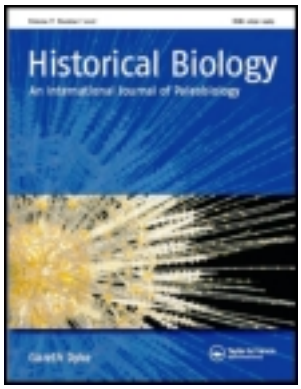

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Cajus G. Diedrich [a] & Thomas Rathgeber [b]

[a] PaleoLogic, Nansenstr. 8, D-33790, Halle/Westphalia, Germany

[b] Staatliches Museum für Naturkunde Stuttgart, Rosenstein, Gewann 1, D-70191, Stuttgart, Germany

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Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss 1810) skeleton remains of the Upper Rhine Valley (SW Germany) and contributions to their sexual dimorphism, taphonomy and habitus

Cajus G. Diedrich[a]* and Thomas Rathgeber[b]

[a]*PaleoLogic, Nansenstr. 8, D-33790 Halle/Westphalia, Germany;* [b]*Staatliches Museum für Naturkunde Stuttgart, Rosenstein, Gewann 1, D-70191 Stuttgart, Germany*

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The Upper Rhine Valley (SW Germany, Europe) has delivered 20,000 Late Pleistocene megafaunal remains found at gravel pit sites in the past decades and only 0.1% carnivore remains including a nearly complete lion skeleton of a small male *Panthera leo spelaea* (Goldfuss, 1810) and also skeleton parts of two more grown-up to even older males from different localities, such as the additional isolated bones. Less than 1% of the bone material belongs to adolescent animals; cub material is completely absent. The material from the Upper Rhine Valley was compared with many caves and few open-air sites of central Europe, indicating strong sexual dimorphism in the last lions of Europe, but problematic remains in the glacial/interglacial size variation. Some lions are in the open air, and all cave localities are overlapping with hyena and cave bear den sites; in some cases, they seem to have been in the open-air hyena den sites in the Upper Rhine Valley. Proofs for hyena or other large carnivore scavenging activities on lion carcasses are cracked lower jaws and chewed long bones. The 'steppe lion' habitus is reconstructed by comparisons with French cave art figurations. Finally, a first overview of the steppe lion paleobiogeography in SW Germany is presented.

Keywords: *Panthera leo spelaea* (Goldfuss, 1810); open-air skeleton remains; central Europe; sexual dimorphism; paleoecology and biogeography; Late Pleistocene

Introduction

Late Pleistocene Eurasian lion *Panthera leo spelaea* (Goldfuss, 1810) remains are extremely rare at open-air sites of Europe, especially originally articulated skeletons from individuals, like the only known male skeleton from Siegsdorf (Bavaria, Germany; Gross 1992), to which here new skeletons and many single bones can be added from SW Germany, including an overview of the steppe lion sites of Baden-Württemberg.

In the year 1700, the historically first Late Pleistocene lion remains from Baden-Württemberg were found during the famous mammoth excavations near Uffkirche in Stuttgart-Bad Cannstatt. Some of the specimens are described and figured by Jäger (1839; Figure 1). Berckhemer (1927) reported 17 sites in Baden-Württemberg with lion remains, mostly of a Late Pleistocene age, but without locality map or bone plates. During that time, in the German Upper Rhine area, lions were known only from four localities; two are from Middle Pleistocene and two from Upper Pleistocene age (Klähn 1922). Adam (1966) published few more bone material from the collection of the including lion remains from some caves. In other publications (e.g. Berckhemer and Peters 1935; Kley 1966; Böttcher et al. 2000), lion bones were mentioned or figured from southern German caves, also a rare cub cranium (Rathgeber 1982). Ziegler (1994, 1996) finally published a short incomplete overview of Pleistocene lion remains in southern Germany. The material described herein was figured only with one of the lion skulls of Huttenheim (Geissert et al. 1986).

Within Recent Late Pleistocene (Eemian, Weichselian) steppe lion *P. l.spelaea* research in Europe (Diedrich 2004–2010a–f; Barnett et al. 2009; Diedrich et al. 2010; Figure 2(A), the quite high amount of open-air site material from southern Germany is of importance to understand the largest predators of the Ice Age in their life, prey relationship, competition and antagonism to the second large carnivore, the Ice Age spotted hyenas *Crocuta crocuta spelaea* (Goldfuss, 1810; Diedrich 2007a, 2008b). Although most of the lion remains in Europe are from cave sites (e.g. Dawkins and Sanford 1900; Argant 1988; Fischer 1994; Diedrich 2010b, 2010d), remains from open-air localities are rarer (Gross 1992; Diedrich 2004, 2007b, 2010a, 2010c).

A programme to study the *P. l. spelaea* material from German cave and open-air localities was started in different regions to obtain as much as possible data about the lion bone taphonomy and sexual dimorphism and inter-species

*Corresponding author. Email: cdiedri@gmx.net/www.paleologic.de

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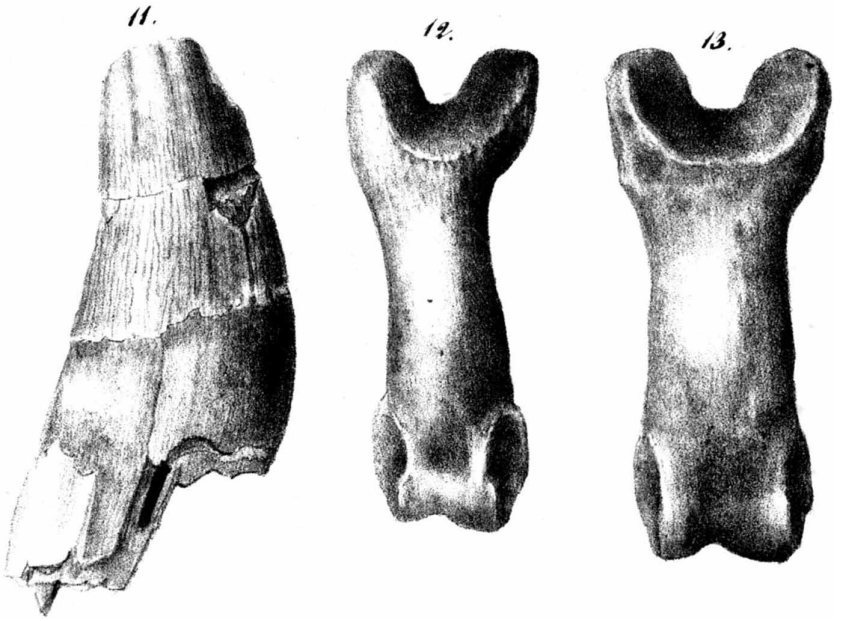

Figure 1. Remains of the Upper Pleistocene steppe lion *P. l. spelaea* (Goldfuss, 1810) from an open-air site near Uffkirche in Stuttgart-Bad Cannstatt. The illustration as figured in Jäger (1839, pl. XV, Figs. 11–13) shows a damaged canine (SMNS no. 30923.3) and two phalanges (SMNS no. 30923.1-2).

life or prey adaptations of the last lions of Europe. Although in northern Germany many sites were already studied (Diedrich 2004–2010a), in southern Germany, an intensive lion research is continued with this contribution, after the recent intensive studies of the holotype and paratype material and hyenas or cave bear bone taphonomy of the largest European Upper Pleistocene steppe lion population of the Zoolithen Cave, Bavaria (Diedrich 2010b).

