New genera and new species of scolecodonts (fossil annelids) with paleoenvironmental and evolutionary considerations

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ABSTRACT: New genera and species are coined in the paranatural classification. These new taxa are *Dualigenys* new genus, *D. erecta* new species; *Nothrites vergonsensis* new species; *Ottawina elegans* new species; *Pterogenys* new genus, *P. dubius* new species; *Sinugenys* new genus, *S. robusta* new species. The affinities of certain of them with both Paleozoic and modern-day forms are suggested.

The family Onuphidae appeared during the Upper Triassic. Up to present the oldest-known members of the family were Upper Cretaceous. Jaw apparatus remains of Errantida polychaetes in Mesozoic black shales, that are regarded as representing anoxic events, provide arguments for suboxic deposits. These chewing pieces belong to the families Dorvilleidae and Mochtyellidae, which constitute the oldest-known identity in the natural fossil taxonomy of burrowing worms. Mochtyellidae, up to now only reported from the Paleozoic, present both modern and ancestral characteristics interpreted as neotenic and progenetic evolutionary modes. Scolecodonts provide a good tool both to distinguish suboxic and anoxic deposits and to interpret some of the mechanisms of Errantida polychaete evolution.

INTRODUCTION

Fossil remains of annelids are rare, although they are one of the most important invertebrate groups in modern-day marine environments. Most sedentarida polychaete fossils are known from their tubes. In the case of Errantida, traces such as burrows are the most common fossil types and body prints, although very rare, have also been described (Ehlers 1868, 1869; Rovereto 1904). Trace fossils belong to paranatural taxonomy with no relationship with natural taxonomy; the exact nature of the worms that created the traces are still unknown.

The skeletominal jaw apparatus, first described by Pander (1856), found only in Errantida polychaetes, are poorly known. They are named scolecodonts (Croneis and Scott 1933). The oldest have been described in Ordovician strata but they are of little stratigraphical interest because of the difficulties of reconstructing jaw apparatuses. These reconstructions are the only annelid components with a sense in the natural classification and in many cases with a stratigraphical utility. This explains why the field discipline, that could have been named "scolecodontology", has few actual followers.

Recent discoveries of Mesozoic pieces (components of jaw apparatuses) make the use of the two existing nomenclatures (orthonatural for jaw apparatuses, prints or modern annelids and paranatural for scolecodonts) difficult because both have been determined for Paleozoic and recent jaws. I proposed an adapted terminology for the dental formula for Mesozoic forms (Courtinat 1988). New forms are described using open nomenclature in a paper dealing with the revision of Post-Paleozoic fossil genera (Courtinat 1990).

In this paper new genera and species (corresponding to the pieces described in opened nomenclature) are named using the paranatural classification, using terminology of the dental formula I have proposed (Courtinat 1990). Affinities with both Paleozoic and modern-day forms are evoked; affinities provide an opportunity to discuss some possible ways of evolution of the forms that could be considered the most frequent Mesozoic Errantida Polychaete annelids.

SYSTEMATIC PALEONTOLOGY

Genus ***Dualigenys*** Courtinat **n. gen.**
Nov. gen D COURTINAT 1990, p. 329-330, pl. 1, fig. 7, 8

Type species: Dualigenys erecta new species fig. 4

Diagnosis: Elementary piece with dentary line of two rows of denticles; row of 1st order simple denticles begins with a fang; row of 2nd order denticles composed by very small, straight, simple denticles; heel round. Myocoele slightly enclosed in posterior position. No bight, lobe or ramal arch present.

Dental formula: $\mathbf{(1)2}$ - - - X $_{x+1}$ - - - $_{x+n}$

Dualigenys erecta Courtinat **sp. nov.**
Plate 1, figure 4

Arabellites sp. 2 COURTINAT 1983, p. 31, pl. 1, fig. 17.
Croneisigneys sp. COURTINAT 1989 a, p. 36, pl. 2, fig. 4, 5.
Croneisigneys sp. 1 COURTINAT, BODERGAT, CUBAYNES and RUGET 1989, p. 105, pl. 1, fig. 4, 5
Nov. gen D sp. 1 COURTINAT 1990, pl. 1, fig. 7, 8.
Nov. gen D sp. 2 COURTINAT, ATROPS and FERRY 1991b, p. 102, pl. 1, fig. 16.

