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First record of gorgonocephalid ophiuroids (Echinodermata) from the Middle Miocene of the Central Paratethys

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The shallow-water (sublittoral) coarse sandy sediments of the Hartl Formation (Langhian, Middle Miocene) which outcrop north of Eisenstadt (Burgenland, Austria) have yielded abundant disarticulated ophiuroid material, mostly large streptospondylous vertebrae. These are here assigned to the Gorgonocephalidae, on the basis of arm branching and the presence of an open ventral groove along the entire arm. Oral plates found associated with these vertebrae are described as a new species, *Astrodendrum*? *pilleri* n. sp. The fossil record of gorgonocephalid ophiuroids is very poor; the present material represents the first unquestionable record of this group from the Central Paratethys, and at that, the stratigraphically oldest. To date, only few ophiuroids have been recorded from Neogene strata of the Paratethys; these are listed in an Appendix.

KEY WORDS: Echinodermata, Ophiuroidea, Gorgonocephalidae, Miocene, Austria, Central Paratethys, new species.

Introduction

The Gorgonocephalidae have a very poor fossil record, which is rather surprising since extant representatives are found in a large variety of habitats, ranging from the subpolar to tropical climate zones (Döderlein, 1927; Mortensen, 1933; Baker, 1980; Hendler *et al.*, 1995). In addition, they may be common in shallow-water habitats (Baker, 1980; Hendler *et al.*, 1995) and generally possess numerous large and relatively sturdy ossicles.

The first, and only, unquestionable report of fossil gorgonocephalids thus far is that by Pomel (1885-1887), who described dissociated vertebrae from the 'Sahélien' (= Upper Miocene-Pliocene; see Durand-Delga, 1962) of Algeria, under the name of *Astrophyton saheliensis* Pomel, 1885. One of his illustrations (Pomel, 1885-1887, pl. D II, fig. 7) clearly shows a branching vertebra. Subsequent authors have often overlooked this record; a rare exception is Sieverts-Doreck's (1954) compilation. Another report of fossil gorgonocephalids is found in Spencer & Wright (1966, p. U91), who noted, 'An undescribed genus occurs in the Oligocene of New Zealand (Fell, *in litt.*).' Assessment of this statement is difficult, in the absence of illustrations and/or description of the material both in Spencer & Wright (1966) and, as far as I know, in subsequent literature sources. The material on which this record is based is currently housed at the Institute of Geological and Nuclear Sciences (Lower Hutt, New Zealand), labelled 'Ophiurid vertebral ossicle – *Gorgonocephalus* [*sic*]'; it is from the Caversham Sandstone (Lower Miocene) at Burnside near Dunedin (IGNS, locality number GS 1890) (pers. comm. J. Simes, February 2003). On the basis of photographs I received of these specimens (three 'non-branching' vertebrae), I am unable to either confirm or dismiss Fell's identification. The third record pertains to a small collection of dissociated gorgonocephalid vertebrae from Pliocene strata penetrated in borehole IJsselmuiden-1 (eastern Netherlands; see Kroh & Jagt, in press).

Apart from these three records that explicitly refer to gorgonocephalids, there are several reports of euryalid-type vertebrae from deposits of Cainozoic age (*e.g.*, Vadász, 1915 – Miocene, Hungary; Valette, 1928 – Burdigalian (Miocene), France, misidentified as brachials of the comatulid crinoid '*Antedon' rhodanicus*; and Donovan & Paul, 1998 - Upper Pliocene, Jamaica). However, it is not clear whether any of these records do indeed represent gorgonocephalids or are merely similar vertebrae of other ophiuroid groups with streptospondylous vertebral type (*e.g.*, Hemieuryalidae, Euryalidae, Ophiobyrsinae, Asteroschematidae and others).

The fossil record of euryalids, another extant family with branching, streptospondylous vertebral type, is similarly poor. An early report of *Euryale*? *liasica* Quenstedt, 1876 has subsequently been shown to consist of resting traces of indeterminate brittle stars with unbranching arms, with the impression of branched arms having been produced by multiple traces of moving arm tips (Seilacher, 1953). Records of *Trichaster*? *ornatus* (Rasmussen, 1950) and *Trichaster*? sp. from the Campanian and Maastrichtian of the SE Netherlands and NE Belgium (Jagt, 2000, pp. 8, 9; pl. 1, figs 5-10) and from the Maastrichtian of Rügen (Germany) and Møn (Denmark; see Jagt & Kutscher, 1998; Kutscher & Jagt, 2000, pp. 51-53; pl. 32, figs 1-7) comprise dissociated streptospondylous vertebrae with an open ventral groove, originally attributed with a query to *Asteronyx* by Rasmussen (1950, 1972). Although superficially similar to vertebrae of the genus *Trichaster*, the attribution of these fossil ossicles to the Euryalidae and in particular to this genus is questionable. In all extant euryalids, the ventral furrow is closed by a 'bridge-like' structure in distal arm portions (Mortensen, 1933, pp. 3, 4). In many Recent taxa only a few proximal vertebrae have open grooves, *e.g.* in *Asteroceras pergamenum* Lyman, 1879 only the first and second vertebrae. In addition, neither Jagt (2000) nor Kutscher & Jagt (2000) recorded any branching vertebrae, while extant *Trichaster* have arms branching up to ten times.

The post-Eocene ophiuroid record in the Paratethys appears to be extremely poor, despite the fact that the first papers on echinoderm fossils from this area were published more than 150 years ago. This may be an artifact, however, since earlier workers preferentially considered more or less complete and well-preserved specimens. In fact, disarticulated skeletal material was commonly ignored. Recent examination of bulk samples from Neogene strata in Austria has revealed that ophiuroid ossicles are in fact a common element in echinoderm palaeocommunities (Kroh, research in progress). The Appendix lists all post-Eocene ophiuroids from the Paratethys; most taxa are in urgent need of revision, having been based mostly on single specimens only or with little extant material for comparison at hand.

The present paper is the third in a series of studies of Neogene echinoderms. Earlier papers were devoted to echinoderm faunas from the 'Retz Sands' (Lower Miocene), with emphasis on the palaeoecology of echinoid-bearing levels and on more global aspects, such as echinoid migration (Kroh & Harzhauser, 1999), and from the Lower Badenian (Langhian) as represented in the Molasse Zone and the northern Vienna Basin (Kroh, 2003).

