is 1.9 mm long and it is mostly preserved as an imprint.

The jaws are 0.5 mm long and 0.3 mm wide in the holotype, 0.25 mm long and 0.15 mm wide in the paratype. They are smooth-bordered, medially joined along 3/4 of their length, quite divaricate and rounded at the anterior extremities so that they form an heart-shaped complex.

Two strong mandibular processes are preserved in both the considered specimens and they are 1 mm long in the holotype, 0.35 mm in the paratype. In the counterpart of MSNM i20610 some longitudinal grooves are preserved on the surfaces of the mandibular processes.

In the paratype, the external margin of the left forcep and the basal part of the right forcep are preserved as imprints. The forceps laterally protrude beyond the lateral borders of the jaws and they extend as far as the posterior borders of the same structures.

Two very long and slender carriers (3 mm in holotype, 1.1 mm in paratype) are linked for a short distance to the forceps. In the same way as the other elements of the pharyngeal apparatus, the carriers are preserved as imprints, apart from a small sector of the right one and a basal portion of both which are formed a black and shiny material.

In the counterpart of the holotype some fragments of the two plates that comprise the left and the right maxilla II are preserved.

In the paratype a few imprints of aciculae appear scattered on both sides of the body. The poor quality of preservation of the aciculae did not allow the number of elements on each metamere to be established.

The superimposition of the mandibular processes on the maxillary apparatus suggests a ventral preservation for the specimens examined.

Remarks: the assignment of the specimens examined to *Phoeniciarabella* n. gen. is mostly justified on the basis of the shape of the carriers and the kind of preservation of the pharyngeal armature. In the same way as the other species of the genus, the carriers of *P. caesaris* n. gen. n. sp. are long, slender and are not equipped with a third unpaired piece. The pharyngeal armature shows mineralization by a black and shiny material. In *P. pinnulata* n. gen. n. sp. the carriers are provided with a lateral pinnula and are joined for about 1/3 of their length, whereas in *P. orensanzi* n. gen. n. sp. the carriers lack these pinnulae and are joined for about 4/5 of their length. In *P. caesaris* n. gen. n. sp. the carriers do not have any kind of pinnula and are joined along a median line over their entire length. Moreover, *P. caesaris* n. gen. n. sp. may be distinguished from the other species of the same genus by the shape of the jaws: subtriangular and fused in a subtrapezoidal complex with regard to *P. pinnulata* n. gen. n. sp., subelliptical and separated in *P. orensanzi* n. gen. n. sp. and subelliptical and fused in a V-shaped complex in *P. caesaris* n. gen. n. sp.

Family Didonidae n. fam.

Diagnosis: elongate (50-150 mm) and thick eunicidans (1.5-3 mm). Jaw apparatus lacking mandibular processes. White and pearly jaws equipped with a black and shiny maxillary apparatus. Maxillary apparatus consisting of two longitudinal rows of pieces located on both sides of the pharyngeal armature. Presence of a single, unpaired carrier linked for a short distance to the forceps.

Remarks: the assignment of the specimens described below to a new family within the eunicemorph polychaetes is justified on the basis of several characters that determine the position of this new group as intermediate between the labidognath oenonoideans such as the lumbrinerids, the prionognath eunicidans such as the histriobdellids and oenonids, and the dorvilleids.

The didonids share with the lumbrinerids the architecture and conservation of the jaws. Their jaws have a very similar pattern to that of some living species of the genus *Lumbrineris*. They are comprised of a white and pearly material in the same way as both the living labidognath eunicidans and those from the Cenomanian of Lebanon, but differently from the oenonids. The pharyngeal armature of the latter can bear jaws very similar in shape to those of some *Lumbrineris* and didonids but it is formed of a very different material. However, the jaw apparatus of the didonids lacks the mandibular processes that are typically present in the similarly shaped jaws of the lumbrinerids, other labidognath eunicidans and the oenonids. Furthermore, the carrier of the didonids is elongate and has a short linkage with the forceps, characteristics that are more fitting with the pharyngeal armature of the prionognath eunicidans and dorvilleids. Among the modern prionognath eunicidans only the histriobdellids possess an unpaired carrier quite similar to that of the didonids. Neverthless, the histriobdellids are symbiotic polychaetes that show some adaptations to a parasitic mode of life, such as the very reduced dimensions, the absence of chateae and the presence of two posterior appendixes equipped with a sucker at the terminal end of the body. These characteristics together with the shape of the jaws indicate that the histriobdellids, parasites of crustacean gills, are very different from the free-living didonids and from all free-living polychaetes known. The disposition of the maxillae of the didonids closely recalls that of both the prionognath oenonoideans and the dorvilleids however, their conservation and consistence seem typically labidognath. In the examined specimens the maxillary apparatus is preserved by a black, shiny material, very similar to the heavily sclerotinized material enriched with metal-ions that comprises the maxillary apparatus of the prionognath eunicidans and of the oenonids from the Cenomanian of Lebanon. Furthermore, in the same way as the didonids, the carriers of both the prionognath eunicidans and dorvilleids show a short linkage with the forceps. However, the maxillary apparatus of the didonids differs from both that of the labidognath and prionognath eunicidans as it does not include paired and symmetrical carriers but, in the same way as the dorvilleids, it bears a single unpaired carrier.

Didone n. gen.

Diagnosis: as the type species.

Derivatio nominis: dedicated to Didone, mithological

Queen of the Phoenicians, ancient inhabitants of Lebanon.

Type species: *Didone pulcherrima* n. sp.

Didone pulcherrima n. sp.
Pl. XI (Figs. C, D); Pl. XII

Diagnosis: elongate and subelliptical jaws, posteriorly joined for about 3/4 of their length, anteriorly divaricate, forming a V-shaped complex and lacking in mandibular processes. Two longitudinal rows of hooked shaped maxillae. Maxillary apparatus supported by a single elongate and scythe-shaped carrier.

Derivatio nominis: from the Latin *pulcherrimus* (= very beautiful), due to the excellent preservation of the examined specimens.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 5 specimens. MSNM i20617 (holotype, part and counterpart), MSNM i20624 and MSNM i25457 (paratypes), MSNM i20619 and MSNM i23415.

Description: apart from MSNM i20624, all the examined specimens are preserved for the entire length of their bodies. They measure from 23 mm (MSNM i23415) to 150 mm (MSNM i25457) in length. The holotype is 115 mm in length while in MSNM i20624 only a 50 mm fragment including the cephalic extremity is preserved. The width of the body is constant and it measures from 1.3 mm (MSNM i20617) to 35 mm (MSNM i20619), with the exceptions of MSNM i20617 and MSNM i25457 that show a significant broadening at the level of the pharyngeal region, from 1.3 mm to 3.5 mm and from 3 mm to 5 mm respectively. The soft parts are not preserved, with the exception of some short, dark traces of the alimentary canal and the body outline.

Each specimen has the pharyngeal apparatus preserved, the length reaches 8 mm in MSNM i25457, 4.5 mm in MSNM i20624, 4 mm in MSNM 20619 and 3.6 mm in MSNM i23415. The jaws have smooth borders and longitudinally grooved surfaces. They are 2.2 mm long in MSNM i25457, 1.4 mm in MSNM i20617, 1.2 mm in MSNM i20624 and 1 mm in MSNM i20619. The jaw apparata are preserved both as imprints and reliefs.

The maxillary elements are positioned along two longitudinal rows on both sides of the pharyngeal armature. They seem like small hooked-shaped plates whose tips are turned laterally and slightly backward. In the holotype at least five of these maxillary plates are evident along the right side of the stomodaeal apparatus and three along the left side. Three of these maxillary plates are preserved in the paratype only along the right side.

The basal parts of the forceps are preserved in MSNM i20617, MSNM i20624 and MSNM i25457. In MSNM i20624 they appear to be linked for a short distance to the carrier.

In each specimen the maxillary apparatus appears to be equipped with a single asymmetrical carrier the original scythe shape of which may clearly be recognized in the holotype and MSNM i20619.

The aciculae are preserved as imprints along both body flanks of MSNM i20317, MNSM i20624, and MSNM i25457. In MSNM i25457 they have a length of approximately 2 mm.

As the jaw apparatus appears superimposed on the maxillary apparatus in both the holotype and paratype, the ventral preservation of these specimens may be implied.

Remarks: the complex morphology of the stomodaeal apparatus allows the examined specimens to be placed within the Eunicida. The most significant features of the pharyngeal apparatus are the absence of the mandibular processes, the maxillae arranged in two longitudinal rows and the presence of an unpaired carrier. Although the shape of the jaws of *Didone* n. gen. resembles that of some lumbrinerids superficially, the arrangement of the maxillae seem typically prionognath. In addition the carrier is not heavily linked to the first pair of maxillae as happens in the click-mechanism of the lumbrinerid-onuphid-eunicid labidognath line (Fauchald, *in litt.*) and the shape of the carrier is typically dorvilleidean. Thus, *Didone* n. gen. and the group to which it belongs may be related to the oenonid-dorvilleid line.

Order Phyllodocida Dales, 1962
Superfamily Aphroditacea Fauchald, 1977
Family Aphroditidae Malmgren, 1867
Genus *Paleoaphrodite* Alessandrello & Teruzzi, 1986

Paleoaphrodite libanotica n. sp.
Pl. XIII

Diagnosis: small-sized and elliptical body equipped with biramous parapodia bearing long chaetae grouped in two strong tufts. Each tuft formed of two setal types.

Derivatio nominis: from the Latin *libanoticus* (= from Lebanon), referred to country of origin of the examined material.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 6 specimens. MSNM i16288 (holotype), MSNM i23085 and MSNM i23086 (paratypes), MSNM i12397, MSNM i23087 and MSNM i24937.

Description: the bodies of the examined specimens are whole-preserved, apart from MSNM i23087 and MSNM i24937. The latter two specimens retain only a short fragment of the posterior body part, measuring 23 mm and 8 mm in length respectively. The body measures between 15 mm (MSNM i23085) and 20 mm (MSNM i23086) in length, between 2 mm (MSNM i23085) and 5 mm (MSNM i23086) as maximum width. MSNM i23086 and MSNM i24937 are full-preserved as imprints.

Excluding the body outline and alimentary canal, the latter preserved as a dark imprint in MSNM i24937, the soft parts are never evident. Along the alimentary canal of MSNM i24937 some small fish vertebrae are preserved: they could be interpreted as traces of predation.

The segmentation of the body is also not evident even if the metamerical organization is revealed by the parapodial arrangement of the chaetae which have allowed at least 12 metameres in MSNM i24937, 16 in MSNM i16288, 17 in both MSNM i12397 and MSNM i23085 to be counted. The chaetae appear clumped in two tufts on each side of the metameres: this arrangement is clear evidence of biramous parapodia. Since there are no morphological differences among the chaetae that provide the tufts of the same metamere side, it is not possible to distinguish between the neuropodial and notopodial tufts of each parapodium nor to hypothesize whether the dorsal or ventral surfaces of the examined specimens are exposed. Each tuft is composed of several thread-like chaetae, measuring from 2 mm (MSNM i23085) to 6 mm (MSNM i23086) in length, and of a smaller number of stronger and thicker chaetae, which may be aciculae, preserved in MSNM i23087, MSNM i12397 and MSNM i24397. The shorter chaetae are those of the anterior and posterior metameres, while the longer ones are those of the central metameres. Most of the chaetae are directed backward but the number of elements that equip each tuft may not be recognized due to the poor quality of preservation.

Remarks: the general body morphology allows the examined material to be related to family Aphroditidae, while the arrangement of the chaetae in two tufts on the sides of each metamere suggests a relationship with the genus *Paleoaphrodite*. The Triassic genus *Homaphrodite* is slightly different from *Paleoaphrodite* in the general morphology of the body and in the architecture of the aciculae. The shape of *H. speciosa* resembles closely that of a typical worm-like metazoan and the specimen described by Gall & Grauvogel (1966) seems to possess only thin chaetae: on the contrary, the body of *P. libanotica* n. sp. has the typical shape of a scale-worm and it is equipped with two chaetal types. However, the two genera are hardly comparable as *H. speciosa* has the antennae and elytrae preserved and these are not evident in *P. libanotica* n. sp.

The studied specimens show a strong similarity to two of the species described to date under *Paleoaphrodite*: the Triassic species *P. raetica* and the Jurassic species *P. gallica* (Alessandrello & Teruzzi, 1986b; Alessandrello *et al.*, 2004). *P. libanotica* n. sp. is similar to *P. raetica* in the oval/elliptical shape of the body but it differs from *P. raetica* in the strong similarity between the notopodial and neuropodial chaetae. This means that in *P. libanotica* n. sp. each setal tuft includes both thread-like chateae and strong chaetae, while in *P. raetica* a tuft is formed of thread-like chaetae only while the other tuft includes both thin and strong chaetae. In *P. gallica* the two tufts of each parapodium are composed of both strong and thin chaetae as in *P. libanotica* n. sp. but the body is fusiform.

Superfamily Glyceroidea Grube, 1850
Family Goniadidae Kingberg, 1866
Genus *Ferragutia* n. gen.

Diagnosis: as the type species.

Derivatio nominis: dedicated to Marco Ferraguti, who kindly donated one of the specimens among the examined material.

Type species: *Ferragutia cenomaniana* n. sp.

Ferragutia cenomaniana n. sp.
Pl. XIV

Diagnosis: pharyngeal apparatus armoured with a micrognaths circlet and two rows of chevrons. Macrognaths absent. Presence of longitudinal muscle bundles.

Derivatio nominis: referred to the geological age of the Haqel outcrop.

Geological age: Cenomanian.

Type locality: Haqel.

Material: 14 specimens. MSNM i8340 (holotype), MSNM i12423, MSNM i12426 (part and counterpart) and MSNM i25439 (paratypes), MSNM i9203, MSNM i9357, MSNM i12410 (part and counterpart) and MSNM i13291 (part and counterpart), MSNM i13306 I, MSNM i13306 II, MSNM i12425 (part and counterpart), MSNM i16295, MSNM i19512, MSNM i24961 and MSNM i24973.

