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#### Evolutionary relationships among bullhead sharks (Chondrichthyes: Heterodontiformes)

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Key words:	Heterodontus, elasmobranch evolution, Paracestracionidae, morphology, bullhead sharks, Late Jurassic



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2 3 4	1	Evolutionary relationships among bullhead sharks (Chondrichthyes:
5 6 7	2	Heterodontiformes)
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10 11	4	by TIFFANY S. SLATER <sup>1,2*</sup> , KATE ASHBROOK <sup>1</sup> , and JÜRGEN KRIWET <sup>3</sup>
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31 32	13	
33 34	14	*Corresponding author
35 36 37	15	
38 39	16	Abstract: The evolution of modern sharks, skates and rays (Elasmobranchii) is largely
40 41	17	enigmatic due to their possession of a labile cartilaginous skeleton; consequently, taxonomic
42 43	18	assignment often depends on isolated teeth. Bullhead sharks (Heterodontiformes) are a group
44 45 46	19	of basal neoselachians, thus their remains and relationships are integral to understanding
47 48	20	elasmobranch evolution. Here we fully describe <i>†Paracestracion danieli</i> – a bullhead shark
49 50	21	from the Late Jurassic plattenkalks of Eichstätt, Germany (150–154 Ma) – for its inclusion in
51 52 53	22	cladistic analyses (employing parsimonious principles) using morphological characters from
54 55	23	complete <i>†Paracestracion</i> and <i>Heterodontus</i> fossil specimens as well as extant forms of the
56 57	24	latter. Results confirm the presence of two separate monophyletic clades within
58 59 60	25	Heterodontiformes based on predominantly non-dental characters, which show a strong

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26	divergence in body morphology between <i>†Paracestracion</i> and <i>Heterodontus</i> (the latter
27	possessing a first dorsal fin and pectoral fins that are placed more anterior and pelvic fins that
28	are placed more posterior). This study emphasizes the importance of including non-dental
29	features in heterodontiform systematics (as compared to the use of dental characters alone)
30	and supports the erection of the family †Paracestracionidae. Further, phylogenetic analysis of
31	molecular data from five extant species suggests that crown heterodontiforms arose from a
32	diversification event 42.58 Ma off the west coast of the Americas.
33	
34	Key words: elasmobranch evolution, Late Jurassic, Paracestracionidae, Heterodontus,
35	morphology, bullhead sharks
36	
37	CHONDRICHTHYANS have a very long evolutionary history with their earliest fossil
38	evidence from the Upper Ordovician (Andreev et al. 2015). The cartilaginous fishes
39	include the Holocephali, or modern chimaeroids (Maisey 2012), and the Elasmobranchii
40	(sensu Maisey 2012; = Neoselachii of Compagno 1977), i.e. the modern sharks, skates and
41	rays, which experienced rapid diversification in the Jurassic period and are the
42	predominant group of living chondrichthyans (Kriwet et al. 2009a). Morphological and
43	molecular studies support two major monophyletic shark clades within Elasmobranchii, the
44	Galeomorphii and the Squalomorphii (Carvalho & Maisey 1996; Maisey et al. 2004;
45	Winchell et al. 2004; Human et al. 2006; Mallatt & Winchell 2007; Naylor et al. 2012).
46	Although both groups are well represented in the fossil record, their labile cartilaginous
47	skeleton leads to a taphonomic bias towards isolated teeth (Kriwet & Klug 2008).
48	Consequently, much of the early evolutionary history of elasmobranchs is either highly
49	contested or unknown (Klug 2010).
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51	Bullhead sharks (Heterodontiformes) are the most plesiomorphic galeomorphs (Naylor et
52	al. 2012), with their remains first appearing in the Early Jurassic (c. 175 Ma).
53	Heterodontiforms are therefore among the oldest groups in the fossil record for modern
54	sharks and have the potential to provide insight into early elasmobranch evolution (Thies
55	1983; Maisey 2012). Several genera of Heterodontiformes seemingly evolved in the
56	Jurassic (Kriwet 2008, Hovestadt 2018): <i>†Proheterodontus, †Palaeoheterodontus,</i>
57	<i>Procestracion</i> and <i>Paracestracion</i> (all represented by isolated teeth and the last also by $\frac{1}{2}$
58	complete specimens) disappear from the fossil record before the Cretaceous, while
59	Heterodontus underwent further radiation and still occupies our waters today (Kriwet
60	2008). <sup>†</sup> <i>Protoheterodontus</i> briefly appears in the Campanian (Guinot et al. 2013,
61	Hovestadt 2018) but did not make a significant contribution to Late Cretaceous
62	biodiversity.
63	
64	Bullhead sharks possess a durotrophic littoral ecomorphotype and are characterized by a
65	distinct heterodont dentition with cuspidate anterior teeth to grab invertebrate prey and
66	robust and flattened posterior teeth to crush armoured prey items or small bony fish (Strong
67	1989; Maia et al. 2012). The Eichstätt and Solnhofen areas in southern Germany (and
68	Dover in the U.K.) formed part of an archipelago in the Jurassic that was surrounded by
69	shallow waters of the Tethys Sea (Kriwet & Klug 2008), which likely promoted allopatric
70	speciation in heterodontiforms (Cuny & Benton 1999). Understanding the evolutionary
71	history and past taxonomic diversity of elasmobranchs, however, is encumbered by
72	preservation and collecting biases (Guinot & Cavin 2015).
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74	Completely articulated specimens of elasmobranchs are of utmost importance because they

75 provide abundant anatomical characters for exact taxonomic identification and can inform

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76	on morphological, ontogenetic and ecological adaptive changes in their evolution. Here we
77	provide a formal description of <i><i>Paracestracion danieli</i> – a subadult specimen from the</i>
78	Tithonian of Eichstätt, Germany (150–154 Ma) that was previously identified as a new
79	species (Slater 2016).
80	
81	Relationships within Heterodontiformes have received surprisingly little attention despite
82	their important phylogenetic position (Maisey 1982, 2012), with recent work including
83	only dental characters (Hovestadt 2018). Anatomical characters from <i>†Paracestracion</i> and
84	Heterodontus fossils, as well as extant species from the latter, were used in cladistic
85	analyses to examine the evolutionary relationships within heterodontiforms. Taxa based on
86	teeth alone were not included here and, despite recent advances (Hovestadt 2018), their
87	validity remains untested. A taxonomic diversity analysis based solely on extinct and extant
88	heterodontid dentition was, however, performed using data from Hovestadt (2018) and Reif
89	(1976) for comparison. Additionally, the phylogenetic relationships of extant Heterodontus
90	were investigated using molecular data from five species. Elucidation of the
91	interrelationships of heterodontiforms will help inform key questions regarding the
92	biodiversity and evolutionary history of heterodontiforms.
93	
94	MATERIAL AND METHODS
95	Taxonomic analysis of †Paracestracion danieli
96	Ultraviolet light was used to expose delicate fossil structures in <i>†Paracestracion danieli</i> .
97	High-resolution casts were made of significant anatomical features, such as teeth and placoid
98	scales, which were photographed using a KEYENCE 3D Digital VHX-600 microscope.
99	
100	Multivariate statistical analysis of heterodontids