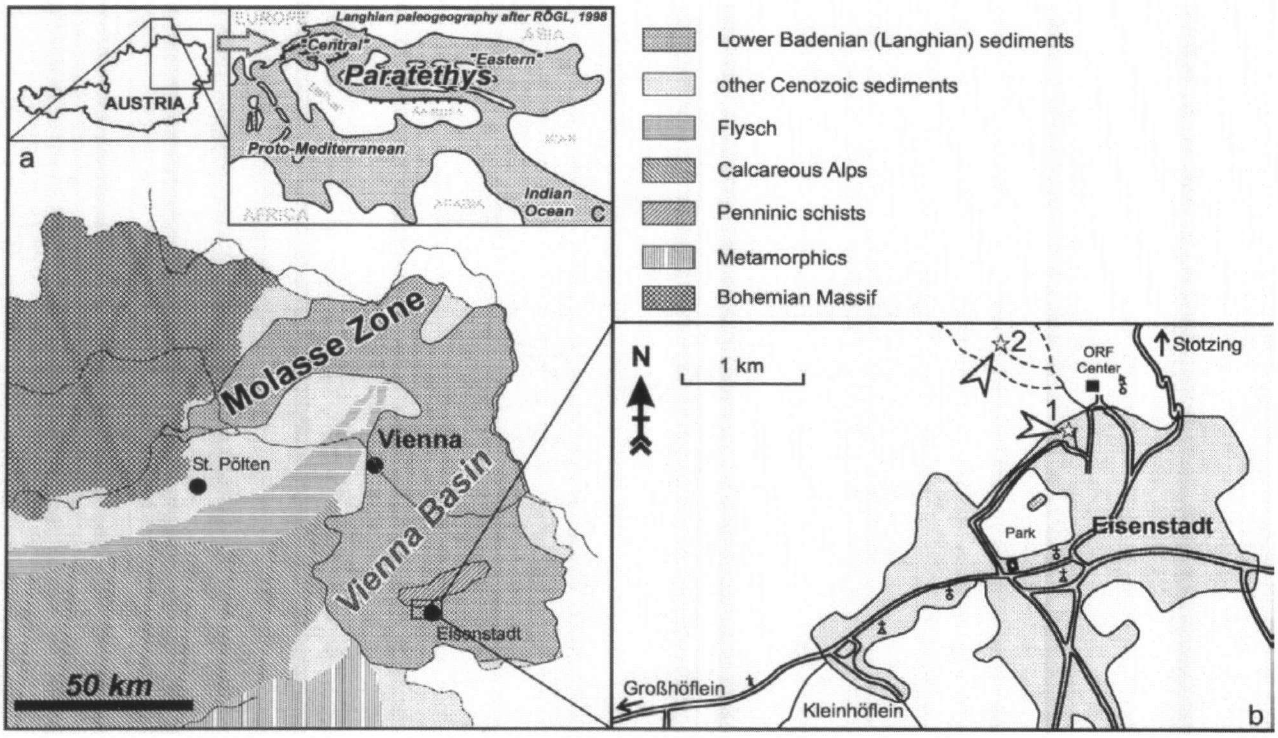

Figure 1. Geographic and stratigraphic position of localities mentioned in the text. A: distribution of Lower Badenian (Langhian) sediments in Austria (slightly modified from Mandic *et al.*, 2002 [courtesy of O. Mandic and F. Rögl]; B: location of sections studied, 1 - Hartl-Lucke; 2 – Johannesgrotte (modified from Kroh *et al.*, in press); C: Langhian palaeogeography after Rögl (1998).

Study area

Material studied comes from the type section 'Hartl-Lucke' of the Hartl Formation, north of Eisenstadt in Burgenland/Austria (ÖK 50 map, sheet 77) (Figure 1). Gorgonocephalid vertebrae are found throughout the section, but are particularly abundant in the basal part. For detailed sections, lithological descriptions, microfacies and sedimentological data, as well as a discussion of regional geology reference is made to Kroh *et al.* (in press).

The study area belongs to the Eisenstadt-Sopron Basin, a small, strongly asymmetrical subbasin of the Vienna Basin complex, which is part of the Central Paratethys, displaying a more or less trigonal size of about 20 x 20 km in width (Piller & Vávra, 1991). In the north, it is bounded by the NE-SW trending Leitha Mountains and the associated SE-dipping Eisenstadt fault (Fodor, 1992), in the east by the N-S trending Rust faults, and the Rust-Fertörakos hills, which separate the basin from the Danube Basin. The southern margin of the Eisenstadt-Sopron is defined by the crystalline ridge of the Rosalia Mountains, which separates it from the Styrian Basin complex.

Strata of the Hartl Formation have recently been dated on foraminiferal evidence as Early Badenian (Late Langhian, Middle Miocene) by Kroh *et al.* (in press).

Material and methods

Field work was carried out in the Spring/Summer of 2001 and in the Spring of 2002. In the field, both unconsolidated and consolidated sediments were sampled; of the former 250 g samples were first dried and then disintegrated using H_2O_2. Subsequently, the samples were washed using standard sieve-sets (0.063 mm, 0.125 mm, 0.25 mm, 0.5 mm, 1 mm, 2 mm, 4 mm, and 8 mm). Additional bulk samples of about 2.5 kg each were taken to investigate the macrofauna. These were washed on a 2 mm sieve and residues were handpicked under a stereo microscope. For quantitative component analysis, thin sections of the consolidated sediments were prepared. Unconsolidated sediments were embedded in resin and also thin-sectioned to produce comparable results. Both the washed samples and the thin sections were subjected to quantitative analysis in order to assess the distribution of biogenic components within the sections. Detailed results of sieve, carbonate and thin section analysis will be presented elsewhere (Kroh *et al.*, in press). To split the gorgonocephalid vertebrae into size classes, a set of sieves from 1.0 to 5.0 mm size in 0.5 mm gradation were used. These sieves were prepared by drilling closely spaced holes into polystyrol boxes, with the size of the holes controlled with an electronic caliper, not varying more than +/- 0.05 mm. Experiments with standard analysis sieve sets had earlier shown to yield unreliable results due to the rectangular shape of the holes. The round holes of the sieves ensured splitting in equal size classes. Both bulk samples and picked ophiuroid material are deposited at the Geologisch-Paläontologische Abteilung of the Naturhistorisches Museum Wien (NHMW); the thin sections at the Institute für Geologie und Paläontologie of the Universität Graz.

A number of extant gorgonocephalid species housed in the collections of the United States National Museum (USNM) were examined for comparison with fossil specimens, thanks to the courtesy of Cynthia Ahearn, *viz. Astrocaneum spinosum* (USNM E34453), *Astrocladus dofleini* (USNM 15767), *Astroboa nuda* (USNM E1470), *Astrodendrum sagaminum* (USNM 25665), *Astroglymma sculptum* (USNM E1476), *Astrochalcis micropus* (USNM E1463), and *Astrophyton muricatum* (USNM E44551). A small piece of the middle portion of an arm was removed from each specimen, the soft tissue then dissolved using sodium hypochlorite (30% solution). After a period in clean water, the ossicles were air dried and examined under a light microscope. Specimens used for SEM analysis were cleaned with hydrogen peroxide and an ultrasonic bath, and then mounted on stubs and gold coated.