Although from the studied localities, and others of the Upper Rhine Valley, the hyenas *C. c. spelaea*

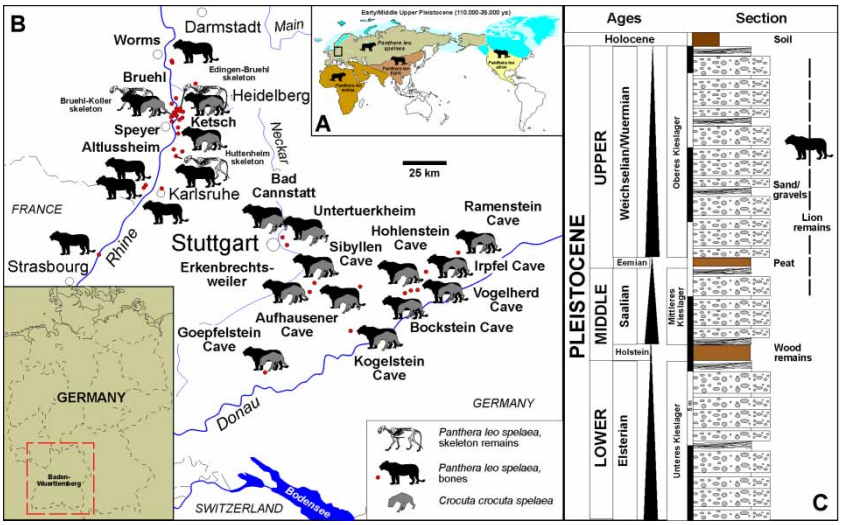

Figure 2. (A) Several lion subspecies were present in the Early to Middle Weichselian (Upper Pleistocene) with *P. l. spelaea* represented in Eurasia (phylogeography modified after Barnett et al. 2009). (B) Upper Pleistocene steppe lion *P. l. spelaea* (Goldfuss, 1810) from open-air and cave sites in SW Germany. In the caves, lion remains generally were found in hyena dens and, in most cases, probably as a result of hyena–lion conflicts. Also, at three open-air sites in the Upper Rhine Valley, hyena open-air den sites seem to have been present (hyena sites in Baden-Württemberg after Diedrich 2008b). (C) Generalised Upper Rhine River terrace lion bearing gravel sequences (section composed after Bartz 1982; Ziegler and Dean 1998).

Table 1. *Panthera l. spelaea* (Goldfuss, 1810) male skeleton remain (6816.5.6.73.1-36) from Huttenheim, Huttenheimer Kammer, Upper Rhine Valley open-air site in SW Germany.

No.	Inventory number	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Original	Date of find
1	6816.5.6.73.1	Skull	Incomplete, length 375 mm, P4 width 32 mm, condyl width 71 mm, frontal width 113 mm			Early adult	Male		x	5 Jun 1973
2	6816.5.6.73.2	Mandible	Ramus, fragment	x		Early adult	Male		x	5 Jun 1973
3	6816.5.6.73.24	Scapula	Incomplete, glenoid width 58 mm		x	Early adult	Male		x	5 Jun 1973
4	6816.5.6.73.25	Scapula	Incomplete, glenoid width 58 mm	x		Early adult	Male		x	5 Jun 1973
5	6816.5.6.73.26	Humerus	Complete, length 355 mm, distal width 96 mm		x	Early adult	Male		x	5 Jun 1973
6	6816.5.6.73.30	Ulna	Incomplete, maximal width 70 mm		x	Early adult	Male		x	5 Jun 1973
7	6816.5.6.73.28	Ulna	Complete, length 404 mm, maximal width 69 mm	x		Early adult	Male		x	5 Jun 1973
8	6816.5.6.73.29	Radius	Complete, length 331 mm, distal width 68 mm		x	Early adult	Male		x	5 Jun 1973
9	6816.5.6.73.27	Radius	Complete, length 332 mm, distal width 70 mm	x		Early adult	Male		x	5 Jun 1973
10	6816.5.6.73.3	Cervical vertebra	Atlas, occipital diameter 72 mm			Early adult	Male		x	5 Jun 1973
11	6816.5.6.73.4	Cervical vertebra	Axis, centrum diameter 42 mm, centrum length 92 mm			Early adult	Male		x	5 Jun 1973
12	6816.5.6.73.5	Cervical vertebra	C3, centrum diameter 37 mm, centrum length 40 mm			Early adult	Male		x	5 Jun 1973
13	6816.5.6.73.6	Cervical vertebra	C4, centrum diameter 48 mm, centrum length 37 mm			Early adult	Male		x	5 Jun 1973
14	6816.5.6.73.7	Cervical vertebra	C6, centrum diameter 37 mm, centrum length 35 mm			Early adult	Male		x	5 Jun 1973
15	6816.5.6.73.8	Cervical vertebra	C7, centrum diameter 37 mm, centrum length 36 mm			Early adult	Male		x	5 Jun 1973
16	6816.5.6.73.9	Thoracic vertebra	T1, centrum diameter 36 mm, centrum length 34 mm			Early adult	Male		x	5 Jun 1973
17	6816.5.6.73.10	Thoracic vertebra	T2, centrum diameter 35 mm, centrum length 35 mm			Early adult	Male		x	5 Jun 1973
18	6816.5.6.73.11	Thoracic vertebra	T3, centrum diameter 37 mm, centrum length 36 mm			Early adult	Male		x	5 Jun 1973
19	6816.5.6.73.12	Thoracic vertebra	T4, centrum diameter 32 mm, centrum length 35 mm			Early adult	Male		x	5 Jun 1973
20	6816.5.6.73.13	Thoracic vertebra	T6-8			Early adult	Male		x	5 Jun 1973
21	6816.5.6.73.14	Thoracic vertebra	T10-12			Early adult	Male		x	5 Jun 1973
22	6816.5.6.73.15	Lumbar vertebra	L1, centrum diameter 49 mm, centrum length 51 mm			Early adult	Male		x	5 Jun 1973

23	6816.5.6.73.16	Lumbar vertebra	L2, centrum diameter 50 mm, centrum length 55 mm			Early adult	Male	x	5 Jun 1973
24	6816.5.6.73.17	Lumbar vertebra	L3, centrum length 58 mm			Early adult	Male	x	5 Jun 1973
25	6816.5.6.73.18	Lumbar vertebra	L4, centrum diameter 48 mm, centrum length 60 mm			Early adult	Male	x	5 Jun 1973
26	6816.5.6.73.19	Lumbar vertebra	L5, centrum diameter 50 mm, centrum length 65 mm			Early adult	Male	x	5 Jun 1973
27	6816.5.6.73.20	Lumbar vertebra	L6, centrum diameter 54 mm, centrum length 63 mm			Early adult	Male	x	5 Jun 1973
28	6816.5.6.73.21	Lumbar vertebra	L7, centrum diameter 56 mm, centrum length 54 mm			Early adult	Male	x	5 Jun 1973
29	6816.5.6.73.22	Costa	No. 1		x	Early adult	Male	x	5 Jun 1973
30	6816.5.6.73.23	Costa	Middle, half	x		Early adult	Male	x	5 Jun 1973
31	6816.5.6.73.31	Pelvis	Half, acetabulum diameter 53 mm	x		Early adult	Male	x	5 Jun 1973
32	6816.5.6.73.32	Pelvis	Half, acetabulum diameter 51 mm		x	Early adult	Male	x	5 Jun 1973
33	6816.5.6.73.33	Femur	Proximal half	x		Early adult	Male	x	5 Jun 1973
34	6816.5.6.73.33a	Femur	Distal fragment			Early adult	Male	x	5 Jun 1973
35	6816.5.6.73.34	Tibia	Complete, length 367 mm, distal width 67 mm	x		Early adult	Male	x	5 Jun 1973
36	6816.5.6.73.35	Metatarsus	III	x		Early adult	Male	x	5 Jun 1973
37	6816.5.6.73.36	Metatarsus	IV	x		Early adult	Male	x	5 Jun 1973

Note: All in the collection of the SMNS.

Table 2. *Panthera l. spelaea* (Goldfuss, 1810) male skeleton remain from the Edingen (Brühl), Edinger Ried, Upper Rhine Valley open-air site in SW Germany.