Description: the presence of some whole-preserved specimens allowed the body length to be measured, from 2.6 mm (MSNM i9357) to 54 mm (MSNM i12410 and MSNM i13291), and the maximum width, from 0.3 mm (MSNM i24973) to 3.5 mm (MSNM i12423). The width of the body is not constant but it seems to decrease from the caudal extremity to the cephalic one.

Most of the examined specimens preserve both micrognaths and chevrons, while few specimens preserve the chevrons only (MSNM i9203, MSNM i12410, MSNM i13291 and MSNM i19512). Sometimes only a single row of chevrons is preserved (MSNM i9203, MSNM i24973). The micrognaths and chevrons of the examined specimens are preserved as small, black, shiny structures probably still composed of the original heavily sclerotinized material enriched with metal-ions. MSNM i12423 lacks both micrognaths and chevrons but can be reasonably assigned to the goniadid here described because of the presence of some longitudinal muscle bundles. In the whole-preserved specimens identical soft structures are particularly evident in the posterior part of the body. Also the relative dimensions of MSNM i12423, 53 mm in length and 3.5 mm in width at the mid-length, suggest the affinites with the other specimens described here. The presence of longitudinal muscle bundles in specimen MSNM i24961, which has only a short length of the posterior part of the body preserved, allows comparisons with *F. cenomaniana* n. gen. n. sp. Near the more slender extremity of this short section a low-preserved eunicemorph stomodaeal apparatus is preserved: it may represent evidence of predation even if it is difficult to distinguish whether the goniadid body and the eunicemorph apparatus are simply superimposed.

The poor quality of preservation of many examined specimens contributed to the distortion (MSNM i9357 and MSNM i12426), splitting (MSNM i8340, MSNM i9203 and MSNM i25439), disturbance (MSNM i12425) or/and interference (MSNM i12410 and MSNM i13291) of the rows of chevrons. However, well-preserved rows of chevrons are evident in MSNM i19512, where a single row of 20 elements is preserved, in MSNM i24973, where a single row (0.7 mm long) of 30 elements is preserved at a distance of 0.5 mm from the micrognaths, and in MSNM i13306 II, where both rows are preserved at a distance of 1 mm from the micrognaths. The largest chevrons are those of the central part of each row, while the smallest are those of the extremities. The micrognaths are also often disturbed or disrupted so that they form a mass in which their borders and shape may no longer be distinguished.

Only a few specimens preserve some imprints of aciculae that measure from 0.3 mm (MSNM i24973) to 0.7 mm (MSNM i12410 and MSNM i13291) in length. In MSNM i12423 the aciculae do not appear on both sides of the body as in the other specimens that show a dorsoventral preservation however, particularly in the posterior sector, their arrangement seems to support a lateral compression during diagenesis. The poor quality of preservation of the examined material did not facilitate an investigation of how the aciculae provide each parapodium and in turn provide information regarding where the parapodia are uniramous and where biramous: furthermore, in modern goniadids the parapodia are uniramous anteriorly, biramous posteriorly (Fauchald, 1977).

In addition to the longitudinal muscle bundles (MSNM i12401, MSNM i12423, MSNM i13291, MSNM i19512 and MSNM i24961) the preserved soft parts include the body outline and dark traces of the alimentary canal, particularly evident in the posterior part of the body. The trunk segmentation is hardly recognizable.

Remarks: a pharyngeal armature consisting of micrognaths and/or chevrons is typical of the goniadid polychaetes. The stomodaeum of the goniadids is an axial eversible pharynx (proboscis) armoured with jaws around the terminal aperture and, in some *taxa*, also with chevrons toward the base. The jaws consist of a circlet of micrognaths sometimes added to some paired macrognaths that appear as larger and denticulate structures. The chevrons support the proboscis and are usually arranged along two longitudinal rows (Hartman, 1950; Fauchald & Rouse, 1997). However, among the examined specimens evidence of an everted pharynx has not been found.

Among the modern goniadids three genera possess chevrons (Hartman, 1950; Fauchald, 1977; Fauchald & Rouse, 1977) in the same way as *Ferragutia* n. gen.: *Goniada*, *Goniadella* Hartman, 1950 and *Progoniada* Hartman, 1965. Neverthless, the lack of macrognaths in all the examined specimens, can hardly be considered an artifact of fossilization but rather as due to a prospective primitive organization (Hartman, 1950), which discriminates *Ferragutia* n. gen. from the modern representatives of this family and from the Missisipian fossil species described by Schram (1979) as *Carbosesostris megaliphagon*. The lack of macrognaths has already been observed in 32 specimens of the Carboniferous *Pieckonia helenae*, which may be distinguished from *Ferragutia cenomaniana* n. sp. as it also lacks chevrons (Thompson, 1979).

Furthermore, the pharyngeal armature of *Ferragutia* n. gen. seems strongly sclerotinized and strengthened by metal-ions in the same way as the living genera *Glycinde* Müller, 1858 and *Bathyglycinde* Fauchald, 1972, whose pharynxes are characterized, in contrast to *Ferragutia* n. gen., by the absence of the chevrons (Hartman, 1950; Fauchald, 1977).

PALEOBIOLOGY AND PALEOECOLOGY

Feeding habits

A lot of the considered specimens preserve a strong pharyngeal apparatus which, in some cases may suggest a predatory habit. However, among the modern polychaetes that possess a stomodaeum armoured with jaws and maxillae, some *taxa* are omnivorous (Kay & Brafield, 1973) or detritivorous (Sanders, 1956; Banse & Hobson, 1968; Goerke, 1971). The carnivorous polychaetes predate crustaceans, molluscs, fish, nematodes or other worms, but also less active preys, such as hydrozoans, bryozoans and poriferans (Mileikovsky, 1962; Hamond, 1969). Among the examined material several specimens preserve traces of the digestive tube as homogeneous, rust coloured thin bands. The preservation of these traces has probably been assisted by the presence of alimentary remains inside the digestive tube at the time of death, however, the food source is never recognizable. Nevertheless, a predatory habit for the aphroditid *Paleoaphrodite libanotica* n. sp. and for the goniadid *Ferragutia cenomaniana* n. gen. n. sp. are hypothesized here. The undetermined MSNM i12402 (Fig. 3) preserves a nematode buccal apparatus along the dark trace of the alimentary canal, the aphroditid specimen MSNM i24937 (Fig. 4) has 2-3 vertebrae of a tiny fish preserved along the reddish trace of the alimentary canal, the goniadid specimen MSNM i24961 preserves an eunicemorph pharyngeal armature in the posterior part of the body. The modern goniadids are actually carnivorous and they use their eversible proboscis crowned with jaws to capture prey (Hartman, 1950): only a few species use their jaws to grasp detritus particles. The modern aphroditids generally live in and on soft muddy bottoms where they slowly bulldoze their way through the sediment in search of organic detritus and small infauna to feed on. Although other living aphroditids tend to be carnivorous on small invertebrates and vertebrates rather than being primarily detritivorous like the sand-dwelling species (Hutchings & McRae, 1993).

Fig. 3 - MSNM i12402, undetermined specimen preserving possible traces of predation.

Reproduction

Among the living polychaetes some particular reproductive phoenomena, such as epitoky and stolonization, are known (Giangrande, 1997). The epitokous specimens are pelagic reproductive specimens that originate from the atokous specimens, or rather from non-reproductive individuals that undergo a direct, complete and profound trasformation, as happens in some nereidids. In other cases the atokous specimens are simply involved in the trasformation and separation of the posterior part of the body (schizogamy), as happens in some syllids and eunicids. The epitokous metameres appear profoundly modified with respect to the others so that the body of the worm seems to be divided in two morphologically distinct regions.

In the same way of the epitochy, the stolonization is an sexual reproductive process that implies the formation of some stolons at the caudal extremity of the specimens involved: through a rapid growth and their consequent separation, the stolons become new individuals.

Among the examined material, the indeterminate specimen MSNM i25433 (Fig. 5) shows profound morphological and morphometrical differences between the anterior and posterior metameres: this may be evidence of epitochy or stolonization but the poor quality of preservation did not allow further information to be obtained.

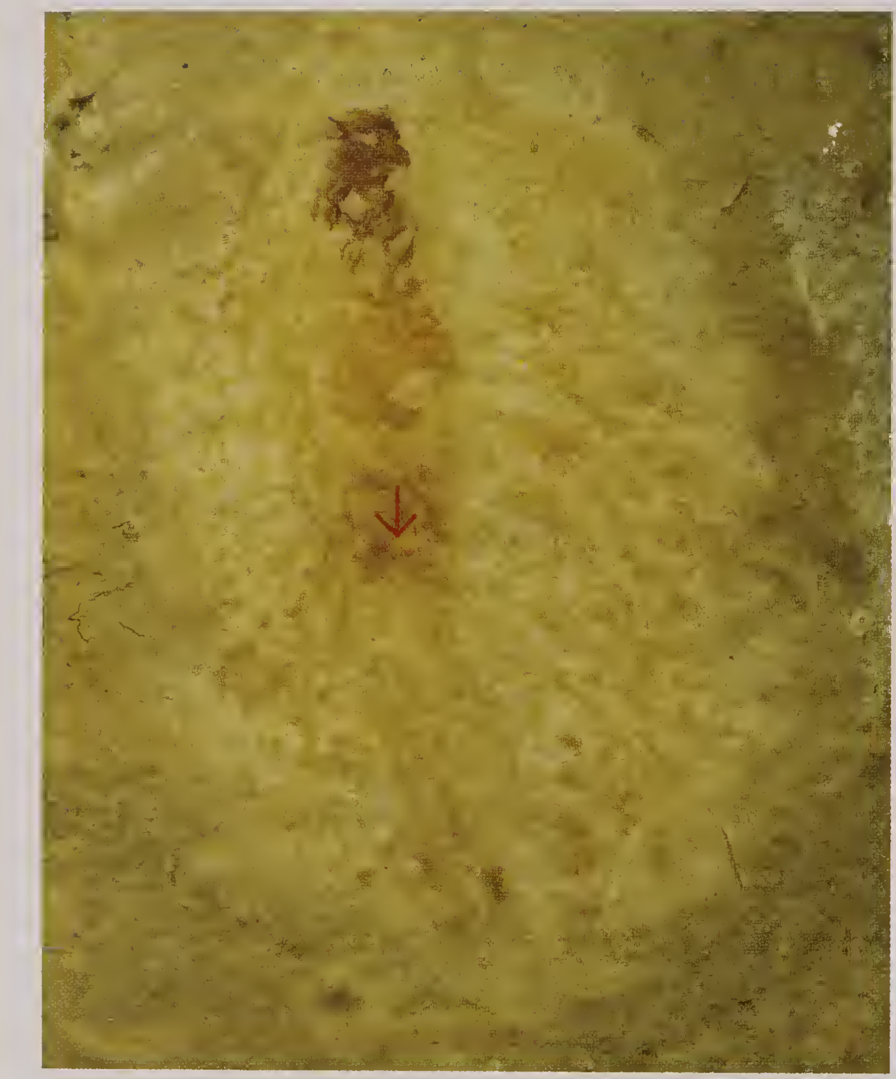

Fig. 4 - *Paleoaphrodite libanotica* n. sp., MSNM i24937, preserving possible traces of predation.

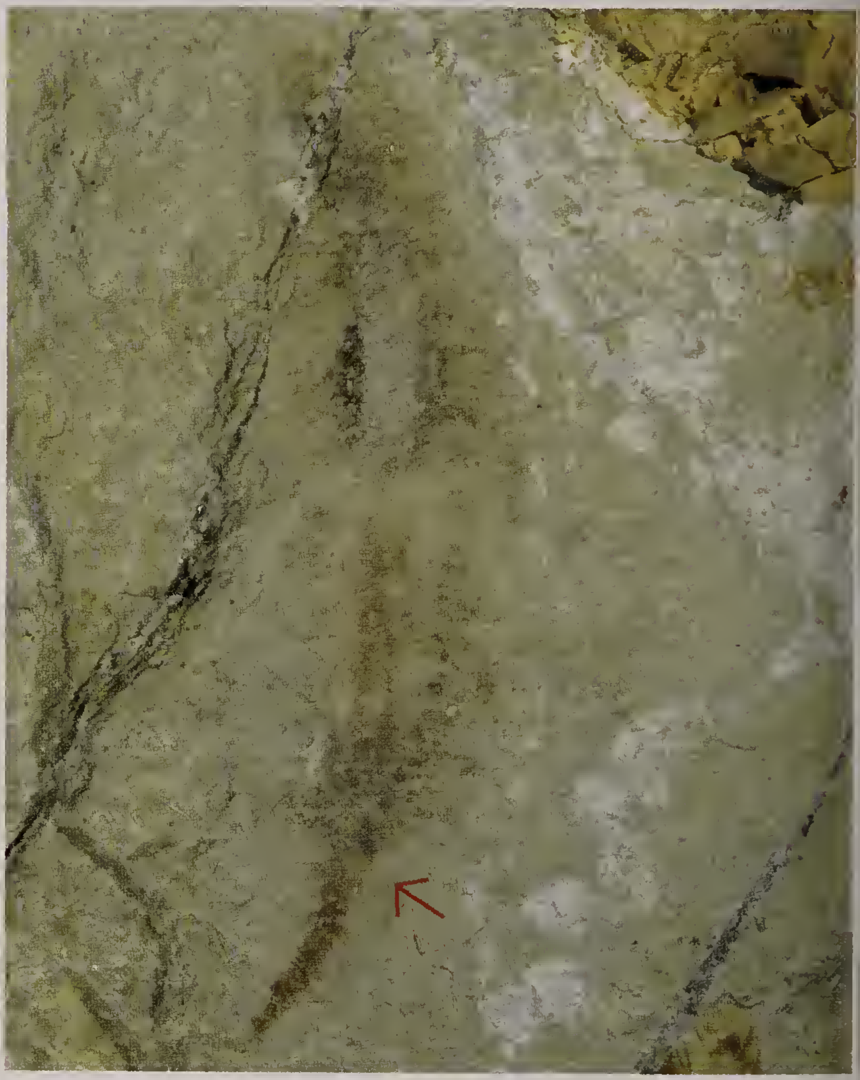

Fig. 5 - MSNM i25433, undetermined specimen showing possible traces of epitochy/stolonization.