Higher-order systematics follow Smith *et al.* (1995), terminology of oral plates is after Murakami (1963) and that of vertebrae follows Irimura & Fujita (2003).

Systematic description

Class Ophiuroidea Gray, 1840
Subclass Ophiuridea Gray, 1840
Order Euryalina Lamarck, 1816
Family Gorgonocephalidae Ljungman, 1867
Genus *Astrodendrum* Döderlein, 1911

Astrodendrum? *pilleri* n. sp.

Figures 2, 3

Types – Holotype, an oral plate, is NHMW 2003z0010/0002; paratype, another oral plate, is NHMW 2003z0010/0003.

Locus typicus – Eisenstadt, Burgenland (Austria).

Stratum typicum – Hartl Formation, Lower Badenian (Langhian), Middle Miocene.

Sample	Fraction (ø in mm)	> 5.0	> 4.5	> 4.0	> 3.5	> 3.0	> 2.5	> 2.0	> 1.5	> 1.0	Sum
Hartl1	"normal" vertebrae	3	4	24	34	123	205	193	27	3	616
	branching vertebrae (sym.)	1	2	4	5	2	2	4	-	-	20
	branching vertebrae (asym.)	-	-	2	7	16	17	19	2	-	63
	ratio (nV:bV)	1:3	1:2	1:4	1:2.8	1:6.9	1:10.8	1:8.4	1:13.5	-	-
	overall ratio	1:3.3				1:7.9			1:13.5	-	1:7.4

Table 1. Size distribution of dissociated gorgonocephalid vertebrae from sample Hartl-Lucke.

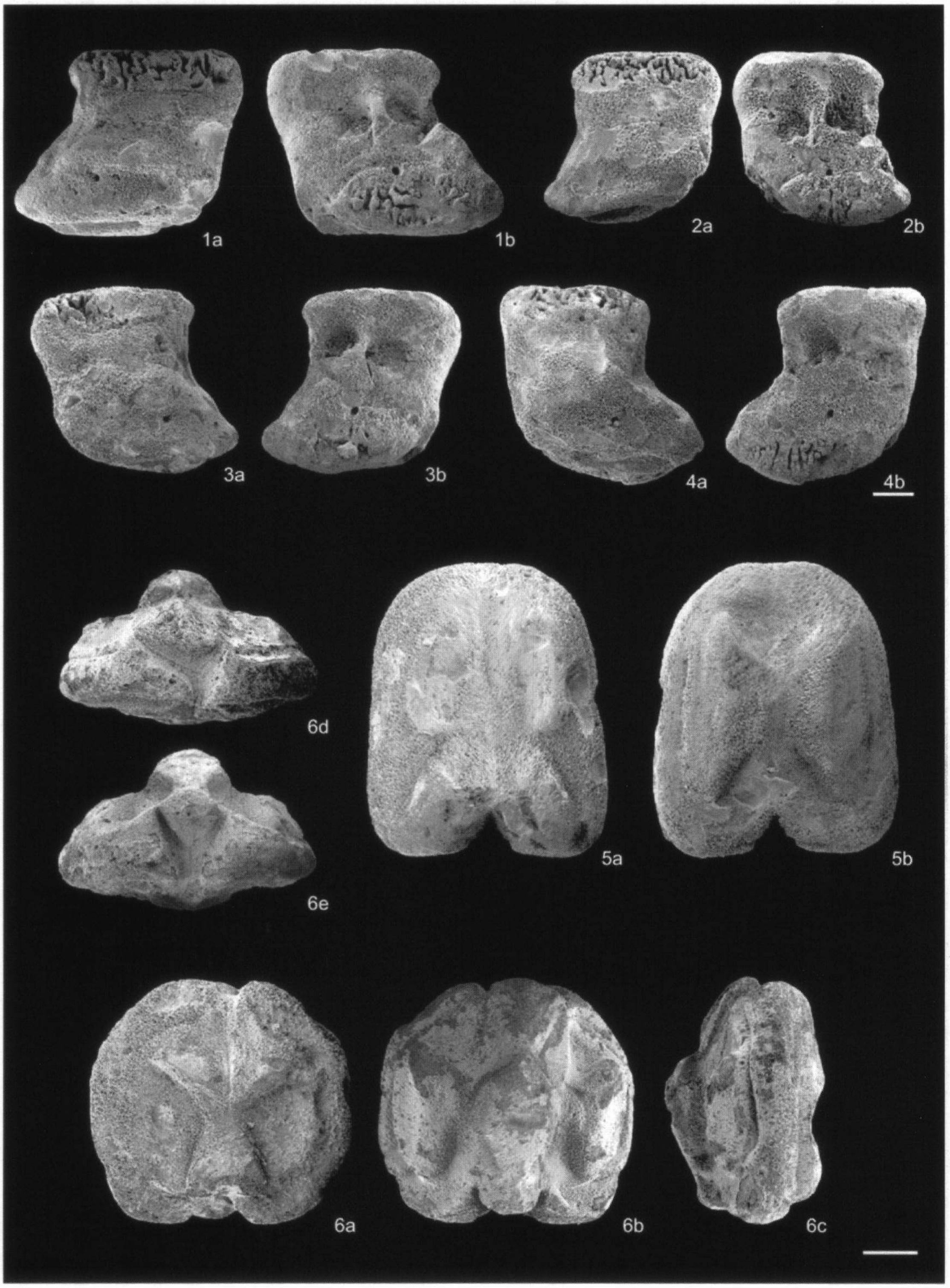

Figure 2. *Astrodendrum*? *pilleri* n. sp.; Hartl-Lucke, Eisenstadt (Burgenland, Austria), basal Hartl Formation (Lower Badenian, Langhian, Middle Miocene). Scale bars equal 1 mm.

1-4 oral plates, in abradial and adradial views, respectively; 1 - NHMW 2003z0010/0001;

2 - NHMW 2003z0010/0002, **holotype**;

3 - NHMW 2003z0010/0003, **paratype**; 4 - NHMW 2003z0010/0004.

5 first vertebra, in proximal and distal views, respectively (NHMW 2003z0010/0005).

6 bifurcating vertebra; in proximal, distal and lateral (distal to left), aboral and oral views, respectively (NHMW 2003z0010/0006).