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101	Seven distance measurements were taken from <i>†Paracestracion danieli</i> , <i>†P. falcifer</i> (AS-
102	VI-505), extant juveniles of <i>H. japonicus, H. zebra, H. portusjacksoni</i> and two adult <i>H.</i>
103	japonicus to identify differences in body shape between genera (Slater et al. 2019, table
104	S1, S2). Measurements taken were total body length, length between the anterior and
105	posterior dorsal fin, length between posterior dorsal fin and caudal fin, distance between
106	the pectoral fin and pelvic fin, length between the pelvic fin and anal fin, and widths of the
107	pectoral and pelvic girdle. Distance measurements were corrected for allometry in the
108	software package PAST v.3.20 (Hammer et al. 2001) and a Principal Components
109	Analysis (PCA) was performed.
110	
111	Cladistic analysis of heterodontiforms
112	Three extant species of <i>Heterodontus</i> and fossil specimens of <i>†Paracestracion</i> ,
113	<i>Heterodontus</i> and <i>Palaeospinax</i> – a stem-group representative of Elasmobranchii used to
113 114	<i>Heterodontus</i> and <i>Palaeospinax</i> – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix
<ul><li>113</li><li>114</li><li>115</li></ul>	<ul> <li>Heterodontus and <i>Palaeospinax</i> – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey &amp; Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this</li> </ul>
<ol> <li>113</li> <li>114</li> <li>115</li> <li>116</li> </ol>	<ul> <li>Heterodontus and †Palaeospinax – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey &amp; Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this study). Morphological trait analysis was carried out using the protocol from Klug (2010).</li> </ul>
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<ol> <li>113</li> <li>114</li> <li>115</li> <li>116</li> <li>117</li> <li>118</li> </ol>	<ul> <li>Heterodontus and †Palaeospinax – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey &amp; Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this study). Morphological trait analysis was carried out using the protocol from Klug (2010). Irrelevant and particularly labile characters were removed and characters specific to Heterodontiformes were added: two cranial (#96, 103), 15 postcranial (#94, 97–102, 104–</li> </ul>
<ol> <li>113</li> <li>114</li> <li>115</li> <li>116</li> <li>117</li> <li>118</li> <li>119</li> </ol>	<ul> <li><i>Heterodontus</i> and <i>Palaeospinax</i> – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey &amp; Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this study). Morphological trait analysis was carried out using the protocol from Klug (2010).</li> <li>Irrelevant and particularly labile characters were removed and characters specific to Heterodontiformes were added: two cranial (#96, 103), 15 postcranial (#94, 97–102, 104–112), two fin spine (#93, 113), 13 dental (#76–80, 83–84, 86–91) and one denticle</li> </ul>
<ol> <li>113</li> <li>114</li> <li>115</li> <li>116</li> <li>117</li> <li>118</li> <li>119</li> <li>120</li> </ol>	Heterodontus and <i>Palaeospinax</i> – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey & Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this study). Morphological trait analysis was carried out using the protocol from Klug (2010). Irrelevant and particularly labile characters were removed and characters specific to Heterodontiformes were added: two cranial (#96, 103), 15 postcranial (#94, 97–102, 104– 112), two fin spine (#93, 113), 13 dental (#76–80, 83–84, 86–91) and one denticle character (#92).
<ol> <li>113</li> <li>114</li> <li>115</li> <li>116</li> <li>117</li> <li>118</li> <li>119</li> <li>120</li> <li>121</li> </ol>	Heterodontus and † <i>Palaeospinax</i> – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey & Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this study). Morphological trait analysis was carried out using the protocol from Klug (2010). Irrelevant and particularly labile characters were removed and characters specific to Heterodontiformes were added: two cranial (#96, 103), 15 postcranial (#94, 97–102, 104–112), two fin spine (#93, 113), 13 dental (#76–80, 83–84, 86–91) and one denticle character (#92).
<ol> <li>113</li> <li>114</li> <li>115</li> <li>116</li> <li>117</li> <li>118</li> <li>119</li> <li>120</li> <li>121</li> <li>122</li> </ol>	<ul> <li>Heterodontus and *Palaeospinax – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey &amp; Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this study). Morphological trait analysis was carried out using the protocol from Klug (2010). Irrelevant and particularly labile characters were removed and characters specific to Heterodontiformes were added: two cranial (#96, 103), 15 postcranial (#94, 97–102, 104–112), two fin spine (#93, 113), 13 dental (#76–80, 83–84, 86–91) and one denticle character (#92).</li> <li>A total of 113 characters were used to create a character matrix in the software program</li> </ul>
<ol> <li>113</li> <li>114</li> <li>115</li> <li>116</li> <li>117</li> <li>118</li> <li>119</li> <li>120</li> <li>121</li> <li>122</li> <li>123</li> </ol>	<ul> <li>Heterodontus and *Palaeospinax – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey &amp; Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this study). Morphological trait analysis was carried out using the protocol from Klug (2010). Irrelevant and particularly labile characters were removed and characters specific to Heterodontiformes were added: two cranial (#96, 103), 15 postcranial (#94, 97–102, 104–112), two fin spine (#93, 113), 13 dental (#76–80, 83–84, 86–91) and one denticle character (#92).</li> <li>A total of 113 characters were used to create a character matrix in the software program Mesquite v.3.51 (Maddison &amp; Maddison 2018). Morphological characters from</li> </ul>
<ol> <li>113</li> <li>114</li> <li>115</li> <li>116</li> <li>117</li> <li>118</li> <li>119</li> <li>120</li> <li>121</li> <li>122</li> <li>123</li> <li>124</li> </ol>	<ul> <li>Heterodontus and *Palaeospinax – a stem-group representative of Elasmobranchii used to polarize characters (Klug 2010) – were examined to create a robust character matrix (Harvey &amp; Pagel 1991; see Slater <i>et al.</i> 2019 for information on specimens used in this study). Morphological trait analysis was carried out using the protocol from Klug (2010). Irrelevant and particularly labile characters were removed and characters specific to Heterodontiformes were added: two cranial (#96, 103), 15 postcranial (#94, 97–102, 104–112), two fin spine (#93, 113), 13 dental (#76–80, 83–84, 86–91) and one denticle character (#92).</li> <li>A total of 113 characters were used to create a character matrix in the software program Mesquite v.3.51 (Maddison &amp; Maddison 2018). Morphological characters from †<i>Palidiplospinax</i> were all coded as [0] (Klug 2010). Soft tissue characters were removed</li> </ul>