Holotype: Plate 1, figure 4; Kimmeridgian - Eudoxus zone - Montépile section (Jura, France)- Repository for type specimen: University Claude-Bernard-Lyon 1. Center of the Earth Sciences.

Dimensions: total length = 69µm; length of the fang = 15µm; length of the 1st order denticle = 10 to 3µm ; length of the 2nd order denticle = 1µm

Description: Elementary piece with dentary line of two denticles rows ; row of first order simple denticles begins with straight to anterogyre fang; bars present or absent between the cups; row of second order denticles composed of very small straight, simple denticles; heel round. Myocoele slightly enclosed, in posterior position. No pillar, bight, lobe or ramal arch present. Probably MI.

Dental formula: **(1) 2+ . . . [6 or 7]** 7 or 8 - - = - - (24 to 30)

Total length: 58 to 85µm.

Comparisons: In paranatural classifications no known genera are comparable to *Dualigenys* new genus. In orthonatural taxonomy some MI of the family Onuphidea have similar features. No known elementary pieces are similar to *Dualigenys erecta* new species. However, left MI of embryo or juvenile onuphid have 1st order and 2nd order simple denticles. The multielementary species *Leptoecia vivipara* figured by Averincez (1972) *in* Orensanz (1990) shows the two kinds of row of denticles and a well-developed fang; the row of 1st order simple denticles begin with a fang and is composed by 7 denticles. According to these similarities, *D. erecta* probably belongs to the family Onuphidea Kinberg 1865.

Distribution: Morocco (Callovian to Aptian; Agadir/Essaouira basin) - France (Domerian, Toarcian; Quercy - Kimmeridgian; Jura - Cenomanian; Vocontian basin).- Unpublished data: Portugal (Toarcian; Rabaçal area) - France (Carnian; Monts d'Or-Lyon)

Genus NOTHRITES Stauffer 1933

Nothrites vergonsensis Courtinat **n. sp.**
Plate 1, figure 5

Nothrites sp. FOUCHER and TAUGOURDEAU 1975, p. 25.

Holotype: Plate 1, figure 5; Cenomanian - Archeocretacea zone - Vergons section (Vocontian Basin, France).

Repository for type specimen: University Claude-Bernard-Lyon 1. Center of the Earth Sciences.

Dimensions of holotype: total length = 80µm

Description: Elementary piece with rectilinear gable bearing up to 7 denticles. Denticles slightly roundish; head gradually joining the shaft. Shaft short to long, straight.

Total length: 68 to 80µm.

Comparisons: This species exhibits strong similarities with numerous mandibles of dorvilleid as *Ophryotrocha antartica* (Szaniawski and Wrona, 1987,fig. 3), unamed mandible of dorvilleid (Colbath 1988, pl. 1, fig. 11), *Schistomeringos mediofurca* (Jumars 1974 ; fig. 3F), *Protodorvillea* (Orensanz 1990, pl. 33, fig. e; left mandible) and *Parougia furcata* (Orensanz 1990, pl. 34, fig. i). Szaniawski and Wrona (1987) cited a comparable elementary piece (Family, genus and species undetermined 2) in the Cape Melville Formation (Lower Miocene of the King George Island, Antartica). They have already noticed the resemblance between their unamed element and the Dorvilleidae.

Distribution: France (Valanginian; Vocontian basin - Albian; Pas-de-Calais - Cenomanian; Vocontian basin).

Genus *Ottawina* Wilson 1948

Ottawina elegans Courtinat **n. sp.**
Plate 1, figure 6

Arabellites sp. 1 COURTINAT 1983, p. 31, pl. 1, fig.14.
Palurites sp. 2 COURTINAT, BODERGAT, CUBAYNES and RUGET 1989, p. 105, pl. 1, fig. 9, 10.
Ottawina sp. COURTINAT 1990, p. 341, pl. 2, fig. 2.
Ottawina sp. 1 COURTINAT, CRUMIÈRE and MÉON 1990, p. 390, pl. 1, fig. 5 ; pl. 2, fig. 10.