DISCUSSION AND CONCLUSIONS

With 379 specimens the Lebanese collection of the fossil free-living polychaetes held by the Museo Civico di Storia Naturale di Milano represents the richest and most varied polychaete paleofauna known within the Mesozoic and, after the Field Museum (Chicago, U.S.A.) collection from the Carboniferous of Mazon Creek (Thompson, 1979), one of the most renowned and numerous in the world. A systematic definition at species level has been possible for 114 specimens: 2 specimens have been already described by Alessandrello & Teruzzi (1986), 112 (110 from Haqel, 2 from Hadjula) have been described in this work. To date 2 orders (Eunicida and Phyllodocida), 6 families (Aphroditidae, Didonidae n. fam., Eunicidae, Goniadidae, Lumbrineridae and Oenonidae), 7 genera (*Didone* n. gen., *Eunicites*, *Ferragutia* n. gen., *Lumbriconerites*, *Paleoaphrodite*, *Phoeniciarabella* n. gen. and *Teruzzia* n. gen.) and 17 species (*Didone pulcherrima* n. gen. n. sp., *Eunicites diopatroides* n. sp., *Eunicites falcatus* n. sp., *Eunicites joinvillei* n. sp., *Eunicites mariacristinae* n. sp., *Eunicites phoenicius*, *Ferragutia cenomaniana* n. gen. n. sp., *Lumbriconereites garassinoi* n. sp., *Lumbriconereites hadjulae* n. sp., *Paleoaphrodite libanotica* n. sp., *Phoeniciarabella caesaris* n. gen. n. sp., *Phoeniciarabella orensanzi* n. gen. n. sp., *Phoeniciarabella pinnulata* n. gen. n. sp., *Teruzzia gryphoeides* n. gen. n. sp., *Teruzzia pezzolii* n. gen. n. sp., *Teruzzia pusilla* n. gen. n.

sp. and *Teruzzia sagittifera* n. gen. n. sp.) of polychaetous annelids have been recorded from the Cenomanian fossiliferous levels of Lebanon. A systematic definition to species level was not possible for 265 specimens (Fig. 6): 226 still remain undetermined, due to the absence of diagnostic features related to the architecture of the pharyngeal armature or to the soft tissues that are rarely preserved in fossils, 31 have been classified to generic level (1 *Lumbriconereites*, 4 *Eunicites* and 26 *Teruzzia* n. gen.) while only 8 were identified to family level (8 Lumbrineridae).

Among the 363 specimens from Haqel there are (Fig. 7) 212 undetermined specimens, 106 Lumbrineridae, 16 Eunicidae, 14 Goniadidae, 6 Aphroditidae, 5 Didonidae n. fam. and 4 Oenonidae: the most represented genera are the lumbrinerid *Teruzzia* n. gen. (82) and *Lumbriconerites* (16), followed by the eunicid *Eunicites* (16), the goniadid *Ferragutia* n. gen. (14), the aphroditid *Paleoaphrodite* (6), the didonid *Didone* n. gen. (5) and the oenonid *Phoeniciarabella* n. gen. (4). Regarding the Haqel outcrop, the species that include the greatest number of specimens are *Teruzzia pezzolii* n. gen. n. sp. (52) and *Lumbriconerites hadjulae* n. sp. (14), followed by *Ferragutia cenomaniana* n. gen. n. sp. (14), *Paleoaphrodite libanotica* n. sp. (6), *Eunicites joinvillei* n. sp. (5), *Didone pulcherrima* n. gen. n. sp. (5), *Eunicites diopatroides* n. sp. (3), *Eunicites phoenicius* (2), *Teruzzia sagittifera* n. gen. n. sp. (2) and *Phoeniciarabella caesaris* n. gen. n. sp. (2). From the same outcrop only the holotype has been described for *Eunicites falcatus* n. sp., *Eunicites mariacristinae* n. sp., *Lumbriconereites garassinoi* n. sp., *Phoeniciarabella orensanzi* n. gen. n. sp., *Phoeniciarabella pinnulata* n. gen. n. sp., *Teruzzia gryphoeides* n. gen. n. sp. and *Teruzzia pusilla* n. gen. n. sp.

With regard to the outcrops of Hadjula and Al-Namoura there are few data on the polychaete paleodiversity as only 15 specimens for the former and 1 specimen for the latter have been collected from these sites to date. Futhermore, among the 15 specimens from Hadjula, a systematic definition to the species level has been possible only for two: they belong to *Lumbriconereites hadjulae* n. sp.

To date an investigation of the relative abundance of the polychaete families from a single paleobasin has been

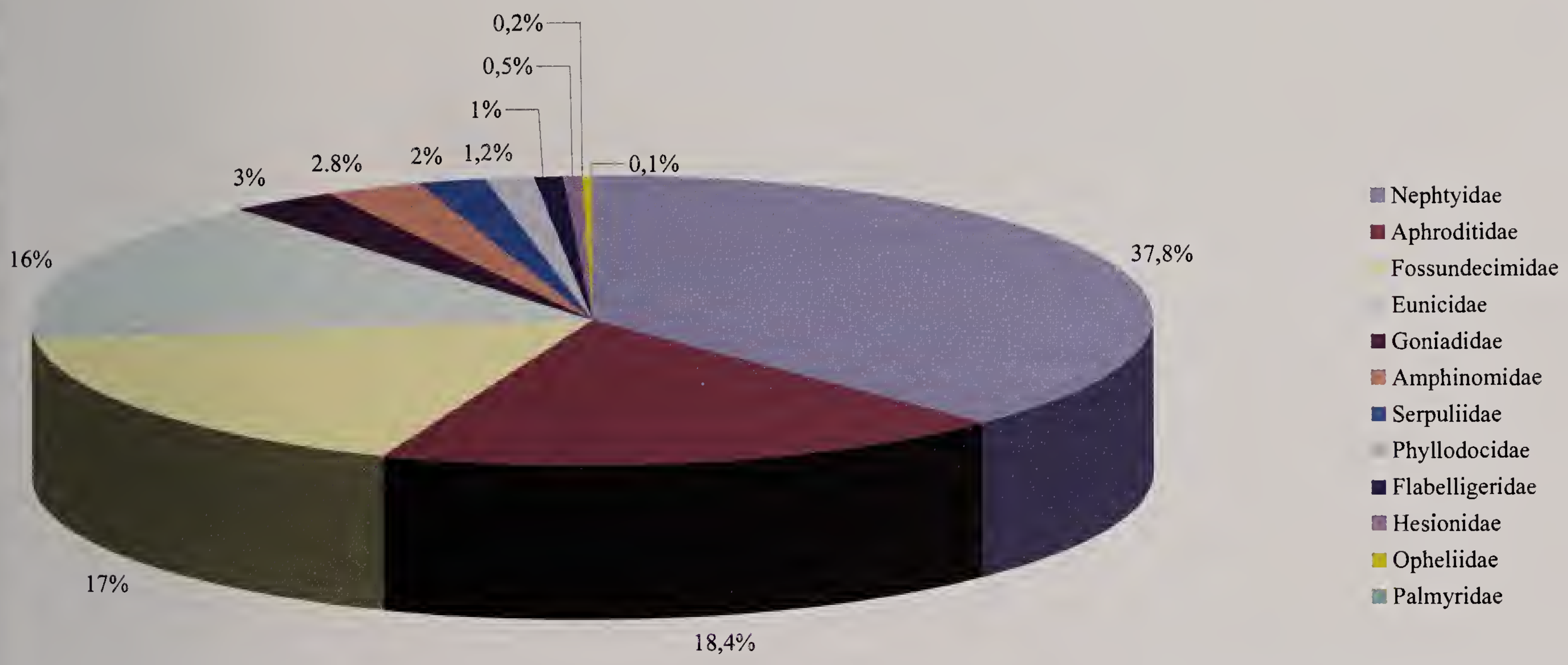

Fig. 6 - Distribution of the examined material among undetermined specimens, determined to species level, generic level or to family level.

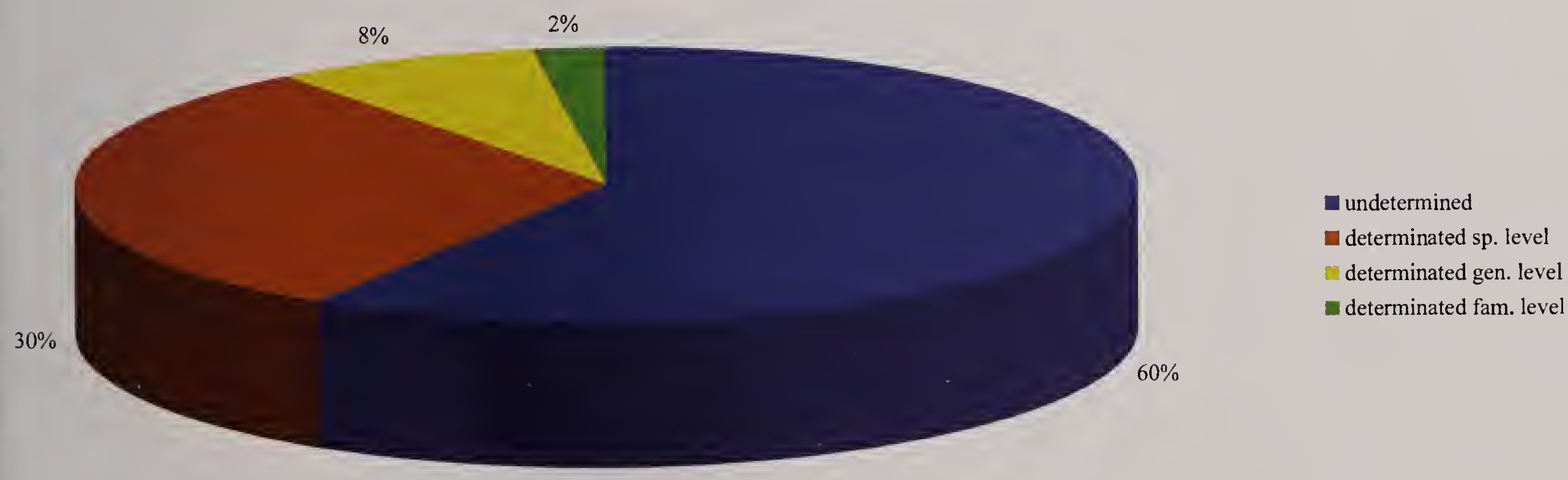

Fig. 7 - Distribuiton of the examined material from Haqel among undetermined specimens, Eunicidae, Lumbrineridae, Oenonidae, Didonidae, Aphroditidae and Goniadidae.

possible only for the Essex Carboniferous biota where at least 1085 polychaete specimens assigned to 12 families have been discovered (Thompson & Johnson, 1977; Thompson, 1979; Hay, 2002). The first difference that can be pointed out through the comparison of the polychaete fauna from Haqel and that from Essex is the presence of sedentary polychaetes in the latter: they represent about 3 % of the total specimens and they have been assigned, in order of abundance, to the flabelligerids, serpulids and opheliids. With regard to the free-living polychaetes, the Essex fauna is mostly comprised of, in order of abundance, nephtyids, aphroditids, fossundecimids and eunicids, followed by small percentages of amphinomids, goniadids, phyllodocids, hesionids and palmyrids (Fig. 8). The differences between the polychaete fauna from Haqel and that from Mazon Creek are probably related to the different paleoenvironments of these outcrops. Haqel was a small, deep paleobasin characterized by restriction of water circulation, stagnation, hypersalinity and oxygen depletion. On the contrary the Francis Creek Member from which most of the specimens described by Thompson (1979) and Hay (2002) were collected represents a delta complex influenced by sea-level and salinity fluctuations. There were distributary channels, interdistributary bays and a proximal prodelta as well as transitions from marine to estuarine and terrestrial facies (Schellenberg, 2002).

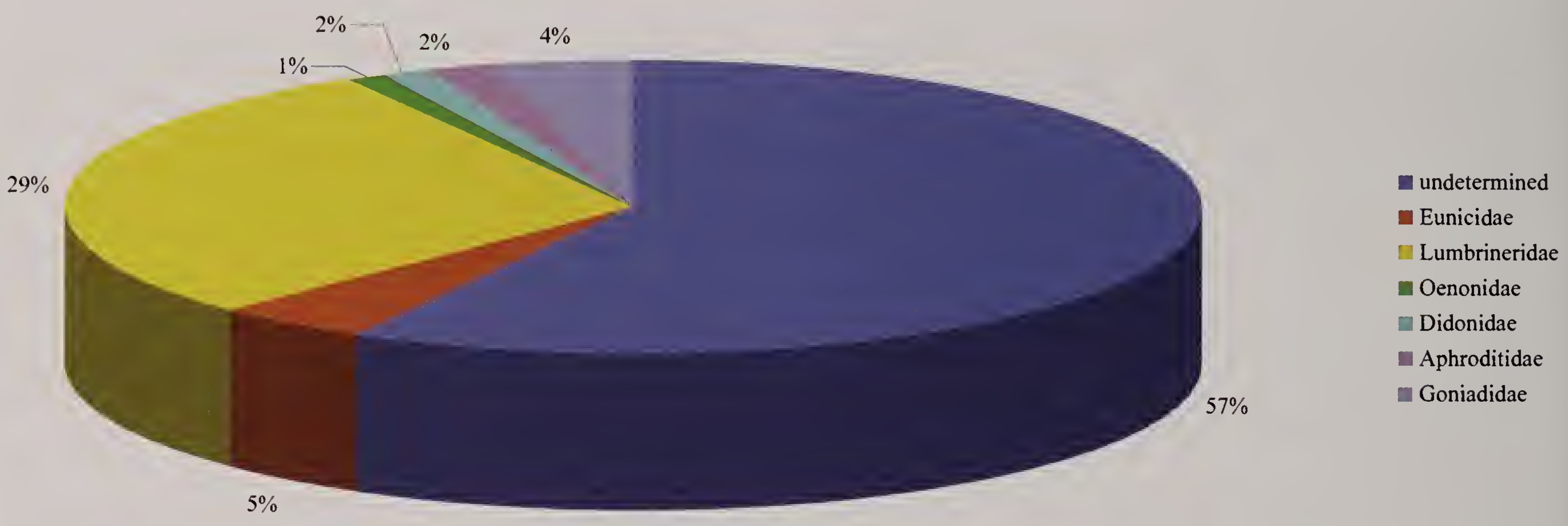

Fig. 8 - Systematic distribution of the polychaete fauna from Mazon Creek according to Thompson (1979) and Hay (2002).