No.	Inventory number	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Original	Date of find
1	6617.1.9.79.2	Cranium	Incomplete, restored, length 440 mm, condyl width 66 mm, P3 right width 26 mm			Senile	Male			27 Sep 1979
2	6617.1.7.89.3	Humerus	Proximal joint, joint length 114 mm	x		Senile	Male		x	25 Jul1989
3	6617.1.7.89.4	Ulna	Complete, length 432 mm		x	Senile	Male		x	25 Jul 1989
4	6617.1.7.89.2	Costa	Without proximal joint	x		Senile	Male		x	25 Jul 1989
5	6617.1.10.89.1	Cervical vertebra	C5, incomplete, centrum width 40 mm, centrum length 42 mm			Senile	Male		x	25 Nov 1989
6	6617.1.7.89.1	Lumbar vertebra	L7, incomplete, pathology, centrum width 58 mm, centrum length 52 mm			Senile	Male		x	25 Jul 1989
7	6617.1.7.89.5 6617.1.2.90.1	Femur proximal part distal part	Incomplete, length 440 mm, proximal joint width 51 mm, distal width 96 mm	x		Senile	Male		x	25 Jul 1989
8	6617.1.7.89.6	Tibia	Complete, length 383 mm	x		Senile	Male		x	25 Jul 1989

All in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS).

Table 3. *Panthera l. spelaea* (Goldfuss, 1810) male skeleton remain from Brühl (Koller), Schlangenwinkel, Upper Rhine Valley open-air site in SW Germany.

No.	Inventory number	Bone type	Commentary	left	right	Individual age	Sex	Bite marks	Original	Date of find
1	6616.17.3.82.2	Skull	Fragment, maxillary, P4 width 39 mm	x		High adult	Male			10 Mar 1982
2	6616.17.3.82.3 + 4	Skull	Fragment, maxillary, temporal, P4 width 39 mm		x	High adult	Male		x	10 Mar 1982
3	6616.17.7.81.1	Mandible	Nearly, complete, with C, P4, M1, length 165 mm, P4 width 28 mm, M1 width 28 mm	x		High adult	Male		x	09 Jul 1981
4	6616.17.3.82.8	Scapula	Incomplete, glenoid width 59 mm		x	High adult	Male		x	10 Mar 1982
5	6616.17.3.82.9	Humerus	Complete, legth 375 mm, distal width 96 mm		x	High adult	Male		x	10 Mar 1982
6	6616.17.3.82.10	Humerus	Complete, legth 375 mm, distal width 96 mm	x		High adult	Male		x	10 Mar 1982
7	6616.17.3.82.11	Radius	Complete, legth 351 mm, distal width 76 mm	x		High adult	Male		x	10 Mar 1982
8	6616.17.3.82.5	Thoracic vertebra	T1, incomplete, centrum width 36 mm, centrum length 38 mm			High adult	Male		x	10 Mar 1982
9	6616.17.3.82.6	Thoracic vertebra	T14, incomplete, centrum width 49 mm, centrum length 50 mm			High adult	Male		x	10 Mar 1982
10	6616.17.3.82.7	Lumbar vertebra	T1, incomplete, centrum width 53 mm, centrum length 70 mm			High adult	Male		x	10 Mar 1982
11	6616.17.3.82.12	Tibia	Complete, Legth 368 mm, distal width 69 mm	x		High adult	Male		x	10 Mar 1982
12	6616.17.7.81.2	Metatarsus	III, complete, length 148 mm	x		High adult	Male		x	09 Jul 1981

All in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS).

Table 4. *Panthera l. spelaea* (Goldfuss, 1810) bones from different Upper Rhine Valley sites in SW Germany. All in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS).

No.	Inventory number locality	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Original	Date of find
1	6617.3.1.67.18 Brühl, Spieswiesen-Ost	Cranium	Brain case fragment			Adult to senile			x	23 Jan 1967
2	6617.1.5.77.1 Edingen (Brühl), Edinger Ried	Cranium	Frontal, fragment							03 May 1977
3	6316.2.5.84.1 Lampertheim, In der Tanne	Mandible	Nearly, complete, length 280 mm M1 width 32 mm		x	Adult	Male		x	09 May 1984
4	6417.1.12.76.1 Heddesheim, Neuwiesen	Mandible	Incomplete with C, P3-4, M1, P4 width 29 mm, M1 width 30 mm, cracked by hyenas		x	High adult	Female	x	x	16 Dec 1976
5	6616.4.9.85.1 Otterstadt, Altrhein-Süd	Mandible	Incomplete with C, P3-4, M1, P4 width 27 mm, M1 width 28 mm, cracked by hyenas		x	Senile	Female	x	x	12 Sep 1985
6	6617.2.3.69.91 Brühl, Spielwiesen-West	Mandible	Fragment, with P3-4, M1, P4 width 23 mm		x	High adult	Female		x	25 Mar 1969
7	6816.5.8.70.1 Huttenheim, Huttenh. Kammer	Canine	Lower jaw	x		Adult	Female		x	19 Aug 1970
8	6616.7.2.87.1 Otterstadt, Waldwiesen	Humerus	Complete, length 357 mm, distal width 89 mm		x	Adult to senile	Female		x	17 Feb 1987
9	6717.2.7.65.1 Altlussheim, Almendwiesen	Humerus	Without proximal joint, distal width 94 mm		x	Adult to senile	Female		x	19 Jul 1965
10	6716.14.11.87.1 Huttenheim, Sandfeld	Humerus	Complete, length 330 mm, distal width 84 mm		x	Adult to senile	Female		x	26 Nov 1987
11	6616.14.12.83.1 Speyer, Deutschof	Humerus	Without proximal joint, distal width 86 mm		x	Adult to senile	Female		x	15 Dec 1983
12	6617.1.4.81.1 Edingen (Brühl), Edinger Ried	Humerus	Without proximal joint, distal width 95 mm		x	Adult to senile	Male		x	15 Apr 1981
13	6916.3.7.64.1 Karlsruhe, Neureut	Humerus	Without proximal joint, distal width 106 mm		x	Adult to senile	Male		x	07 Jul 1964
14	6617.7.9.62.20 Ketsch, Kreuzwiese	Humerus	Distal joint, width 80 mm		x	Adult to senile	Female		x	26 Sep 1962
15	6915.3.7.70.1 Wörth, Geisbögel	Humerus	Shaft		x	Late juvenile	Female		x	09 Jul 1970
16	6717.4.7.67.1 Altlussheim, Eichelgarten	Humerus	Complete, length 386 mm, distal width 102 mm	x		Adult to senile	Male		x	01 Jul 1967
17	6616.2.6.89.1 Brühl (Koller), Rheingewann	Humerus	Complete, length 371 mm, distal width 97 mm	x		Adult to senile	Male		x	29 Jun 1989
18	6617.6.8.79.1 Ketsch, Hohwiesen	Ulna	Complete, length 423 mm, largest width 72 mm		x	Adult to senile	Male		x	16 Aug 1979
19	6316.2.12.75.1 Lampertheim, In der Tanne	Ulna	Incomplete, largest width 75 mm		x	Adult to senile	Male			10 Dec 1975
20	6616.16.12.92.1 Otterstadt, Altrhein-Nord	Ulna	Incomplete, largest width 60 mm		x	Late juvenile	?Female		x	22 Dec 1992
21	6616.15.7.73.1 Altlussheim, Silzwiesen	Ulna	Fragment, largest width 76 mm	x		Adult to senile	Male			31 Jul 1973
22	6616.7.4.81.1 Otterstadt, Waldwiesen	Radius	Complete, length 362 mm, distal width 76 mm	x		Adult to senile	Male	x	x	23 Apr 1981
23	6617.2.9.67.30 Brühl, Spieswiesen-West	Radius	Distal half, distal width 74 mm		x	Adult to senile	Male		x	25 Sep 1967
24	6915.2.12.69.1 Wörth, Rheinanlagen	Radius	Shaft		x	?	?		x	19 Dec 1969
25	6616.16.4.81.1 Otterstadt, Altrhein-Nord	Cervical vertebra	Atlas, incomplete			Adult to senile			x	23 Apr 1981
26	6616.4.1.87.3 Otterstadt, Altrhein-Süd	Cervical vertebra	C5, incomplete, centrum width 41 mm, centrum length 33 mm			Adult to senile			x	09 Jan 1987
27	6816.5.5.74.4 Huttenheim, Huttenh. Kammer	Lumbar vertebra	L5, incomplete, centrum width 55 mm, centrum length 68 mm			Adult to senile			x	01 May 1974
28	6316.3.3.80.1 Lampertheim, Lüderitzbucht	Sacrum	Centrum width 58 mm			Adult to senile			x	20 Mar 1980
29	6617.2.8.83.1 Brühl, Spieswiesen-West	Pelvis	Half, joint width 49 mm		x	Adult to senile	Male		x	02 Aug 1983
30	6616.16.4.81.2 Otterstadt, Altrhein-Nord	Pelvis	Half, joint width 46 mm	x		Adult to senile	Female		x	23 Apr 1981
31	6616.8.9.78.1 Otterstadt, Waldwiesen	Pelvis	Half, joint width 49 mm		x	Adult to senile	Male	x	x	19 Sep 1978
32	6417.1.10.76.1 Heddesheim, Neuwiesen	Femur	Complete, length 385 mm, distal width 83 mm, proximal joint diameter 42 mm		x	Adult to senile	Female		x	12 Oct 1976
33	6717.13.8.83.1 Wiesental, Allmendweg	Femur	Incomplete, distal width 42 mm	x		Adult to senile	Female	x	x	10 Aug 1983
34	6617.6.9.62.7 Ketsch, Hohwiesen	Femur	Shaft	x		Late juvenile	?		x	26 Sep 1962