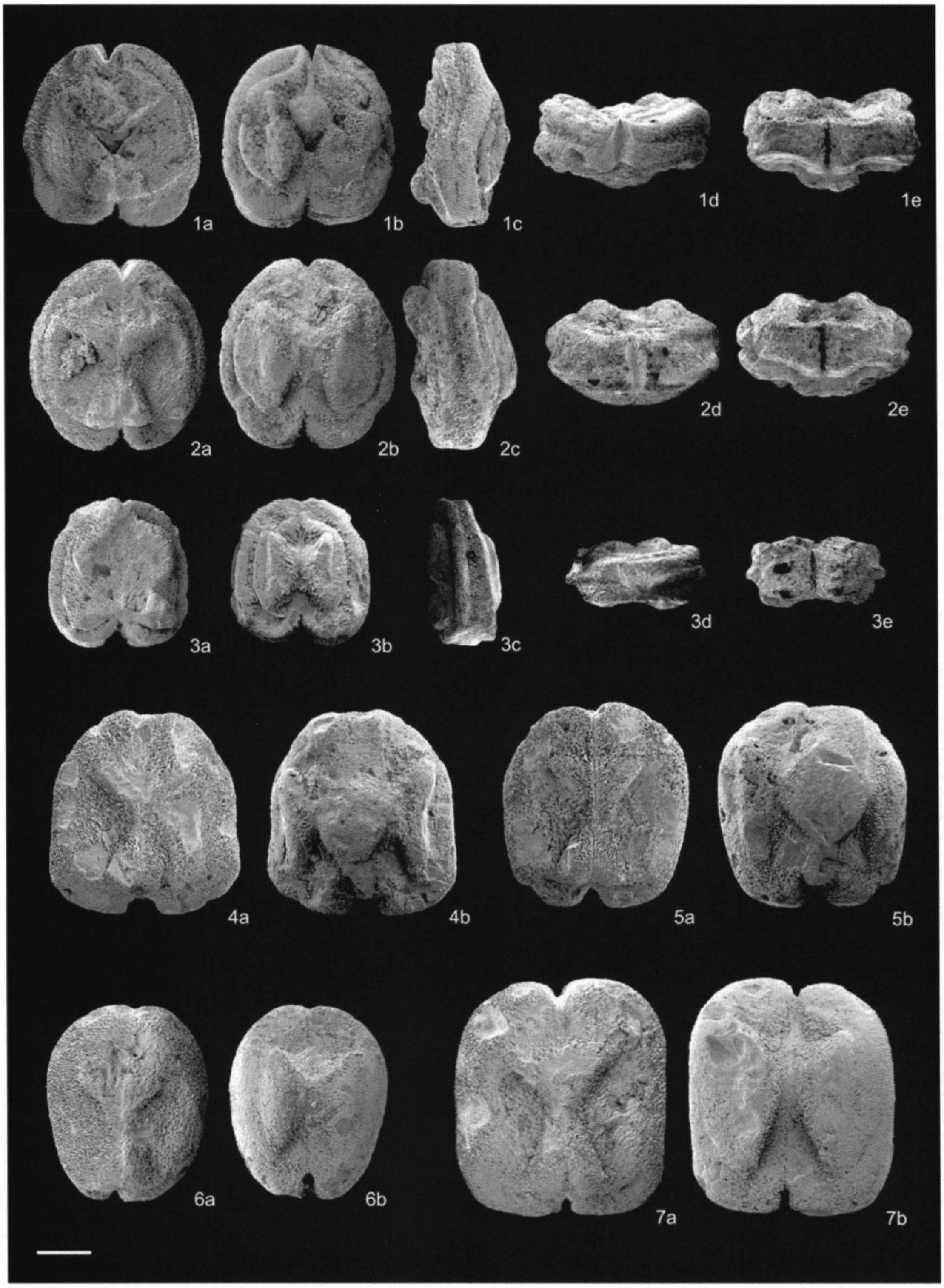

Figure 3. *Astrodendrum*? *pilleri* n. sp.; Hartl-Lucke, Eisenstadt (Burgenland, Austria), basal Hartl Formation (Lower Badenian, Langhian, Middle Miocene). Scale bars equal 1 mm.

1 medial vertebra, in proximal, distal, lateral (distal to left), aboral and oral views, respectively (NHMW 2003z0010/0007);
2 medial vertebra, in proximal, distal, lateral (distal to left), aboral and oral views, respectively (NHMW 2003z0010/0008);
3 first vertebra, in proximal, distal, lateral (distal to left), aboral and oral views, respectively (NHMW 2003z0010/0009);
4 symmetrically bifurcating proximal vertebra, in proximal and distal views, respectively (NHMW 2003z0010/0010);
5 asymmetrically bifurcating proximal vertebra, in proximal and distal views, respectively (NHMW 2003z0010/0011);
6 vertebra from just proximal of bifurcation, in proximal and distal views, respectively (NHMW 2003z0010/00012);
7 proximal vertebra, in proximal and distal views, respectively (NHMW 2003z0010/00013).