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Paleodiversity of the free-living polychaetes (Annelida, Polychaeta) and description of new *taxa* from the Upper Cretaceous *Lagerstätten* of Haque, Hadjula and Al-Namoura
Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano
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Appendix - Complete listing of the examined specimens

The specimens marked with '*' are from Hadjula, those marked with '**' from Al-Namoura, all the others from Haqel.

MSNM v1168I	und.	und.	und.	und.	
MSNM v1168II	und.	und.	und.	und.	
MSNM v1168III	und.	und.	und.	und.	
MSNM v1168IV	und.	und.	und.	und.	
MSNM v1187	und.	und.	und.	und.	
MSNM v2148	und.	und.	und.	und.	
MSNM v3703	und.	und.	und.	und.	
MSNM i7843	Eunicida	Eunicidae	*Eunicites*	*phoenicius*	holotype
MSNM i7844	Eunicida	Eunicidae	*Eunicites*	*phoenicius*	paratype
MSNM i8338	und.	und.	und.	und.	
MSNM i8339	und.	und.	und.	und.	
MSNM i8340	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	holotype
MSNM i8342	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i8343	und.	und.	und.	und.	
MSNM i8344	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i8345	und.	und.	und.	und.	
MSNM i8346	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i8347	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i8348	und.	und.	und.	und.	
MSNM i8349	und.	und.	und.	und.	
MSNM i8350	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i8378	und.	und.	und.	und.	
MSNM i8379	Eunicida	Lumbrineridae	*Teruzzia*	*pusilla*	holotype
MSNM i8380	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i8381 (A+B)	und.	und.	und.	und.	
MSNM i8382	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i8383(A) + MSNM i8387(B)	und.	und.	und.	und.	
MSNM i8384	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i8385	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i8386	und.	und.	und.	und.	
MSNM i8388	und.	und.	und.	und.	
MSNM i8389	und.	und.	und.	und.	
MSNM i8390	und.	und.	und.	und.	
MSNM i8391	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i8472	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i8473	und.	und.	und.	und.	
MSNM i8474	und.	und.	und.	und.	
MSNM i8475	und.	und.	und.	und.	
MSNM i8476	Eunicida	Lumbrineridae	*Teruzzia*	*sagittifera*	paratype
MSNM i8479	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i8480	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i8481	und.	und.	und.	und.	
MSNM i8482	und.	und.	und.	und.	
MSNM i8483	Eunicida	Lumbrineridae	*Teruzzia*	und.	

MSNM i8487	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i8488	Eunicida	Eunicidae	*Eunicites*	*falcatus*	holotype
MSNM i8489	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i8490	Eunicida	Eunicidae	Eunicites	*mariacristinae*	holotype
MSNM i9178	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i9179	und.	und.	und.	und.	
MSNM i9180	und.	und.	und.	und.	
MSNM i9182I	und.	und.	und.	und.	
MSNM i9182II	und.	und.	und.	und.	
MSNM i9183	und.	und.	und.	und.	
MSNM i9184	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i9185	und.	und.	und.	und.	
MSNM i9186	und.	und.	und.	und.	
MSNM i9187	und.	und.	und.	und.	
MSNM i9190	Eunicida	Lumbrineridae	und.	und.	
MSNM i9192	Eunicida	Lumbrineridae	und.	und.	
MSNM i9193	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i9194	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i9195	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i9196	und.	und.	und.	und.	
MSNM i9197	und.	und.	und.	und.	
MSNM i9199	und.	und.	und.	und.	
MSNM 9200	und.	und.	und.	und.	
MSNM i9201	und.	und.	und.	und.	
MSNM i9202	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i9203	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM 9206I	und.	und.	und.	und.	
MSNM 9206II	und.	und.	und.	und.	
MSNM i9207	und.	und.	und.	und.	
MSNM i9208	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i9209	und.	und.	und.	und.	
MSNM i9210	und.	und.	und.	und.	
MSNM i9211	und.	und.	und.	und.	
MSNM i9212	und.	und.	und.	und.	
MSNM i9213	und.	und.	und.	und.	
MSNM i9214	und.	und.	und.	und.	
MSNM i9355(A)+MSNM i20618(B)	Eunicida	Lumbrineridae	*Lumbriconereites*	*garassinoi*	holotype
MSNM i9356	und.	und.	und.	und.	
MSNM i9357	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i9258	und.	und.	und.	und.	
MSNM i9359 (A+B)	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i9360	und.	und.	und.	und.	
MSNM i9361	und.	und.	und.	und.	
MSNM i9362	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
**MSNM i9363	und.	und.	und.	und.	
MSNM i9367	und.	und.	und.	und.	

MSNM i9369	und.	und.	und.	und.	
MSNM i9370	und.	und.	und.	und.	
MSNM i10402	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	paratype
MSNM i10762	und.	und.	und.	und.	
MSNM i10763	Eunicida	Lumbrineridae	und.	und.	
MSNM i10968	und.	und.	und.	und.	
MSNM i12396	und.	und.	und.	und.	
MSNM i12397	Phyllodocida	Aphroditidae	Paleoaphrodite	*libanotica*	
MSNM i12398	und.	und.	und.	und.	
MSNM i12400	und.	und.	und.	und.	
MSNM i12401	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i12402	und.	und.	und.	und.	
MSNM i12403	und.	und.	und.	und.	
MSNM i12404	und.	und.	und.	und.	
MSNM i12405	und.	und.	und.	und.	
MSNM i12406	und.	und.	und.	und.	
MSNM i12407	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i12408(A)+MSNM i12412(B)	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i12409	und.	und.	und.	und.	
MSNM i12410(A)+MSNM i13291(B)	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i12411	Eunicida	Oenonidae	*Phoeniciarabella*	*pinnulata*	holotype
MSNM i12413	und.	und.	und.	und.	
MSNM i12414	Eunicida	Eunicidae	*Eunicites*	*joinvillei*	paratype
MSNM i12415(A)+MSNM i13305(B)	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i12417	und.	und.	und.	und.	
MSNM i12419	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i12420	Eunicida	Eunicidae	*Eunicites*	*joinvillei*	holotype
MSNM i12421	und.	und.	und.	und.	
MSNM i12422	und.	und.	und.	und.	
MSNM i12423	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	paratype
MSNM i12424 (A+B)	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	holotype
MSNM i12425 (A+B)	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i12426 (A+B)	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	paratype
MSNM i12626	und.	und.	und.	und.	
MSNM i12628	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i12629	und.	und.	und.	und.	
MSNM i12630	und.	und.	und.	und.	
MSNM i12631	und.	und.	und.	und.	
MSNM i12632 (A+B)	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	paratype
MSNM i12936	Eunicida	Lumbrineridae	und.	und.	
MSNM i13283	Eunicida	Oenonidae	*Phoeniciarabella*	*orensanzi*	holotype
MSNM i13284	Eunicida	Eunicidae	*Teruzzia*	*pezzolii*	
MSNM i13286	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i13287	und.	und.	und.	und.	
MSNM i13288 (A+B)	Eunicida	Eunicidae	*Eunicites*	*diopatroides*	paratype
MSNM i13289	und.	und.	und.	und.	

MSNM i13290	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	holotype
MSNM i13292	und.	und.	und.	und.	
MSNM i13293	und.	und.	und.	und.	
MSNM i13294	und.	und.	und.	und.	
MSNM i13295	und.	und.	und.	und.	
MSNM i13296	und.	und.	und.	und.	
MSNM i13297	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i13298	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i13299	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i13301	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i13302	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i13303	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i13304	Eunicida	Eunicidae	*Eunicites*	*joinvillei*	paratype
MSNM i13306I	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i13306II	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i13307	und.	und.	und.	und.	
MSNM i13308	und.	und.	und.	und.	
MSNM i13309	und.	und.	und.	und.	
MSNM i13311	Eunicida	Eunicidae	*Eunicites*	und.	
MSNM i13312	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i13606(A) + MSNM i16303(B)	und.	und.	und.	und.	
MSNM i16275I	und.	und.	und.	und.	
MSNM i16275II	und.	und.	und.	und.	
MSNM i16276	und.	und.	und.	und.	
MSNM i16278	und.	und.	und.	und.	
MSNM i16279	Euncida	Lumbrineridae	und.	und.	
MSNM i16282	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i16287	und.	und.	und.	und.	
MSNM i16288	Phyllodocida	Aphroditidae	*Paleoaphrodite*	*libanotica*	holotype
MSNM i16291	und.	und.	und.	und.	
MSNM i16293	Eunicida	Lumbrineridae	und.	und.	
MSNM i16294	und.	und.	und.	und.	
MSNM i16295	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i16296	und.	und.	und.	und.	
MSNM i16299	und.	und.	und.	und.	
MSNM i16308	und.	und.	und.	und.	
MSNM i19512	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i20654	und.	und.	und.	und.	
MSNM i20593	Eunicida	Eunicidae	*Eunicites*	und.	
MSNM i20595	und.	und.	und.	und.	
MSNM i20597	und.	und.	und.	und.	
MSNM i20599	und.	und.	und.	und.	
MSNM i20600	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20601	und.	und.	und.	und.	
MSNM i20603I	und.	und.	und.	und.	
MSNM i20603II	und.	und.	und.	und.	

MSNM i20608	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20609	und.	und.	und.	und.	
MSNM i20610 (A+B)	Eunicida	Oenonidae	*Phoeniciarabella*	*caesaris*	holotype
MSNM i20611	Euncida	Lumbrineridae	*Teruzzia*	*pezzolii*	paratype
MSNM i20612	Eunicida	Eunicidae	*Eunicites*	*joinvillei*	
MSNM i20613	Eunicida	Eunicidae	*Eunicites*	*diopatroides*	paratype
MSNM i20614	Eunicida	Eunicidae	*Lumbriconereites*	*hadjulae*	paratype
MSNM i20615	und.	und.	und.	und.	
MSNM i20616	und.	und.	und.	und.	
MSNM i20617 (A+B)	Eunicida	Didonidae	*Didone*	*pulcherrima*	holotype
MSNM i20619	Eunicida	Didonidae	*Didone*	*pulcherrima*	
MSNM i20620	und.	und.	und.	und.	
MSNM i20621	und.	und.	und.	und.	
MSNM i20623	Eunicida	Eunicidae	*Lumbriconereites*	*hadjulae*	
MSNM i20624	Eunicida	Didonidae	*Didone*	*pulcherrima*	paratype
MSNM i20625	und.	und.	und.	und.	
MSNM i20627	und.	und.	und.	und.	
MSNM i20628	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20629	und.	und.	und.	und.	
MSNM i20630	und.	und.	und.	und.	
MSNM i20632	und.	und.	und.	und.	
MSNM i20633	und.	und.	und.	und.	
MSNM i20638	und.	und.	und.	und.	
MSNM i20639	und.	und.	und.	und.	
MSNM i20640	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20641	und.	und.	und.	und.	
MSNM i20642	und.	und.	und.	und.	
MSNM i20643	und.	und.	und.	und.	
MSNM i20644	und.	und.	und.	und.	
MSNM i20645	und.	und.	und.	und.	
MSNM i20646	und.	und.	und.	und.	
MSNM i20647	und.	und.	und.	und.	
MSNM i20648	und.	und.	und.	und.	
MSNM i20649	und.	und.	und.	und.	
MSNM i20651	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20653	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20654	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20656	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20657	und.	und.	und.	und.	
MSNM i20658	und.	und.	und.	und.	
MSNM i20659	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i20661	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i20662	und.	und.	und.	und.	
MSNM i20663	und.	und.	und.	und.	
MSNM i22829	und.	und.	und.	und.	
MSNM i22830	und.	und.	und.	und.	