Table 4 – *continued*

No.	Inventory number locality	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Original	Date of find
35	6616.2.6.89.2 Brühl (Koller), Rheingewann	Femur	Incomplete, length 405 mm, proximal joint width 44 mm		x	Adult to senile	Female	x	x	29 Jun 1989
36	6516.6.5.75.1 Altrip, Neuhofener Altrhein	Femur	Shaft		x	?	?		x	?
37	7213.3.7.76.1 Lichtenau, Hasenkopf	Femur	Distal joint		x	Adult to senile	?		x	08 Jul 1976
38	6616.12.6.66.1 Speyer, Binsfeld-Südost	Tibia	Complete, legth 340 mm, distal width 61 mm		x	Adult to senile	Female		x	29 Jun 1966
39	6816.5.11.87.5 Huttenheim, Huttenh. Kammer	Tibia	Without distal joint	x		Adult to senile	Male		x	26 Nov 1987
40	6717.12.8.83.1 Wiesental, Viehweg	Tibia	Incomplete, strong pathology	x		?Senile	?Female		x	10 Sep 1983
41	6617.2.7.67.63 Brühl, Spieswiesen-West	Phalanx	1, complete			Adult to senile			x	08 Jul 1967

(Goldfuss, 1823) were published recently (Diedrich 2008b; Figure 2(B)), the brown bear and the cave bear *U. arctos* and *U.* cf. *spelaeus* materials are under investigations. Additionally to those carnivores, a few remains of wolves *Canis lupus* subsp. and only a single pelvic of *P. pardus* were collected over the years. Coincidently, occurrence of hyena den sites and lion remains is often overlapping and is also recorded at the cave localities (Figure 2(B)). The distribution of lions, which is a special taphonomic result, is relating very often to hyena dens (cf. Diedrich 2009a, 2010b) and cave bear dens (Diedrich 2009e, 2010d). Only a few lion localities are without the presence or indirect proof of hyena activities.

However, the last lions of Eurasia have coexisted with two other lion subspecies such as the north American *P. l. atrox* (cf. Harington 1969) and the African *P. l.* subsp. and with tigers such as the *P. l. tigris* in different geographical regions (cf. Barnett et al. 2009; Figure 2(A)), but in central Europe in the glacial, there seem to have been only one large felid with *P. l. spelaea* and one medium-sized *P. pardus*, both being recorded in the Upper Rhine River Valley in a ratio of 100:1, demonstrating the rareness of l.pards in lowland environments.

Material and methods

About 20,000 mostly unstudied bones were mainly collected from the gravel pit sieving dumps between 1955 and 2007. The material is housed in the Staatliches Museum für Naturkunde Stuttgart (SMNS). Another single lion jaw is in the Senckenbergmuseum Frankfurt (SMF).

Three *P. l. spelaea* skeleton remains, one skeleton and two possible skeleton relicts with mainly large bones, were collected from Baden-Württemberg for the Upper Rhine Valley (Figure 2(B)). All of them are described and figured monographically with all the bones listed separately in the tables with other single bone records found at 28 localities along the Rhine River (Tables 1–4).

The osteometric scheme for the sex identifications and comparisons is followed by Gross (1992), whereas the data from the Upper Rhine Valley lion bones are compared to available data from the literature.

Also, the lion bone damages were compared to other Pleistocene bone materials from different caves and open-air sites, which are recently published for many localities of Germany and Czech Republic. The bone taphonomy was, in general, compared with the open-air sites of NW Germany and with the modern African hyena den sites.

Finally, the main important cave art figurations of Upper Pleistocene lions from French caves were used for the illustration reconstruction of the habitus of the last lions of Europe.