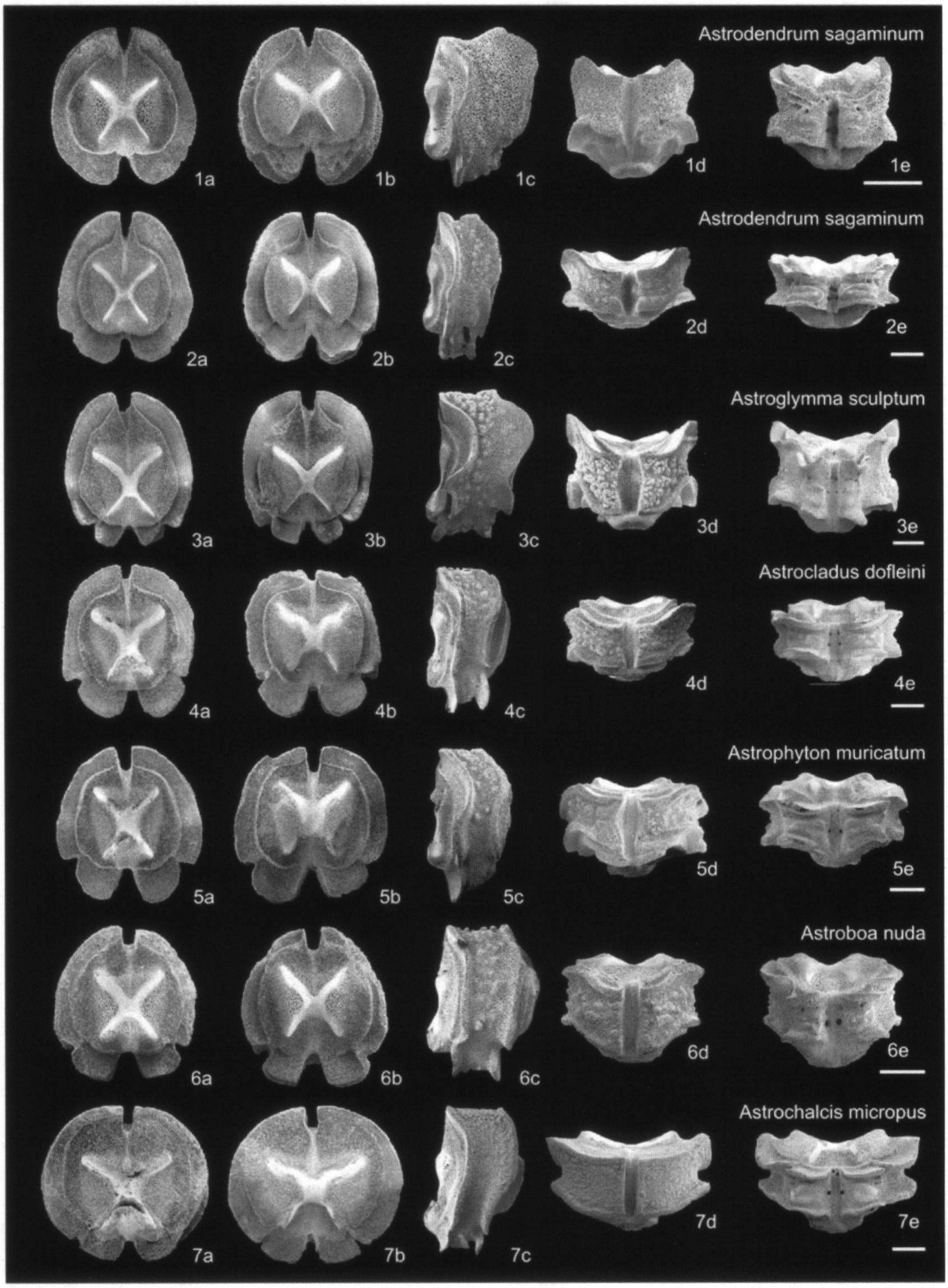

Figure 4. Proximal and medial vertebrae of extant gorgonocephalids, all in proximal, distal, lateral (distal to left), aboral and oral views, respectively. Scale bars equal 1 mm.

1 *Astrodendrum sagaminum* (Döderlein, 1902), USNM 25665, from medial portion of arm;
2 *A. sagaminum*, USNM 25665, from proximal portion of arm;
3 *Astroglymma sculptum* (Döderlein, 1896), USNM E1476, from medial portion of arm;
4 *Astrocladus dofleini* Döderlein, 1911, USNM 15767, from proximal portion of arm;
5 *Astrophyton muricatum* (Lamarck, 1816), USNM E44551, from medial portion of arm;
6 *Astroboa nuda* (Lyman, 1874), USNM E1470, from medial portion of arm;
7 *Astrochalcis micropus* Mortensen, 1912, USNM E1463, from medial portion of arm.

		branched					No. of vertebrae between branchings**				Geographical Distribution								Climatic Distributio					
Genus	unbranched	single	multiple	Type of branching (asym/sym)	No. of branchings (disc diameter)	Maximum size (disc ø in mm)	proximal (before 1st branching)	middle	distal	Depth range	Eastern Pacific	Carribean	Eastern Atlantic	Mediterranean	Western Indian	Indopacific	Artic + Bering	Antarctic	Northern Polar	Northern Subpolar	Northern Cool	Northern Warm	Tropic	Southern Warm
Eospondylidae (Early Devonian)																								
Eospondylus	✓																							
Kentrospondylus		✓																						
Onychasteridae (Early Carboniferous)																								
Onychaster	✓																							
Asteronychidae (Late Cretaceous - recent)																								
Asteronyx	✓									109-2963	✓	✓	✓		✓	✓					▨	◐	■	◐
Astrodia	✓					17				510-3720	✓	✓	✓			✓						◐	■	◐
Asteroschematidae (recent)																								
Asteroschema	✓					14				57-1747	✓	✓	✓		✓	✓					▨	▨	■	◐
Asterobrachion	✓					22				15-550						✓								◐
Astrocharis	✓									522-1089						✓						◐	■	
Astrocolex	✓																							
Ophiocreas	✓					28				146-2000						✓						◐	■	◐
Ophiuropsis	✓					5				108-180						✓							■	
Gorgonocephalidae (Oligocene - recent)																								
Asteroporpa	✓					23				37-508		✓				✓						◐	■	◐
Asteroporpa (Astromoa	✓					10				71-301						✓							■	◐
Astracme			✓							146-527		✓				✓							■	
Astroboa			✓	sym-asym*	25-30 (30 mm)	92	2-4	5-8 (3-9)	6-10	0-256					✓	✓						◐	■	◐
Astrocaneum			✓	sym	25 (30 mm)	64	6	7-11	14-16	17	✓	✓										◐	■	
Astrochalcis			✓		13 (17 mm)	75	3	4-6	8-9	13-180						✓							■	
Astrochele	✓					12				366-2933							✓				▨			
Astrochlamys	✓					14				200-567								✓						
Astrocladus			✓	sym-asym*	20-25 (30 mm) - 38 (63 mm)	93	2-4	6-9	7-13	2-600					✓	✓					▨	◐	■	◐
Astroclon			✓	sym-asym*	>6 (55 mm)	65	23-35			200-457						✓						◐	■	◐
Astrocnida			✓			30	40-100			5-220		✓											■	
Astrocrius	✓					35				366-730						✓					▨	▨	■	◐
Astrocyclus			✓		13 (25 mm) - 20 (30 mm)	38	5-6	6-13	15-41	5-229		✓											■	
Astrodendrum			✓	sym-asym*	-20 (37 mm)	99	5	5-11	13-15	0-926	✓				✓	✓						◐	■	◐
Astrodictyum			✓	sym			5	7-9		?	✓												■	◐
Astroglymna			✓	sym-asym*	20 (30 mm) - 24 (48 mm)	65	3-5	6-9	9-13	73-300			✓		✓	✓							■	
Astrogomphus	✓					10				146-1089		✓											■	
Astrogordius			✓		13-15 (30 mm)			13-17	20+	36		✓											■	
Astrohamma	✓					8				150-457								✓						
Astrohelix	✓					17				190-275						✓						◐	■	
Astrophyton			✓	sym-asym*	12 (10 mm) - 32 (58 mm)	52	4-5	3-7	8-10	2-70 (508?)		✓	✓										■	
Astroplegma			✓		26		4	5-6		188						✓							■	
Astrosierra			✓	sym	7-10	37	10-23	8-11		18-457						✓								■
Astrospartus			✓		20 (30 mm) - 30 (48 mm)	63	6-7	6-13	15+	50				✓								■		
Astrostephanus	✓					22				135-520						✓							■	
Astrothamnus	✓					21				296-622						✓						◐	■	
Astrothorax	✓					28				73-998					✓	✓					◐	◐	■	◐
Astrothrombus	✓					14				37-751						✓						◐	■	◐
Astrotoma	✓					36				4-1183						✓		✓					■	
Astrozona	✓					8				1089						✓							■	
Conocladus			✓	sym	8 (18 mm) - 10 (55 mm)	55	4-14	11-19		6-240						✓								◐
Gorgonocephalus			✓	sym	10-12 (30 mm) - 15 (70 mm)	83	4-8	14-29	40-120	15-1850		✓	✓	✓	✓	✓	✓	✓			▨	▨	■	◐
Ophiocrene																								
Schizostella		✓		sym	1 (rarely 2; 4 mm)	4	6	11-34	16-24	12-46		✓											■	
Euryalidae (recent)																								
Asteromorpha	✓									200-300					✓	✓							■	◐
Asterostegus																								
Astroceras	✓					14				60-1185						✓						◐	■	◐
Euryale			✓		14 (16 mm)	49	5-6			0-290						✓						◐	■	◐
Sthenocephalus			✓	sym	7-9	50	8-33	16-24 (10-34)	30-35	36-714						✓							■	
Trichaster			✓		3-4	37	34-66	14-16	75-100	106-146						✓					▨	◐	■	◐