Holotype: Plate 1, figure 6; Cenomanian - Archeocretacea zone - Vergons section (Vocontian Basin, France).

Repository for type specimen: University Claude-Bernard-Lyon 1. Center of the Earth Sciences.

Dimensions of holotype: total length = 70µm; length of the fang = 13µm

Description: Elementary piece with a line begining with a fang and composed by simple straight or posterogyre denticles. Inner margin completely denticulated; heel round. Myocoele slightly enclosed, in posterior position. Pillars slighty developped. No bight, lobe or ramal arch present. On some forms, denticles of the first half dentary line gently spaced by bars.

Variations of the dental formula:
(1) - 2 - 3 - 4 - 5 + - - - 10 to 12
(1) 2 - 3 + - - - 10 to 12
(1) - 2 - - - + 5 - 6 - - = - - 10 to 12

Total length: 70 to 97µm.

Comparisons: Only one species of *Ottawina* is known in the Canadian Ordovician (Wilson 1948). *Ottawina elegans* shows strong affinities with dentate robust MI of arabellids and onuphids. *Ottawina elegans* is firstly described (Courtinat, 1983) in a partial apparatus in association with *Dualigenys erecta*. The assemblage assigned to Oenonidae (Arabellidae or Atraktoprionidae) in 1984 (Courtinat, figure 2) is highly questionable taking into account the probable affinity with the Onuphidae.

Distribution: Morocco (Aptian; Agadir/Essaouira basin) - France (Toarcian; Quercy - Cenomanian; Vocontian basin).

Genus ***Pterogenys*** Courtinat **n. gen.**
Nov. gen E COURTINAT 1990, pl. 1, fig. 11

Type species: Pterogenys dubius Courtinat new species, plate 1, figure 2.

Diagnosis: Elementary pieces paired of carrier, forming a small V-shaped element that looks like a wing. The two pieces are proximally fused. Inner margin denticulated and composed of very small, simple denticles.

Comparisons: In dorvilleids *sensu stricto,* none of the wing-shaped elements are denticulated and free such is the case of the genus *Schistomeringos* Jumars 1974 where the carriers may be fused with the basal plates. On the other hand free and fused denticulated carriers are known in the *Dorvillea* group (genera *Dorvillea, Protodorvillea, Meiodorvillea* and *Exallopus*).

Pterogenys dubius Courtinat **n. sp.**
Plate 1, figure 2

Genres et espèces indéterminés COURTINAT 1989 a, p. 49, fig. 19 c, pl. 2, fig. 17.
Gen nov, species ind. COURTINAT, BODERGAT, CUBAYNES and RUGET 1989, p. 106, pl. 1, fig. 3.
Nov. gen E, n. sp. 1 COURTINAT 1990, pl. 1 , fig. 11.
Gen. new, sp. nov COURTINAT, CRUMIÈRE and MÉON 1990, p. 390, pl. 2, fig. 7.

Holotype: Plate 1, figure 2 ; Toarcian - Serpentinum zone - Penne section (Quercy, France).

Repository for type specimen: University Claude-Bernard-Lyon 1. Center of the Earth Sciences.

Dimensions of holotype: total length = 57μm; length of the denticles = 1μm

Description: Elementary pieces paired and free, forming a small wing-shaped element where the two branches are curved. Two elementary pieces proximally fused. Each element bears a row of micrometrical, simple denticles.

Total length of an element of the pair: 34 to 57μm; length of the denticles = up to 1μm.

Comparisons: A pair of posteriorly fused carriers similar to *Pteroenys dubius* new species is known in dorvilleids excluding iphitimidinophilids (genera *Schistomeringos* Jumars 1974, *Dorvillea* Parfitt 1866, *Protodorvillea* Pettibone 1961, *Meiodorvillea* Jumars 1974, *Exallopus* Jumars 1974, *Parougia* Wolf 1986 and *Pettibonia* Orensanz 1973 emend. Blake 1979).

Distribution: France (Toarcian; Quercy - Oxfordian; Southern Jura - Cenomanian; Vocontian basin).

