ISOLATED OSSICLES OF THE FAMILY EOSPONDYLIDAE SPENCER et WRIGHT, 1966, IN THE LOWER DEVONIAN OF BOHEMIA (CZECH REPUBLIC) AND CORRECTION OF THE SYSTEMATIC POSITION OF EOSPONDYLID BRITTLESTARS (ECHINODERMATA: OPHIUROIDEA: OEGOPHIURIDA)

FREDERICK H. C. HOTCHKISS

Marine and Paleobiological Research Institute, P.O. Box 1016, Vineyard Haven, MA 02568 U.S.A.

RUDOLF J. PROKOP

Department of Palaeontology, Museum of Natural History, National Museum, Václavské náměstí 1, 115 79 Praha 1, Czech Republic

VÁCLAV PETR

(Research Associate of the Marine and Paleobiological Research Institute, Vineyard Haven, U.S.A.)
Milánská 451, 109 00 Praha 10, Czech Republic

Abstract. Isolated ophiuroid vertebrae from the Barrandian white beds are identified as belonging to the genus *Eospondylus* (*Eospondylus* cf. *primigenius*) by comparing them with partially exposed vertebrae in Hunsrück Slate body fossils. The vertebrae are from the relatively shallow-water Loděnice Limestone (Pragian Stage) and also from the relatively deep-water, low-energy Dvorce-Prokop Limestone (Pragian Stage) and Třebotov Limestone (Dalejan Stage, Emsian). The morphology of the isolated vertebrae is used to question and correct the systematic position of eospondylid brittlestars (*Eospondylus* and *Kentrospondylus*). The family Eospondylidae has been classified in the Order Euryalida based on specimens of *Eospondylus* that show dorso-ventral flexure of the rays and intimate association with crinoids. In this study we show that the vertebrae of *Eospondylus* are not of the euryalid hourglass type. The architecture of the articulating surfaces is both zygospondylous and auluroid. The canal for the radial water vessel is in the center of the zygosphene knob and zygotreme pit. This architecture occurs also in the vertebrae of *Furcaster*. We reclassify the Eospondylidae next to the Furcasteridae in the Suborder Zeugophiurina, Order Oegophiurida. The first undoubted euryalids are post-Triassic.

■   Echinodermata, Ophiuroidea, Euryalida, Oegophiurida, Eospondylidae, systematics, phylogeny, Lower Devonian, Barrandian area, Czech Republic, Hunsrück Slate, Germany.

Introduction

SEM study of isolated ossicles of brittlestars picked from Barrandian Devonian washings reveals six or seven families of ophiuroids. No ophiuroids have been reported as whole body fossils from the Barrandian Devonian. In this contribution we document ossicles of the Family Eospondylidae (Pragian and Dalejan age), while previously we have documented ossicles of the families Cheiropterasteridae (Pragian and Dalejan age) and Klasmuridae (Dalejan age) – see Hotchkiss, Prokop et Petr (1999a, b). Material that is yet to be reported includes ossicles attributable to the families Furcasteridae, Ophiurinidae and one or both of Protasteridae and Encrinasteridae. The washings include arm ossicles (ambulacral vertebrae and halves of vertebrae; lateral plates = side arm plates) and ossicles of the mouth frame (of varied terminology: half jaws, oral plates, first or second ambulacrals, etc.).

The echinoderm fauna of the non-reefal facies of the Pragian age (i.e., transitional and deeper-water facies) is known almost exclusively from washings of the so-called "white beds". But here, being often the main rock-forming component, echinoderms are even much more diverse and abundant than in the reefal facies. With the exception of calyces of some small crinoids and microcrinoids, the skeletal elements are typically wholly disarticulated, with frequently well-preserved stereom. Crinoids are most common but representatives of other echinoderm classes, including ophiuroids, are also encountered.

In the transitional facies between high-energy shallow-water reef flank and low-energy deeper-water environment, the most diverse and rich echinoderm fauna has been obtained by second of the authors from the Loděnice Limestone. All possible parts of echinoderm skeletons have been discovered. Minute complete calyces of several inadunate families, esp. of pygmaeocrinids (three distinct species of

the genus *Pygmaeocrinus*), calceocrinids (esp. *Eohalysiocrinus*), and ramacrinids (esp. *Junocrinus*) are typical but disintegrated skeletal elements of other crinoid families and other echinoderm classes also dominate the invertebrate assemblage. Calyx plates of other inadunates are frequent, esp. of elicrinids, cyathocrinitids and tiaracrinids, as well as those of the camerates of the genus *Hexacrinites* or of the flexible crinoid *Lecanocrinus*. Thecal plates of cystoids (*Bulbocystis* of Diploporita, and pleurocystitids of Rhombifera), portions of calyces of blastoids (esp. *Caryoblastus*), plates from the submarginal rings of cyclocystoids (*Cyclocystoides* and *Sievertsia*), plates from the peripharyngeal rings of holothuroids, disarticulated Aristotle's lanterns, interambulacral plates and spines of echinoids are all abundant. Representatives of edrioasteroids (*Rhenopyrgus*) and ophiocistioid teeth (*Klukovicella*) are less common. In the rich material there are also thecal plates of asteroids, ambulacral (i.e. half-vertebrae) and lateral plates of oegophiurid brittlestars, and several specimens of a distinctive type of ophiuroid vertebrae identified here as belonging to the genus *Eospondylus*.

The echinoderm fauna of the deeper-water low-energy environment of the Pragian age, Dvorce-Prokop Limestone, is not very different in abundance and species composition. Probably the most important difference is in the presence of the cup plates of the flexible crinoid *Edriocrinus* (it is unknown from the Loděnice Limestone, while relatively common in the Dvorce-Prokop Limestone). The difference may be associated with the unusual mode of life of this crinoid (basal circlets of its cups are typically attached to various hard objects, e.g. to rugose corals, orthocone nautiloid shells, pluricolumnals of other crinoids, and rarely to the shells of orthothecid hyoliths). The rich material includes several specimens of the distinctive vertebrae identified here as belonging to the ophiuroid genus *Eospondylus*.

The echinoderm fauna of the Dalejan age is known predominantly from the deeper-water low-energy Třebotov Limestone and again almost exclusively from washings of the so-called "white beds". Here, the echinoderm species are typically very small, with thin minute plates. However, being often the main (or at least one of the main) rock-forming component, the echinoderm fauna of the Třebotov Limestone is extremely rich and diverse. Inadunates are represented by small and microcrinoid genera, such as *Eohalysiocrinus*, *Minicrinus*, *Ramacrinus*, *Theloreus*, *Pygmaeocrinus*, *Aureocrinus*, *Briseocrinus*, *Holynocrinus*, *Resetocrinus*, *Treocrinus*, *Timocrinus*, etc., but other small thin-plated crinoids and remains of other echinoderms are equally common, especially undescribed tiny ophiuroid vertebrae, disarticulated parts of Aristotle's lanterns of echinoids and skeletal ossicles of holothuroids. In the rich material collected by the second of the authors there are also several specimens of the distinctive vertebrae that belong to the genus *Eospondylus*.

Methods and materials

At an early stage in this study (1992) just three isolated vertebrae and one lateral plate were identified tentatively as *Eospondylus*, and these specimens have been the main focus of research. Described vertebrae NM L 36903 and

NM L 36904 and the one lateral plate NM L 36910 are from the Loděnice Limestone 'Červený lom' quarry near Praha-Klukovice. Described vertebra NM L 36905 and mentioned vertebrae NM L 38365 and NM L 38366 are from the Třebotov Limestone "Prastav" quarry at Praha-Holyně. We made the preliminary identification from comparison with the published drawings of Spencer (1925, p. 311, Text-fig. 206). Additional collections have been sorted and now, at the end of the study, twenty-three *Eospondylus* vertebrae (two of them as half-vertebrae) have been picked from the washings. The localities, facies and stratigraphical positions of all the *Eospondylus* vertebrae are detailed in Tab. 1.

Table 1. *Eospondylus* vertebrae specimens and localities in the so-called "white beds" in the Barrandian area, including the stratigraphical position. The co-occurrence of an eyelet-type of vertebra representing an undescribed species and perhaps a new genus of the family Eospondylidae is also noted in this table, but its description is deferred (see Methods and materials section).

I) *Eospondylus* vertebrae from the relatively shallow-water limestone, Lower Devonian, Pragian, Loděnice Limestone, localities
a) "Červený lom" quarry near Praha-Klukovice – one early specimen (found by RP in 1964) and two additional specimens (the illustrated NM L 36903 and L 36904) [co-occurrence of one eyelet-type vertebra collected by Budil 1991]. Co-occurrence also of the one lateral plate NM L 36910.
b) "Na Konvářce" at Praha-Smíchov (left pit in situ) – one specimen (found by Radvan Horný in 1999)
c) "Dívčí hrady" at Praha-Smíchov (back-filled quarry beyond the viaduct) – one specimen
II) Eospondylus vertebrae from the deeper-water limestone of a low-energy environment, Lower Devonian, Pragian as well as Dalejan Stages
1) Localities in Lower Devonian, Pragian, Dvorce-Prokop Limestone
a) quarry in a valley of a brook, locality Praha-Malá Chuchle – two specimens found by Josef Bouška [co-occurrence of three eyelet-type vertebrae on the same slide and 22 additional on another slide]
b) "lom u Svatého Prokopa" (St. Prokop quarry) below the rock where St. Prokop Church stood at Praha-Hlubočepy (eastern wall along the road) – two specimens found by RP in 1993 [co-occurrence of one eyelet-type collected by František Hanuš in 1931]
c) "Červený lom" quarry near Praha-Klukovice – a half-vertebra specimen of the standard type found by RP directly above the base of Dvorce-Prokop Limestone [co-occurrence of one eyelet-type vertebra on same slide; also three eyelet-type collected by Ivan Kolebaba at "Bílá rokle"]
2) Localities in Lower Devonian, Dalejan Stage, Třebotov Limestone
a) "Prastav" quarry at Praha-Holyně – eight specimens (including specimen NM L 36905) coll. musei; one specimen collected by Josef Bouška [co-occurrence of 15 eyelet-type vertebrae on same slide]; a half-vertebra specimen collected by František Hanuš; and a slide with the interesting NM L 38365 (elongate swayback version of standard type) together with NM L 38366 (standard type of very small size)
b) highway roadcut at Praha-Barrandov, about 20 cm below the base of Choteč Limestone – one specimen
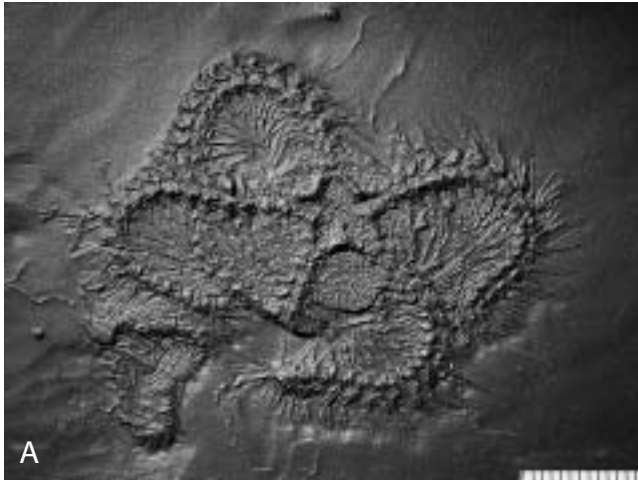
Text-fig. 1. *Eospondylus primigenius* (STÜRTZ) Bundenbach, Eschenbach-Bocksberg quarry, Lower Devonian, Lower Emsian (Zlichovian), Hunsrück Slate, specimens PWL 1996 57LS (NMM) top image (A) x 1.5, and PWL 1996 66LS (NMM) bottom image (B) x 1.7.
Specimen with rays bent into strong curves. Such flexibility and attitudes of rays differentiate the behavioral ecology of *Eospondylus* from all other Hunsrück Slate ophiuroids. Delicateness of the top specimen and robustness of the bottom specimen is perhaps the combined result of real phenotypic differences, differences of preserved detail, and differences of distortion of the rock. [courtesy of Herbert Lutz and Thomas Engel; photos by Alexander Glass].