Sources: Lyman, 1865, 1874, 1875, 1877, 1878; Studer, 1881, 1884; Döderlein, 1902, 1911, 1927, 1930; Boone, 1933; Mortensen, 1933; Spencer & Wright, 1966; Baker, 1980

* proximal 1st to 2nd branching symmetrical, others (distal) asymmetrical

** values were obtained by counting the tube feet (literature data were corrected for oral plates and branching vertebrae)

Table 2. Arm branching in the suborder Euryalina, compiled from literature sources.

Diagnosis – A gorgonocephalid with grossly rhomboid oral plate with a concave dorsal margin and a large, undivided, vertically elongated adradial muscular area, shaped like a spoon with bent handle.

Derivatio nominis – Named after my friend and colleague Werner E. Piller, head of the Institut für Geologie und Paläontologie at the Karl-Franzens-University Graz.

Material studied – Ten oral plates (NHMW 2003z0010/0001-4, 14-15) and ~ 1,000 vertebrae (NHMW 2003z0010/0005-13, 16-18; see Table 1), all originating from bulk samples taken from the basal Hartl Formation at the Hartl-Lucke section, Eisenstadt (Burgenland, Austria). Although this cannot be demonstrated beyond doubt, oral plates and vertebrae are here considered to be conspecific.

Taxonomic procedure Most fossil ophiuroid material is preserved in the form of dissociated ossicles. Although extant species usually are defined upon disc plating, oral frame structure and presence/absence of oral and dental papillae, provisional generic attributions of fossil brittlestars are possible (*e.g.*, Jagt, 2000). In fossil material, lateral arm plates have been shown to produce the most reliable results (Hess, 1962a, b, 1963, 1965, 1966, 1975a, b). In various papers, Hess also demonstrated that in most cases dissociated vertebrae could not be used, since similar types occur in different genera and families. Moreover, these ossicles exhibit a wide range of morphological variation along the arm. In gorgonocephalids, however, lateral arm plates are rather small and reduced; so far none have been recognised in the bulk samples available. This is probably related to the fact that most ossicles smaller than 2 mm in diameter are obscured by epitaxial cement, often beyond recognition.

In extant gorgonocephalid material borrowed from the United States National Museum (USNM), the variation in vertebral structure along the arm turns out to be less wide than in other ophiuroid groups. In addition, proximal and medial vertebrae in the specimens studied reveal marked differences in shape, size of oral fossae and ornament (Figure 4). For the new species, an oral plate is here designated holotype, since of this type of ossicle there is only one (morpho)type, whereas vertebral morphology changes along the arm. Besides, there is considerable variation in the shape of these plates amongst genera in the family Gorgonocephalidae (Murakami, 1963), which allows a provisional generic attribution of the fossils to be made. Matsumoto (1917) noted that oral plates are of considerable taxonomic importance in extant ophiuroids.

Description

'Normal' vertebrae — Vertebrae range in size from less than 1 to *c.* 5.5 mm in diameter, and show a characteristic hourglass-shaped streptospondylous articulation. In lateral view, most are relatively narrow; the lateral furrow between the proximal and distal insertion areas is rather narrow and no traces of ornament could be found in any ossicle. The aboral groove is V-shaped, the oral groove U- to V-shaped. Where preserved, oral fossae are large and not well differentiated from the remaining ossicles surface; a similar condition is found in vertebrae of extant *Astrodendrum*, while those of other genera exhibit well-differentiated oral fossae (see Figures 4.3-4.7). Proximal vertebrae (*e.g.* Figures 2.5, 3.4 and 3.7) are trapezoidal to rectangular in proximal/distal view; medial ones are more rounded in outline (*e.g.*, Figures 3.1, 3.2). Similar changes in the shape of vertebrae along the arm have been observed in extant material (see *e.g.*, Figures 4.1, 4.2). Vertebrae just distal of a branching vertebra are smaller horizontally and have a vertically elongated outline (see Figure 3.6). The first arm vertebrae (see Figures 2.5 and 3.3) could also be identified in the material studied; these occur in the size classes down to diameters of > 2.5 mm.

Branching vertebrae — Branching vertebrae are slightly wider than 'normal' ones, their proximal faces being closely similar, but the distal face has two inclined articulation surfaces. In the present material there are vertebrae that are symmetrical in distal view as well as asymmetrical ones in distal view. In larger (*i.e.*, from proximal arm portions) size classes there are mainly (near-)symmetrical branching vertebrae, whereas the smaller size classes predominantly yield the asymmetrical type (see Table 1).

Oral plates — Oral plates of *Astrodendrum*? *pilleri* n. sp. are grossly rhomboidal in outline, with a concave dorsal margin; however, the distinct notch in the dorsal margin present in many gorgonocephalids (*e.g.*, *Astrocladus coniferus* or *Astrothamnus bellator*; compare Murakami, 1963, pl. 3) is absent here. The abradial muscular area is barely visible, but appears to be small; the adradial area is undivided, large, vertically elongated and is shaped like a spoon with bent handle, the dorsal part being distinctly enlarged. Both ab- and adradial articulation areas are large and well developed. The arrangement of depressions for the first and second oral tentacles is very similar to that seen in oral plates of *Astrodendrum sagaminum*.

The oral plates consist of fused first and second ambulacrals (Hendler, 1978; Stewart, 2000), rather than of first adambulacral and second ambulacral as stated by Murakami (1963).