MSNM i22831	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i22832	und.	und.	und.	und.	
MSNM i22833	und.	und.	und.	und.	
MSNM i22835	und.	und.	und.	und.	
MSNM i22836	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i22837	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i22838	und.	und.	und.	und.	
MSNM i22839	und.	und.	und.	und.	
MSNM i22840	und.	und.	und.	und.	
MSNM i23046	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i23048	und.	und.	und.	und.	
MSNM i23051	und.	und.	und.	und.	
MSNM i23053	und.	und.	und.	und.	
MSNM i23056	und.	und.	und.	und.	
MSNM i23058	und.	und.	und.	und.	
MSNM i23059	und.	und.	und.	und.	
MSNM i23083	und.	und.	und.	und.	
MSNM i23084	Eunicida	Eunicidae	*Eunicites*	*diopatroides*	holotype
MSNM i23085	Phyllodocida	Aphroditidae	*Paleoaphrodite*	*libanotica*	paratype
MSNM i23086	Phyllodocida	Aphroditidae	*Paleoaphrodite*	*libanotica*	paratype
MSNM i23087	Phyllodocida	Aphroditidae	*Paleoaphrodite*	*libanotica*	
MSNM i23414	und.	und.	und.	und.	
MSNM i23415	Eunicida	Didonidae	*Didone*	*pulcherrima*	
MSNM i23416	und.	und.	und.	und.	
MSNM i23417I	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i23417II	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i23419I	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i23419II	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i23421	Eunicida	Oenonidae	*Phoeniciarabella*	*caesaris*	paratype
MSNM i23424	und.	und.	und.	und.	
MSNM i23425	und.	und.	und.	und.	
MSNM i23426	und.	und.	und.	und.	
MSNM i23427	und.	und.	und.	und.	
MSNM i23428	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i23429	und.	und.	und.	und.	
MSNM i23436	Eunicida	Lumbrineridae	*Teruzzia*	*sagittifera*	holotype
MSNM i23440	und.	und.	und.	und.	
MSNM i23441	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i23443	und.	und.	und.	und.	
MSNM i23447	und.	und.	und.	und.	
MSNM i23448	und.	und.	und.	und.	
MSNM i23450	und.	und.	und.	und.	
MSNM i23453	und.	und.	und.	und.	
MSNM i23454	Eunicida	Lumbrineridae	und.	und.	
MSNM i23455	und.	und.	und.	und.	
MSNM i23457	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	

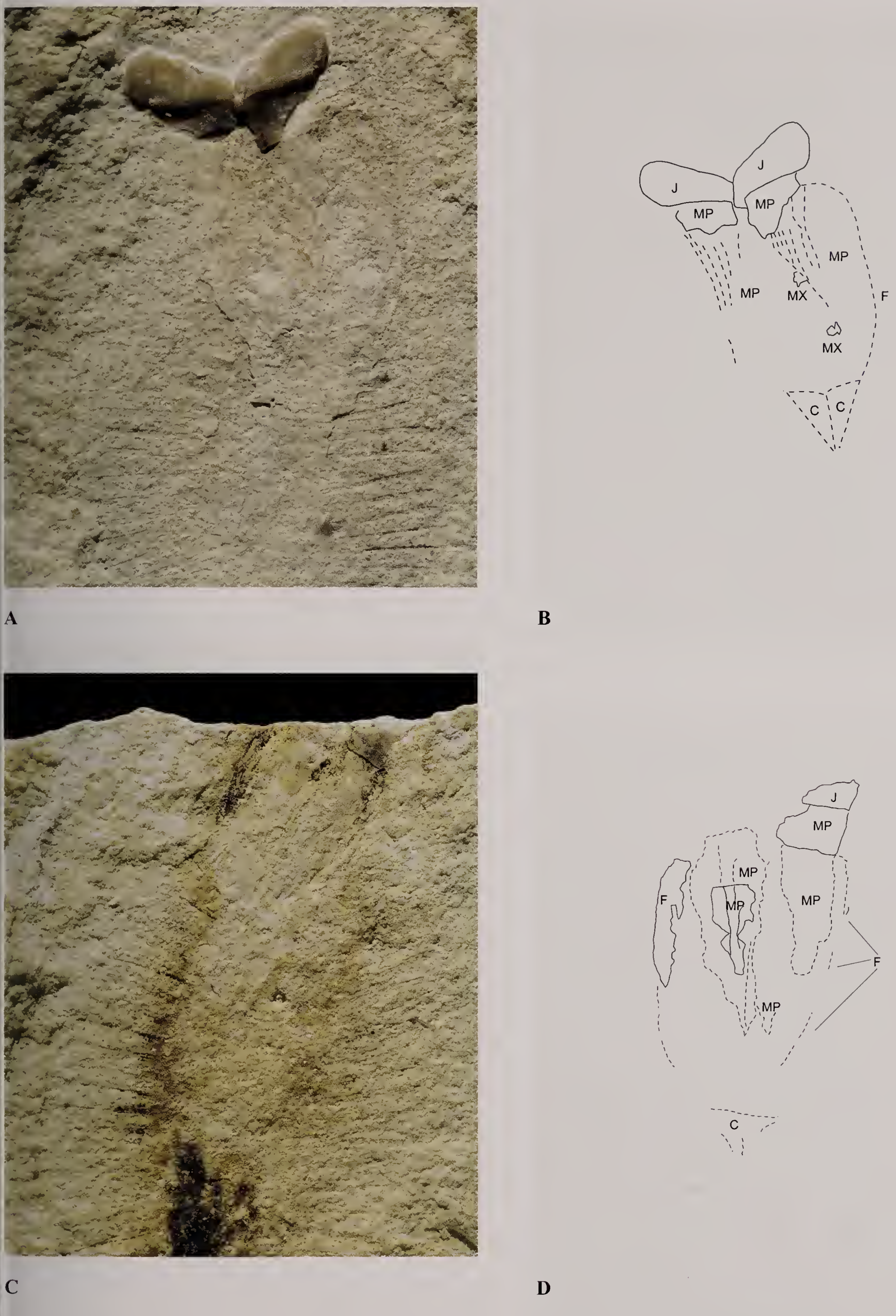
MSNM i23458	und.	und.	und.	und.	
MSNM i24812	Eunicida	Eunicidae	*Eunicites*	und.	
MSNM i24813	und.	und.	und.	und.	
MSNM i24814 (A+B)	und.	und.	und.	und.	
MSNM i24911	und.	und.	und.	und.	
MSNM i24913	Eunicida	Lumbrineridae	und.	und.	
MSNM i24915 (A+B)	und.	und.	und.	und.	
MSNM i24917	und.	und.	und.	und.	
MSNM i24918	und.	und.	und.	und.	
MSNM i24919	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i24926 (A+B)	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i24930	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i24933	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i24935	und.	und.	und.	und.	
MSNM i24936 (A+B)I	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i24936 (A+B)II	und.	und.	und.	und.	
MSNM i24937	Phyllodocida	Aphroditidae	*Paleoaphrodite*	*libanotica*	
MSNM i24940	und.	und.	und.	und.	
MSNM i24943	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	paratype
MSNM i24944	und.	und.	und.	und.	
MSNM i24945	und.	und.	und.	und.	
MSNM i24946	und.	und.	und.	und.	
MSNM i24961	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i24965	und.	und.	und.	und.	
MSNM i24964	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i24966	und.	und.	und.	und.	
MSNM i24967	Eunicida	Lumbrineridae	*Teruzzia*	*gryphoeides*	holotype
MSNM i24970 (A+B)	und.	und.	und.	und.	
MSNM i24972	und.	und.	und.	und.	
MSNM i24973	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	
MSNM i24976	und.	und.	und.	und.	
MSNM i24977	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i24989	und.	und.	und.	und.	
MSNM i24990	und.	und.	und.	und.	
MSNM i24991	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i24992	und.	und.	und.	und.	
MSNM i24944	und.	und.	und.	und.	
MSNM i25000	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i25001	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i25002	und.	und.	und.	und.	
MSNM i25003	und.	und.	und.	und.	
MSNM i25004	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i25005	und.	und.	und.	und.	
MSNM i25007	und.	und.	und.	und.	
MSNM i25009 (A+B)	und.	und.	und.	und.	
MSNM i25011	und.	und.	und.	und.	

MSNM i25014	und.	und.	und.	und.	
MSNM i25015 (A+B)	und.	und.	und.	und.	
MSNM i25019	und.	und.	und.	und.	
MSNM i25020 (A+B)	und.	und.	und.	und.	
MSNM i25088	und.	und.	und.	und.	
MSNM i25089	und.	und.	und.	und.	
MSNM i25090	und.	und.	und.	und.	
MSNM i25091	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i25092	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i25093 (A+B)	und.	und.	und.	und.	
*MSNM i25107	und.	und.	und.	und.	
*MSNM i25108	und.	und.	und.	und.	
*MSNM i25109	und.	und.	und.	und.	
*MSNM i25110	und.	und.	und.	und.	
*MSNM i25113	und.	und.	und.	und.	
*MSNM i25115 (A+B)	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
*MSNM i25116	und.	und.	und.	und.	
MSNM i25117	und.	und.	und.	und.	
MSNM i25118	Eunicida	Eunicidae	*Eunicites*	und.	
*MSNM i25119	und.	und.	und.	und.	
*MSNM i25120	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i25433	und.	und.	und.	und.	
MSNM i25434	und.	und.	und.	und.	
MSNM i25435	und.	und.	und.	und.	
MSNM i25436	und.	und.	und.	und.	
MSNM i25437	und.	und.	und.	und.	
MSNM i25438	Eunicida	Lumbrineridae	*Teruzzia*	*pezzolii*	
MSNM i25439	Phyllodocida	Goniadidae	*Ferragutia*	*cenomaniana*	paratype
MSNM i25440	und.	und.	und.	und.	
MSNM i25441 (A+B)	und.	und.	und.	und.	
MSNM i25442	Eunicida	Lumbrineridae	*Teruzzia*	und.	
*MSNM i25443	und.	und.	und.	und.	
MSNM i25444	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i25445	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i25446	Eunicida	Lumbrineridae	*Lumbriconereites*	*hadjulae*	
MSNM i25447	und.	und.	und.	und.	
MSNM i25448	und.	und.	und.	und.	
MSNM i25449	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i25450	und.	und.	und.	und.	
MSNM i25451	und.	und.	und.	und.	
MSNM i25452 (A+B)	und.	und.	und.	und.	
MSNM i25453	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i25454	Eunicida	Lumbrineridae	*Teruzzia*	und.	
MSNM i25455 (A+B)	und.	und.	und.	und.	
MSNM i25456	Eunicida	Eunicidae	*Eunicites*	*joinvillei*	
MSNM i25457	Eunicida	Didonidae	*Didone*	*pulcherrima*	paratype

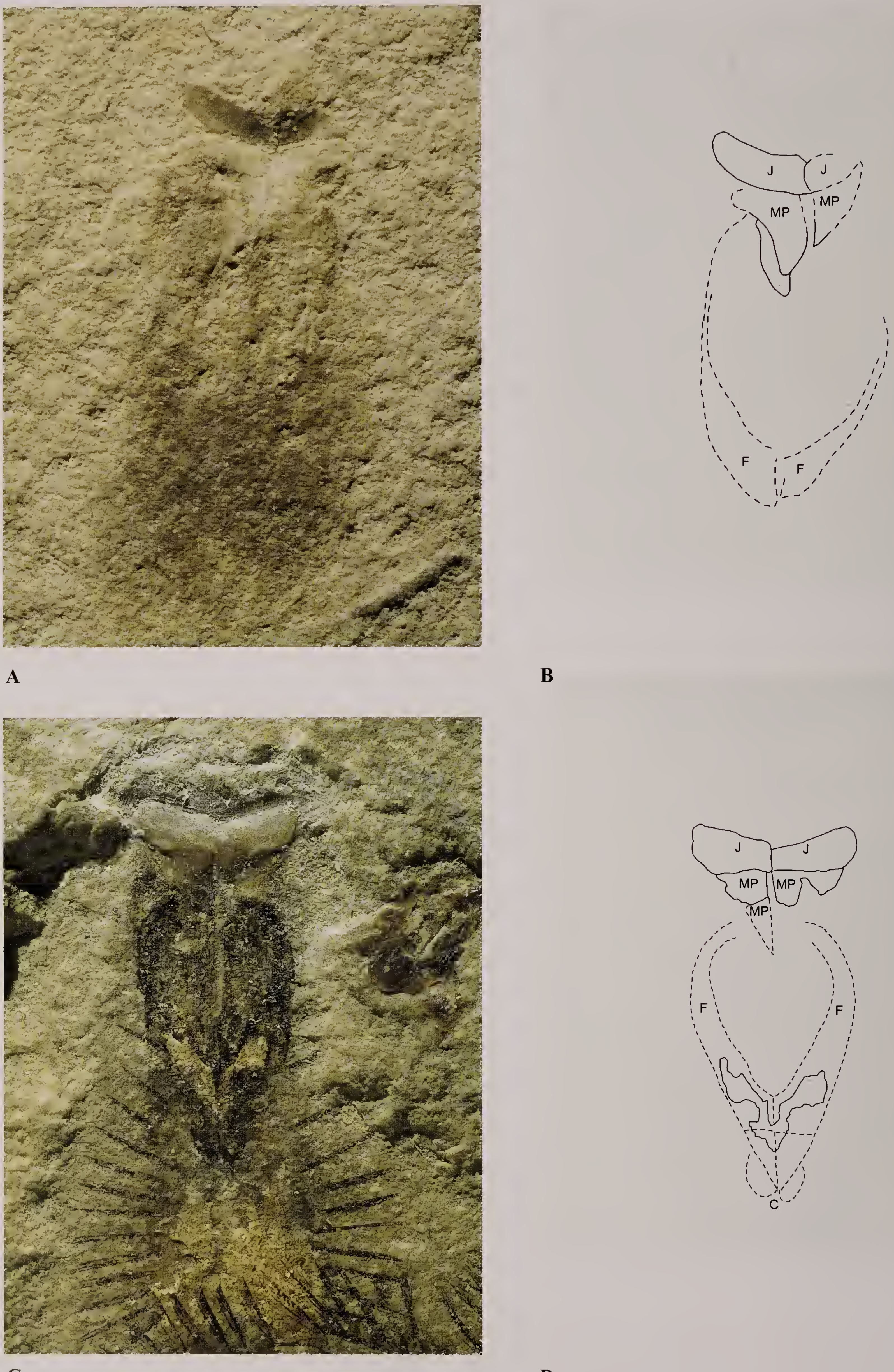
MSNM i26326	und.	und.	und.	und.	
MSNM i26327	und.	und.	und.	und.	
MSNM i26328	und.	und.	und.	und.	
MSNM i26329	und.	und.	und.	und.	
MSNM i26330	Eunicida	Lumbrineridae	*Lumbriconereites*	und.	
*MSNM i26332	und.	und.	und.	und.	
MSNM i26333	und.	und.	und.	und.	
*MSNM i26335 (A+B)	und.	und.	und.	und.	
*MSNM i26336	und.	und.	und.	und.	
MSNM i26337	und.	und.	und.	und.	
*MSNM i26338	und.	und.	und.	und.	
MSNM i26339	und.	und.	und.	und.	
MSNM i26340	und.	und.	und.	und.	