The plan of research was to verify the identification by study of comparative reference material of Hunsrück Slate *Eospondylus primigenius* (STÜRTZ). As a rule, however, Hunsrück Slate stelleroids do not clearly reveal the morphological details of individual skeletal elements (Boczarowski 2001:8). It was a matter of luck that eventually we acquired Hunsrück Slate specimens that had sufficiently revealing views of the vertebrae to allow truly confident identification. Meanwhile the first report on isolated vertebrae of *Eospondylus* was published by Boczarowski (2001) in a comprehensive and richly illustrated monograph on isolated ossicles of Devonian non-pelmatozoan echinoderms from the Holy Cross Mountains, Poland. We agree with his identification. Because of the difficulty in adequately describing

the complex high relief articulations of the vertebrae we provide stereo-pair scanning electron microscope images.

The vertebrae identified here as *Eospondylus* vertebrae are a good match with the vertebrae of *E. primigenius* comparative reference specimens and can be called *Eospondylus* vertebrae of standard or normal type. For completeness we mention that the washings contain a second type of vertebra that has *Eospondylus*-type articulation features but represents an undescribed species and perhaps a new genus of the family Eospondylidae. In upper surface view, the wings of these other related vertebrae have a distinctive eyelet shape which, however, is not seen anywhere along the length of the arm of *E. primigenius* comparative reference specimens. These eyelet vertebrae will be presented in a separate paper. However it can be mentioned here that the eyelet type co-occurs with the normal type and is more abundantly represented in the pickings (Table 1).

Abbreviations: Národní Museum, Praha (NM); The Natural History Museum [formerly British Museum of Natural History], London (BMNH); National Museum of Natural History [Smithsonian Institution], Washington (USNM); Cincinnati Museum Center (CMC); Field Museum of Natural History, Chicago (FMNH); University of Chicago (UC) [UC specimens are in the FMNH]; Royal Ontario Museum, Toronto (ROM); Department of Earth and Planetary Sciences, Washington University, St. Louis (WU), Naturhistorisches Museum in Mainz (NMM).

Comparative reference material: Hunsrück Slate specimens of *Eospondylus primigenius* (STÜRTZ). NM S 4764 (arms curved ventrally; Text-fig. 2), NM S 4765 (aboral

Text-fig. 2. *Eospondylus primigenius* (STÜRTZ) Bundenbach, Eschenbach-Bocksberg quarry, Lower Devonian, Lower Emsian (Zlichovian), Hunsrück Slate,, NM S 4764, x 3.
Specimen with ventral arm coiling. The specimen is on its dorsum in slate with all five rays curled ventrally inward toward mouth area on underside of disk. Barely visible are tips of two jaws; slightly exposed are proximal parts of rays in oral view extending outward from disk. The location of abrupt ventral bending of rays is indicated by emergence from slate of five rays in aboral view that point inward toward buried disk. Based on ventral bending of rays and intimate association with crinoids *Eospondylus* has been interpreted as stratigraphic first occurrence of Order Euryalida, which contains epizoic gorgonocephalid and euryalid basket-stars of modern oceans. This status is rejected using new evidence from isolated vertebrae. [Photo by Alexander Glass].

arm flexure), NM S 4766 (two individuals on one slab; larger specimen with good undersurface views of vertebrae and of groove spines; Text-fig. 6; Text-fig. 10), NM S 4767 (extreme horizontal arm bending), NM S 4768. NM S 4764 – NM S 4768 were donated by the Marine and Paleobiological Research Institute. BMNH E3353 (extreme horizontal arm bending with half twist; Text-fig. 7A; figured Spencer 1925, Text-fig. 206b, 206e, pl. 21 Text-fig. 9; Owen 1965; Lewis 1993), BMNH E3355 (figured Stürtz 1890, pl. 26, Text-fig. 6; figured Spencer 1925, Text-fig. 206c), BMNH 3356 (coll. Stürtz 1891), BMNH E3357 (figured Stürtz 1890, pl. 26, Text-fig. 7; figured Spencer 1925, Text-fig. 206d), BMNH E3358 (good views of lateral plates; Text-fig. 7B; coll. Stürtz 1891; figured Spencer 1925, Text-fig. 206a; figured Smith 1985, pl. 7.7.2), BMNH E5094. USNM 370166, USNM 370175, USNM 485334. CMC IP50701. FMNH 18888 (two specimens, from Stürtz). UC 39129, UC 39133. ROM 11474 (old no. 1432D) and ROM 11475 (both coll. Stürtz 1908), ROM 12954. WU 860033 (Original label: Korff No. 60; excellently prepared; shows upper and the lower surfaces of vertebrae).

Overview of descriptive terms of ophiuroid vertebrae

Proximal: adoral, inner, anterior.
Distal: aboral, outer, posterior.
Ventral: under, oral, actinal.
Dorsal: upper, aboral, apical, abactinal.
Lateral: side. Left and right: consistent with anterior-posterior and dorsal-ventral terminology.

Multiple related terms exist for describing the protrusions and hollows on ophiuroid vertebrae. For brevity they are mentioned without source. Additional morphological structures and terms that relate to particular taxa are presented by Clark (1914) and by Irimura et Fujita (2003). Spencer (1925) demonstrated a broad congruence between the protrusions, hollows, hinges, and muscle insertions of the Paleozoic *Hallaster* and the Recent *Ophioglypha* (= *Ophiura*). This congruence implies homology and favors using the same descriptive terms for Paleozoic and Recent vertebrae wherever possible.

Protrusions: knob, peg, nose, umbo, condyle, articular condyle, ball, articulation boss, projection, bulge, protuberance, process, apophysis, Gelenkhöcker, hinges, articular shoulder.

Hollows: groove, socket, receptacle, pit, depression, socket-like depression, Gelenkgruben.

Additional articulation terms: articular facet (Bray 1985, LeClair 1996), saddle, flange.

Conjugate surface: mating surface.

Horizontal articulation: horizontal hinges, adoral hinges (k), aboral hinges (K), paired knobs and sockets, lateral knobs and sockets, paired lateral knobs and sockets, **zygocondyles** (= paired knobs of distal surface), **zygapophyses** (= paired knobs of proximal surface). The unnamed paired dorsolateral pits (sockets) of the proximal surface that lodge the paired zygocondyles of the preceding vertebra seldom are mentioned in the literature, perhaps because they are mistaken as paired dorsal longitudinal muscle fields. Exceptions are MacBride (1906, p. 482, as "two dorso-lat-

eral pits"), Müller (1950, p. 14, Tab. 3, as "horizontale Artikulation, laterale Gelenkgruben") and LeClair (1996, p. 246, Text-fig. 1, as "area for intervertebral ligament"). These dorsolateral pits are part of Müller's (1950) trispondylous arrangement of knobs and sockets.

Vertical articulation: vertical hinges, unpaired dorsal or ventral knob and socket, dorsal or ventral nose and groove, **epanapophysis** (= unpaired dorsal knob of proximal surface), **zygosphene** (= unpaired ventral knob of distal surface), **zygotreme** (= unpaired ventral socket of proximal surface), and a new term **epanotreme** for the unpaired dorsal receptacle on the distal articulating surface (= "shoulder on the outer face to receive the umbo", Lyman, 1882, p. 355, label 4). The epanotreme lodges the epanapophysis.

Wing of vertebra: the upper and lateral central part of the vertebra between the insertions for the dorsal longitudinal muscles (Spencer 1925, p. 250), bounded proximally and distally by ridges called alar ridges or lateral ridges. Wing of vertebra **upper surface terms**: dorsal notch, groove, aboral groove, aboral hollow, vertical cylindrical hole, sulcus, pore, canal, cleft, furrow. **Areas for muscle attachment:** muscle area, muscle fossae, attachment fossae, insertion field. **Fulcral ridges:** ridges that separate the dorsal longitudinal muscle fossae from the ventral longitudinal muscle fossae (Bray 1985).

Auluroid canal: tubular passage for the radial water vessel through a vertebra (the radial water vessel is completely enclosed by the vertebrae). Although the name Auluroidea is disparaged (e.g. Fell et Pawson 1966: 34 footnote), we find the terms 'auluroid canal' and 'auluroid condition' descriptive and useful. **Cup for tube feet:** podial basin. **Cupola:** dome structure that projects from the sides of the vertebrae and below which the podial basin forms [terminology of Boczarowski (2001) especially concerning *Astutuaster* and *Umerophiura*].

Zygospondyline, zygospondylous: peg-and-socket vertebral joints that permit horizontal flexure but limit vertical flexure (Bell 1892, p. 177; Matsumoto 1917, p. 8). **Streptospondyline, streptospondylous:** vertebral articulations in which saddle-shaped faces are well developed and the articular peg is very rudimentary or absent, enabling vertical and horizontal flexure (Bell 1892, p. 177; Matsumoto 1917, p. 8; Mortensen 1933, p. 10, 11, footnote). The definition of streptospondyline given by Spencer et Wright (1966, p. U30) is problematic because it refers to "simple ball-and-socket joints" and does not mention saddle-shaped or hourglass shaped articulations. The definition of Spencer et Wright is traceable to statements by Bell (1892, p. 179-180): "*Ophioteresis* is a streptospondyline Ophiurid" and "The Streptophiurae are Ophiurids in which the ambulacral ossicles articulate with one another by means of a more or less simple ball-and-socket joint." However, as shown by Mortensen (1913) the observations on "*Ophioteresis*" by Bell turned out to be faulty. This history arguably damaged the value of the term streptospondyline until its use was clarified and stabilized by Mortensen (1933, p. 11, footnote).

For examples of current research on vertebrae of Recent ophiuroids see Bray (1985), Litvinova (1994), LeClair (1995, 1996), LeClair et LaBarbera (1997) and Irimura and Fujita (2003). Bray's (1985) analysis of the vertebral ossi-

cles of *Ophiocoma echinata* is original and insightful. Bray goes beyond looking at the shapes of conjugate surface areas by locating and describing the positions and orientations of the articular facets of these areas. He describes the unpaired ventral umbo and conjugate pit in conventional terms. What is insightful is his description of "paired oral and aboral processes" on the distal face and on the proximal face of the ossicle. Analysis of his text and diagrams shows that he counts the **epanapophysis** (= unpaired dorsal knob of proximal surface) as two aboral articular processes because it has two articular facets of imperforate stereom. These proximal-surface paired aboral facets articulate with distal-surface paired aboral facets located on the upper surface of the **zygocondyles** (= paired knobs of distal surface). The lower surface of the zygocondyle has a pair of facets of imperforate stereom that are Bray's "paired oral processes" and these articulate with proximal-surface paired oral facets located on the upper surface of the **zygapophyses** (= paired knobs of proximal surface). Bray's observations provide a solution to an important problem. Namely, by using the articular facets of imperforate stereom as the reference for topological analysis of the articulation, it becomes clear that this system of paired oral and aboral facets in *Ophiocoma* is mechanically equivalent and developmentally transformable into the system of facets that is present in the streptospondylous hourglass articulations of the Euryalida. This leaves the presence or absence of the unpaired ventral peg and socket as the only essential difference between zygospondylous and streptospondylous articulations. Štorc (2004) explains the morphogenetic trajectory from peg and socket zygospondylous articulations to hourglass-shaped streptospondylous articulation surfaces from study of *Ophiosmilax? alternatus* vertebrae. *O.? alternatus* has vertebrae that are intermediate between the hourglass-type and the zygospondyline type (Kutscher et Jagt 2000, p. 48) and Štorc (2004) used the terminology **transspondylous** vertebrae and transspondylous vertebral type (terms traceable to Müller 1950). *Ophiosmilax* and other members of the subfamily Ophiobyrsinae are classified 'incertae ordinis et familiae' as they appear related to both the Ophiomyxidae and to the euryalids (Smith, Patterson et Lafay 1995; in which morphological characters nos. 7-11 relate to vertebrae).