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42 43 44	14
45 46	14
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126	(such as the presence of molariform teeth in juvenile heterodontids or in the absence of
127	preservation) were coded as [?]. Parsimonious approaches were used in the software
128	program PAUP* v4.0 and 1000 replicates were performed using the heuristic search mode
129	by stepwise addition to obtain bootstrap values (Felsenstein 1985; Swafford 2002). All
130	characters were treated with equal weight. Both ACCTRAN and DELTRAN algorithms
131	were used as they assign character changes as closely as possible to the nodes and tips,
132	respectively (Agnarsson & Miller 2008). Sixty phylogenetically uninformative and/or
133	constant characters were removed (#1-17, 19-26, 28, 30-39, 42-48, 50-51, 53-57, 62,
134	64–65, 67, 70, 73, 75–76, 104, 112).
135	
136	Taxonomic diversity analysis
137	The standing diversity of heterodontiforms was determined for species presented in
138	Hovestadt (2018). Genera of ambiguous systematic position within Heterodontiformes
139	were omitted and 95% confidence intervals (CI) were calculated to obtain a measure for
140	the significance of results. We also consider the stratigraphic distribution of the two dental
141	morphotypes proposed for extant and extinct heterodontiforms by Reif (1976) and
142	Hovestadt (2018).
143	
144	Molecular phylogeny of extant heterodontids
1.4.5	
145	Homologous NADH2 mitochondrial gene sequences for <i>Chimaera phantasma</i> (accession
146	number JQ518719.1), Torpedo fuscomaculata (JQ518934.1), Raja montagui (JQ518886.1),
147	Heterodontus galeatus <mark>(JQ518722.1)</mark> , H. portusjacksoni <mark>(JQ519033.1)</mark> , H. zebra
148	(KF927894.1), H. mexicanus (JQ519166.1) and H. francisci (JQ519165.1) were aligned using
149	ClustalW in MEGA v7.0 (Kumar et al. 2016). C. phantasma was used as the outgroup and a
150	maximum likelihood phylogeny was produced using a GTR+Γ model and an analytical

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1 2		
3 4	151	variance estimation with nucleotide substitutions and a strong branch swap filter. Gaps and
5 6	152	missing data were treated as complete deletions and 1000 bootstrap replications were
7 8 0	153	executed. A time tree was constructed using a local clock and a minimum and maximum
9 10 11	154	divergence date between Rajiformes and Torpediniformes (187.8-209 Ma) for calibration
12 13 14	155	(Inoue <i>et al.</i> 2010; Aschliman <i>et al.</i> 2012).
15 16	156	
17 18 19	157	GEOGRAPHICAL AND GEOLOGICAL SETTING
20 21	158	†Paracestracion danieli (PBP-SOL-0005) was excavated from the Solnhofen limestone
22 23	159	(ca. 153 Ma, early Tithonian, Late Jurassic) near Eichstätt (South Germany; Fig. 1). The
24 25 26	160	fossil-yielding layers consist of finely laminated and strongly silicified calcarenites and
27 28	161	calcisiltites (for information about the geology and geography of this area see Kriwet $\&$
29 30	162	Klug 2004).
31 32 33	163	
34 35	164	Institutional abbreviations. BSPG, Bayerische Staatssammlung für Paläontologie und
36 37	165	Geologie Munich, Germany; JME, Jura Museum Eichstätt, Germany; SMNS, State
38 39 40	166	Museum of Natural History Stuttgart, Germany; PBP-SOL, Wyoming Dinosaur Center,
40 41 42	167	USA.
43 44	168	
45 46	169	SYSTEMATIC PALAEONTOLOGY
47 48 49	170	Superclass CHONDRICHTHYES Huxley, 1880
50 51	171	Class ELASMOBRANCHII Bonaparte, 1838
52 53	172	Cohort EUSELACHII Hay, 1902
54 55	173	Subcohort NEOSELACHII Compagno, 1977
50 57 58	174	Superorder GALEOMORPHII Compagno, 1973
59 60	175	Order HETERODONTIFORMES Berg, 1940

1		
2 3 4	176	Family PARACESTRACIONIDAE
5 6	177	LSID. urn:lsid:zoobank.org:act:XXXXXXXXX
7 8 0	178	
9 10 11	179	Genus †PARACESTRACION Koken, in Zittel, 1911
12 13	180	
14 15 16	181	Type species. †Cestracion falcifer Wagner, 1857 (BSPG AS-VI-505); lower Tithonian of
17 18	182	Solnhofen, South Germany.
19 20	183	
21 22 23	184	<i>†Paracestracion danieli</i>
24 25	185	Figure 2
26 27	186	
28 29 30	187	Derivation of name. Named in honour of J. Frank Daniel for his work on the endoskeleton of
30 31 32	188	extant heterodontiform sharks.
33 34	189	
35 36 27	190	Holotype. PBP-SOL-0005, complete specimen preserved in part and counterpart.
37 38 39	191	
40 41	192	<i>Diagnosis</i> . <sup>†</sup> <i>P. danieli</i> is characterized by the following combination of plesiomorphic and
42 43	193	autapomorphic (indicated by an asterisk) morphological traits: labial ornamentation on
44 45 46	194	anterior teeth; absence of distal curvature in parasymphyseal teeth; pectoral girdle positioned
47 48	195	at the 12 <sup>th</sup> vertebra*; and first dorsal fin spine placed at the 32 <sup>nd</sup> and 33 <sup>rd</sup> vertebrae*.
49 50	196	
51 52 53	197	Description. The part and counterpart of † <i>P. danieli</i> display organic preservation of the body
54 55	198	shape and a complete and fully articulated cartilaginous skeleton (Fig. 2A–B). The paired fins
56 57	199	are represented by a single fin each: the pectoral fin is ovular in shape (i.e. possesses no
58 59 60	200	distinct margins) and is most broad near its trailing edge, while the pelvic fin – ventral to the