PLATES I - XVI: LIST OF ABBREVIATIONS

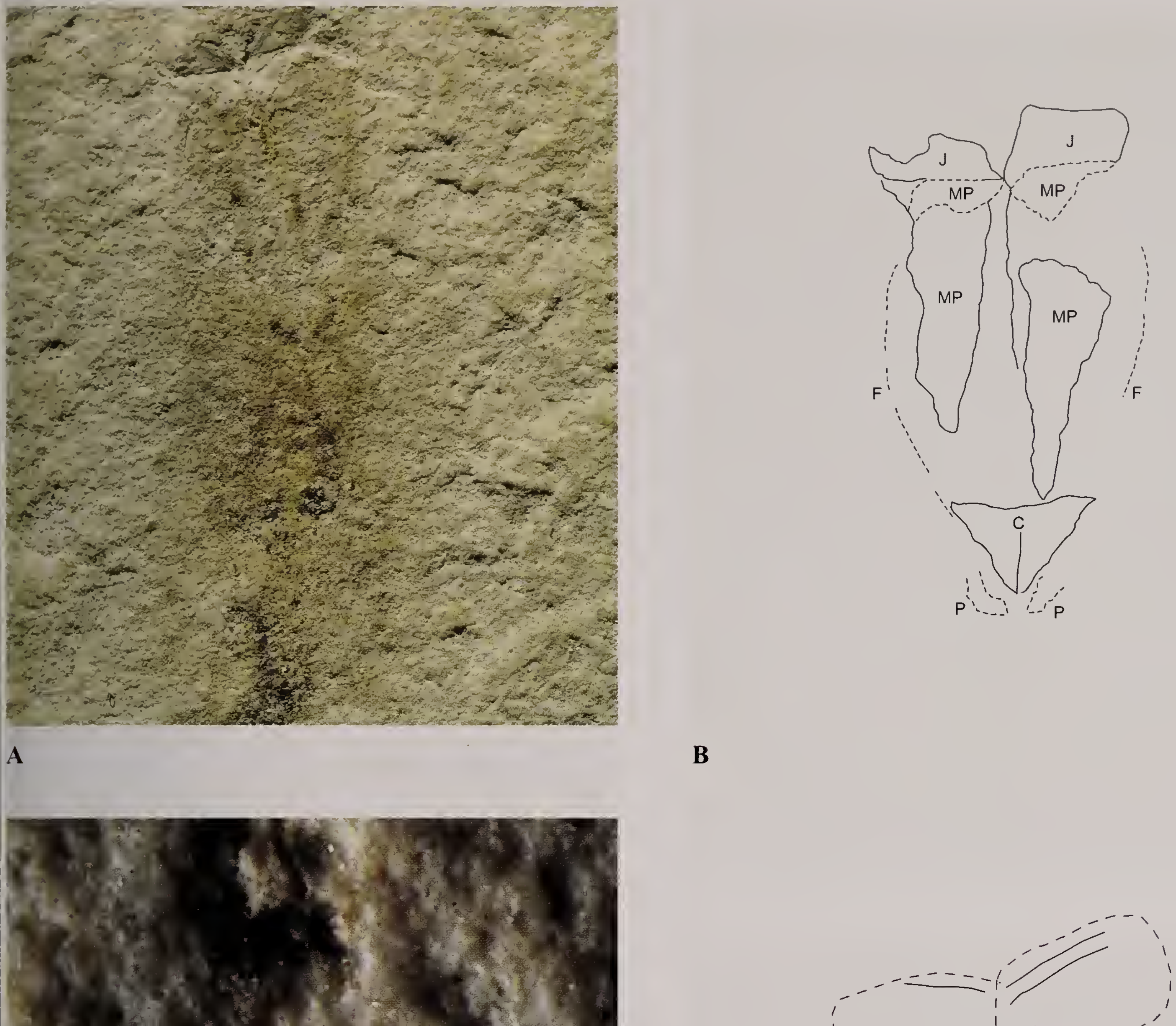
C = maxillary carriers
F = forceps
J = jaws
Japp = jaw apparatus
M = maxilla
MP = mandibular processes



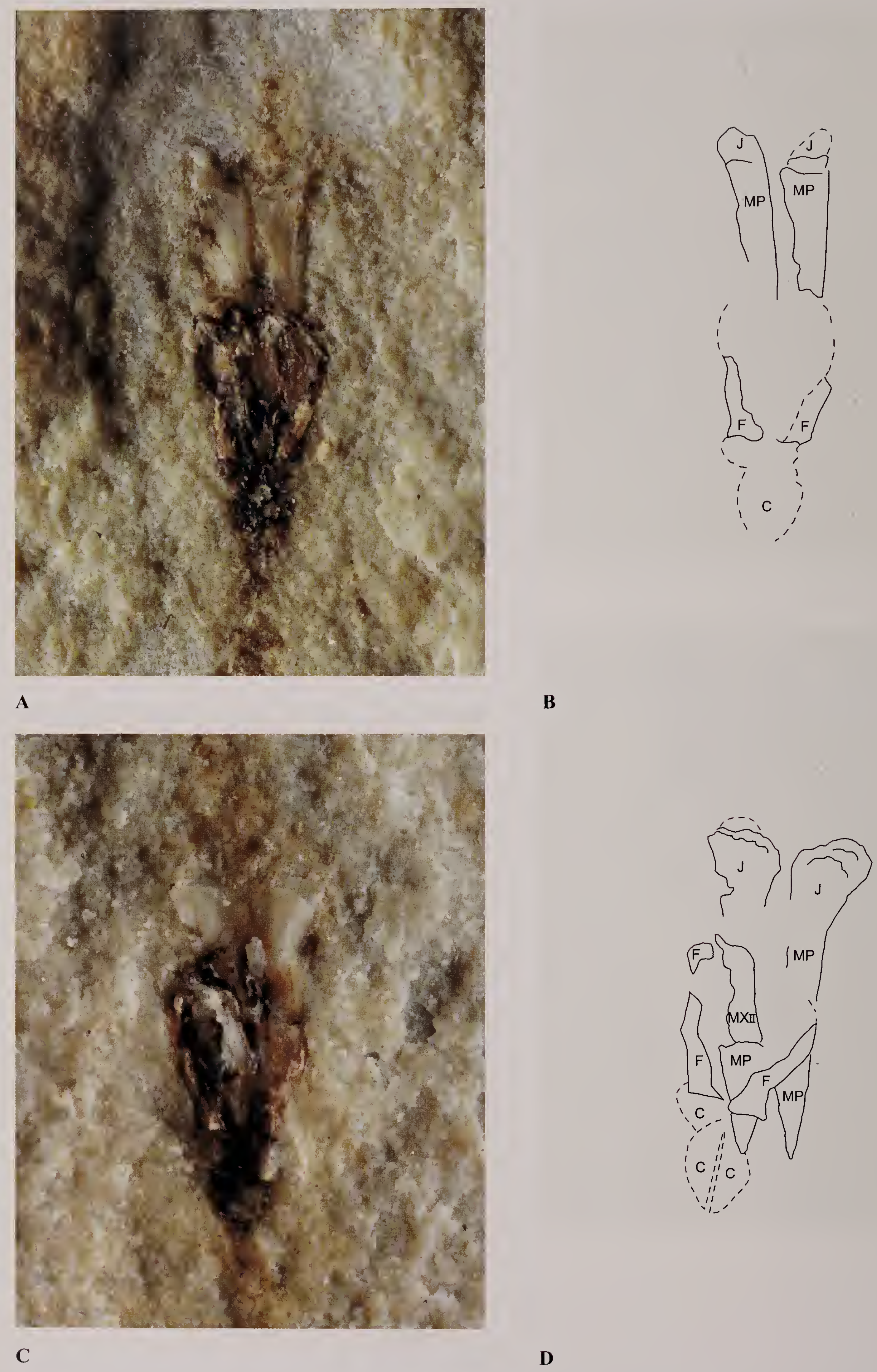
Pl. I - *Eunicites joinvillei* n. sp., MSNM i12420, holotype (A: x 4.8; B: x 4.5); *Eunicites joinvillei* n. sp., MSNM i12414, paratype (C: x 5.2; D: x 7.3).



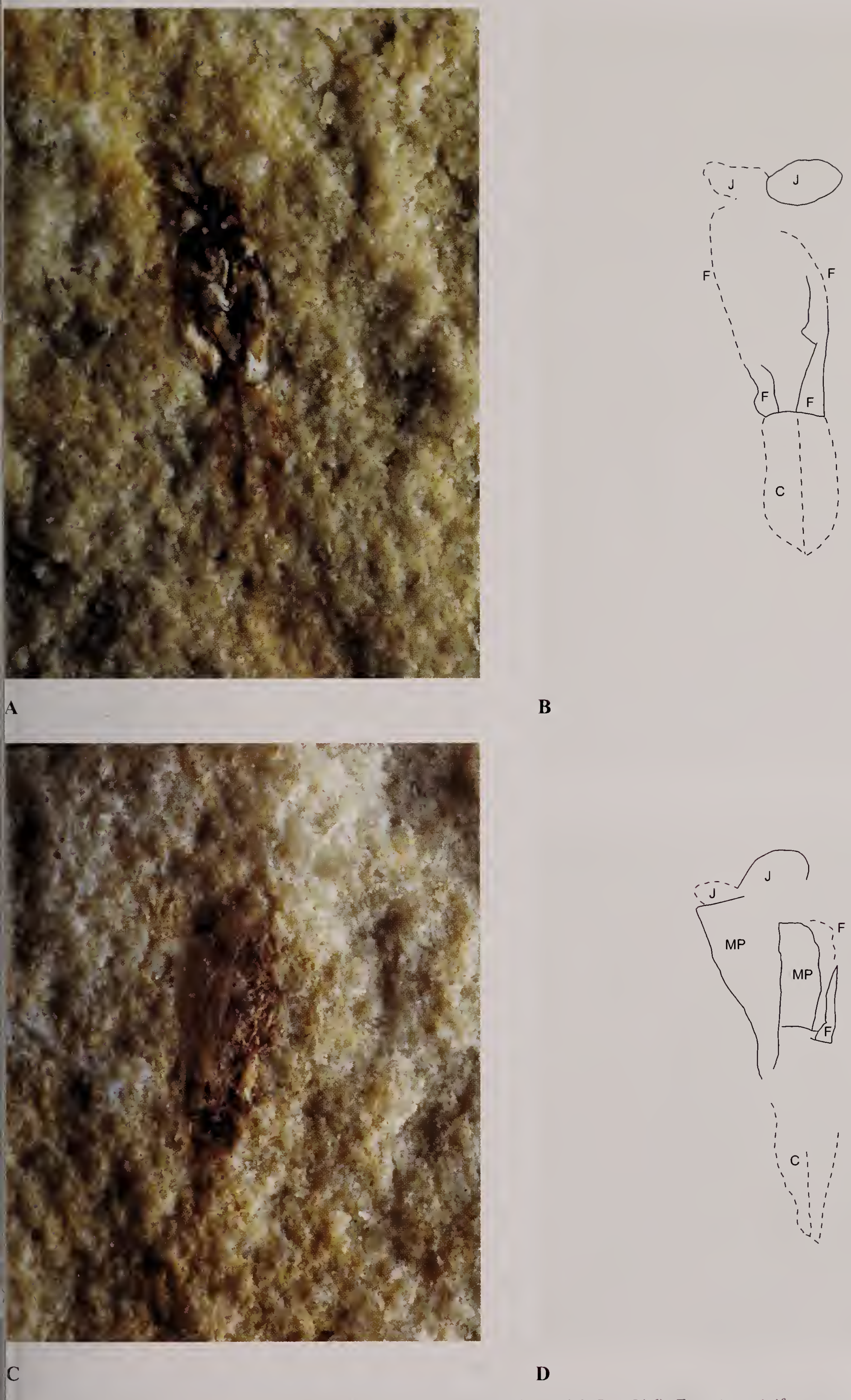
Pl. II - *Eunicites falcatus* n. sp., MSNM i8488, holotype (A: x 11.6; B: x 8.4); *Eunicites diopatroides* n. sp., MSNM i23084, holotype (C: x 7; D: x 7.4).



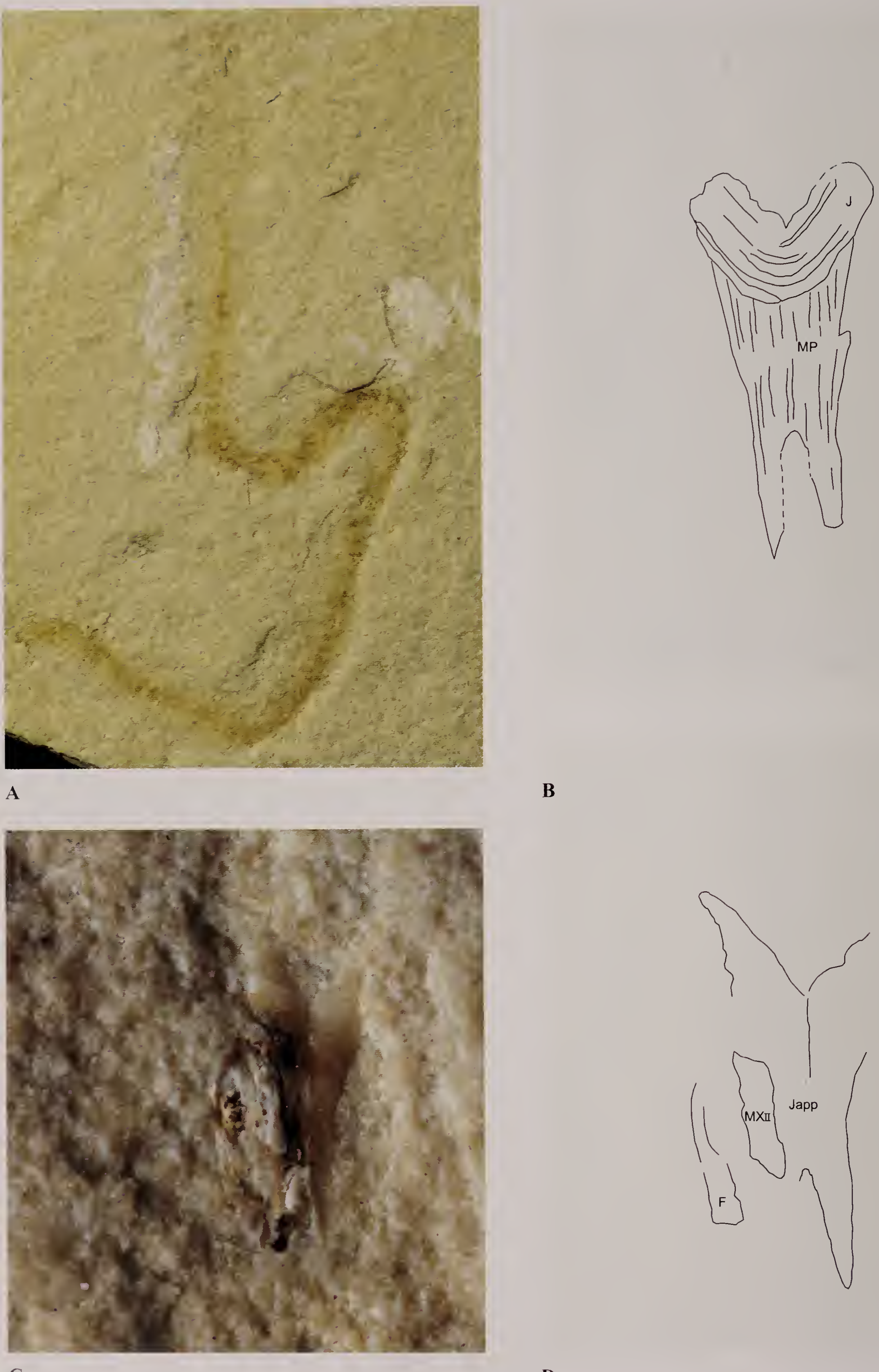
Pl. III - *Eunicites diopatroides* n. sp., MSNM i20613, paratype (A: x 10; B: x 10.3); *Eunicites mariacristinae* n. sp., MSNM i8490, holotype (C: x 100; D: x 120).