Conventions in this paper for presenting the figures of isolated vertebrae: Dorsal (upper) and ventral (lower) views are presented with the proximal end at the top. Lateral, proximal and distal views are presented with the dorsal (apical) surface on top. In left lateral view, proximal (= anterior) is to the left. In right lateral view, proximal (= anterior) is to the right.

Scanning electron microscopy: SEM stereopair imaging was done by Dr. Rudolf F. Turner, Indiana Molecular Biology Institute Microscopy Facility at Indiana University (Dr. Barry D. Stein, Microscopy Facility Supervisor). For each view, vertebrae were mounted individually on stubs and coated with 60:40 gold:palladium in a SEM Coating Unit E5100 (Polaron Equipment Ltd.) and examined with a JEOL JSM-5800LV scanning electron microscope. Stubs were tilted six degrees between image captures to obtain stereopair images.

Systematics

Family **Eospondylidae** Spencer et Wright 1966
Genus *Eospondylus* Gregory 1897

The family Eospondylidae contains *Eospondylus* with five rays and *Kentrospondylus* with ten rays. Gregory (1897) erected the genus *Eospondylus* with type species *Ophiurella primigenia* Stürtz, 1886. Stürtz (1886) described *O. primigenia* as an ophiuroid of Mesozoic aspect and placed it in the genus *Ophiurella* Agassiz, 1836. Many excellent photographs of *E. primigenius* have been published (e.g. Smith 1985, pl. 7.7.2; Bartels, Briggs et Brassel 1998, Text-fig. 194). In a large museum collection of Hunsrück Slate ophiuroids, *E. primigenius* ranked ninth in number of specimens and comprised 5% of the collection (Südkamp 1994). Material-based key papers are by Stürtz (1886, 1890, 1893), Spencer (1925), Lehmann (1957) and Boczarowski (2001). The location and registration numbers of the type specimens of *E. primigenius*, including designating lectotype and paralectotype specimens, is being researched by Alexander Glass (personal communication, May 2005). Starting with its initial description and up to the present, *E. primigenius* holds an important place in discussions on the origination and ancestry of crown group ophiuroids (especially Stürtz 1893; Spencer et Wright 1966).

Distinguishing morphological characteristics of *Eospondylus* include: Disk circular, small (incorporates only two arm vertebrae), without oral shields, without radial shields, and without calycinal plates (primary rosette is not evident in post-juvenile stages but is likely in early growth stages). A madreporite is present on the underside of the disk, interradially, near the mouth frame (Lehmann 1957) (very rarely seen). Arms high, robust, without dorsal or ventral arm plates. Individual segments of the arm long. Ambulacral ossicles completely fused into vertebrae. A median dorsal cleft deeply indents the upper surface of each vertebra. The vertebrae have complex articular processes and facets, including an unpaired ventral median articular process that is perforated by the radial water vessel channel (Boczarowski 2001). Laterals well separated on the aboral surface and not conspicuous except for the vertical spine ridge. The spine ridges carry long spines, of unequal length, splayed outward from the direction of the arm length, creating a dramatic appearance. Laterals conspicuous on the oral surface of arms, closely approximated, somewhat pear-shaped, and bearing spaced minute pointed groove spines.

Eospondylus grew to fairly large size and had fairly large arm vertebrae. Spencer (1925, p. 309) listed "arm high" and "individual segments of the arm long" as generic characters. The arms appear to be about as high as wide. In BMNH E3355 the length of the rays is >150 mm; the disk diameter (distorted) is 30 mm x 16 mm; the vertebrae are 4 mm to 5 mm wide (width of ray); the arm segment length is 3.1mm (24 arm segments in 75 mm arm length). Spencer (1925, p. 312) reported the length of an arm segment in BMNH E3355 as 4.0mm, and in BMNH E3353 and E3358 as 2.4 mm. In NM S 4767 the disk extends to junction of 2nd and 3rd vertebrae; mouth frame 11 mm x 7 mm (distorted by rock deformation); longest arm is 117 mm and appears not distorted; the arm segment length is 2.5 mm (17 proximal segments in 43 mm arm length); the vertebrae are approxi-

mately 3 mm wide (versus distorted arm width of 7 mm). In NM S 4768 the mouth frame is approximately 6mm diameter; the arm segment length is 1.6 mm (proximal 7 arm segments in 11.5 mm arm length); proximal vertebrae approximately 3 mm wide (width of ray at 5th and 6th arm segments).

Eospondylus primigenius and *E. primigenius* var. *compactus* occur in the Lower Devonian Hunsrück Slate, Germany (Lehmann 1957). The age of the Hunsrück Slate is end of Pragian (Siegenian) to middle of the Lower Emsian (Bartels, Briggs et Brassel 1998, p. 19). *Eospondylus tenuis* was described by Withers et Keble (1934) from the Silurian Yarravian series, Moonee Ponds, Victoria, Australia (Clark 1946, p. 165). Gill et Caster (1960, p. 32) listed *Eospondylus* cf. *tenuis* from the Lower Devonian, Collins' Quarry, Kinglake, Victoria, Australia. Australia was included in the distribution records of *Eospondylus* by Spencer (1950, p. 407) and Ubaghs (1953, p. 821) but not by Spencer et Wright (1966, p. U90), perhaps indicating their opinion that *E. tenuis* does not belong in this genus. Haude (1998, see also 2004) listed *Eospondylus*? n. sp., from the Lower Devonian Talacasto Formation (Lochkovian to Emsian) of the Argentine Precordillera. Boczarowski (2001) described *Eospondylus ingens* from vertebrae and lateral plates that were chemically extracted from the Middle Devonian, Early Givetian, Skały Beds, Holy Cross Mountains, Poland. *Eospondylus* sp. was reported from the upper part of the Selscheid Beds (Middle Devonian, Upper Eifelian) of the Attendorn-Olpe area (western Sauerland) by May (2003). We report *Eospondylus* sp. isolated vertebrae and a lateral plate from the Dvorce-Prokop Limestone (Pragian age), the Loděnice Limestone (Pragian age) and the Třebotov Limestone (Dalejan age, Late Emsian).

A feature of the Hunsrück Slate ophiuroid *Eospondylus primigenius* (Text-fig. 1) is that the rays often are bent into strong curves (Spencer 1925, Pl. 21, Text-fig. 9; Lehmann 1957, Pl. 15). Usually the bending of the rays is horizontal but sometimes is vertical (Spencer 1925, p. 310, Bonn specimen, Lehmann 1957, Pl. 16). A clump of *Eospondylus* with tangled arms was reported by Lehmann (1957). During this study we obtained a specimen with arms curved ventrally under the disk in euryalid fashion (NM S 4764; Text-fig. 2) and one with aboral arm flexure (NM S 4765). Such flexibility and attitudes of the rays is not seen in other Hunsrück ophiuroids (Lehmann 1957) and differentiates the behavioral ecology of *Eospondylus* from other ophiuroids. It also has been noticed that *Eospondylus* and crinoids sometimes are preserved in intimate association and may have lived together (Stürmer 1968, figs 2, 3; Bartels, Briggs et Brassel 1998, figs 151, 155; Bartels et al. 1997, figs 48, 56). Haude (2004, p. 418) reported from the Lower Devonian of Argentina "an eospondylid that lived as a commensalist on large rheophilic crinoids."

The above observations on the behavioural ecology of *Eospondylus*, especially the vertical bending and flexibility of the rays and the intimate association with crinoids, were used by Spencer et Wright (1966) to classify *Eospondylus* in the Order Euryalida, which contains the epizoic gorgonocephalid and euryalid basket-stars of modern oceans. Thus Spencer et Wright (1966, p. U27-28) wrote [we paraphrase] that by Devonian time two ophiuroid groups had developed, one with arms that allowed for active movement on the sea floor, the other with arms that allowed for a commensal life attached to crinoids and other hosts. The second of these groups had arms that could climb up and grip onto hosts such as crinoids by means of the vertical rolling of the arms and small hooked spines. This group consists of suspension-feeders collecting organic particles by their own ciliary action, aided by that of their hosts. With this prologue, Spencer et Wright (1966, p. U90) reclassified *Eospondylus* into its own Family Eospondylidae, and placed that family in the Suborder Euryalina. They listed the content of the Euryalina as the Palaeozoic families Eospondylidae and Onychasteridae, and the Recent families Asteronychidae, Asteroschematidae, Gorgonocephalidae and Euryalidae (Spencer et Wright 1966, p. U38). Fell et Pawson (1966, p. 36) suggested from retained metapinnular structure in Asteronyx that the Euryalida "derived from some stock nearer to the somasteroids than the Oegophiurida" and thus are of great antiquity. Latest classifications treat the Euryalina as the Order Euryalida (Smith, Paterson et Lafay 1995) (see also Clark et Courtman-Stock 1976, p. 127 [footnote]). Spencer et Wright (1966) clearly recognized the appearance of *Eospondylus* in the Lower Devonian as the stratigraphic first occurrence of the Euryalida. This status is an important reason to review the classification of *Eospondylus* using the new evidence from isolated vertebrae.

Species *Eospondylus* cf. *primigenius* (Stürtz)

Text-figs 3-5, 8, 9A, 9B, 11.

Horizon: Loděnice Limestone, Třebotov Limestone, Lower Devonian

Material: NM L 36903, NM L 36904, NM L 36905, NM L 36910, NM L 38365, NM L 38366, 10 unnumbered specimens from Dalejan and 8 unnumbered specimens from Pragian

Occurrence: Praha – Klukovice, Červený lom quarry (Pragian); Holyně, Prastav quarry (Dalejan)

Description of vertebrae

The complex shape and the general proportions of the ossicles are best understood by examining the SEM stereopair dorsal and ventral (Text-fig. 3), proximal and distal (Text-fig. 4), and left and right (Text-fig. 5) views of each vertebra. The vertebrae carry some damage, especially the fragile cupola structures for the tube feet are broken or missing. Of twenty-three vertebrae, two are half-vertebrae and twenty-one are entire. Traces of the suture between the two firmly-joined halves are evident particularly on the proximal and distal surfaces. The vertebrae are pierced lengthwise by the auluroid canal for the radial water vessel of the water vascular system. The following features are useful to orient the vertebrae. The dorsal surface has a median dorsal cleft. The ventral surface is flat and plastron like and has distal lateral cupola structures for the tube feet. The proximal surface has a prominent unpaired dorsal knob and the opening of the auluroid canal is a deep funnel. On the distal surface the auluroid canal is concentric with the zygosphene knob (hence like a spout), and the zygocondyles look like raised wings of a bird (eagle).