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1 2		
2 3 4	201	anterior dorsal fin and abutting the pectoral fin – is pointed at both its apex and free rear tip
5 6	202	and has an anterior and posterior margin of similar length. The anterior dorsal fin (height, 23
7 8 0	203	mm; length, 40.4 mm) is larger than the posterior (height, 25.9 mm; length, 30.2 mm) but
9 10 11	204	both possess a rounded apex and a gently curved posterior margin. The anal fin is ventral to
12 13	205	the posterior dorsal fin, is its own length to the caudal fin and is pointed at its apex. A pointed
14 15	206	ventral tip joins the pre- and postventral margin of the caudal fin, with the postventral margin
16 17 18	207	extending dorsocaudally to a ventral posterior tip. The dorsal lobe predominates the caudal
19 20	208	fin, whereby the upper postventral margin continues anterodorsally to a broad subterminal
21 22	209	notch. The posterior margin and the dorsal posterior 'tip' are rounded and possess no distinct
23 24 25 26 27 28 29 30 31 32	210	boundaries.
	211	
	212	A dense layer of denticles obstructs the view of the neurocranium. The hyomandibula, hyoid
	213	and branchial apparatus are embedded in sediment. Segments of the Meckel's cartilage join at
33 34	214	the symphysis to form a bulbous rostrum and then extend in a posterolateral fashion (Fig. 2C).
35 36	215	One mandible segment is fully exposed in lateral view and maintains a similar height along its
37 38 39 40 41	216	entire length; the posterior end does not possess a strong process but is negatively cambered
	217	(i.e. the ventral margin extends more laterally than the dorsal margin) before it curves
42 43	218	dorsally to form the quadrato-mandibular joint. Features of the palatoquadrate are obscured
44 45	219	by sediment. Two dorsal fin spines are positioned directly anterior to each dorsal fin (Fig.
46 47 48	220	3A–B). The posterior fin spine is larger and more recurved than the anterior and the caps of
49 50	221	each bear no tuberculation. Skeletal features such as the propterygium, mesopterygium and
51 52	222	metapterygium are visible, however much of their features are embedded in the sediment.
53 54 55	223	Supraneural elements are present and are along the posterior end of the caudal fin.
56 57	224	
58 59 60	225	Exposed teeth on the Meckel's cartilage are preserved in situ and are symmetrical and possess

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3 4	2
5 6	2
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9 10 11	2
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18 19 20	2
21 22	2
23 24	2
25 26 27	2
28 29	2
30 31	2
32 33	2
34 35 36	2
37 38	2
39 40	2
41 42 43	2
44 45	2
46 47	2
48 49 50	2
50 51 52	2
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226	a gentle slope. Three small, lateral cusps flank each side of a large, central cusp – all of which
227	possess distinct vertical striations on their labial face (Fig. 2D–F). The pair of cusps most
228	proximal to the central cusp are well developed when compared to the other cusplets. The
229	cusps are not lingually bent and the lateral and posterior teeth are not distally inclined.
230	Anterior teeth are taller than they are wide and exhibit a slightly convex basal labial edge that
231	juts out over the crown/root junction (Fig. $2E-F$ ). Lateral teeth are wider than they are tall,
232	and the basal labial edge is less prominent than in anterior teeth (Fig. 2D). No molariform
233	teeth are present, which supports that the specimen is subadult. The root is gently curved in
234	basal view and the vascularisation is of the holaulacorhize type. Single, circular nutritive
235	foramina are located in the centre of a nutritive groove, which divides the root into two lobes
236	(Fig. 2G). No nutritive foramina are visible on the lateral faces of the root lobes.
237	
238	The most rostral part of the cranium is densely covered in denticles that are preserved in
239	apical view and have a slightly convex crown surface and a wide posterior margin that gently
240	tapers to a rounded anterior tip (Fig. 2H). Denticle crowns on the rest of the cranium possess
241	(in apical view) a delicate mid-ridge and an arrow-like morphology that is nearly as wide as it
242	is long (Fig. 2I); the ventral side of the body is flanked with denticles of similar morphology
243	but are longer than they are wide (and thus are more pointed at their apex) and have a more
244	prominent mid-ridge in apical aspect (Fig. 2J). Denticles along the anterior margins of the
245	paired fins are again arrow-like in shape but have a weak mid-ridge and a much shorter 'stem'
246	
	than cranial and ventral denticles (Fig. 2K). Many dorsal denticles possess the same
247	than cranial and ventral denticles (Fig. 2K). Many dorsal denticles possess the same morphology as those on the ventral side of the body; some, however, are thorn-like in apical
247 248	than cranial and ventral denticles (Fig. 2K). Many dorsal denticles possess the same morphology as those on the ventral side of the body; some, however, are thorn-like in apical view (Fig. 3C). Anterior to the fin spines are dorsal thorns, which – unlike denticles – sit
247 248 249	than cranial and ventral denticles (Fig. 2K). Many dorsal denticles possess the same morphology as those on the ventral side of the body; some, however, are thorn-like in apical view (Fig. 3C). Anterior to the fin spines are dorsal thorns, which – unlike denticles – sit perpendicular to the body, are slightly concave in lateral view and have a broad base that