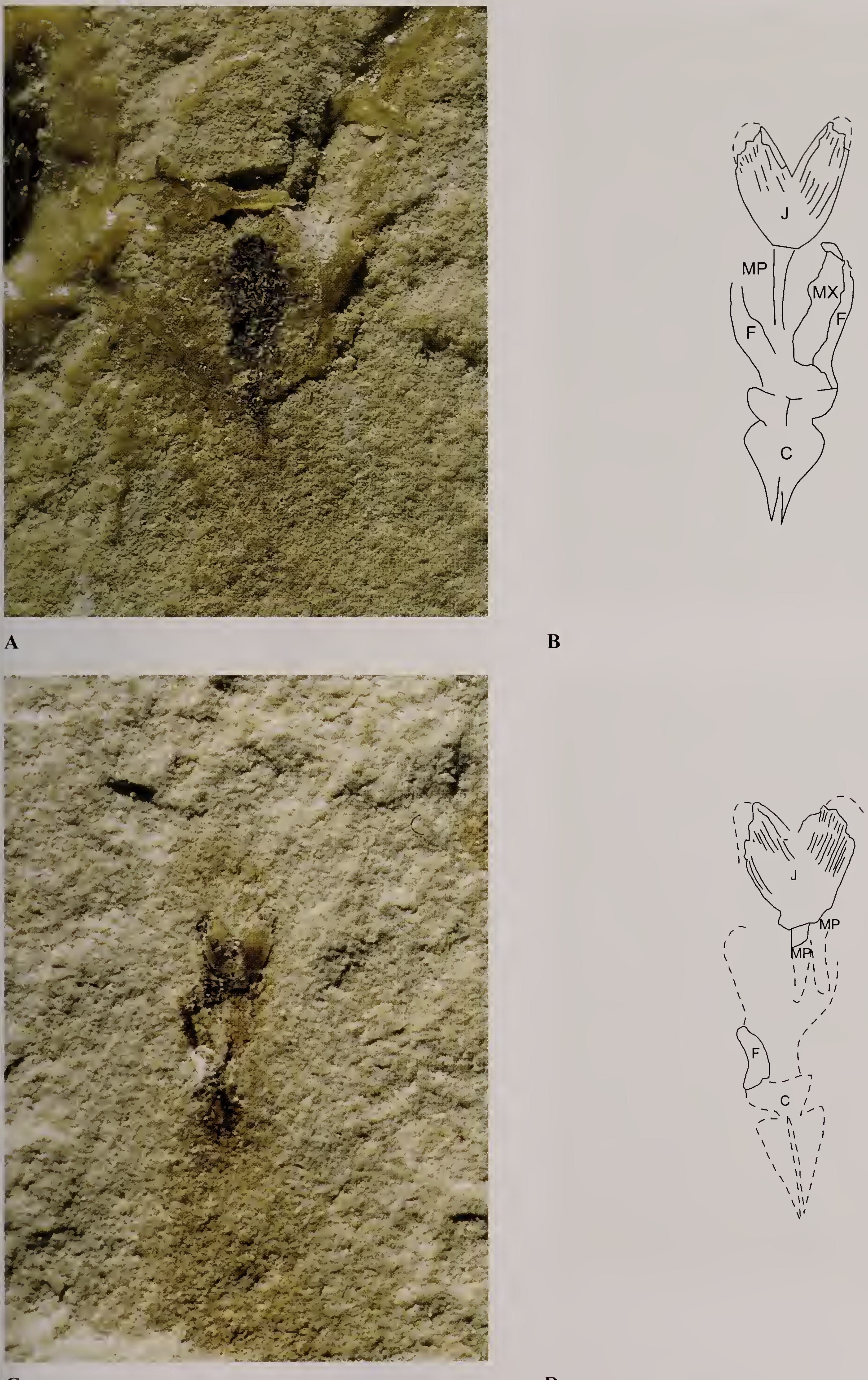
Pl. IV - *Teruzzia pezzolii* n. gen. n. sp., MSNM i13290, holotype (A: x 93; B: x 94); *Teruzzia pezzolii* n. gen. n. sp., MSNM i20611 (C: x 23; D: x 28.5).



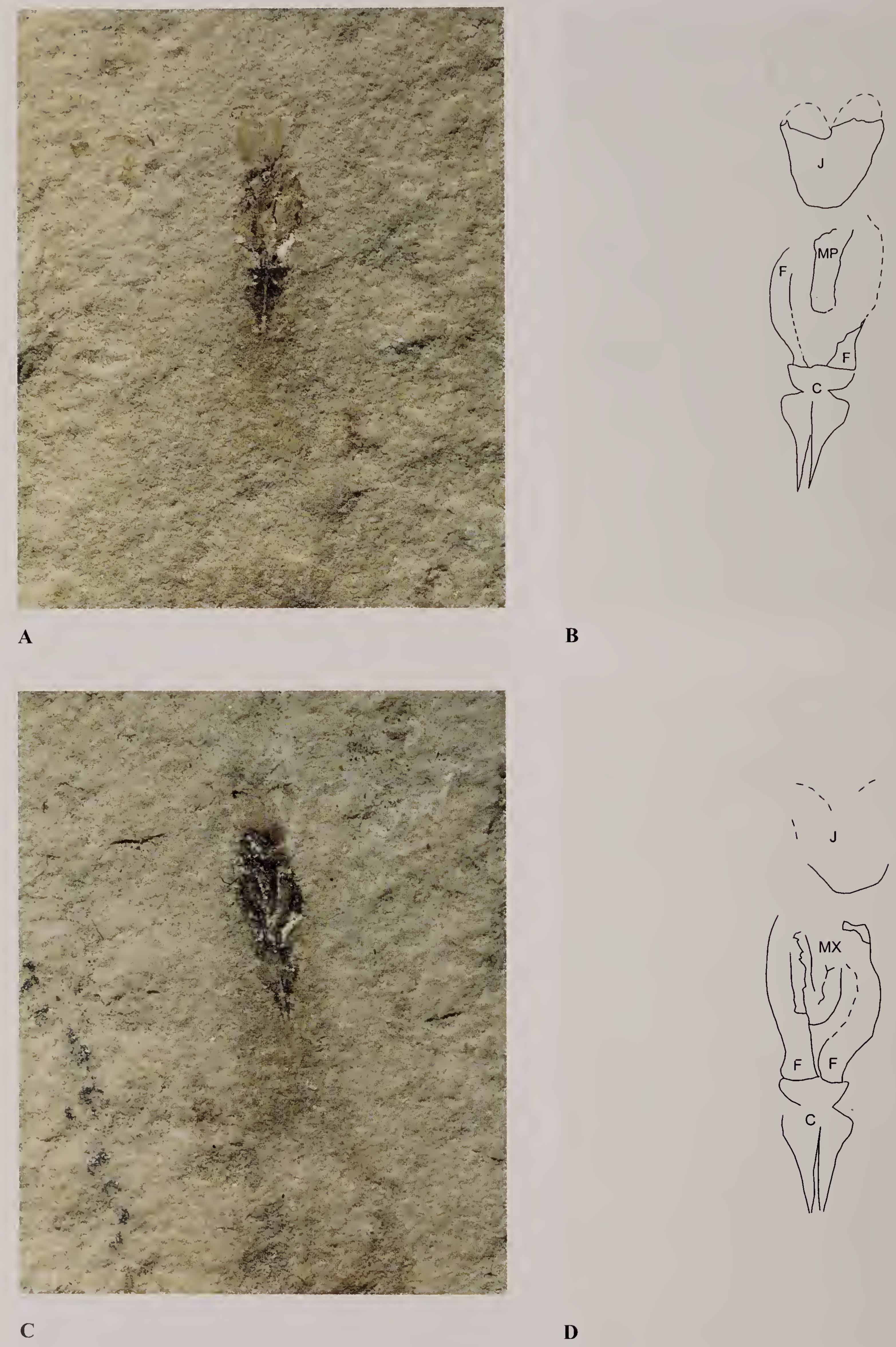
Pl. V - *Teruzzia sagittifera* n. gen. n. sp., MSNM i23436, holotype (A: x 52.3; B: x 54.6); *Teruzzia sagittifera* n. gen. n. sp., MSNM i8476, paratype (C: x 47; D: x 54.6).



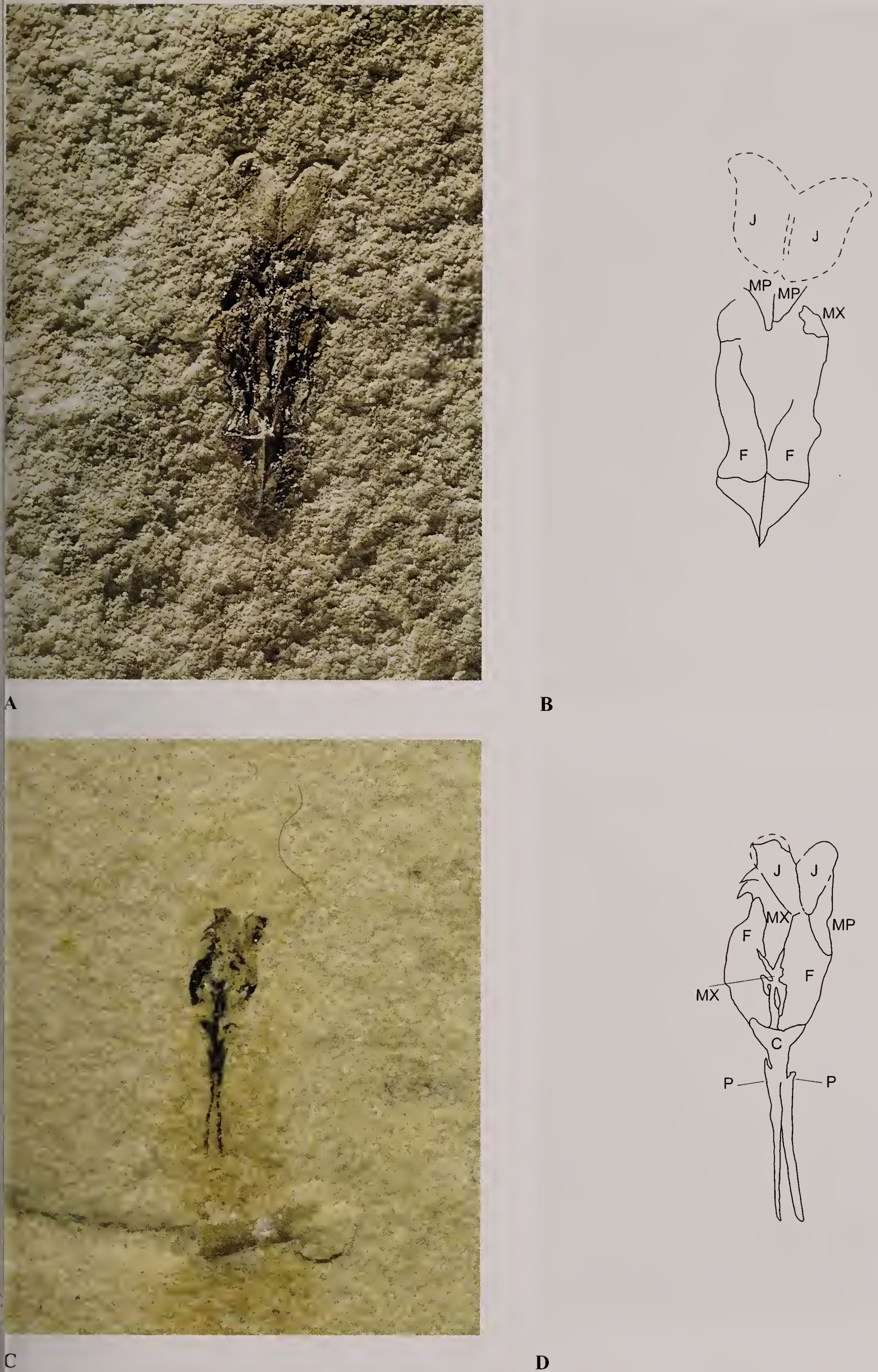
Pl. VI - *Teruzzia pusilla* n. gen. n. sp., MSNM i8379, holotype (A: x 10; B: x 128); *Teruzzia gryphoeides* n. gen. n. sp., MSNM i24967, holotype (C: x 36.6; D: x 46.6).