DORSAL   **VENTRAL**
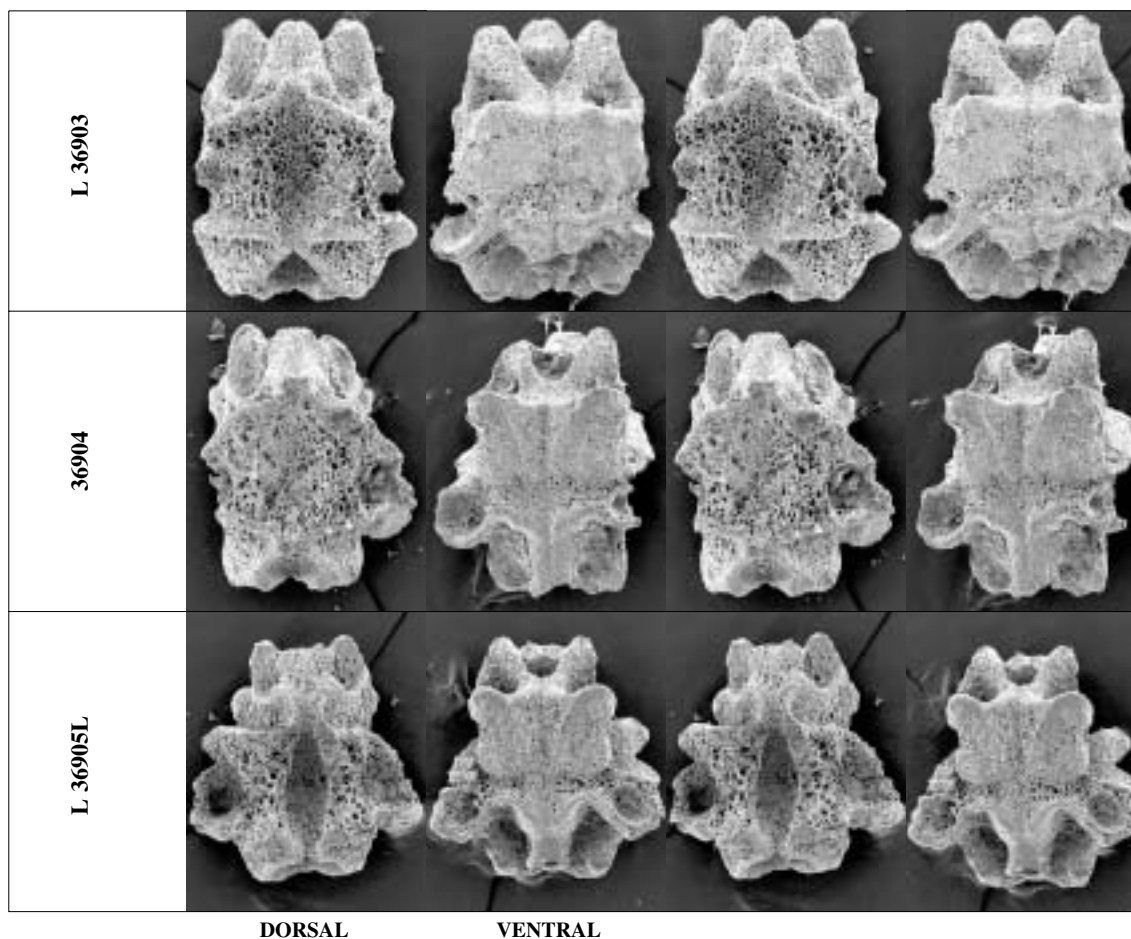
Text-fig. 3. *Eospondylus* cf. *primigenius* (STÜRTZ)
NM L 36903 "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, x 23,
NM L 36904 "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, x 25,
NM L 36905 "Prastav" quarry at Praha-Holyně, Třebotov Limestone, Lower Devonian, Dalejan, x 24,
Vertebrae. Dorsal (left stereoimage) and ventral (right stereoimage) views oriented with the proximal end at the top. The dorsal surface has a median dorsal cleft. The ventral surface is flat and plastron like and has distal lateral cupola structures for the tube feet. Six degree tilt between image captures. See text for descriptions. [SEM images by Dr. Rudolf F. Turner].

Under surface of vertebrae (Text-fig. 3): The portion of the under surface of the vertebrae that corresponds with the floor of the ambulacral groove is essentially flat and plastron-like. This part of the ossicle is exposed in the normal outward movement of the lateral plates in articulated specimens. A shallow indent with abundant stereom perforations is present on the mid-line of the plastron. Proximally the perforations define a nearly triangular zone, widest at the proximal edge of the undersurface, and narrowest near the mid-length of the vertebra where indented lateral branches of perforate stereom lead toward the location of the lateral arm plates and the cups for the tube feet. The midline triangle of perforate stereom divides the proximal undersurface of the vertebrae into left and right islands of stereom that lack obvious perforations. The proximal edge of these islands extends as a lobe that partly hides the ventral muscle fossae of the proximal surface. The lateral branches of perforated stereom are succeeded distally by a small area of stereom that lacks obvious perforations. This area is contiguous with a spout-like structure that contains the radial water vessel (auluroid condition). These features are visible in the ambulacral groove of some articulated *E. primigenius*.

At the mid-length of the vertebra the lateral branches of perforated stereom form a transverse belt. Disto-laterally to this belt the width of the vertebrae expands into the cupola structure of the cups for the tube feet. The cupola structures project from the sides of the vertebrae and are intact in specimen NM L 36905. The cupola structures are broken off on one side of NM L 36904 and off both sides of NM L 36903. Likewise they are broken off both sides of the vertebrae illustrated by Boczarowski (2001, figs 9L, 9M). Although broken off, nevertheless a part of the rim of the cupola is evident in NM L 36903 and in Boczarowski's Text-fig. 9M. In articulated *E. primigenius* the cupola structures normally are concealed by the lateral plates. Specimen NM S 4766 is an exception in that a few lateral plates are displaced and expose the cupola area (Text-fig. 6).

The lateral ridges (the proximal and distal borders of the wings of the vertebrae) converge ventrally with the rim of the cupola such that the proximal lateral ridge is seen from the under surface. The cupola hides the distal lateral ridge.

The proximal lateral ridge projects significantly from the side of the vertebra in NM L 36905, but due to breakage it projects only slightly in NM L 36904, and does not project into view in NM L 36903.

The under surface view of the isolated vertebrae includes a profile view of the proximal and distal articulation and muscle insertion features which, although prominent, are not part of the under surface. The articular processes strongly project beyond the plastron and cupola regions. At the distal border can be seen: the conspicuous spout-like zygosphene (unpaired ventral knob of distal surface) that contains the radial water vessel, deep paired hollows (the ventral muscle fossae and the pits for the zygapophyses of the conjugate surface are quite confluent), and the zygocondyles (paired knobs of distal surface). At the proximal border can be seen the ventral muscle fossae, the zygapophyses (paired knobs of proximal surface) and the epanapophysis (unpaired dorsal knob of proximal surface). At the distal border of the undersurface of the vertebrae exposed in the ambulacral groove of some articulated *E. primigenius* (Text-fig. 6) can be seen the recesses of the ventral muscle fossae, the spout-like zygosphene, and even evidence that the zygosphene is penetrated by the auluroid canal. Likewise, at the proximal border can be seen part of the funnel-like ventral socket (the reentrant between the zygapophyses) and parts of the surfaces for the attachment of the ventral intervertebral muscles.

Upper surface of vertebrae (Text-fig. 3): The halves of vertebrae are solidly fused, without visible suture. The stereom in the aboral groove and on the wings of the vertebrae has abundant large perforations. The aboral groove (median dorsal cleft) is deeply sculpted and broadest at its median part. In NM L 36905 the aboral groove has a lenticular shape and looks like a median pore, but it is only a deep hollow. The upper and lateral part of the vertebra between the insertions for the dorsal longitudinal muscles is the wing of the vertebra. In all specimens the wing of the vertebra is widest at the lateral ridges. Between the lateral ridges the wings are deeply excavated and vertical-sided to the level of the circular cupola. In NM L 36905 the excavation goes more deeply into the ventrolateral area, making a ventrolateral pit just above the cupola. The upper surface of the cupola has a conspicuous hollow. The proximal and distal lateral ridges are confluent with the margin of the cupola. In some articulated *E. primigenius* (ROM 11474, WU 860033) the prominent spine-bearing ridge of the lateral plate lies precisely over the distal lateral ridge, and we believe that this is the undisturbed position. In BMNH E3357 the lateral plate appears to have slipped off the lateral ridge and into the concavity of the side of the vertebra (Spencer 1925, text-Text-fig. 206).

The proximal and distal articular processes strongly project beyond the lateral ridges of the vertebrae. This was observed also by Boczarowski (2001, p. 38) and written into his diagnosis of *Eospondylus ingens*. The proximal processes project considerably more, and the distal processes project less. In NM L 36905 upper surface view the distal processes project very little beyond the lateral ridge, and this is true also in a vertebra of *E. ingens* interpreted by Boczarowski (2001, Pl. 1, Text-fig. 17) as coming from the middle part of the arm. At the proximal border in all speci-

mens can be seen the conspicuous epanapophysis (unpaired dorsal knob of proximal surface) and the zygapophyses (paired knobs of proximal surface). The articular processes at the distal border are the epanotreme (unpaired dorsal receptacle that lodges the epanapophysis) and the zygocondyles (paired knobs of distal surface, but not looking like knobs in this upper surface view). In articulated *E. primigenius* the upper surface of the vertebrae is not covered by any plating. The peg on the proximal surface (the epanapophysis) is lodged in a shoulder-socket on the distal surface (the epanotreme) when the vertebrae are in close contact (but in many specimens successive vertebrae are not in close contact). The space for the dorsal intervertebral muscles is fairly large as a consequence of the setback of the lateral ridges from the extremities of the articular processes. The setback for the muscles is greatest in NM L 36905 and involves a small curl in the lateral ridge where the ridges converge behind the epanapophysis.

Proximal surface of vertebrae (Text-fig. 4): The proximal articulating surface presents a strong image of a central triangular area in the foreground and a peripheral region that is the wing of the vertebra in the background. The shape in NM L 36905 is like a tall isosceles triangle with ventral base, dorsal vertex and rounded angles. In NM L 36903 the triangle is almost equilateral. The triangular area contains all the articulating knobs and pits, the canal for the radial water vessel, and the ventral intervertebral muscle fields. The base of the 'triangle' is a profile of the under surface of the vertebra. The profile in NM L 36905 shows a shallow dihedral angle. The profile in NM L 36903 and NM L 36904 shows a shallow ventral groove. The articulation knobs of the proximal surface are the epanapophysis (unpaired dorsal knob of proximal surface) and the zygapophyses (paired knobs of proximal surface). The articulating pits (sockets) of the proximal surface are the zygotreme (unpaired ventral socket of the proximal surface) and two unnamed dorsolateral sockets. The dorsal knob is shaped somewhat like a square that is standing on its diagonal. In this orientation it contributes two articular facets, each at forty-five degrees to the horizontal (following the insight of Bray 1985). The vertical suture of the two fused ambulacral plates is plainly visible on the dorsal knob. Looking a bit like an inverted flask, the dorsal knob is connected below to a median saddle ridge which extends to the opening of the auluroid canal. The canal opening is at the bottom of a deep depression that serves as a socket (zygotreme) for the ventral knob of the conjugate surface. Paired ventral knobs (zygapophyses) are on either side of the canal opening. These angular knobs are somewhat pyramidal with three very steep surfaces: one surface faces toward the dorsolateral paired sockets, one faces toward the ventral intervertebral muscle fields, and one faces toward the radial water vessel. In the perimeter space between the dorsal knob and the paired ventral knobs are the dorsolateral sockets for the horizontal hinge knobs (zygocondyles) of the conjugate surface. Depressions for the ventral muscles are situated at the lower outer corners of the triangular area; the fossae are deeply excavated and of moderate cross section. The dorsal intervertebral muscle fields lie outside of the triangular articulating surface and at a more distant plane (the wing of the vertebra).