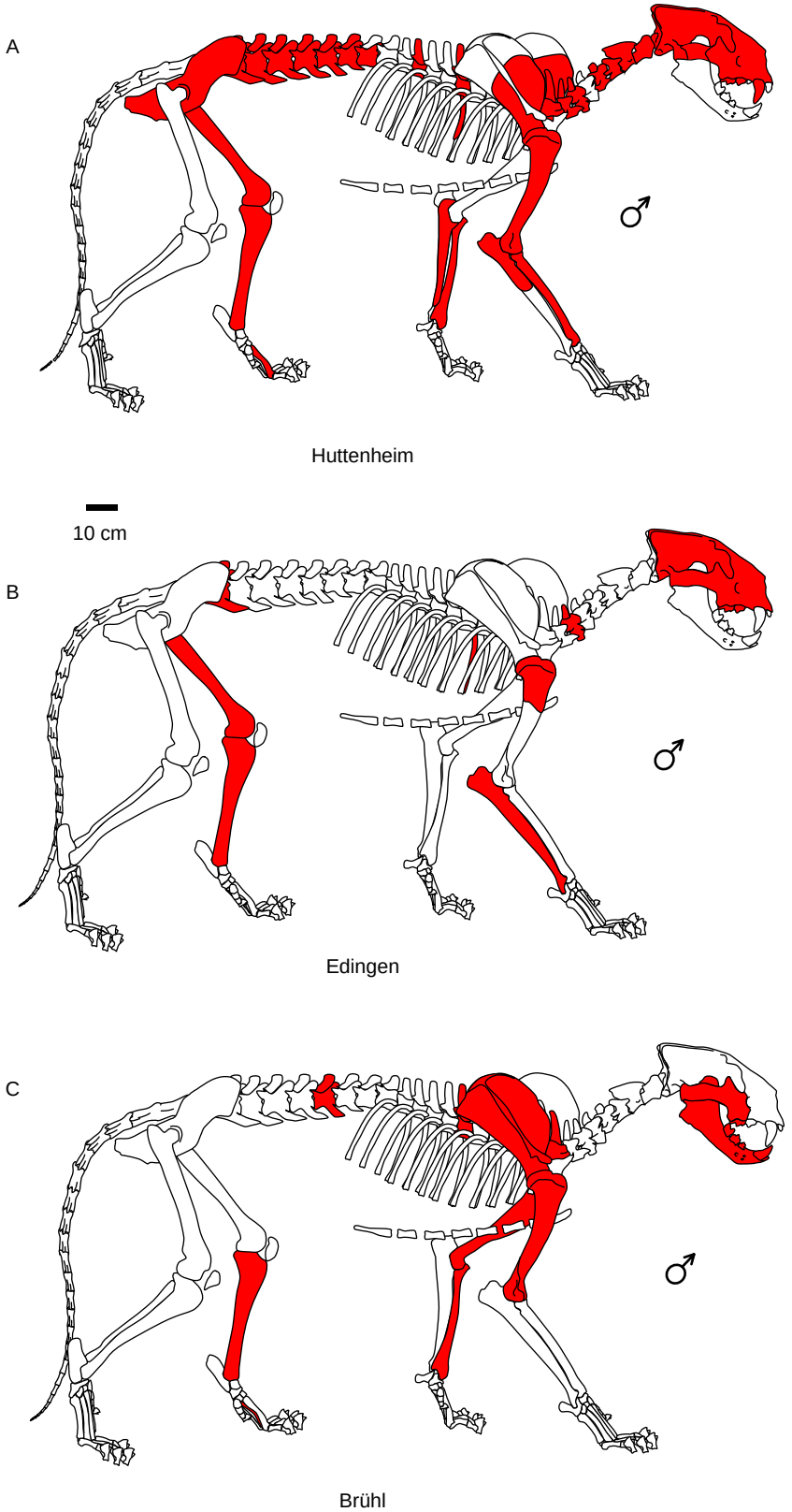

Figure 3. Material of at least three *P. l. spelaea* skeleton remains from three localities of the Upper Rhine Valley (Germany). (A) One of the most complete skeleton finds in a German open-air locality is the small male from Huttenheim, Huttenheimer Kammer. (B) In the skeleton from Edingen (Brühl), Edinger Ried, the skull is remarkable. (C) The lion remain of Brühl (Koller), Schlangenwinkel is most incomplete.

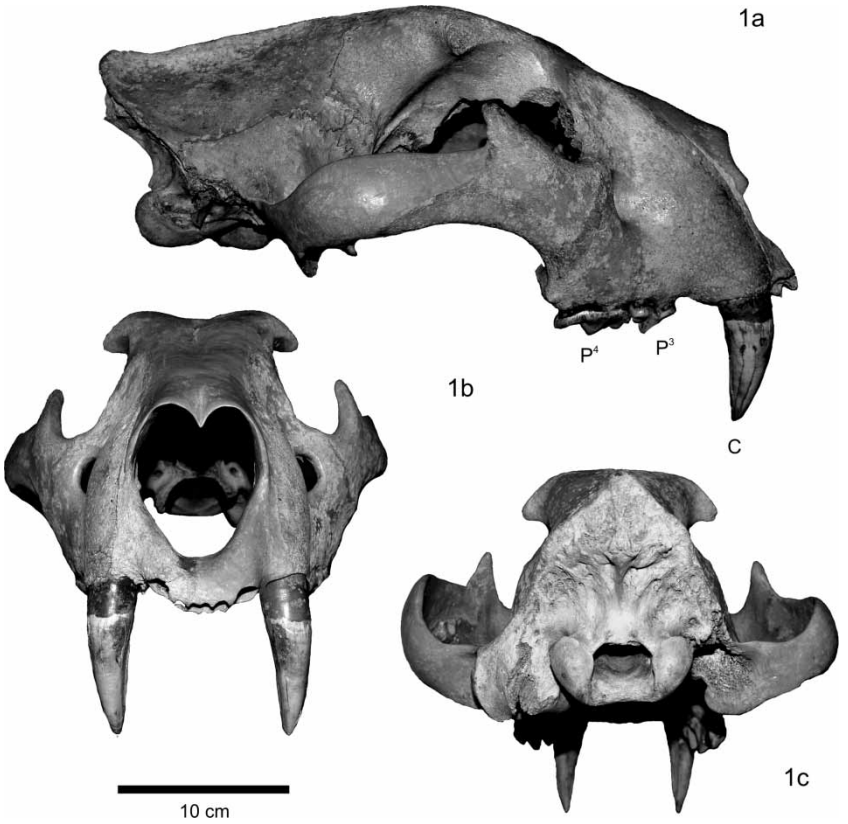

Figure 4. (1) Skull from the early adult small male skeleton of Huttenheim, Huttenheimer Kammer (Germany) (SMNS no. 6816.5.6.73.1), (a) lateral right, (b) frontal and (c) occipital.

Geology and dating

The Upper Rhine Valley terrace stratigraphy of about 100 m thick Early to Late Pleistocene fluvial gravel-dominated sediments was published by Bartz (1982) for the Karlsruhe region, whereas for the upper part, into which most of the gravel pits reach only 30 m deep, such as in Reilingen (Ziegler and Dean 1998); here, the latter stratigraphy is used for a generalised section to demonstrate the most probable lion bone layers (Figure 2(C)). The main gravel material originates from the Alps, but side rivers also transported material into the Rhine Graben structure; and the terrace is 100 m above sea level today (Bartz 1982).

There are three main Pleistocene gravel 'layers' (Figure 2(C)). The lower 'Unteres Kieslager' gravels are dated as Early Pleistocene Elsterian deposits ending in a sedimentary sequence with an interglacial wood-bearing layer of the Holsteinian (Bartz 1982; Ziegler and Dean 1998). The second 'Mittleres Kieslager' is suggested of Middle Pleistocene Saalian. Finally, the Upper Pleistocene starts with the Eemian warm period layers, which are pond and swamp (peat) sediments. Those are overlayed by the last gravel series, the 'Oberes Kieslager'. In general, those Upper Pleistocene 'Niederterrassen' (lower terraces) of the Upper Rhine Valley are about 8 km wide extended fluvial gravels, sands and resulting dunes (Bartz 1982).

Most of the megafauna of the Upper Rhine Valley gravel pits are of Upper Pleistocene and mainly of glacial Weichselian/Wuermian age (see Figure 2(C)), but several cases of the bone material of interglacial mammals proved to be of Eemian ages (Adam 1966; Geissert et al. 1986; Rathgeber 1994; Rathgeber and Ziegler 2003). Most of the lion bones are due to their bone preservation from the Upper Pleistocene (Eemian–Weichselian/Wuermian), whereas it cannot be excluded, which in a few cases even older and reworked material is present, reaching into the late Middle Pleistocene, which is indicated by the presence of few Middle Pleistocene faunal elements such as *Mammuthus trogontherii*, *Alces latifrons*, *Bubalus murrensis* and *Trogontherium cuvieri*.

The mainly Upper Pleistocene megafauna bone materials collected with the lion material at the Upper Rhine Valley localities (Figure 2(B)) consist of mixed glacial elements such as *M. primigenius*, *Equus caballus przewalskii*, *E. hydruntinus*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Bison priscus*, *Ovibos moschatus*; an intermediate fauna: *E. c. germanicus*, *Stephanorhinus*