1 2		
3 4	251	
5 6	252	Occurrence. Late Jurassic (Tithonian, ca. 153 Ma).
/ 8 0	253	
9 10 11	254	RESULTS
12 13	255	Comparison and multivariate statistical analysis of meristic characters
14 15	256	<i>†Paracestracion danieli</i> is characterized by seven cusps in anterior teeth at a body length of
16 17 18	257	225 mm while the holotype of † <i>P. falcifer</i> (AS-VI-505) exhibits a single cusp in anterior teeth
19 20	258	at a body length of 400mm (Fig. 4). The position of various features along the body column
21 22	259	(e.g. at the $n^{\text{th}}$ vertebrae) are markedly different between $\dagger P$ . danieli and $\dagger P$ . falcifer: the
23 24 25	260	dorsal fin spines in the former (anterior: 32 <sup>nd</sup> –33 <sup>rd</sup> ; posterior: 62 <sup>nd</sup> –63 <sup>rd</sup> ) – as well as the
25 26 27	261	pectoral and pelvic girdle (12 <sup>th</sup> and 32 <sup>nd</sup> , respectively) – are placed more posterior along the
27 28 29 30 31 32 33 34	262	body when compared to † <i>P. falcifer</i> (anterior fin spine: 23 <sup>rd</sup> –24 <sup>th</sup> ; posterior fin spine: 43 <sup>rd</sup> –
	263	44 <sup>th</sup> ; pectoral and pelvic girdle: 10 <sup>th</sup> and 24 <sup>th</sup> , respectively; Slater 2016, table 1). This is
	264	confirmed by multivariate statistical analysis, which reveals that the distance between the
35 36	265	pectoral and pelvic fins accounts for the majority of the variation (PC1=78.9%) in body shape
37 38	266	between † <i>P. danieli</i> , † <i>P. falcifer</i> as well as extant species of <i>Heterodontus</i> : the distance
39 40 41	267	between the posterior dorsal and caudal fin (PC2) explain 15.9% of the variation (Fig. 5).
41 42 43	268	
44 45	269	Cladistic analysis of heterodontiforms
46 47	270	The cladistic analysis produced one most parsimonious tree with a tree length of 61, a
48 49 50	271	consistency index of 0.9016 (indicating a low amount of homoplasy in the dataset) and a
51 52	272	retention index of 0.9062 (indicating that the proportion of terminal taxa retaining the
53 54	273	character identified as a synapomorphy is high). Unless specified, characters were assigned
55 56 57 58 59 60	274	to nodes and terminal taxa by both ACCTRAN and DELTRAN optimizations. Results from

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275	our analysis support two monophyletic groups, a clade that includes <i>†Paracestracion</i>
276	species and one that contains extinct and extant forms of <i>Heterodontus</i> (Fig. 6).
277	
278	Characters supporting the monophyly of node B are the presence of a root shelf that
279	surrounds the entire circumference of the tooth (likely anchoring them in the mucosal
280	tissue), pelvic fins that are ventral to the first dorsal fin and, as assigned by ACCTRAN
281	optimization, abutting the pectorals (Fig. <mark>6</mark> ). The vertebrae above which the first dorsal fin
282	spine is inserted is considered an autapomorphic character for $\dagger P$ . viohli, $\dagger P$ . falcifer and
283	<i>†P. danieli</i> (22–23rd, 24–25th and 32–33rd vertebrae, respectively).
284	
285	Node C is characterized by pelvic fins that abut the pectorals and seven cusps on the
286	symphysial teeth as a juvenile, which are both supported by DELTRAN optimization.
287	Specimen SMNS 11150 is identified as a separate species from <i>†P. falcifer</i> due to the
288	presence of five cusps on its anterior teeth as a juvenile (ACCTRAN optimization; Fig.
289	S1). <i>†Paracestracion viohli</i> (JME Sha 728) is characterized by ornamentation on the
290	lingual tooth crown face and a lack thereof on the labial face in anterior teeth.
291	
292	Node D features dorsal thorns (DELTRAN optimization) and an absence of distal curvature
293	in the parasymphysial teeth of juveniles. †Paracestracion danieli features an additional two
294	characters: a pectoral girdle at the 12 <sup>th</sup> vertebra and the aforementioned position of the first
295	dorsal fin spine.
296	
297	Node E identifies a monophyletic clade that is supported by a low number of tooth families
298	(Section Acceleration), an absence of labial tooth crown ornamentation in
299	anterior teeth, an anal fin that is more than its own length in distance to the caudal fin and a

1 2		
3 4	300	pectoral girdle positioned at the eighth vertebrae. <i>†Heterodontus zitteli</i> features accessory
5 6	301	cusplets that are nearly the same height as the central cusp and – as in $\dagger P$ . danieli – dorsal
/ 8 9	302	thorns (DELTRAN optimization) and seven cusps on the anterior teeth (DELTRAN
) 10 11	303	optimization).
12 13	304	
14 15	305	Node F features an absence of a horizontal root on the basal face of anterior teeth, labial
16 17 18	306	faces of the crown that jut out over the crown/root junction, anterior teeth with a convex
19 20	307	labial face, absence of a cylindrical central cusp, presence of a medio-lingual protuberance,
21 22	308	and an absence of fin spine tuberculation. Additional characters are identifiable when
23 24 25	309	ACCTRAN optimization is used: an anal fin that is posterior to the second dorsal fin,
25 26 27	310	absence of dorsal thorns, pectoral fins that are entirely situated anterior to the first dorsal
28 29 30 31 32 33 34 35 36 37 38 20	311	fin, and a high number of vertebral centra. DELTRAN optimization also identifies a low
	312	number of tooth rows to this node. <i>†Heterodontus canaliculatus</i> is recognized by
	313	ACCTRAN as having three cusps in adult anterior teeth.
	314	
	315	Node G is exclusive to extant <i>Heterodontus</i> and shows a relationship between species
39 40 41	316	occupying shallow waters off of the coasts of Australia and the east coast of Asia.
42 43	317	Characters for node G include: two root lobes are inclined and join in the midline of the
44 45	318	lingual side of the tooth, broad molariform teeth with no median crest on the cutting edge
46 47 48	319	in adults, an anal fin that is posterior to the second dorsal fin, pectoral fins that are not
49 50	320	situated anterior to the first dorsal fin, a low number of vertebrae and a single cusp in adult
51 52	321	anterior teeth (the last of which is supported by DELTRAN optimization). Heterodontus
53 54	322	portusjacksoni has enameloid ridges on molariformes, a less pronounced supraorbital crest,
55 56 57	323	and five cusps in juvenile anterior teeth (the last is supported by ACCTRAN optimization).
58 59 60	324	<i>H. japonicus</i> , conversely, has seven cusps in juvenile anterior teeth.