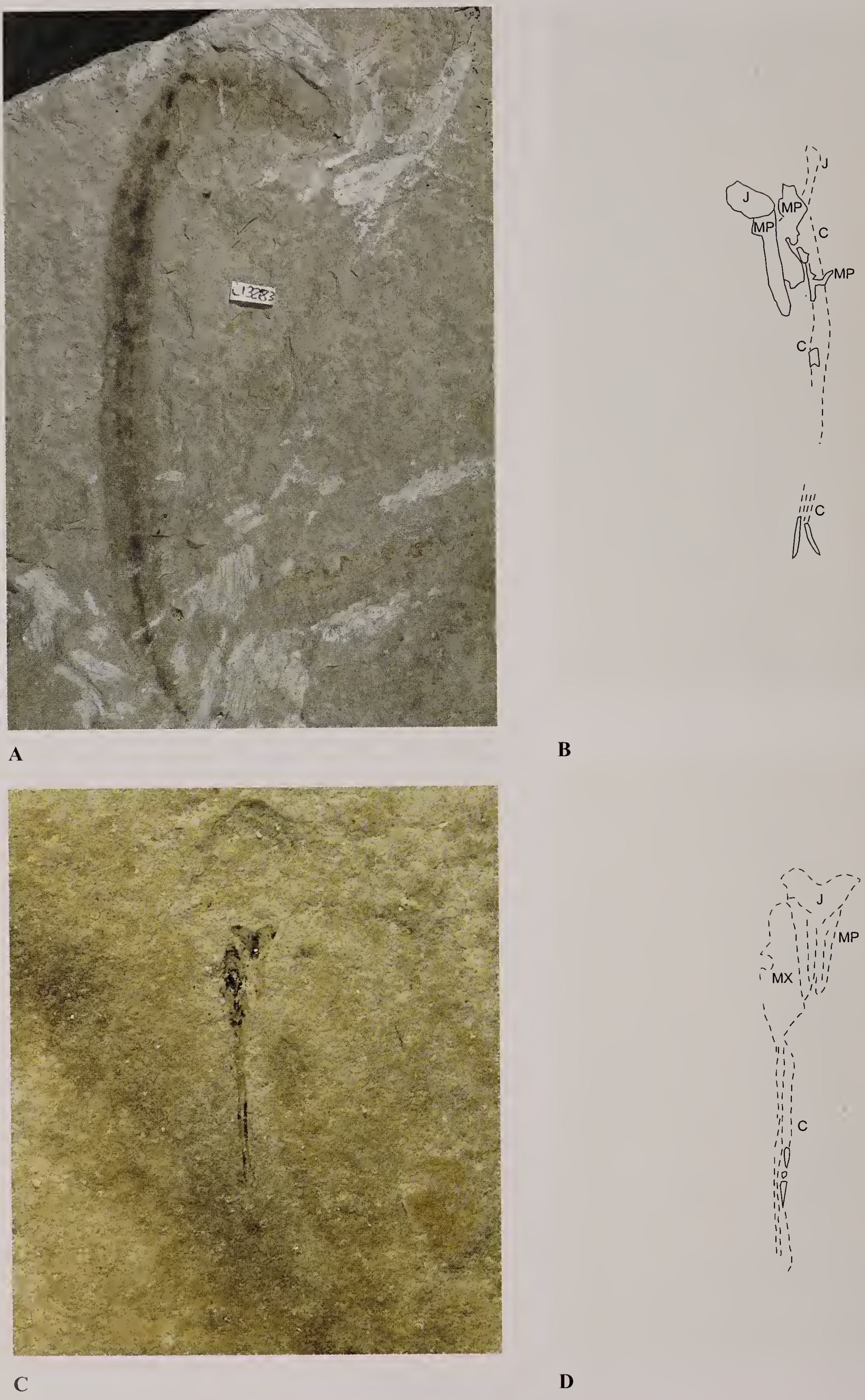
Pl. VII - *Lumbriconereites hadjulae* n. sp., MSNM i12424a, holotype, part, (A: x 9.5; B: x 16); *Lumbriconereites hadjulae* n. sp., MSNM i20614, paratype (C: x 8.8; D: x 16).



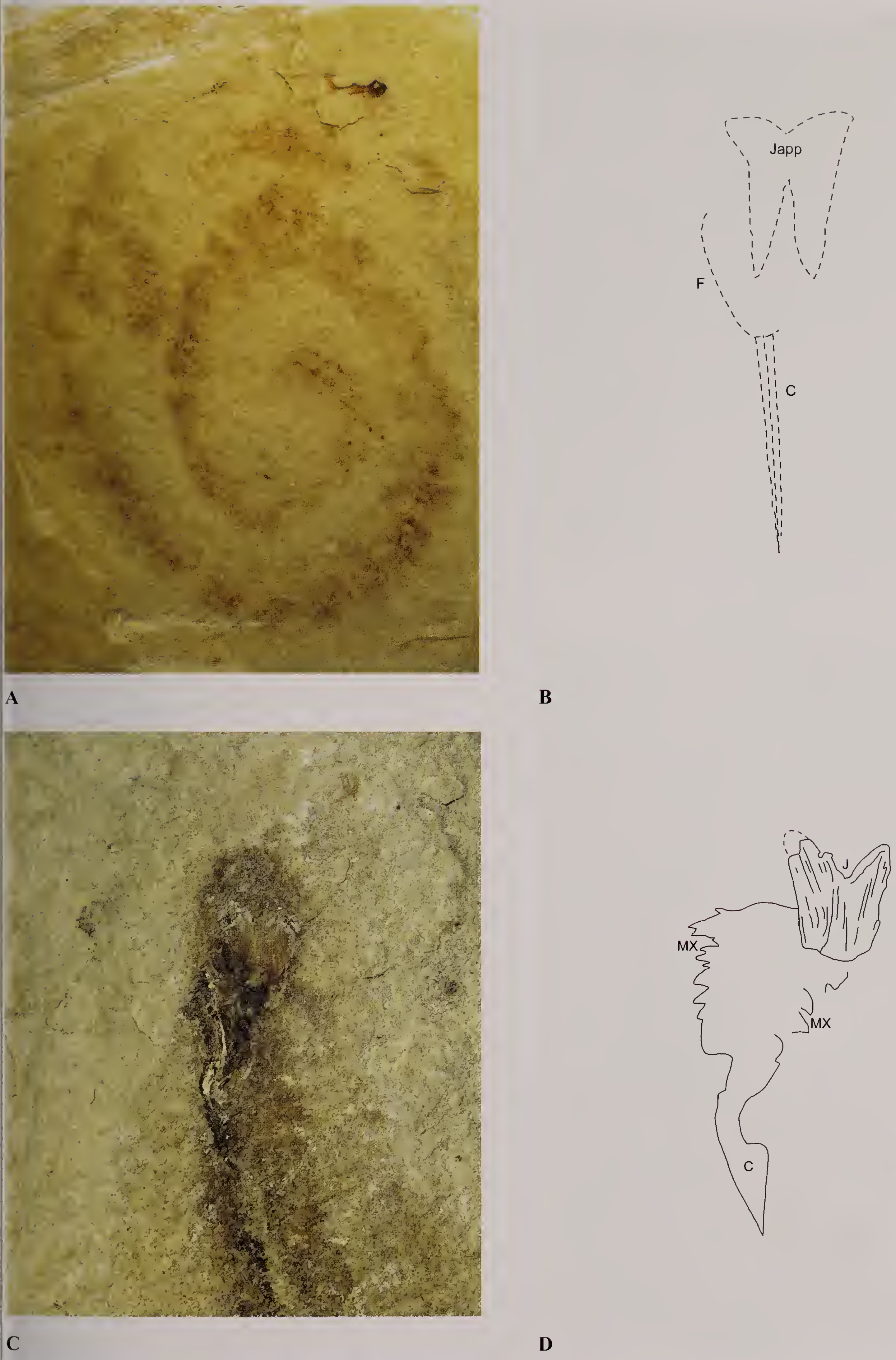
Pl. VIII - *Lumbriconereites hadjulae* n. sp., MSNM i12632a, holotype, part (A: x 10; B: x 17.5); *Lumbriconereites hadjulae* n. sp., MSNM i12632b, holotype, counterpart (C: x 10; D: x 19.2).



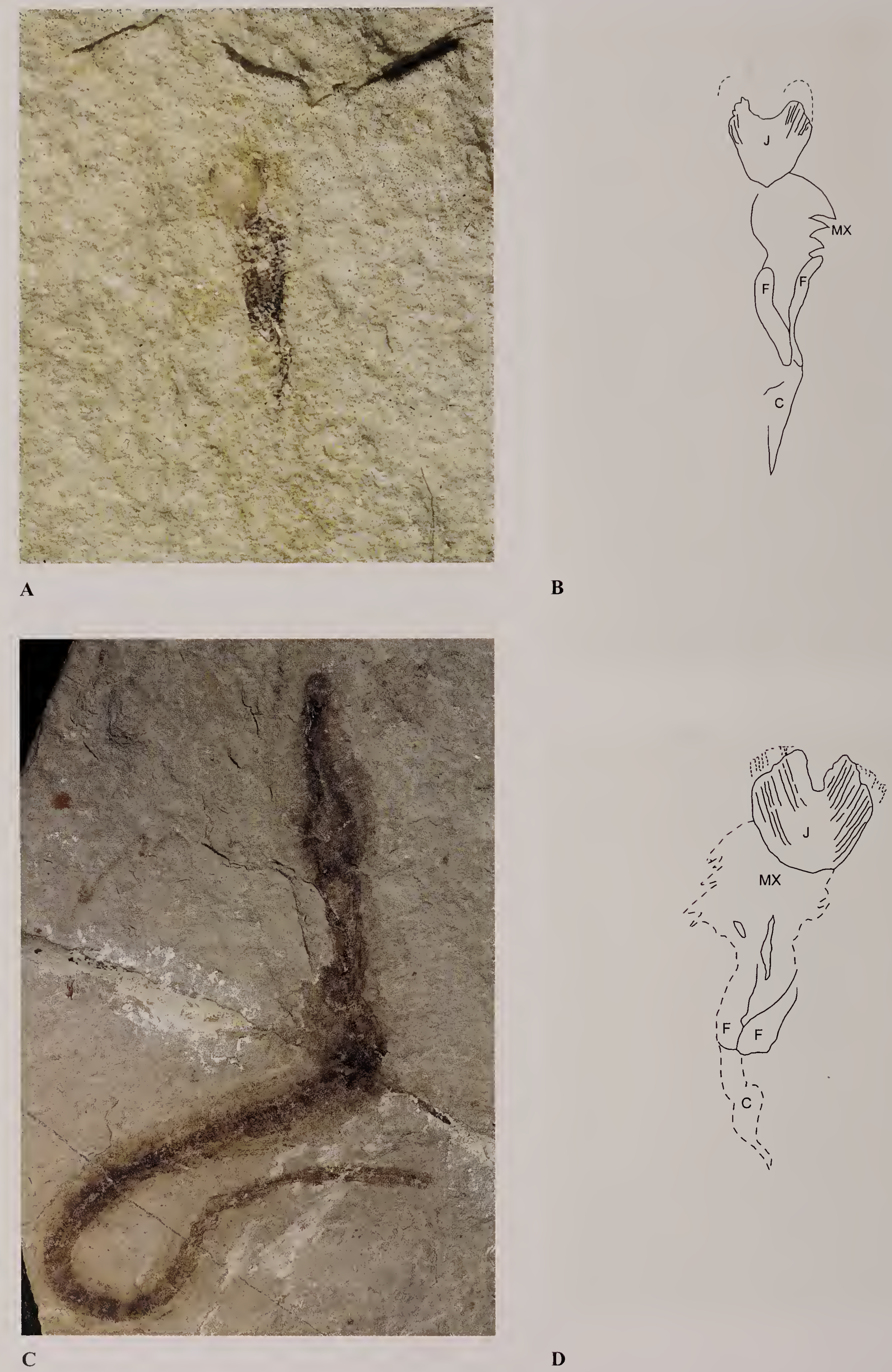
Pl. IX - *Lumbriconereites garassinoi* n. sp., MSNM i9355, holotype (A: x 11.3; B: x 11.6); *Phoeniciarabella pinnulata* n. gen. n. sp., MSNM i12411, holotype (C: x 12; D: x 19).



Pl. X - *Phoeniciarabella orensanzi* n. gen. n. sp., MSNM i 13283, holotype (A: x 0.7; B: x 360); *Phoeniciarabella caesaris* n. gen. n. sp., MSNM i 20610, holotype (C: x 10; D: x 18).



Pl. XI - *Phoeniciarabella caesaris* n. gen. n. sp., MSNM i26421, paratype (A: x 3.6; B: x 36); *Didone pulcherrima* n. gen. n. sp., MSNM i20617, holotype (C: x 9.3; D: x 17).



Pl. XII - *Didone pulcherrima* n. gen. n. sp., MSNM i20624, paratype (A: x 10; B: x 16.2); *Didone pulcherrima* n. gen. n. sp., MSNM i25457, paratype (C: x 2; D: x 10.4).

Pl. XIII - *Paleoaphrodite libanotica* n. sp., MSNM i16288, holotype (x 11.3).

Pl. XIV - *Ferragutia cenomaniana* n. gen. n. sp., MSNM i8340, holotype, (A: x 60; B: x 70); *Ferragutia cenomaniana* n. gen. n. sp., MSNM i12426, paratype (C: x 4; D: x 60).

Pl. XV - *Eunicites diopatroides* n. sp., MSNM i23084, holotype (x 4).

Pl. XVI - *Teruzzia pezzolii* n. gen. n. sp., MSNM i23419 (x 1.1).

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