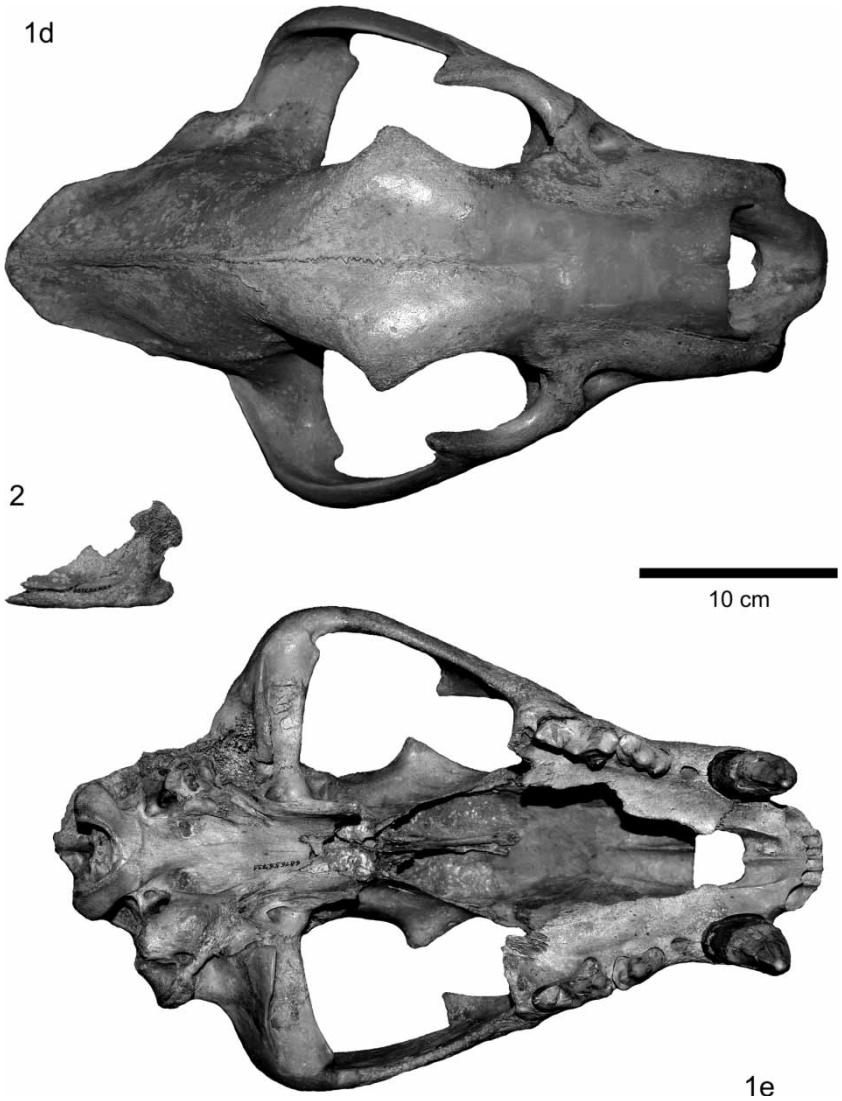

Figure 5. Skull from the early adult small male lion skeleton of Huttenheim, Huttenheimer Kammer (Germany). (1) Cranium (SMNS no. 6816.5.6.73.1), (d) dorsal and (e) ventral. (2) Left mandible fragment (SMNS no. 6816.5.6.73.2), lateral.

hemitoechus, *Megaloceros giganteus*, *Cervus elaphus*, *Bos primigenius*, *C. c. spelaea*, *P. pardus*, *C. lupus* subsp., *Vulpes vulpes*, *U. spelaeus* cf. *spelaeus*; and interglacial ones: *Palaeoloxodon antiquus*, *S. kirchbergensis*, *Sus scrofa*, *Hippopotamus amphibius*, *A. alces*, *Dama dama*, *Capreolus capreolus*, *Castor fiber*, *U. arctos* and *Lynx lynx*.

Systematic paleontology

Family *Felidae* (Gray 1821)
Genus *Panthera* (Oken 1816)
Species *Panthera l.* (Linnaeus 1758)
Panthera l. spelaea (Goldfuss, 1810)

Figures 4–22

The Pleistocene lion material from the Upper Rhine Valley consists of three skeleton remains (Figure 3) and many isolated bones, whose exact datation is not possible. The preserved skeletons are only of the larger bones, and there is only one small male lion skeleton remain from Huttenheim, that is much more complete, being one of the most complete skeletons from Late Pleistocene open-air sites of Europe. The other two skeleton parts sadly include only a few bones which indicate originally complete skeletons in articulation at those sites. At Huttenheim, at least the lion skeleton must have been originally 100% complete, but the problem at all those gravel pit sites is the exploring techniques, at which generally all small bones got lost, such as seen in the all skeleton remains presented herein (Figure 3).

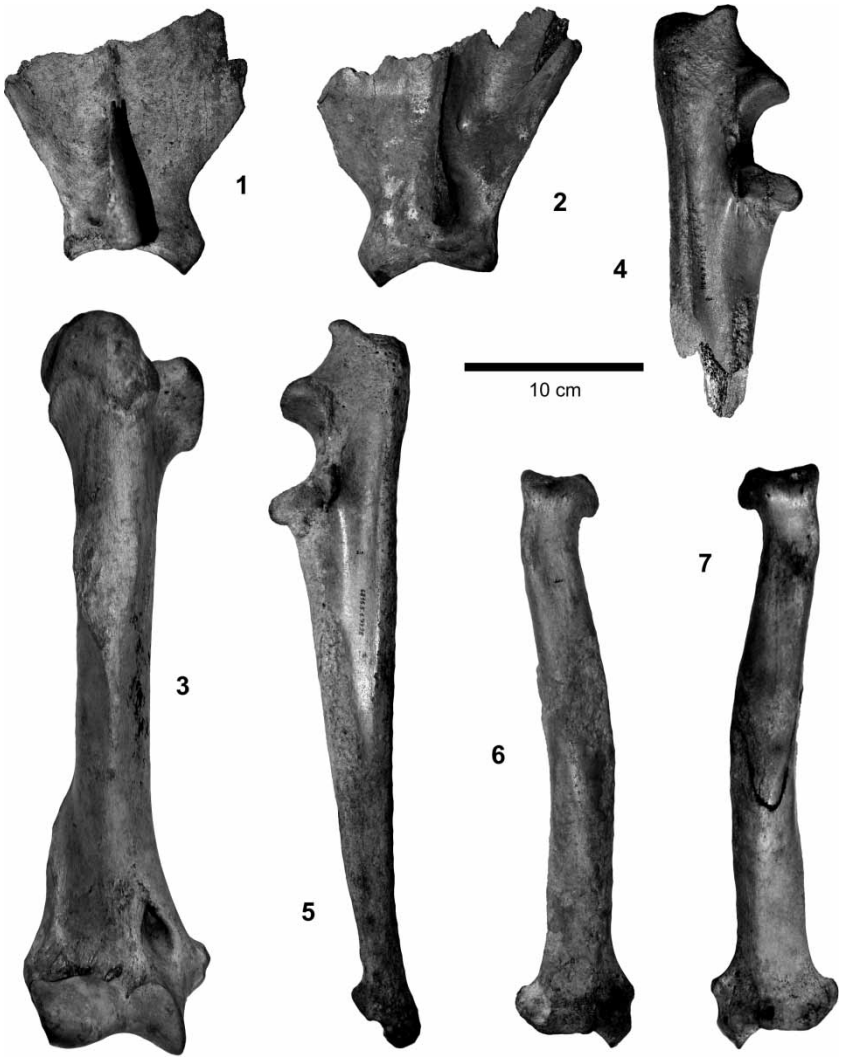

Figure 6. Forelimb bones from the early adult small male lion skeleton of Huttenheim, Huttenheimer Kammer (Germany). (1) Right scapula (SMNS No. 6816.5.6.73.24), lateral. (2) Left scapula (SMNS No. 6816.5.6.73.25), lateral. (3) Right humerus (SMNS No. 6816.5.6.73.26), cranial. (4) Right ulna fragment (SMNS No. 6816.5.6.73.30), lateral. (5) Left ulna (SMNS No. 6816.5.6.73.28), lateral. (6) Right radius (SMNS No. 6816.5.6.73.29), lateral. (7) Left radius (SMNS No. 6816.5.6.73.27), lateral.

Small male lion skeleton from Huttenheim, Huttenheimer Kammer

This is the most complete skeleton from the Upper Rhine Valley consisting of 37 large bones including the most complete skull (Figures 3(A), 4–8, Table 1). The *skull* (Figures 4 and 5) is few incomplete but has only left with the C, P^{3-4}-dentition preserved on both sides. In total length, it is 375 mm with an occipital width of 50 mm. The teeth are not much used and indicate an individual of a medium adult age, which was, therefore, possibly not fully grown up. Both P^4 lengths measure 32 mm. This *post-cranial* skeleton consists of seven forelimb bones (Figure 6). Both scapulae are half preserved. The right humerus and the right ulna are complete as in both radii. From the left ulna, only the proximal half was collected. The vertebral column is one of the most complete in open-air skeleton finds of Europe and consists of six cervical including atlas and axis, six thoracic and all seven lumbar vertebrae (Figure 7). Two incomplete ribs (Figure 8.7 and 8.8) are preserved, one is the right first one, the other is from the left middle thorax region. The pelvic (Figure 8.1 and 8.2) is lacking the sacrum and other smaller parts. The hind legs are represented by the incomplete left femur, the one complete left tibia and the left metatarsalia III and IV (Figure 8.3–8.6).