PROXIMAL   DISTAL
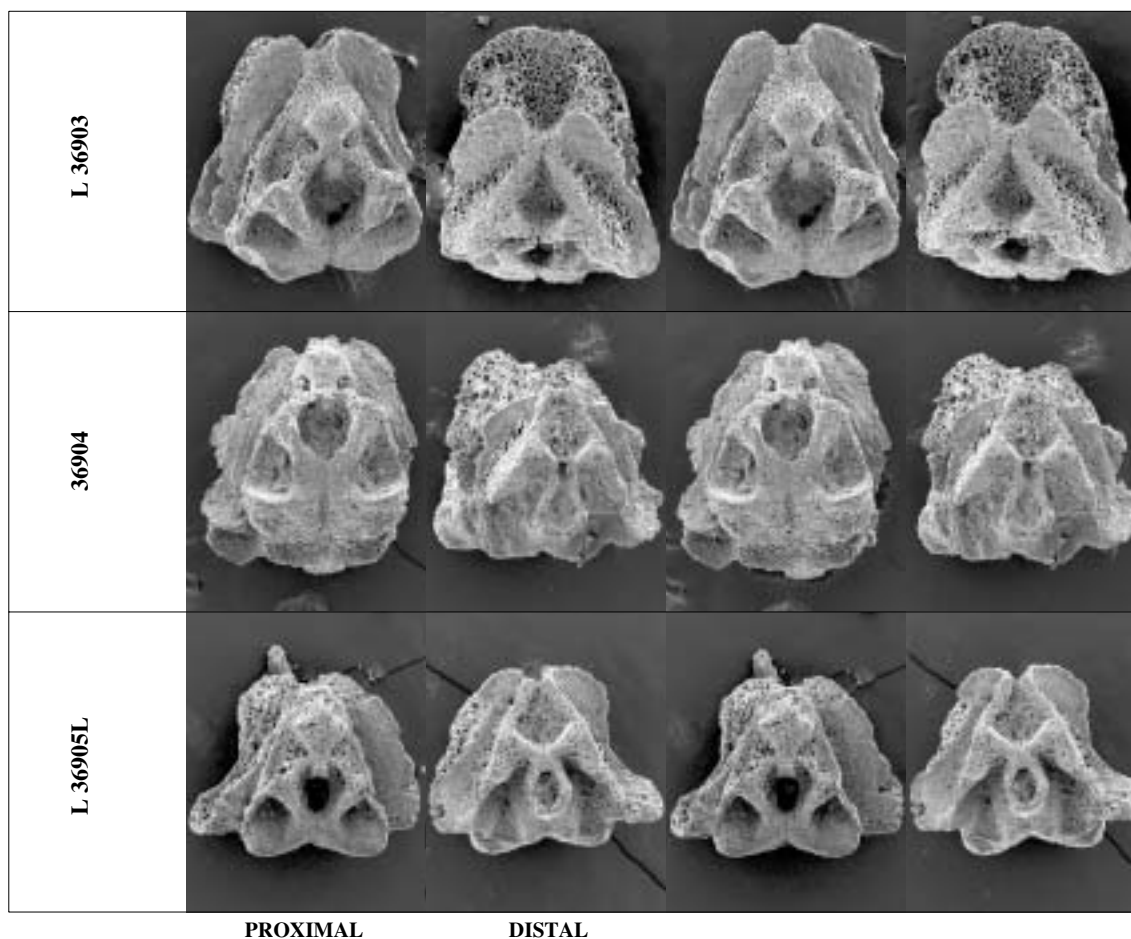
Text-fig. 4. *Eospondylus* **cf.** *primigenius* (Stürtz)
NM L 36903 "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, x 25,
NM L 36904 "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, x 28,
NM L 36905 "Prastav" quarry at Praha-Holyně, Třebotov Limestone, Lower Devonian, Dalejan, x 20,
**Vertebrae. Proximal (left stereoimge) and distal (right stereoimage) views oriented with dorsal surface on top. Proximal surface has an unpaired dorsal knob, paired zygapophyses, and opening auluroid canal is deep funnel. On distal surface auluroid canal is concentric with zygosphene knob, and zygocondyles look like raised wings of a bird. The distal view of NM L 36903 (top row) is tilted down. Proximal view of NM L 36904 (middle row) is tilted up. See text for descriptions. [SEM images by Dr. Rudolf F. Turner].**

Point of discussion: In *Eospondylus*, at the proximal end of the vertebrae the insertion surfaces for the dorsal intervertebral muscles are at a more distal plane than the ventral muscle insertion surfaces. This is the reverse of the relative locations of these surfaces in the Order Ophiurida (e.g. see Palaeocoma in Hess 1962, p. 617, Text-fig. 7, lateral view). This difference applies only to the proximal end of each vertebra. The relative location of muscle insertion surfaces at the distal end of the vertebrae is the same in *Eospondylus* and in the Order Ophiurida. At the distal end of the vertebrae the insertion surfaces for the dorsal intervertebral muscles are at a more proximal plane than the ventral muscle insertion surfaces.

Distal surface of vertebrae (Text-fig. 4): The articulation processes of the distal surface present the general impression of a bird image ("vogelähnliches Gebilde" of Hess 1962, p. 615). The zygocondyles (paired dorsal knobs of distal surface) look like raised wings. The zygosphene (unpaired ventral knob of distal surface) looks like a bird body suspended beneath the wings. The upper surfaces of the two zygocondyles form a V and acted as paired aboral articular facets

(analysis of articular facets follows the insight of Bray 1985). The lower surfaces of the two zygocondyles are configured as / and \ and acted as paired oral articular facets. The outer surfaces of the zygocondyles are steep flat surfaces that bordered the dorsal longitudinal muscles. The large auluroid canal opening is subcircular, is located in the lower half of the vertebra, and is concentric with the zygosphene knob. The canal opening is surrounded by a raised rim. The articulating pits of the distal surface are the epanotreme (unpaired dorsal socket) and unnamed paired ventrolateral pits that merge imperceptibly with deep fossae for the ventral longitudinal muscles. The muscle fields for the dorsal longitudinal muscles are the wings of the vertebra.

Lateral surfaces of vertebrae (Text-fig. 5): Both sides of NM L 36903 and NM L 36904 have similar appearances, but only the left side of NM L 36905 is used for description because the right side is damaged and has a substantially different appearance (major loss of proximal lateral ridge). The side view dorsal profile of NM L 36905 is a swayback shape, and consequently this vertebra has a lower profile in its midregion than do the vertebrae NM L 36903 and NM L

LEFT SIDE   RIGHT SIDE
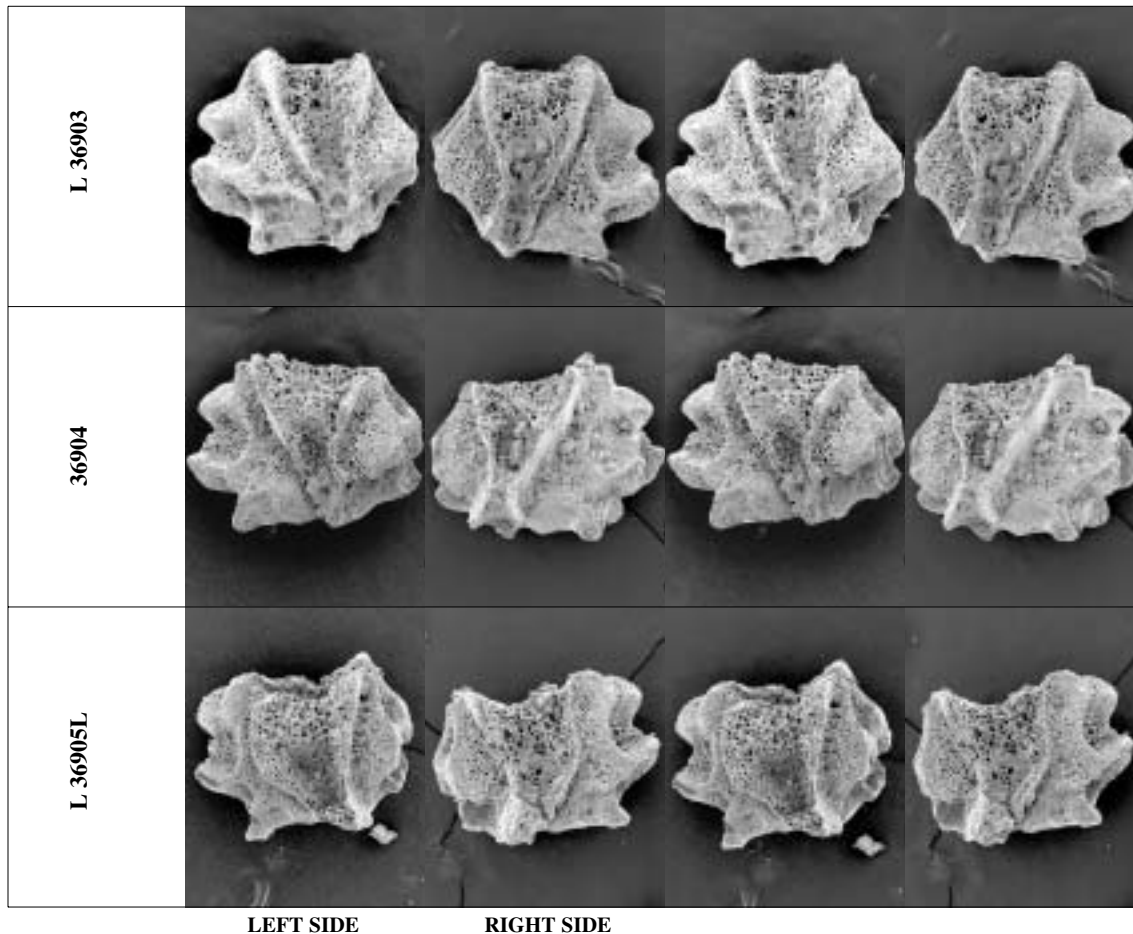
Text-fig. 5. *Eospondylus* cf. *primigenius* (Stürtz)
NM L 36903 "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, x 23,
NM L 36904 "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, x 28,
NM L 36905 "Prastav" quarry at Praha-Holyně, Třebotov Limestone, Lower Devonian, Dalejan, x 21,
Vertebrae. Left (left stereoimage) and right (right stereoimage) lateral views oriented with dorsal surface on top. In left lateral view, proximal (anterior) is to the left. In right lateral view, proximal (anterior) is to the right. At ends of the vertebrae articulating surfaces are seen in profile. In midregion, wing of the vertebra lies between proximal and distal lateral ridges. The right side of NM L 36905 (bottom row) is damaged. See text for descriptions. [SEM images by Dr. Rudolf F. Turner].