Genus ***Sinugenys*** Courtinat **n. gen.**
Nov. gen A COURTINAT 1990, pl. 1, fig. 1, 2.

Type species: Sinugenys robusta Courtinat new species, plate 1, figures 1, 3.

Diagnosis: Elongated piece with heterometric denticles. Dentary line begin with a major denticle. Behind the major denticle, the others have separate bases with or without bars. Denticles straight or posterogyre. In some case, roundish anterior margin with a sinus, joining the major denticle with a spur. Myocoele in posterior position, slightly enclosed. No bight and lobe. Heel round to ogival.

Dental formula: 1____n

Sinugenys robusta Courtinat **n. sp.**
Plate 1, figures 1, 3

Palurites sp. COURTINAT 1989, p. 41- 42 , pl. 2, fig. 19.
Nov. genus A *sensu* COURTINAT 1990, p. 332.

Holotype: Plate 1, figure 3; Oxfordian - Bifurcatus zone - Apremont section (Southern Jura, France).

Repository for type specimen: University Claude-Bernard-Lyon 1. Center of the Earth Sciences.

Dimensions of holotype: total length = 112μm; length of the denticles = up to 10μm.

Description: Elongated piece with heterometric denticles. Dentary line begining with a major straight denticle. Behind the major denticle, others have separate bases, a bar occuring between the denticles 4 and 5. Denticles 1 to 4 straight, 5 to 8 one posterogyre. Roundish anterior margin showing a sinus joining the major denticle with a small spur. Myocoele in posterior position, slightly enclosed. No bight and lobe; heel ogival.

Dental formula: 12 - - - - + 4 - 5 + - - - - 8

Total length: 90 to 112μm

Comparisons: Some elementary or multielementary fossil genera can be compared to *Sinugenys*. MI or MII of *Pernerites* Zebera 1935 do not exhibit anterior sinus, spur and lobe and have a hook; *Arabellites* Hinde 1879 have a lobe on the external margin but no sinus; *Delosites* Kozur 1967 and *Lysaretides* Kozur 1971 shows a spur on the external margin without anterior sinus. No known modern forms are similar. The natural affinities of *Sinugenys robusta* new species are unknown up to this day. Only weak analogies appear with the MII of the multielementary triassic species *Delosites raridentatus* Kozur 1967 emend. Zawidzka 1971.

Distribution: France (Oxfordian and Kimmeridgian; Southern Jura)

CONCLUSIONS

Jaw apparatuses or their components are more numerous in Paleozoic strata than Post-Paleozoic ones. Courtinat (1990) assumed that such a condition could result from a modification in the chemical composition of jaws during the Triassic period following the Upper Permian turmoil of the biological world. Colbath (1986) noted that the development of mineralization in the lineages ancestral to some modern forms is probably concomitant with a reduced sclerotization. Following this interpretation, the relatively high abundance of polychaete jaws in Lower Paleozoic rocks might reflect a high fossilization potential whereas the post-Paleozoic record result from a low potential. Jaw apparatuses recovered from Mesozoic sediments look like modern forms and have been mainly assigned to the modern families Glyceridae, Goniadidae, Arabellidae and Dorvilleidae. These families have a high fossilization potential (maxillae without calcite or aragonite). By implication, it is admitted the fossil representatives of the families Eunicidae, Onuphidae or Lumbrineridae have mineralized maxillae (maxillae with calcite or aragonite), and so, scolecodonts are not fossilized.

The analogy evoked concerning the Onuphidae and the triassic elementary pieces *Dualigenys erecta* (see systematic paleontology) makes both the conclusions drawn by Colbath (op. cit.), and my hypothesis of a modification of the chemical composition of jaws during the Triassic period, questionable. If comparisons developped -in affinities sections- are correct, the first appearance of the family Onuphidae dated to the Upper Triassic (Carnian). Up to the present the first appearance of elements assigned to this family has been Upper Cretaceous.