Medium-sized male lion skeleton remain from Edingen (Brühl), Edinger Ried

This skeleton remain only consists of 12 large bones including the cranium (Figures 9–11; Table 2). The *skull* (Figures 9 and 10) was damaged and repaired. Some parts

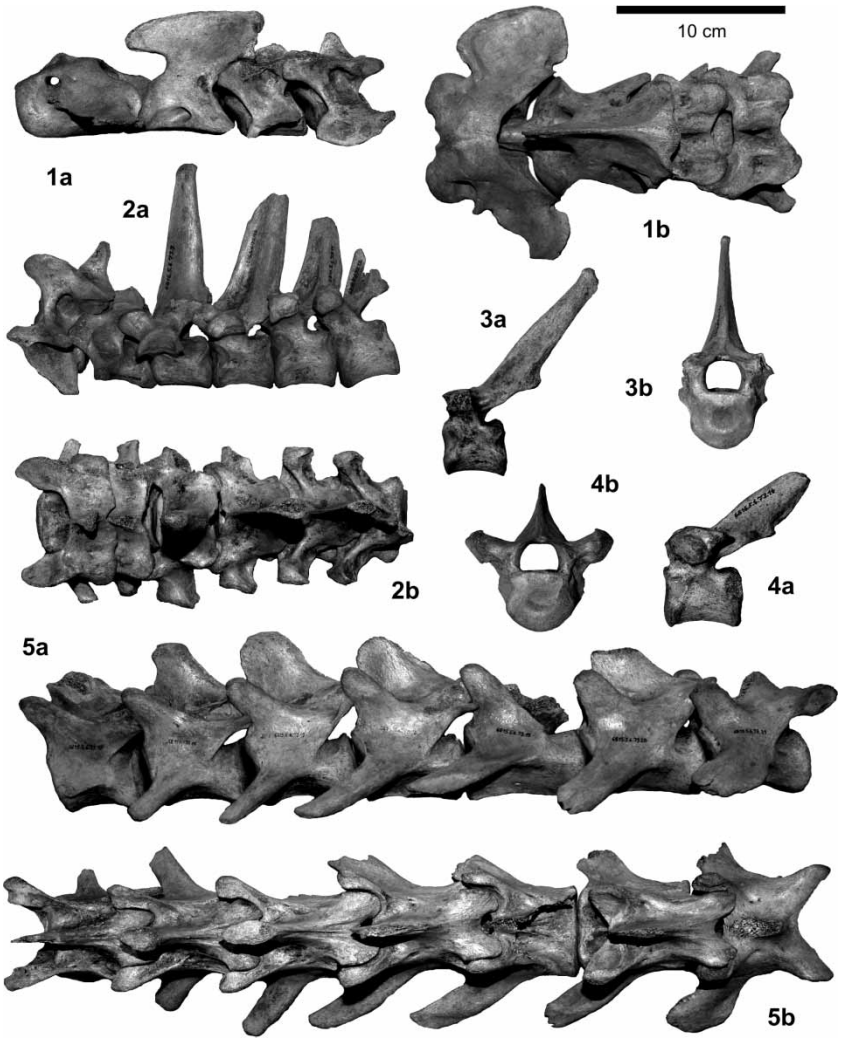

Figure 7. Vertebrae from the early adult small male lion skeleton of Huttenheim, Huttenheimer Kammer (Germany). (1) First four cervical vertebrae including atlas and axis (SMNS No. 6816.5.6.73.3-6), (a) lateral and (b) dorsal. (2) Vertebrae C6 to T4 (SMNS No. 6816.5.6.73.7-12), (a) lateral and (b) dorsal. (3) Thoracic vertebra 6/8 (SMNS No. 6816.5.6.73.13) (a) lateral and (b) cranial. (4) Thoracic vertebra 10/12 (SMNS No. 6816.5.6.73.14), (a) lateral and (b) cranial. (5) All seven lumbar vertebrae (SMNS No. 6816.5.6.73.15-21), (a) lateral and (b) dorsal.

of the premaxillaries, the left zygomatic arch and the occipital part were completed. The only preserved tooth is the incomplete right P^3. Tooth P^4 is preserved only with root remains. The total length is not for sure, but the reconstruction is well done and allows the main important measurements for the sex identification. The *postcranial* remains are few (Figure 11). The right humerus is only the upper third, whereas the right ulna is complete. The vertebral column has only the fifth cervical and the last seventh lumbar vertebra. This one is pathological on the right processus transversus. A middle proximally damaged rib is another thoracic element. Finally, the left hind -limb is preserved with the damaged femur and complete tibia.

Lion skeleton from Brühl (Koller), Schlangenwinkel

Only eight bones are represented including a *skull* fragment and the right mandible (Figures 12–14.1, Table 3). The skull is a right maxillary and zygomatic arch fragment including the P^4. The lower jaw is complete, but is missing all incisives and the P_3. Both the upper P^4 and the lower M_1 are well worn which indicate a high adult animal. The teeth proportions (see Table 3) would fit to males. Postcranial bones are from the fore limb, an incomplete right scapula and both humeri, and finally a left radius (Figures 12.2–12.4 and 13.1). The vertebral column is preserved by three vertebrae: the first thoracic, the last 14th thoracic and the third lumbar (Figure 13.3–13.5). Finally, the hindlimb bones are the

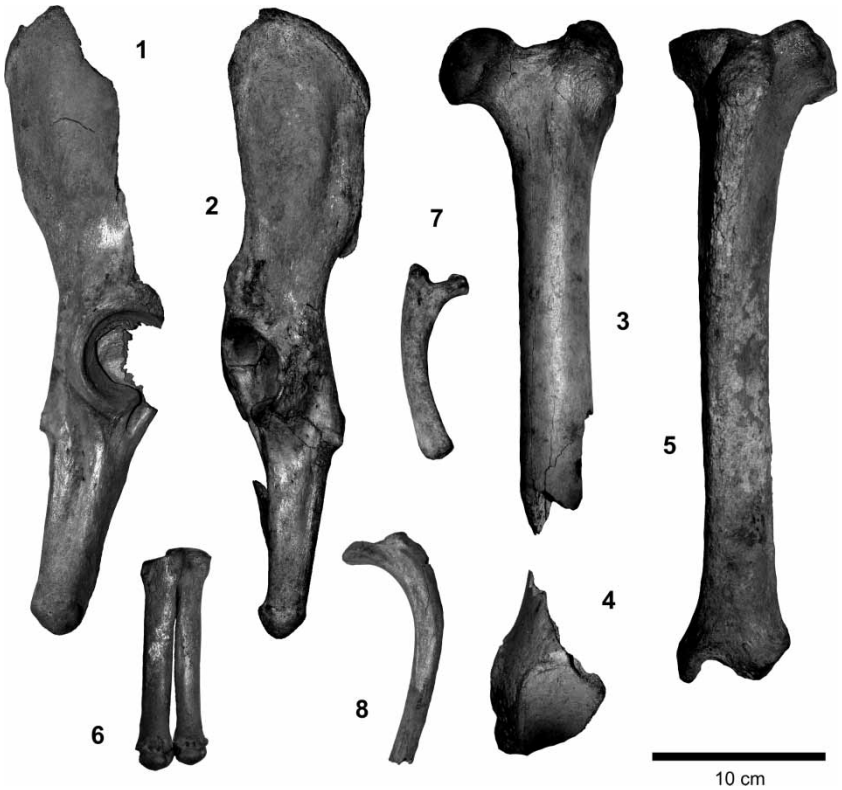

Figure 8. Hind-limb and rib bones from the early adult small male lion skeleton of Huttenheim, Huttenheimer Kammer (Germany). (1) Right pelvis part (SMNS No. 6816.5.6.73.32), lateral. (2) Left pelvis part (SMNS No. 6816.5.6.73.31), lateral. (3) Left femur (SMNS No. 6816.5.6.73.33), cranial. (4) Left femur distal joint fragment (SMNS No. 6816.5.6.73.33a), cranial. (5) Left tibia (SMNS No. 6816.5.6.73.34), cranial. (6) Left metatarsus III and IV (SMNS No. 6816.5.6.73.35 and 36), cranial. (7) First right costa (SMNS No. 6816.5.6.73.22), lateral. (8) Middle left costa (SMNS No. 6816.5.6.73.23), lateral.

left tibia and the left metatarsus III (Figures 12.5 and 13.2).