Discussion

The vertebrae studied clearly are assignable to the Gorgonocephalidae, as this is the only family to include forms with branching arms which have vertebrae with open ventral furrow both in proximal and distal arm positions. The family Euryalidae can definitely be excluded since there the ventral furrow is closed by a 'bridge-like' structure in all but the proximalmost vertebrae (Mortensen, 1933, pp. 3, 4). Additional evidence comes from the oral plates, which are very similar to those of extant gorgonocephalids (compare Murakami, 1963, pls 3, 4).

Generic placement of the present material is difficult. In shape, the oral plates compare well with those of extant *Astrodendrum sagaminum* (compare Murakami, 1963, pl. 3, figs 35, 36), differing only in the presence of an undivided adradial muscular area; this is divided in *A. sagaminum*. In overall shape, the vertebrae are similar in all gorgonocephalids. Nevertheless, examination of a range of extant species in the USNM collections indicates that there are distinct differences in ornament, shape of the aboral groove, size and shape of the oral fossae as well as lateral profile. In view of the fact that larger ossicles usually are better preserved than small ones in the fossil material available, a comparison between them and extant specimens cannot be but restricted to proximal and medial ossicles. In outline and size and shape of the oral fossae, the fossil species compares well with *Astrodendrum sagaminum* (Figure 4.2), and it is here tentatively referred to that genus. The lack of ornament would support this attribution, since *A. sagaminum* shows only very faint, easily obscured ornament, whereas in other genera (*e.g.*, *Astroglymma*, *Astrophyton* or *Astroboa*) ornament is rather coarse.

Assuming all vertebrae to be conspecific, as suggested by the presence of just one type of oral plate, it should also be possible to use the abundance of branching vertebrae to assign the material to an extant genus or group of genera. Of the thirty-four extant gorgonocephalid genera and subgenera, thirteen have simple, unbranched arms (*Asteroporpa* s. str., *Asteroporpa* (*Astromoana*), *Astrochele*, *Astrocrius*, *Astrogomphus*, *Astrohamma*, *Astrohelix*, *Astrostephanus*, *Astrothamnus*, *Astrothorax*, *Astrothrombus*, *Astrotoma* and *Astrozona*) and may thus be excluded from consideration. *Schizostella*, a diminutive genus from the Caribbean has arms which usually show only a single arm branching or, more rarely, two (Clark, 1952; Hendler *et al.*, 1995). The type of branching also provides additional information. In some genera, the arms branch mainly symmetrically (*Astrocaneum*, *Astrodictyum*, *Astrosierra*, *Conocladus* (syn. *Astroconus*) and *Gorgonocephalus*). In a group of genera related to *Astroboa* (*e.g.*, *Astrocladus*, *Astroglymna*, *Astrophyton*, *Astrodendrum*), the proximalmost (usually the first to third) bifurcations are symmetrical, the more distal ones are markedly asymmetrical. The number of vertebrae occurring before the first bifurcation and between bifurcation points in the proximal and medial arm portions also shows some systematic variation and could be useful in classification of fossil material. A summary of these features and additional data on size range, depth range, geographical and climatic distribution of the genera within the order Euryalina may be found in Table 2.

In order to analyse the number of branching vertebrae and their distribution along the arms, all fossil vertebrae from a bulk sample were sorted into nine size classes (using sieves with round holes ranging between 1.0 and 5.0 mm, in grades of 0.5 mm). Within the size classes, 'normal' vertebrae, symmetrical and asymmetrical branching vertebrae were distinguished. The ratio between branching and 'normal' vertebrae was calculated; the resulting data matrix may be found in Table 1.

The distribution of symmetrical *vs* asymmetrical branching vertebrae in the different size classes suggests a branching type similar to that of the extant *Astroboa* group. Symmetrically branching vertebrae are found mainly in the coarse size classes, or proximal portions of arms, whereas the number of asymmetrically branching vertebrae increases in the smaller size ranges, or the distal portions of the arm. The same situation is found in extant gorgonocephalids related to *Astroboa* (*e.g.*, *Astrocladus*, *Astroclon*, *Astrodendrum*, *Astroglymna* and others; compare Table 2, column 5). The overall ratio between branching and 'normal' vertebrae in the present material is 1:7.3. In the different size classes this value is distinctly different. In the four size classes > 3.5 mm, the ratio is 1:3.3. In size classes between 2.0 and 3.0 mm, it rises to 1:7.9 and further to 1:13.5 in the size class >1.5 mm. Although the sediment of the bulk samples has clearly been sorted by currents, this has affected mainly the small fraction < 1 mm grain size, as indicated by a grain size analysis (Kroh, unpublished data). Moreover, sorting is unlikely to have affected the ratios between branching and 'normal' vertebrae, since these are similar in size and gross morphology. If the pattern resulting from the analysis to some extent represents the distribution of bifurcations along the arm and is not a sampling artefact, it also indicates that the material is assignable to the *Astroboa* group. The genera *Astroboa*, *Astrocladus*, *Astrodendrum*, *Astroglymna* and *Astrophyton* in particular show a closely comparable arm structure (compare Table 2, columns 8-10).

This result also fits well the current depth range, geographical and climatic distribution of the genera within the family Gorgonocephalidae. Close extant relatives of echinoderms from the Paratethys are usually found in the Atlantic Ocean (including the Caribbean Sea), the Mediterranean and the western Indian Ocean, whereas taxa currently restricted to the Indo-Pacific region only have rare fossil relatives in the Paratethys/Mediterranean region. The palaeoenvironmental interpretation of the Hartl Formation presented by Kroh *et al.* (in press) indicates a nearshore position and relatively shallow depositional depth for the strata that have yielded the new gorgonocephalid material. This does not contradict with the proposed classification and supports the exclusion of multibranched, deep-water taxa such as *Astracme*, *Astrochlamys* or *Astroclon*.

Implications for gorgonocephalid phylogeny

Döderlein (1927, p. 12) presented an *ad hoc* phylogeny, based on morphological features, of extant representatives of the group, with *Conocladus* as the basal form of nearly all extant gorgonocephalids. However, this genus is endemic to South Australian coastal waters (Baker, 1980, p. 73) and is probably highly derived. Döderlein considered the large number of vertebrae occurring before the first bifurcation in the genera *Astrocnida*, *Astroclon* and *Conocladus* to be a paedomorphic [*sic*] feature. The material from the Middle Miocene of central Europe discussed in the present paper is the oldest unquestionable record of gorgonocephalids from the fossil record and shows multiple branching and branching close to the disc to have occurred already in the Miocene. There is no fossil evidence to suggest that a low number of vertebrae before the first branching can really be considered as the ancestral stage. Since these animals are passive suspension feeders (Fricke, 1968; Macurda, 1976; Hendler, 1982; Wolfe, 1982), bifurcations in proximal arm portions are much better suited to increase the area available for feeding than bifurcations in the distal parts. Additionally, the mesh width of the feeding fan formed by the arms is smaller when there are numerous proximal bifurcations. Smaller mesh widths enable the animals to catch more and smaller prey than with larger widths.