A relatively high abundance of polychaetes and echinoderms have been reported in the oxygen-minimum zone of modern environments (Thomson et al. 1985). The proportion of Sedentarida diminishes with depth, whereas the proportion of burrows, probably built by Errantida polychaetes, increases. Polychaetes are resistant to pollution, and therefore abundant, in the bays of Mikawa and Ise in Japan, whereas crustaceans become rare, as a result of their weak tolerance for variations in oxygen content (Bodergat and Ikeya 1988). These two modern examples illustrate the behaviour of annelid worms (particularly Errantida annelids), to depleted aquatic levels of oxygen, due to either increasing depth or pollution.

Based on these data, mesozoic scolecodonts in black shales argue for suboxic deposits. Their presence is evidence of benthic life. Errantida polychaete annelids rework sediment, though they have in some cases been found in laminated sediments devoid of bioturbation. The burrows of such organisms may disappear after compaction and thus the presence of scolecodonts is not incompatible with the apparent absence of microbioturbation (Courtinat and Howlett 1990).

In most of the black shales studied, common annelid families are the Dorvilleidae and Mochtyellidae. The more common representatives of Dorvilleidae are the new genus *Pterogenys* described in this paper, and numerous species of *Anisocerasites* and *Schistomeringos*. The Mochtyellidae appear with *Mochtyella* spp. (Courtinat, Crumière et al. 1990).

It has been suggested that the families Dorvilleidae and Mochtyellidae are synonymous (Courtinat 1990). This hypothesis appears to be well founded considering the distinct features of the mesozoic forms assigned to *Mochtyella*. These features are the presence of a second ridge and a basal plate which are characteristic of the mochtyellids; and first and second order denticles occur alternating on the M I and on the M II that are dorvilleid characteristics. Mochtyellids and dorvilleids have a jaw apparatus belonging to two types of jaws seen in the Eunicea: the placognatha type and the ctenognatha type both known only from the Ordovician (Kielan-Jaworoska 1966).

Mochtyella Kielan-Jaworwska, regarded as placognatha, is considered to be the most primitive organization which could have given rise to the ctenognatha genus *Pistoprion* Kozlowski ancestor of the Dorvilleidae.

The ctenognatha apparatuses, in contrary to those of the placognatha, are symmetrical and a paired M III is in front of a paired M II, itself in front of the M I, following the initial concept. These differences would be of no significance if the compound M I of *Mochtyella* is considered as two distinctive pieces, either separated or not. Both types could represent symmetrical jaw apparatuses. The anterior teeth have been described as more strongly developped in ctenognatha than in placognatha. Such a characteristic is of little relevance when distinguishing the two types. This point of view could be supported by the arrangement of divided denticles (Courtinat, 1990). In the first divided denticle of the M II, the number of the anterior second order denticles corresponds to the number of anterior lateral denticles of anterior teeth (At). In the same way, there is an equivalent for the posterior denticles. The integration of one At into a M II could be considered either as a specific characteristic or as of the phylogenetic of the Mochtyellidae - modern Dorvilleidae line.

Mochtyellidae survived by adaptating to extreme environments of weak dissolved oxygen content and of great depths. Modern annelids and, probably, Mochtyellidae predominantly consume energy when ventilation water through tubes or burrows. When suboxic, then anoxic conditions are reached, oxic metabolism shifts to anoxic metabolism in a gradual transition (Scott 1976). One effect is a modification of the reproduction mechanisms. In response to this modification, annelid inhabitants of deep-sea hydrothermal vents, compensate for their very low fecundity by continuously reproducing over a long period of time (McHugh 1989). Thus, the relative abundance of scolecodonts in "suboxic fossilized habitats" could be linked to the production of brooded juveniles. The small sized scolecodonts could be interpreted as juvenile forms. In fact, they are probably adults as juvenile forms have jaw apparatuses in chemism which cannot be conserved as the proteins are weakly sclerotized. For all the above reasons, the association of both dorvilleid (modern) and mochtyelleid (ancestral) characteristics could be relevant of neoteny and in the same way small sizes could be considered as a progenetic evolutionary mode.