2 3 4	325	
5 6	326	Taxonomic diversity of heterodontiforms
7 8	327	Analysis of data from Hovestadt (2018) shows that the standing taxonomic diversity of
9 10 11	328	fossil heterodontiforms increased from the Early to the Late Jurassic, followed by a 1.7%
12 13	329	decrease in species across the Jurassic/Cretaceous boundary (Table 1). The Late
14 15	330	Cretaceous represents 26.3% of the total extinct and extant taxonomic diversity for
16 17 18	331	heterodontiforms, with the Cenomanian accounting for most species. Further, an 8.8%
19 20	332	decrease in species standing diversity occurs across the K/Pg boundary but is not
21 22	333	significant. The Palaeogene represents 17.5% of the total diversity of fossil and extant
23 24 25	334	heterodontiforms, while the Neogene represents 12.3%. Three and six extant species
26 27	335	display dental structures of morphotype 1 and 2, respectively.
28 29	336	
30 31 32	337	Molecular phylogeny of extant Heterodontus
32 33 34	338	Results indicate that <i>H. francisci</i> – originating ca. 42.58 Ma – is basal to all other extant
35 36	339	heterodontids included in our analysis and that <i>H. mexicanus</i> and <i>H. zebra</i> diverged from <i>H</i> .
37 38	340	francisci ca. 27.67 Ma and 9.22 Ma, respectively (Fig. 7). H. portusjacksoni and H. galeatus
39 40 41	341	are shown to have diverged from each other 7.14 Ma. The low bootstrap support value,
42 43	342	however, indicates that their relationships remain unresolved.
44 45	343	
46 47 48	344	DISCUSSION
49 50	345	Comparison of Heterodontidae and <i>†Paracestracionidae</i>
51 52	346	Cladistic analysis and comparison of dental and non-dental features between Heterodontus
53 54	347	and $\dagger Paracestracion$ supports the necessity for a family – $\dagger Paracestracionidae$ – to include
55 56 57	348	all extinct forms of the latter.
58 59 60	349	

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1 2		
3 4 5 6 7	350	Post-cranial features. Our findings emphasize the differences in body morphology between
	351	Heterodontidae and †Paracestracionidae and characterizes the latter as having pelvic fins that
/ 8 9	352	are placed more anterior as well as a first dorsal fin that is placed more posterior – two key
10 11	353	features that are possessed by slow swimming epibenthic and benthic sharks (Figs 5, 6; Maia
12 13	354	et al. 2012). In contrast, traits that are generally associated with a more active lifestyle, such
14 15 16	355	as a (1) first dorsal fin and associated fin spine that are placed more anterior (2) pelvic girdle
17 18	356	and fins that are placed more posterior and (3) pectoral girdle that is placed more anterior,
19 20	357	are most clearly manifested in the Heterodontidae. The Late Jurassic culminated in a
21 22 23	358	radiation in teleosts (Arratia 2004) as well as marine transgressions and minor mass
23 24 25	359	extinctions that primarily affected coastal reef habitats (Hallam 1981, 1990, 2001; Moore &
26 27	360	Ross 1994), which would have led to an increase in competition; it is plausible that the body
28 29 30 31 32 33 34 35 36 37 38 39 40 41	361	morphology of Heterodontus contributed to their persistence into the Cretaceous, unlike
	362	Paracestracion.
	363	
	364	<i>Paracestracion</i> has previously been defined by the position of the pelvic fins, whereby they
	365	abut the pectorals and sit below the first dorsal fin (Kriwet et al. 2009b). Interestingly, the
	366	first dorsal fin spine's position along the vertebral column unambiguously distinguishes $\dagger P$ .
42 43	367	<i>falcifer</i> and <i>†P. danieli</i> . Although this is also an autapomorphic character for <i>†P. viohli</i>
44 45 46	368	sexual dimorphism cannot be ruled out (compare Daniel 1915) due to its missing posterior
47 48	369	end and is therefore only characterized by its dental ornamentation in this study. Further, $\dagger P$ .
49 50	370	<i>falcifer</i> (the holotype) and $\dagger P$ . <i>danieli</i> possess thorns. This trait, however, is also present in
51 52	371	$\dagger H$ . zitteli and similar structures present in juvenile angel sharks are lost as they age
53 54 55	372	(Compagno 2001). Investigation of the presence/absence of dorsal thorns in undoubtedly
56 57	373	adult heterodontiforms is thus necessary to determine if it is an ontogenetic or a homoplastic
58 59 60	374	feature.

1		
2 3 4	375	
5 6	376	Dentition. This study identifies an additional key characteristic of †Paracestracionidae to
7 8 9	377	those of previous studies (Kriwet et al. 2009b): teeth exhibit a root shelf whereas in
10 11	378	Heterodontidae the root lobes meet in the midline of the tooth and form a lingual
12 13	379	protuberance. Additionally, the rate at which the number of cusps is reduced throughout
14 15 16	380	ontogeny in extant Heterodontidae is very gradual when compared to †Paracestracionidae
17 18	381	(Reif 1976; Fig. 3). The Meckel's cartilage and palatoquadrate in extant juveniles contains
19 20 21	382	13–17 and 17–21 tooth families, respectively (Reif 1976), while † <i>P. danieli</i> possesses 21 and
22 23	383	23 families, respectively, and the holotype for $\dagger P$ . <i>falcifer</i> possesses 29 on the palatoquadrate:
24 25	384	this may indicate a major difference in feeding ecology between Heterodontidae and
26 27 28	385	<sup>†</sup> Paracestracionidae (Slater 2016). Further studies on the ontogeny of heterodonty in
29 30	386	Heterodontiformes, however, are required to confidently determine differences in dentition
31 32	387	between the two families and examine the impact on their evolutionary fates.
33 34	388	
35 36 37	389	Taxonomy of Heterodontiformes
38 39	390	Extant species of <i>Heterodontus</i> are divided into two groups based on tooth morphology (Reif
40 41 42	391	1976): following this concept, Hovestadt (2018) revises extant and extinct heterodontiform
42 43 44	392	systematics and assigns fossil species to either morphotype 1 or 2 (corresponding to the
45 46	393	Portusjacksoni and Francisci group, respectively, of Reif 1976 for extant species) or, if a
47 48 49	394	combination of characters is present, to a new genus. New genera based exclusively on
50 51	395	isolated fossil teeth were thus introduced: $\uparrow Protoneterodontus$ is represented by a single
52 53	390 207	* <i>Palacehoteredontus</i> by a species in the late Late to early Middle Jurassie and
54 55	391	T undebneter buomus by a species in the late Late to early windule Jurassic and
56 57	398	<i>Procestracion</i> by a single anterior tooth from the Kimmeridgian of southern Germany
58 59 60	399	(Hovestadt 2018). Further, Hovestadt (2018) assumes <i>†Cestracion zitteli</i> to be undiagnosable