36904. This swayback low profile is even more strikingly presented in NM L 38365 (elongate swayback version of standard type). The lateral surface is divided into three successive regions. At the ends of the vertebrae are the exposed proximal and distal articulating surfaces. The central region is the wing of the vertebra, ending at the proximal and distal lateral ridges. The wing extends from the dorsal surface to the ventral edge, ending where the cupola is located. The wing of NM L 36905 is broader than in NM L 36903 and NM L 36904, whereas the dorsal nose of the proximal articulating surface is more prominent in NM L 36903 and NM L 36904 than in NM L 36905. The appropriateness of the term dorsal nose for the epanapophysis is evident in side view. The proximal articulating surface, described from upper part to lower part, is composed of a shoulder leading to the dorsal nose, a reentrant below the nose and also at this level a deep dorsolateral pit, a projection that is the zygapophysis, a deep reentrant that leads to the fossae for the ventral longitudinal muscles, and a final ventral projection that contains the muscle fossae. The zygapophyses project as much (NM L 36905) or slightly more (NM L

36903, NM L 36904) than the dorsal nose projects. The profile of the distal articulating surface has three parts. Beginning at the upper surface, the profile slopes linearly away from the distal lateral ridge; the next part is a vertical profile at midlevel; the bottom part slopes back to the distal lateral ridge at the level of the cupola. The presented surface is uniform and flat. The flatness and the simple profile contrast with the complexity of the epanotreme, the zygocondyles, and the ventrolateral pits and fossae that are behind the top, middle and lower portions of this surface. The zygosphene (unpaired ventral knob pierced by the auluroid canal) is hidden from view, or inconspicuous or visible depending on the tilt of the specimen. The wing of the vertebra is deeply excavated just above the cupola. The shape of the wing of the vertebra is outlined by the lateral ridges. The tilt of the proximal lateral ridge toward the posterior cupola is particularly distinctive.
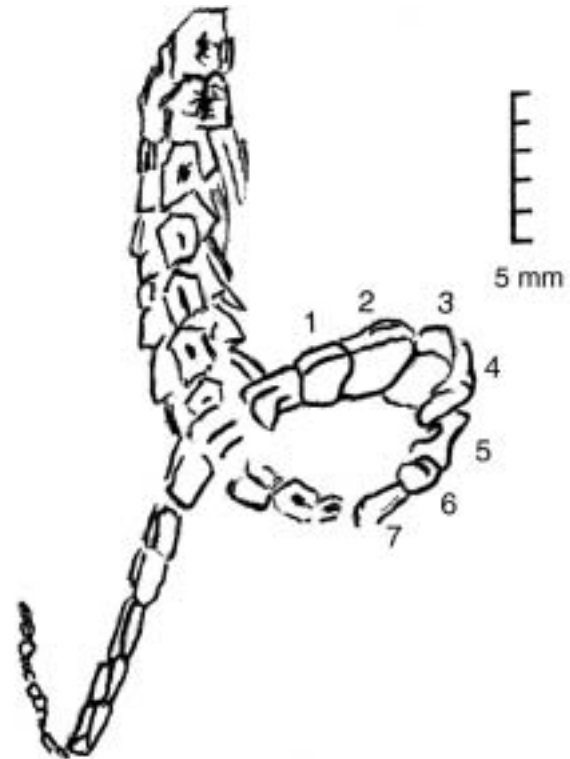
Variation of the vertebrae: Differences between the swayback lower profile vertebra NM L 36905 and the more block-like NM L 36903 and NM L 36904 are recorded throughout the description. Such differences may indicate

12
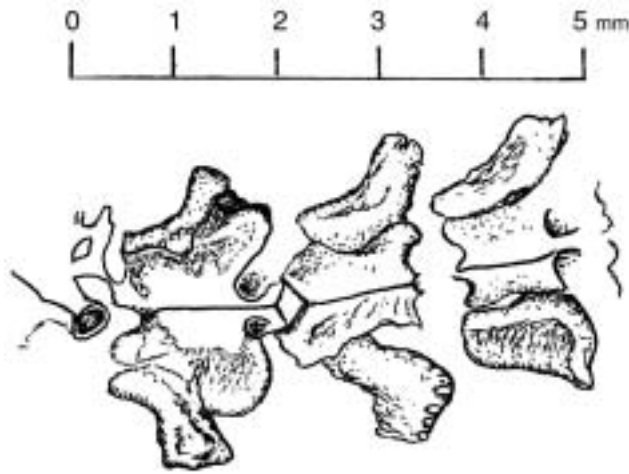
Text-fig. 6. *Eospondylus primigenius* (STÜRTZ) Bundenbach, Eschenbach-Bocksberg quarry, Lower Devonian, Lower Emsian (Zlichovian), Hunsrück Slate, NM S 4766, x 12.5.
Undersurface of arm segments in Hunsrück Slate articulated specimen. A few lateral plates are displaced and expose details of vertebrae. The canal for radial water vessel is in center of zygosphene knob and zygotreme pit, like spout and funnel. At distal outer edges of vertebrae is cupola for tube feet. There are no under arm plates.
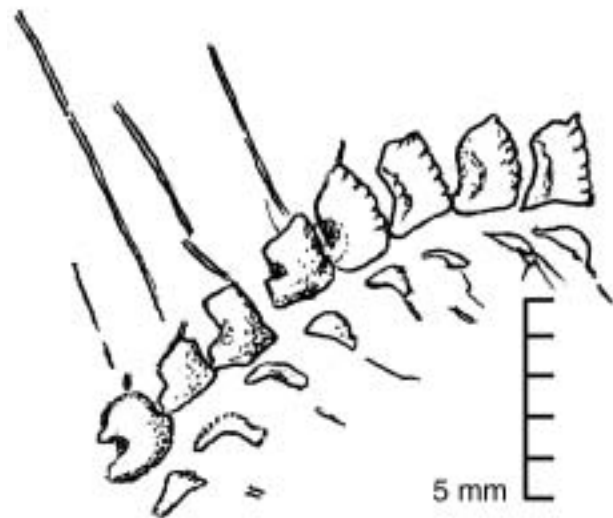

Text-fig. 7A. *Eospondylus primigenius* (STÜRTZ) Bundenbach, Eschenbach-Bocksberg quarry, Lower Devonian, Lower Emsian (Zlichovian), Hunsrück Slate,
BMNH E3353, x 3.
Extreme horizontal arm bending: Arm loop with half-twist in Hunsrück Slate. In the proximal part of the arm the view is of the upper surface, but after the loop the view is of the lower surface. Seven arm segments (six articulations) bend 180 degrees, indicating 30 degrees of bend per articulation.

that the vertebrae came from different parts of the arm (Boczarowski 2001), or that they may represent variation among specimens, or some of both. The elongate swayback vertebra NM L 38365 is probably from the distal region of an arm where segments are elongate. The block-like NM L 36903 and NM L 36904 are probably from the proximal or middle part of an arm. The swayback vertebra NM L 36905 is more equiproportioned than elongate and this suggests that it is a transitional morphology, perhaps coming from a part of the arm that is between the midpart and the distal part of the arm. Specimen NM L 38366 is block-like but of very small size, probably indicating the proximal or middle part of the arm in a small growth stage individual. On the other hand some of the variability may represent phenotypic variation in the population (Text-fig. 1), the reasons for which can vary. For example the living ophiuroid *Ophiocoma echinata* has a more robust form with relatively shorter arms in areas exposed to high energy waves in the swash zone (Bray 1981). Lehmann (1957) recognized *E. primigenius* var. *compactus* as having arm structure different from typical *E. primigenius*. Measurements (length x width) obtained from Národní Museum SEM images printed with a 500 micron scale (the 100 micron scale in the Indiana University images is not as well suited): NM L 36903 1.46 mm x 1.23 mm; NM L 36904 1.48 mm x 1.17 mm; NM L 36905 1.25 mm x 1.25 mm.

Extreme horizontal arm bending (Text-fig. 7A): In articulated *E. primigenius* specimen BMNH E3353 one arm loops over itself in the horizontal plane (no twist or inversion), and a second arm loops over itself with a half-twist (complete inversion); the tightest 180 degree bend involves eight segments (seven articulations) in the former and seven segments (six articulations) in the latter; the calculated bend per articulation is 25.7 degrees and 30 degrees respectively.

Text-fig. 7B. *Eospondylus primigenius* (STÜRTZ) Bundenbach, Eschenbach-Bocksberg quarry, Lower Devonian, Lower Emsian (Zlichovian), Hunsrück Slate, BMNH E3358, x 4.
Hunsrück Slate articulated specimen. Underside of arm showing two contrasting appearances of lateral arm plates in a single arm. The arm is rolled slightly. Of the left lateral arm plates the lateral surface is extensively exposed. The spine ridge faces distally (posteriorly). Of the right lateral arm plates only the ventral edge that borders the ambulacral groove is exposed.

In articulated *E. primigenius* specimen NM S 4767 the distal half of an arm is bent almost 180-degrees, involving 7 segments (6 articulations); the bend per articulation is 30-degrees. These values are consistent with the extremes of intersegmental bending in zygospondylous ophiuroids reported by LeClair et LaBarbera (1997).

Description of lateral arm plate

The one lateral plate NM L 36910 (Text-fig. 8, Text-fig. 9) is assigned to *Eospondylus* based on shape comparisons with lateral plates in articulated *E. primigenius* specimens

Fig. 9A

Fig. 9B
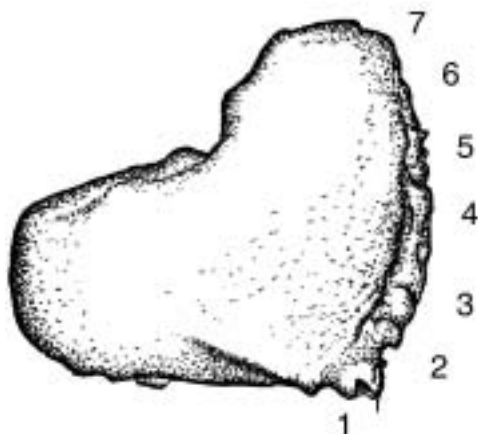
Text-fig. 8. *Eospondylus* **cf.** *primigenius* (Stürtz) "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, NM L 36910, x 25.
Left lateral plate, outer view. The surface leading to the vertical ridge flairs outward. The height profile leaves uncovered part of the side of the arm vertebra.

Text-fig. 9A. *Eospondylus* **cf.** *primigenius* (Stürtz) "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, NM L 36910, x 40.
Left lateral plate. Inner surface view from below. The spine ridge faces distally (posteriorly) and has blunt pointed denticles. Anterior and parallel to denticled part of spine ridge is internal rounded ridge. Ventrolaterally ossicle has slit-like sockets for groove spines.

Text-fig. 9B. *Eospondylus* **cf.** *primigenius* (Stürtz) "Červený lom" quarry near Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, NM L 36910, x 38.
Inner view drawing showing proximal peg and distal ridge that articulated with vertebrae. The vertical spine ridge carried seven spines and faced distally and outward from side of arm.

(Text-fig. 7B). Especially similar are the prominent vertical ridge, the outward flair of the surface that leads to the vertical ridge, the blunt pointed denticles that separate the spine sockets, the count of seven vertical spine sockets, the lack of a distal tongue (successive laterals of *E. primigenius* do not overlap), and the small size of the slit-like groove spine sockets which are five in number. The height profile leaves uncovered part of the side of the arm vertebrae, while ventrally the plate wraps partly under the arm. This lateral plate differs from the proximal, middle and distal lateral plates of *E. ingens* which have a distal tongue (Boczarowski 2001, figs. 9 N-Q). This lateral plate is more similar to the lateral plates of *Furcaster aequoreus* (especially Boczarowski 2001, Text-fig. 11 B) but the *Furcaster* lateral plates have a narrower and more pointed proximal end.

Analysis and conclusions

These vertebrae compare very well with the exposed parts of the vertebrae of Hunsrück Slate *E. primigenius*. In particular they have the identifying characteristic of a median dorsal cleft that deeply indents the upper surface of each vertebra and deep hollows on the dorsolateral surface. With the exception of the elongate distal vertebra NM L 38365, the amount of exposed proximal articulating surface in lateral view is much smaller in the Barrandian ossicles than in
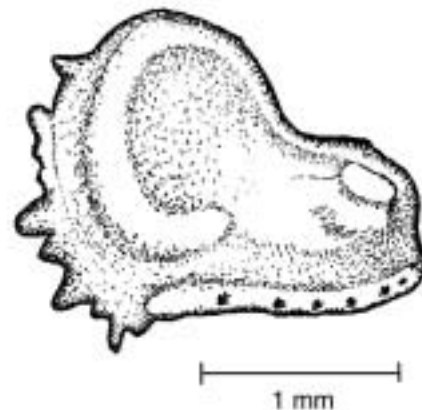
the holotype of *E. ingens* from the Holy Cross Mountains (Boczarowski 2001, Text-fig. 9L3). We identify the Barrandian vertebrae as *Eospondylus* sp., cf. *E. primigenius*.

The conclusion that articulated *E. primigenius* did not have under arm plates (Spencer 1925, p. 311) is supported by the present study. The detailed correspondence of the underside of the isolated vertebrae with the ossicles exposed in the ambulacral groove of articulated *E. primigenius* identifies the ossicles in the ambulacral groove as vertebrae that are not obscured by under arm plates. Even the cupola area of the vertebrae is exposed in rare articulated specimens in which a few lateral plates are sufficiently displaced (Text-fig. 6). In addition, the observation that the side arm plates were movable and could either cover or uncover the ambulacral groove, and the presence of groove spines on the ventral edge of the side arm plates (Text-fig. 10), are consistent with a lack of under arm plates.