Conclusions

The recognition of remains of multibranched gorgonocephalids in the fossil record is important since these animals are highly specialised suspension feeders and thus are useful in palaeoecological reconstructions. Extant species are often found in reef habitats or elevations on mud and sea grass flats, associated with gorgonians, stony corals, fire corals and sponges (Hendler *et al.*, 1995). They are nocturnal, ascend to an elevated perch at dusk and extend their feeding arms in a parabolic array in moderately strong water currents. The stomach content of *Astrophyton muricatum* (Lamarck, 1816) has been shown to consist mainly of small copepods (Davis, 1966; Fricke, 1968;

Wolfe, 1982).

In addition, it is important to have a sound fossil record of animal groups to allow calibration with the outcome of phylogenetic analyses. The fossil record of ophiuroids, and of euryalids in particular, is rather poor. Smith *et al.*. (1995, p. 227) stated that, '... the absence of Euryaline taxa in the earlier part of the Mesozoic is, however, very puzzling, since our analysis suggests that they should have a much longer fossil record'. In fact, the only fossil euryaline taxa listed in Smith *et al.* (1995) are those described by Rasmussen (1950, 1972), plus the cursory mention of gorgonocephalids by Fell (*in litt.*; see Spencer & Wright, 1966, p. U91). In the present paper, at least for one group of the Euryalina an unquestionable fossil record is documented. Hopefully, future studies will focus in more detail on euryaline vertebral ossicles and their confident assignment at the family level.

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Appendix

Post-Eocene ophiuroid taxa recorded from the Paratethys, arranged in alphabetical order. **Note:** Unless species have been reassigned in subsequent papers, generic attribution is that of the original publication.

Amphiura? *badensis* Küpper, 1954
  (Küpper, 1954, p. 163, pl. 15, figs 1, 2; Lower Badenian [Langhian], Baden, eastern Austria)
Amphiura? *gigantiformis* Küpper, 1954
  (Küpper, 1954, pp. 163, 164, pl. 14, figs 1-8; Badenian [Langhian–Serravallian], Mannersdorf, eastern Austria)
  (Kristan-Tollmann, 1964, p. 77; Badenian [Langhian–Serravallian], Müllendorf, eastern Austria)
  (Kristan-Tollmann, 1966, p. 132; same locality and stratigraphy)
Amphioplus? *kuehni* (Binder & Steininger, 1967)
  (Binder & Steininger, 1967, pp. 21-23, pl. 1, figs 1, 2, as *Amphiura*? *kühni*; Karpatian [Upper Burdigalian], Teiritzberg, northeast Austria)
  (Meyer, 2002, pp. 325-331, pl. 1, figs 1, 2; same locality and stratigraphy)
Asteronyx sp.
  (Küpper, 1954, p. 164, pl. 15, fig. 3a-e; Badenian [Langhian–Serravallian], Römerberg near Baden, eastern Austria)
Ephippiellum symmetricum Lomnicki, 1899
  (Lomnicki, 1899, pp. 224-227, fig. 3a-d; Badenian [Langhian–Serravallian], Wieliczka, Poland])
  (Szajnocha, 1899, pp. 387-389; Badenian [Langhian–Serravallian], Wieliczka, Poland])
  (Andrusov, 1899, pp. 248, 249; Miocene, Tschokra Limestone, Kertsch Peninsula; Miocene, marl with *Pecten denudatus*, Cap Tarchan])
  (Lomnicki, 1902, pp. 155-157)
Ophiura? *parviformis* Küpper, 1954
  (Küpper, 1954, pp. 161, 162, pl. 15, figs 4-14; Badenian [Langhian–Serravallian], Rauchstallbrunngraben near Baden, eastern Austria)
Ophiura? *vindobonensis* Küpper, 1954
  (Küpper, 1954, p. 162, pl. 14, figs 9-17; Badenian [Langhian–Serravallian], Römerberg near Baden, eastern Austria)
Pseudaspidura hungarica Kolosváry, 1941
  (Kolosváry, 1941, pp. 307, 308, figs 1-3 [not an ophiuroid at all?]; Oligocene, Kiscell Clay, Hungary
indeterminate ophiuroids
  (Vadász, 1915, pp. 93, 94, figs 4, 5; Middle Miocene; Mátraverebély and Kemence, northern Hungary; the specimen in fig. 5 is assignable to the Euryalae according to Sieverts-Doreck, 1954)
  (Valette, 1928, pp. 31, 32, figs 5.1a-e, 5.2a-e [described as brachials of '*Antedon' rhodanicus*]; Burdigalian, Angeles (Gard), France)
  (Kühn, 1952, p. 124; Eggenburgian [Lower Burdigalian] and Badenian [Langhian–Serravallian], Horn, Brunn and Rauchstallbrunngraben near Baden, northeast Austria)
  (Tollmann, 1955, table 1; Badenian [Langhian–Serravallian], Eisenstadt, Großhöflein and Müllendorf, eastern Austria)
  (Kristan-Tollmann, 1964, p. 79; Lower Badenian [Langhian], Eisenstadt, eastern Austria)
  (Kroh & Harzhauser, 1999, pp. 153, 154, pl. 4, figs 5-13; Upper Eggenburgian [Lower Burdigalian], Unternalb, northeast Austria)
ophiuroid trace fossils
  (Prakfalvi, 1992, figs 9, 10; Eggenburgian [Lower Burdigalian], Mátraszele, northern Hungary)
Asteriacites lumbricalis von Schlotheim, 1820 (interpreted as ophiuroid resting traces by Seilacher, 1953)
  (Heer, 1865, p. 440 as ‚Seesterne'; Muschelsandstein [Burdigalian], Reiden near Luzern, Switzerland)
  (Bachmann, 1868, p. 250 as ‚Abdrücke eines Seestern'; Muschelsandstein [Burdigalian], Reiden near Luzern, Switzerland)
  (Kaufmann, 1872, pp. 279, 281 as ‚Seesterne' and ‚*Astropecten helveticus*'; Burdigalian, Reiden, Switzerland)
  (Mayer, 1872, p. 489 as ‚*Astropecten helveticus* May.'; Muschelsandstein, Helvet II and III [Burdigalian], near Bern, Switzerland)
  (Seilacher, 1953, pp. 94-102; Molasse [Burdigalian], Switzerland)