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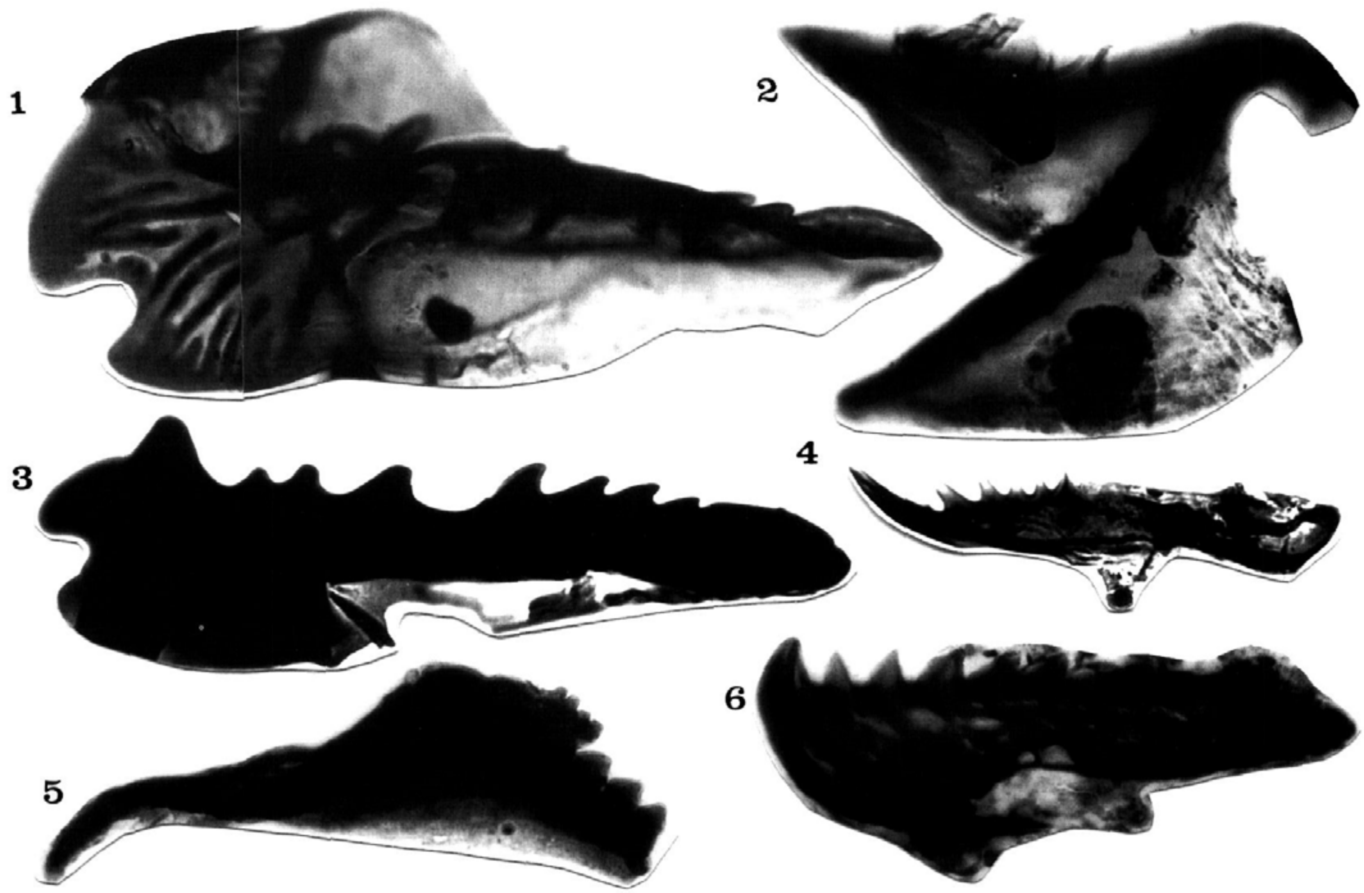

PLATE 1

1 *Sinugenys robusta* new species (Holotype: length =112μm).

2 *Pterogenys dubius* new species (Holotype: length = 57μm),

3 *Sinugenys robusta* new species (other specimen in front view),

4 *Dualigenys erecta* new species (Holotype: length = 69μm).

5 *Nothrites vergonsensis* new species (Holotype: length = 80μm).

6 *Ottawina elegans* new species (Holotype: length = 70μm).

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Manuscript received January 25, 1996
Manuscript accepted July 2, 1997