The architecture of the articulating surfaces of *Eospondylus* is both zygospondylous and auluroid (Text-fig. 11). Weller (1930) described isolated vertebrae with this articu-

DISTAL

3 mm

2

1

0

lateral plates have groove spines

DETAIL „D"
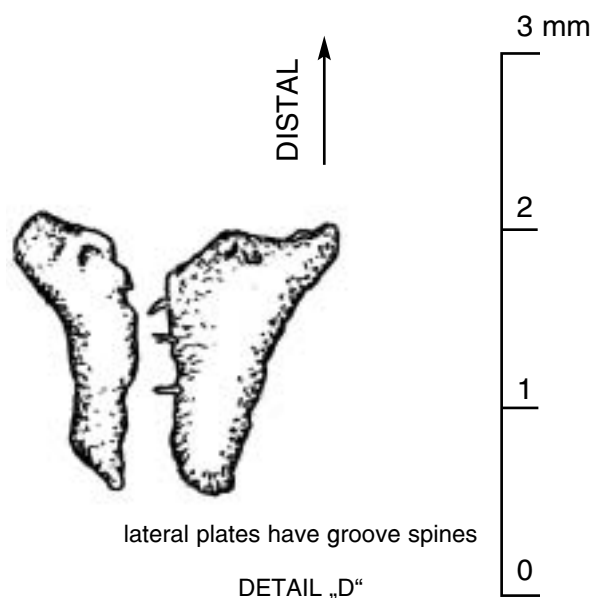
Text-fig. 10. *Eospondylus primigenius* (Stürtz) **Bundenbach, Eschenbach-Bocksberg quarry, Lower Devonian, Lower Emsian (Zlichovian), Hunsrück Slate, NM S 4766, x 26. Lateral plates on undersurface of arm segment in Hunsrück Slate articulated specimen. Short thin groove spines on ventral edge of lateral arm plates protect undersurface of vertebra and partially cover ambulacral groove.**

lation type but he was not able to identify them to family or genus. Identification came when Haude (1982, Text-fig. 3) and Haude et Thomas (1983, Text-fig. 7) found vertebrae of this type plan in partially disarticulated specimens of *Furcaster* n. spp. (Family Furcasteridae). Haude (1982, p. 14) and also Boczarowski (2001, p. 29) recognized several vertebrae illustrated by Becker et Weigelt (1975) as belonging to *Furcaster*. Most recently Boczarowski (2001) described and named *Furcaster aequoreus*, *F. cataphractus* and *Eospondylus ingens* based on isolated vertebrae of this articulation type. In this architecture, (1) the articulations are a topological match to the trispondylous peg-and-socket articulations seen in many Ophiurida, (2) the channel for the radial water vessel is completely enclosed within the vertebra, and (3) the placement of the canal for the radial water vessel is in the center of the zygosphene knob and zygotreme pit. Thus the zygosphene with its hole for the radial water vessel is like a spout or nozzel, and the zygotreme is like a funnel. So far, this type of arm vertebrae with zygospondylous articulations and centered auluroid canal is known only in the Furcasteridae and the Eospondylidae.

P o i n t s   o f   d i s c u s s i o n : A vertebra figured by Becker et Weigelt (1975, plate 4 figs. 6a-e) has some eospondylid features but differs from typical *Eospondylus* and *Furcaster* vertebrae. The orientation of the views should have been stated as follows: 6a right side, 6b dorsal, 6c ventral, 6d distal (posterior), 6e proximal (anterior). This vertebra may possibly belong to the family Eospondylidae.

The proximal vertebrae of *Furcaster cataphractus* have many features in common with *Eospondylus* vertebrae and also significant differences. In proximal and distal end views the articulation processes share significant resem-

blances. In oral view the expanded cupola for the tube feet are quite similar (compare Boczarowski 2001, Text-fig. 13). However in *F. cataphractus* the aboral groove is approximately straight-sided and situated between narrow sharp ridge borders (while it is lens-shaped and situated between wide rounded borders in *Eospondylus*). In *F. cataphractus* the distal wings are so close to the end of the vertebrae that in side view the articulation processes are mostly hidden (while in *Eospondylus* alar ridges set back from the articular surfaces which are visible in side view). In *F. cataphractus* the sides of the vertebrae are broadly concave (but in *Eospondylus* there is the nonhomologous deep excavation in the wing area just over the cupola). So far the Barrandian isolated vertebrae of *Furcaster* and of *Eospondylus* have been easy to separate.

The distal surface of a proximal vertebra of *Palaeocoma gaveyi* figured by Hess (1962, Text-fig. 7) also has the three features of being (1) zygospondylous, (2) auluroid, and (3) with the hole for the radial water vessel at the center of the zygosphene. The Hess vertebra, which is not typical of the rest of the arm vertebrae, suggests that the manner of transition from a centered auluroid canal to an open ventral channel for the radial water vessel might usefully be studied in the arm of *P. gaveyi*. Spencer (1925, p. 251) argued that there is great plasticity in the relation of the radial water vessel to the substance of the vertebra, and therefore he argued that the auluroid condition is not a basis for erecting a Class Auluroidea. His view is confirmed by *Trichaster* (an euryalid with hourglass articulations) in which the radial water vessel is enclosed in a ventral canal that is not part of any articulating surface (Mortensen 1933).

Although sharing generalized topological structure with the vertebrae under discussion, the vertebrae of *Hallaster* and *Lapworthura* as illustrated by Spencer (1925, figs 178, 205) are too different to be considered at length here. In *Lapworthura* each half vertebra has its own functional dorsal nose [not so in *Hallaster* in which the vertebral halves share in forming a single dorsal nose]. In both *Hallaster* and *Lapworthura* the ventral nose is scarcely evident and also the hole for the auluroid canal is very small, inconspicuous, and near the ventral surface.

As is well known, the arms of the Euryalida typically coil ventrally and may branch. In particular, the vertebrae of the Euryalida typically articulate by broad hourglass-shaped surfaces (Mortensen 1933; Spencer et Wright 1966, p. U90). Although *Eospondylus* was capable of ventral arm coiling, aboral arm flexure, and extreme horizontal arm bending, we have shown here that the vertebrae of *Eospondylus* do not have hourglass articulations and are not intermediate between hour-glass type and zygospondyline type. In addition, articulated body fossils of *Eospondylus* do not have radial shields, do not have genital plates, do not have oral shields, do not have adoral shields, and do not have buccal under arm plates, whereas all of these are present in the Euryalida. We argue that the total evidence against classifying *Eospondylus* in the Euryalida is convincing.

From its vertebrae *Eospondylus* is almost a *Furcaster*. We classify the Eospondylidae next to the Furcasteridae in the Suborder Zeugophiurina, in the Order Oegophiurida. This result is much closer to the classification of Spencer (1925) than to the classification of Spencer et Wright
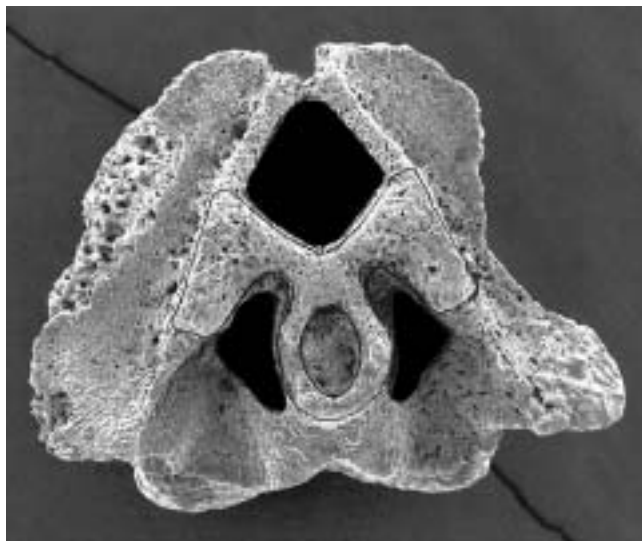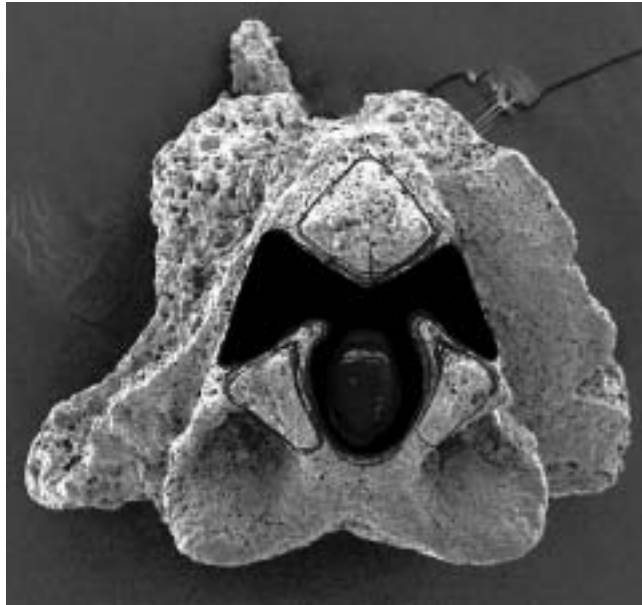
Text-fig. 11. *Eospondylus* cf. *primigenius* (STÜRTZ) "Prastav" quarry at Praha-Holyně, Třebotov Limestone, Lower Devonian, Dalejan, NM L 36905, x 65.
Overlay of proximal and distal articulations. Upper photo is proximal surface with distal bird-like articulation knobs superposed in ink. Lower photo is distal surface with proximal articulation knobs superposed in ink. The architecture of articulation surfaces is both zygospondylous and auluroid. This architecture occurs also in vertebrae of *Furcaster* and indicates that families Eospondylidae and Furcasteridae are closely related.

(1966). Spencer (1925) placed *Eospondylus* in the family Hallasteridae because the long spines are "set at a distinct angle to the direction of the arm-length" (p. 309), and he placed *Furcaster* in its own family Furcasteridae because the arm spines are parallel to the arms. On the other hand, he considered that the vertebrae and side shields of *Hallaster*, *Lapworthura* and *Eospondylus* are so similar to those in *Furcaster* that he placed the family Hallasteridae next to the family Furcasteridae. Certainly more work has to be done to elucidate the morphology of all these genera and to use cladistic methods to formulate hypotheses of relationships among them. Work of this sort is being done by Glass (personal communication, June 2005). In an abstract

for the 2005 Geological Society of America meetings he reports that separation of the Furcasteridae and the Eospondylidae is not supported.

A conclusion from this analysis is that *Eospondylus* is not the first occurrence of the Order Euryalida. It follows that neither is the sister taxon *Kentrospondylus*. According to the classification of Spencer et Wright (1966) the candidate after *Eospondylus* and *Kentrospondylus* for the first occurrence of the Order Euryalida defaults to *Onychaster*. However, retaining *Onychaster* in the Euryalida is not likely to withstand critical reevaluation because it is known that *Onychaster* has an auluroid canal and does not have hourglass articulations (Spencer 1927, text-Text-fig. 217). The classificatory importance that Spencer (1927, p. 333, 325) attached to a single *Onychaster* specimen with a branched arm is greatly diminished by the lack of any similar occurrence despite many examined specimens. The USNM *Onychaster* specimen from Indian Creek with the branched arm has been lost track of (Owen 1965, p. 557). A single instance of a branched arm could be an accident of regeneration. The first undoubted euryalids are post-Triassic.

Acknowledgements

References

Agassiz, L. (1836): Podrome d'une monographie des radiaires ou echinodermes. – Mém. Soc. Sci. natur. Neuchatel, 1(for 1835): 168–199.