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1 2		
3 4	400	(nomina nuda) due to an absence of preserved dentition and considers †P. viohli Kriwet, 2008
5 6	401	as a non-heterodontiform due to the lack of associated dental characters (p. 90). However, in
7 8 0	402	this study, we show that – in addition to dental features – non-dental characters clearly
9 10 11	403	identify <i>†Paracestracion zitteli</i> to represent the most basal member of heterodontids and
12 13	404	support the inclusion of <i>†P. viohli</i> in <i>†Paracestracionidae</i> . Ultimately, systematic assignment
14 15	405	of heterodontiforms based on dental characters alone is likely to provide ambiguous results
16 17 18	406	due to an absence of data on the ontogeny of heterodonty as well as the prevalence of
19 20	407	convergent evolution in elasmobranch dentition. Our study utilizes non-dental features to
21 22	408	distinguish several species within the Heterodontiformes and thus highlights the importance
23 24 25	409	of these characters in taxonomic analyses of heterodontiform fossils.
25 26 27	410	
28 29	411	A new Super Order (Paracestrationiformes) and family (Paracestrationidae) was proposed
30 31	412	(Jacques and Van Waes 2012) to include all members of the <i>†Paracestracion</i> genus however
32 33 34	413	neither was registered. Our study confirms the necessity for the family <i>†</i> Paracestracionidae
35 36	414	however we refrain from introducing a new order to include the <i>†</i> Paracestracionidae family
37 38	415	due to the restriction of taxa in our analyses, which does not reject the interpretation that both
39 40 41	416	families represent sister groups within Heterodontiformes.
42 43	417	
44 45	418	Diversity patterns of heterodontiforms
46 47 49	419	A 1.7% decrease in species across the Jurassic/Cretaceous boundary is likely due to the
40 49 50	420	limited number of species recorded in the Early Cretaceous, which may be a result of
51 52	421	collecting bias: consequently, a significant decrease in heterodontiform diversity across the
53 54	422	Jurassic/Cretaceous boundary cannot be unambiguously established. The Late Cretaceous
55 56 57	423	heralds the highest species diversity in the evolutionary history of heterodontiforms however
58 59 60	424	it is unbalanced among the epochs and is generally rather low.

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2 3 4	425	
5 6	426	Relationships within extant heterodontiforms
7 8	427	Origins of crown heterodontiforms. Divergence dates in this study are based on the minimum
9 10 11	428	and maximum divergence dates between Rajiformes and Torpediniformes, which spans
12 13	429	187.8–209 Ma. Our estimate that crown heterodontiforms originated with <i>H. francisci</i> off the
14 15	430	west coast of the Americas ca. 42.58 Ma largely supports a previous estimate of 47 Ma
16 17 18	431	(Sorenson et al. 2014). Heterodontus quoyi (not included in this study) also occupies waters
19 20	432	off the west coast of South America and was previously posited as the most plesiomorphic
21 22	433	heterodontid due to the proximity of the anal fin to the caudal fin – as in $\dagger H$ . zitteli (Maisey
23 24 25	434	1982). It is therefore critical to obtain molecular information for <i>H. quoyi</i> to elucidate the
26 27	435	origin of crown heterodontiforms.
28 29	436	
30 31 32	437	Ultimately, our molecular phylogeny suggests that pre-Eocene – and especially Cretaceous
33 34	438	heterodontiforms – represent stem group members. This contrasts with Hovestadt (2018), in
35 36	439	which (apart from the absence of morphotype 2 from the Oligocene) both dental morphotypes
37 38 20	440	are present in the Palaeogene, Neogene and the Late Cretaceous (Table 1). If dentitions bear
39 40 41	441	not only a taxonomic but also a phylogenetic signal – which remains to be tested – this would
42 43	442	indicate that species resembling modern heterodontiforms evolved in the late Early
44 45 46	443	Cretaceous. Our results are, nevertheless, consistent with the data from Hovestadt (2018) that
40 47 48	444	indicate that morphotype 2 (Francisci group of Reif 1976) is the most plesiomorphic of
49 50	445	heterodontiform dentitions. We, however, consider the reconstruction of heterodontid
51 52	446	evolution based on dental features alone insufficient: molecular information combined with
53 54 55	447	morphological evidence from complete fossil specimens provides a larger, more robust
56 57	448	dataset than one based on dental morphology.
58 59 60	449	

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1		
2 3 4	450	Eastern Pacific species. During the mid-Eocene shallow waters of the Tethys Sea extended to
5 6	451	what are presently the west coasts of the Americas, the east coast of North America and the
7 8 0	452	Gulf of Mexico and the disparity in the oceanic temperature from the equator to the poles was
9 10 11	453	reduced (Barron 1987; Sluijs et al. 2006; Hines et al. 2017): these conditions may have
12 13	454	contributed to the migration and subsequent speciation of heterodontids during the mid-
14 15 16	455	Eocene due to their strong preference for waters over 21 °C (Compagno 2001).
17 18	456	
19 20	457	Western Pacific species. Results also reveal a monophyletic relation for species along the east
21 22 23	458	Asiatic and Australian coasts (H. zebra, H. portusjacksoni and H. galeatus): future
23 24 25	459	palaeontological discoveries might clarify the migration routes resulting in the divergence of
26 27	460	these species (as well as those not included in this study along the east coast of Saudi Arabia
28 29	461	and Africa) from those in the Eastern Pacific ca. 9.22 Ma (Ebert et al. 2017; Pollom et al.
30 31 32	462	2019). The topology of Western Pacific species in our phylogeny is likely different from that
33 34	463	of Naylor et al. (2012) due to their use of Bayesian principles: further, the positions of H.
35 36	464	portusjacksoni and H. galeatus are considered unresolved here.
37 38 39	465	
40 41	466	CONCLUSIONS
42 43	467	Anatomical characters from complete bullhead shark fossils support the monophyly of
44 45 46	468	Heterodontiformes, which can be separated into two families: one including solely extinct
40 47 48	469	forms of $\frac{1}{Paracestracion}$ – assigned to $\frac{1}{Paracestracionidae}$ and both extinct and extant
49 50	470	forms of <i>Heterodontus</i> within the Heterodontidae. Although we recognize the importance of
51 52	471	tooth morphologies in taxonomic analyses the phylogenetic signal of heterodontiform dental
53 54 55	472	characters requires further investigation. This study emphasizes the importance of using non-
56 57	473	dental features to provide a greater number of informative characters when investigating the
58 59 60	474	systematics of chondrichthyan fossils.

175	
4/3	
476	Molecular phylogenetic analysis reveals that crown heterodontiforms likely originated off the
477	west coast of the Americas due to a diversification event during the mid-Eocene. Further
478	research, however, is required to elucidate the evolutionary history of Heterodontiformes and
479	to clarify migration routes that led to the current distribution of <i>Heterodontus</i> .
480	
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485	collections and G. Cuny for useful comments on the manuscript.
486	
487	DATA ARCHIVING STATEMENT
488	Data for this study are available in the Dryad Digital Repository:
489	https://datadryad.org/review?doi=doi:10.5061/dryad.6p4f83q
490	This published work and the nomenclatural act it contains, have been registered in ZooBank:
491	http://zoobank.org/References/XXXXXXXXX
492	
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9 10 11	721	
12 13	722	FIGURES
14 15 16	723	FIG. 1. Geological map of Eichstätt, Germany and surrounding areas. Stars indicate locality
16 17 18	724	from which <i>†Paracestracion danieli</i> was excavated.
19 20	725	
21 22	726	FIG. 2. Photographs of <i>Paracestracion danieli</i> , a complete fossil subadult heterodontiform.
23 24 25	727	A, UV image. B, counterpart. C, palatoquadrate and Meckel's cartilage with teeth in situ. D,
26 27	728	anterior tooth. E, parasymphysial tooth. F, lateral teeth. G, root vascularization of anterior
28 29	729	teeth. <mark>H</mark> , rostral denticles. <mark>I</mark> , cranial denticles. <mark>J</mark> , ventral denticles. <mark>K</mark> , denticles on leading edge
30 31	730	of pelvic fin. Scale bars represent: 1 cm (A–C); 0.5 mm (D–K).
32 33 34	731	
35 36	732	FIG. 3. A, anterior dorsal fin spine. B, posterior dorsal fin spine. C, dorsal denticles. D, dorsal
37 38	733	thorn. Scale bars represent: 1 mm (A–B); 0.5 mm (C–D).
39 40 41	734	
42 43	735	FIG. 4. Tooth morphology of anterior teeth throughout ontogeny for †extinct and extant
44 45	736	heterodontids. The darker grey region denotes the tooth root for $\dagger P$ . falcifer. Adapted from
46 47 49	737	Reif (1976). All scale bars represent 1 mm.
48 49 50	738	
51 52	739	FIG 5. PCA of allometrically scaled distance measurements taken from extinct and extant
53 54	740	heterodontids. Ellipses, 95% confidence interval. Adapted from Slater (2016).
55 56 57	741	
57 58		
59 60		

2 3 4	742	FIG 6. Morphometric cladogram of extinct and extant heterodontids. Labels on nodes indicate
5 6	743	bootstrap estimates for ACCTRAN and DELTRAN optimization (the latter in bold). Crosses
7 8	744	indicate extinct species. TL, total length; RI, retention index; CI, consistency index.
9 10 11	745	
12 13 14 15 16 17 18 19 20	746	FIG 7. A molecular, maximum likelihood phylogeny of extant Heterodontiformes. Bootstrap
	747	values and divergence times are indicated (the latter in bold).
	748	
	749	TABLE 1. Standing diversity of extinct and extant heterodontiforms through time. Raw data
21 22	750	and stratigraphic information taken from Reif (1976) and Hovestadt (2018) are presented with
23 24 25 26 27	751	respect to the authors' proposed dental morphotypes. CI, confidence interval; N, number of
	752	species.
28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 9 50 51 52 53 45 56 57 58 9 60	754	



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FIG. 1. Geological map of Eichstätt, Germany and surrounding areas. Stars indicate locality from which <sup>†</sup>Paracestracion danieli was excavated.

160x75mm (600 x 600 DPI)



FIG. 2. Photographs of <sup>†</sup>Paracestracion danieli, a complete fossil subadult heterodontiform. A, UV image. B, counterpart. C, palatoquadrate and Meckel's cartilage with teeth in situ. D, anterior tooth. E, parasymphysial tooth. F, lateral teeth. G, root vascularization of anterior teeth. H, rostral denticles. I, cranial denticles. J, ventral denticles. K, denticles on leading edge of pelvic fin. Scale bars represent: 1 cm (A–C); 0.5 mm (D–K).

160x185mm (600 x 600 DPI)





FIG. 3. A, anterior dorsal fin spine. B, posterior dorsal fin spine. C, dorsal denticles. D, dorsal thorn. Scale bars represent: 1 mm (A–B); 0.5 mm (C–D).

160x62mm (600 x 600 DPI)



80x115mm (600 x 600 DPI)



57 58

59

60



FIG 5. PCA of allometrically scaled distance measurements taken from extinct and extant heterodontids. Ellipses, 95% confidence interval. Adapted from Slater (2016).

109x75mm (600 x 600 DPI)



FIG 6. Morphometric cladogram of extinct and extant heterodontids. Labels on nodes indicate bootstrap estimates for ACCTRAN and DELTRAN optimization (the latter in bold). Crosses indicate extinct species. TL, total length; RI, retention index; CI, consistency index.

110x75mm (600 x 600 DPI)



FIG 7. A molecular, maximum likelihood phylogeny of extant Heterodontiformes. Bootstrap values and divergence times are indicated (the latter in bold).

110x75mm (600 x 600 DPI)

2								
3		Morphotype			N		Total	Upper and lower
4				-			species	limits of 95% CI
5		1	2	?	Epoch	Series	(%)	(%)
6	Recent	3	6		9	9	15.8	-8.98/+10.05
0	Pliocene	1	1		2	_ 7	12.3	-7.82/+9.19
/	Miocene	1	4		5			
8	Oligocene	1			1	10	17.5	-9.33/+10.46
9	Eocene	4	3		7	_		
10	Palaeocene	1	1		2			
10	Maastrichtian	1	1	2	3	15	26.3	-11.06/+11.84
11	Campanian	1			1			
12	Santonian	1			1			
13	Coniacian							
14	Turonian		1		1			
15	Cenomanian	4	4	1	9			
15	Aptian/Albian		1	1	2	5	8.8	-6.72/+7.97
16	Barremian			1	1			
17	Hauterivian							
18	Valanginian			2	2			
10	Berriasian							
20	Late Jurassic				6	6	10.5	-7.37/+8.67
20	Middle Jurassic				4	4	7	-5.89/+7.39
21	Early Jurassic				1	1	1.8	-5.89/+7.39
22	Total species					57		
23								