Bartels, C., Briggs, D. E. G., Brassel, G. (1998): The fossils of the Hunsrück Slate: marine life in the Devonian. – Cambridge Palaeobiol. Ser., 3. 309 pp. Cambridge Univ. Press.

Bartels, C., Lutz, H., Blind, W., Opel, A. (1997): Schatzkammer Dachschiefer: die Lebenswelt des Hunsrückschiefer-Meeres. 83 pp., Mainz u. Bochum.

Becker, G., Weigelt, H. (1975): Neue Nachweise von Ophiuroidea im Rheinischen Schiefergebirge. – Not.-Bl. Hess. Landesamt. Bodenforsch. Wiesbaden, 103: 5–36, Taf. 1–8.

Bell, F. J. (1892): A contribution to the classification of ophiuroids, with descriptions of some new and little-known forms. – Proc. Zool. Soc. Lond., 1892: 175–183, pls 11, 12.

Boczarowski, A. (2001): Isolated sclerites of Devonian non-Pelmatozoan echinoderms. – Palaeont. pol., 59: 1–220.

Bray, R. D. (1981): Size variation of the rubble-dwelling ophiuroid *Ophiocoma echinata* of Barbados, West Indies. – *In*: Proceedings of the Fourth International Coral Reef Symposium, Manilla, Philipines (May 18–22, 1981), 2: 619–621.

Bray, R. D. (1985): Stereom microstructure of the vertebral ossicles of the Caribbean ophiuroid *Ophiocoma echinata. – In*: Proceedings of the Fifth International Coral reef Symposium, Tahiti (1985), 5: 279–284.

Clark, A. M., Courtman-Stock, J. (1976): The echinoderms of southern Africa. – British Museum (Natural History), Publication 776: 277 pp. London.

Clark, H. L. 1914. Growth-changes in brittle stars. – Pap. Marine Biol. Lab. Tortugas, 5(7): 91–126.

Clark, H. L. 1946. The echinoderm fauna of Australia, its composition and its origin. – Carnegie Institution of Washington, Publication, 566: iv + 567 pp.

Fell, H. B., Pawson, D. L. (1966): General biology of echinoderms, p. 1–48. *In*: R. A. Boolootian (ed.): Physiology of Echinodermata. Interscience Publishers.

Gill, E. D., Caster, K. E. (1960): Carpoid echinoderms from the Silurian and Devonian of Australia. – Bull. amer. Paleont., 41(185): 1–71.

Glass, A. (2005): A phylogeny of Paleozoic Ophiuroidea (Echinodermata) [Abstract]. – Geological Society of America Abstracts with Programs, 37 (7): 306.

Gregory, J. W. (1897): On the classification of the Palaeozoic echinoderms of the group Ophiuroidea. – Proc. Zool. Soc. Lond., 1896: 1028–1044.

Haude, R. (1982): Ophiuren (Echinodermata) aus dem Karbon des Rheinischen Schiefergebirges. – Geol. Jb. Hessen, 110: 5–26.

Haude, R. (1998): Die Ophiuren (Echinodermata) aus den Fundschichten Bodenbenders im Unter-Devon der argentinischen Präkordillere. – Terra Nostra, 98(5): 65.

Haude, R. (2004): Morphology and palaeobiology of echinoderms in the Lower Devonian of the Argentine Precordillera, p. 417–419. – *In*: T. Heinzeller – J. H. Nebelsick (eds): Echinoderms: München, 633 pp. Taylor & Francis Group. London.

Haude, R., Thomas, E. (1983): Ophiuren (Echinodermata) des hohen Oberdevons im nördlichen Rheinischen Schiefergebirge. – Paläont. Z., 57: 121–142.

Hess, H. (1962): Mikropaläontologische Untersuchungen an Ophiuren. – Eclogae geol. Helv., 55(2): 595–656.

Hotchkiss, F. H. C., Prokop, R. J., Petr, V. (1999a): Isolated skeletal ossicles of a new brittlestar of the Family Cheiropterasteridae Spencer, 1934 (Echinodermata: Ophiuroidea) in the Lower Devonian of Bohemia (Czech Republic). – J. Czech Geol. Soc., 44(1–2): 189–193.

Hotchkiss, F. H. C., Prokop, R. J., Petr, V. (1999b): Isolated vertebrae of brittlestars of the Family Klasmuridae Spencer, 1925 (Echinodermata: Ophiuroidea) in the Devonian of Bohemia (Czech Republic). – J. Czech Geol. Soc., 44(3–4): 329–333.

Irimura, S., Fujita, T. (2003): Interspecific variation of vertebral morphology in the Ophiuroidea, p. 161–167. – *In*: J.-P. Feral, B. David (eds): Echinoderm research 2001, 337 pp. A.A. Balkema, Lisse.

Kutscher, M., Jagt, J. W. M. (2000): Early Maastrichtian ophiuroids from Rügen (northeast Germany) and M*n (Denmark), p. 45–103. – *In*: Jagt, J. W. M. (2000): Late Cretaceous-Early Paleogene echinoderms of the K/T boundary in the southeast Netherlands and northeast Belgium, Part 3. Ophiuroids; with a chapter by M. Kutscher and J. W. M. Jagt. – Scr. Geol. (Leiden), 121: 1–179.

LeClair, E. E. (1995): Microstructural roughness of skeletal calcite in ophiuroid vertebral ossicles: evidence of wear? – Tissue & Cell, 27(5): 539–543.

LeClair, E. E. (1996): Arm joint articulations in the ophiuran brittlestars (Echinodermata: Ophiuroidea): a morphometric analysis of ontogenetic, serial, and interspecific variation. – J. Zool. (London), 240: 245–275.

LeClair, E. E., LaBarbera, M. C. (1997): An *in vivo* comparative study of intersegmental flexibility in the ophiuroid arm. – Biol. Bull., 193: 77–89.

Lehmann, W. M. (1957): Die Asterozoen in den Dachschiefern des rheinischen Unterdevons. – Abh. Hess. Landesamt. Bodenforsch., 21: 1–160 + 55 pls.

Lewis, D. N. (1993): Catalogue of the type and figured specimens of fossil Asteroidea and Ophiuroidea in The Natural History Museum. – Bull. nat. Hist. Mus. (Geol.), 49(1): 47–80.

Litvinova, N. M. (1994): The life forms of Ophiuroidea (based on morphological structures of their arms), p. 449–454. – *In*: B. David, A. Guille, J.-P. Féral, M. Roux (eds): Echinoderms through time, 940 pp. A.A. Balkema, Rotterdam.

Lyman, T. (1882): Report on the Ophiuroidea dredged by H.M.S. Challenger during the years 1873–76. – Challenger Rep. Zool., 5: 1–386, 48 pls.

MacBride, E. W. (1906): Echinodermata, p. 425–623. – *In*: S. F. Harmer and A. E. Shipley (eds): The Cambridge Natural History, Vol. I. MacMillan & Co., NY.

Matsumoto, H. (1917): A monograph of Japanese Ophiuroidea, arranged according to a new classification. – J. Coll. Sci., Tokyo, 38(2): 1–408 + plates 1–7.

May, A. (2003): Die Fossilführung des Mitteldevons im Raum Attendorn-Ole (West-Sauerland; Rechtsrheinisches Schiefergebirge). – Geol. Paläont. Westfalen, 60: 47–79.

Mortensen, Th. (1913): On the alleged primitive ophiuroid *Ophioteresis elegans* Bell; with description of a new species of *Ophiothela*. – Mindeskr. f. J. Steenstrup, X, Bianco Lunos Bogtrykkeri (Kobenhaven), 10: 1–18, 2 pls.

Mortensen, Th. (1933): Studies of Indo-Pacific Euryalids. – Vidensk. Medd. fra Dansk naturh. Foren. (Kobenhavn), 96(2): 1–75 + plates 1–5

Müller, A. H. (1950): Die Ophiuroideenreste aus dem Mucronatensenon von Rügen. – Geologica (Geol. Instit. Univ. Berlin, Greifswald, Halle, Rostock), 5: 1–35 + 3 pls.

Owen, H. G. (1965): The British Palaeozoic Asterozoa: Table of Contents, Supplement and Index. – Palaeontogr. Soc., for 1964, pp. i vii, 541–583, text Text-fig. 349, Table 2.

Smith, A. B. (1985): Echinodermata, p. 153–190. – *In*: J. W. Murray (ed.): Atlas of invertebrate macrofossils. – The Palaeontological Association. Longman; Harlow, Essex.

Smith, A. B., Paterson, G. L. J., Lafay, B. (1995): Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. – Zool. J. Linn. Soc., 114: 213–243.

Spencer, W. K. (1925): A monograph of the British Palaeozoic Asterozoa, Pt. VI, p. 237–324, pls. XVIII–XXII, text-figs 172–212. – Palaeontogr. Soc., for 1922.

Spencer, W. K. (1927): A monograph of the British Palaeozoic Asterozoa, Pt. VII, pp. 325–388, pls XXIII–XXIV, text-figs 213–248. Palaeontogr. Soc., for 1925.

Spencer, W. K. (1950): Asterozoa and the study of Palaeozoic faunas. – Geol. Mag., 87(6): 393–408.

Spencer, W. K., Wright, C. W. (1966): Asterozoans, p. *U4-U*107, text figs 1–89. – *In*: R. C. Moore (ed.): Treatise on Invertebrate Paleontology, Part U, Echinodermata 3, Lawrence, Kansas, University of Kansas Press and Geological Society of America.

Štorc, R. (2004): The Late Cretaceous brittle star *Ophiosmilax*? *alternatus* from Europe and northern Africa. – Geobios (Lyon), 37: 395–401.

Stürmer, W. (1968): Einige Beobachtungen an devonischen Fossilien mit Röntgenstrahlen. – Natur u. Mus., 98(10): 413–417.

Stürtz, B. (1886): Beitrag zur Kenntnis paläozoischer Seesterne. – Palaeontographica, 32: 75–98, pls 8–14.

Stürtz, B. (1890): Neuer Beitrag zur Kenntniss paläozoischer Seesterne. – Palaeontographica, 36: 203–247, pls 26–31.

Stürtz, B. (1893): Ueber versteinerte und lebende Seesterne. – Verh. naturhist. Ver. Rheinl. Westf, 50: 1–92 + plate 1.

Südkamp, W. H. (1994): Echinodermen aus dem Hunsrückschiefer. Teil 1: Flachtiere und Sterntiere. – Fossilien, 11(4): 244–252.

Ubaghs, G. (1953): Classe des Stelleroidea. – *In*: J. Piveteau (ed.): Traité de Paléontologie, vol. III, Les formes ultimes d'invertébrés morphologie et évolution. Onychophores. Arthropodes. Echinodermes. Stomocordés, p. 774–842, figs 1–64. Paris: Masson et Cie.

Weller, J. M. (1930): Ophiuroid remains of Pennsylvanian age. – J. Paleont., 4(1): 1–13.

Withers, R. B., Keble, R. A. (1934): The Palaeozoic brittle stars of Victoria. – Proc. roy. Soc. Victoria, N. S., 47(1): 196–212.

Postscript

Articulated specimens of an eospondylid ophiuroid with eyelet-type vertebrae have now been found in the Middle Devonian Arkona Shale, southwestern Ontario, Canada (collected by Michael Topor and John Topor, Hamtramck, Michigan; identified by FHCH from supplied images). Andreas Kroh included the families Eospondylidae and Onychasteridae in a table summarizing arm branching in the order Euryalida (Kroh, A. 2003. First record of gorgonocephalid ophiuroids from the Middle Miocene of the central Paratethys. Cainozoic Research 2:143-155). He listed *Eospondylus* and *Onychaster* as having simple unbranched arms, but listed *Kentrospondylus* as having branched arms. This latter is a misunderstanding because *Kentrospondylus* has ten simple arms that form ten mouth corners.