Other single lion bone remains from different open-air sites

All in total, 41 more isolated bones were collected at several gravel pits (Table 4). *Cranial* remains are mostly lower jaws, whereas only one is most complete from Lampertheim (Figure 14.2). Another small sized is from an unknown locality in the Upper Rhine Valley (Figure 14.3). Three more jaw fragments are present. The one from the site Brühl, Spieswiesen-West (Figure 15.2), has fresh fractures and was modernly damaged. Here, the P_4 is complete, the M_1 is incomplete and a root fragment sticks in the alveole of the P_3. Two other lower jaws from Heddesheim, Neuwiesen and Otterstadt, Altrhein-Süd are damaged by carnivore (probably hyenid) activities and are typically broken diagonally, both missing the rami (Figure 15.4 and 15.5). Although the first one is from an adult (canine was broken modern), the second one has strongly worn teeth, especially the canine, proving an older individual age. From a lower jaw, one canine of an adult lion was collected in Huttenheim, Huttenheimer Kammer (Figure 15.3). Finally, a brain case fragment of a high adult to older lion was found in Brühl, Spieswiesen-West (Figure 15.1).

Many *forelimb* bones are collected (Figures 16–18), whereas the humeri dominate (9), followed by the ulnae (4) and finally the radii (3). Their localities and metrics and statistical sexual dimorphism analyses can be obtained from Table 4 and Figure 23. Two of the humeri are remarkable. In general, all are from grown-up animals, but one from Speyer, Deutschhof (Figure 16.4) has no proximal joint cap and belonged, therefore, to an early adult individual. Another humerus from Edingen (Brühl), Edinger Ried (Figure 17.4), is from a similar old small individual. One humerus from Brühl (Koller), Rheingewann (Figure 16.1), has a bone growth and an enlarged entepicondylar foramen. The half humerus from Ketsch, Kreuzwiese (Figure 16.5), is strange in its proportions and seems to represent also a pathological remain. Possibly, the single preserved phalanx I from Brühl, Spieswiesen-West (Figure 17.8), is from the fore limb.

A few isolated *vertebrae* are represented in Figure 19.1–19.3. A single atlas was found in Otterstadt, Altrhein-Nord and the fifth cervical vertebra in Otterstadt, Altrhein-Süd, whereas the fifth lumbar vertebra was collected in Huttenheim, Huttenheimer Kammer.

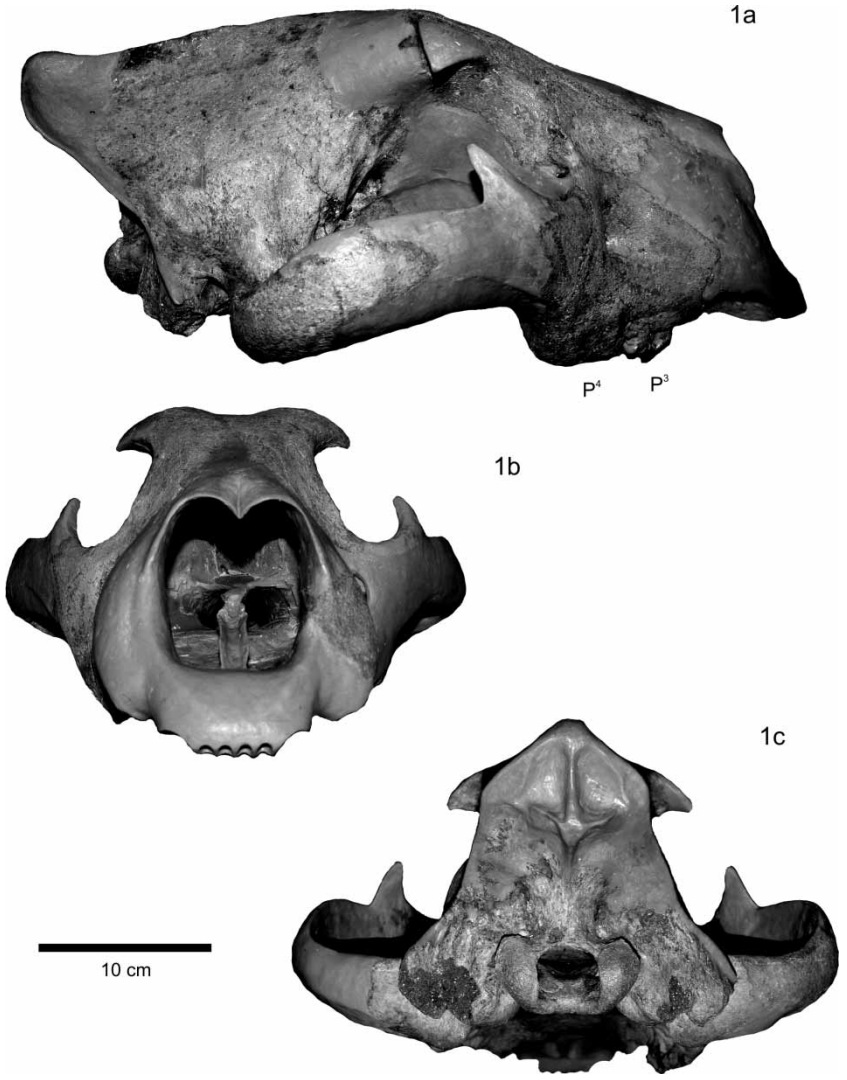

Figure 9. Skull from the adult large lion skeleton of Edingen (Brühl), Edinger Ried (Germany) (SMNS no. 6617.1.9.72.2). (1a) Lateral right, (1b) frontal and (1c) occipital.

The *pelvic* bones (Figure 19.4–19.7) consist of a single sacrum from Lampertheim, Lüderitzbucht and three incomplete remains of fused ilium/ischium/pubis bones from the sites Otterstadt, Altrhein-Nord, Brühl, Spieswiesen-West and Otterstadt, Waldwiesen.

Hind limb remains are represented only by the femora and tibiae (Figures 20–22) again from many different sites (cf. Table 4). Only one femur of Heddesheim, Neuwiesen is complete (Figure 20.1), the others are incomplete; but this resulted not by modern damage, instead by large carnivore activity. At the two femora, one from Wiesental, Allmendweg and the other from Brühl (Koller), Rheingewann (Figures 20.3 and 21.1), similar parts were chewed of at the trochanter major and the distal joint. Also, bite marks on the shafts and joint prove to be the scavenging damages. Finally, there is only one smaller femur shaft without joints of a juvenile (older cub), which is the only record of such a young animal in between all other bones of the Upper Rhine Valley material. One tibia from Speyer, Binsfeld-Südost is complete (Figure 22.1), but in the other much larger one of Hutttenheim, Huttenheimer Kammer (Figure 22.2), the distal joint is missing. Finally, the very pathological tibia of Wiesental, Viehweg (Figure 22.3) is remarkable, which will be discussed under 'Lion diseases: pathologies'.

Discussion

Skeleton finds in Europe

Skeletons of Late Pleistocene steppe lion *P. l. spelaea*, in former times called 'cave lion' (e.g. Dawkins and Sanford 1900), are rare all over Europe and are represented by a few skeletons from Spain, France, Czech Republic (cf. Altuna 1981; Tichy 1985; Diedrich

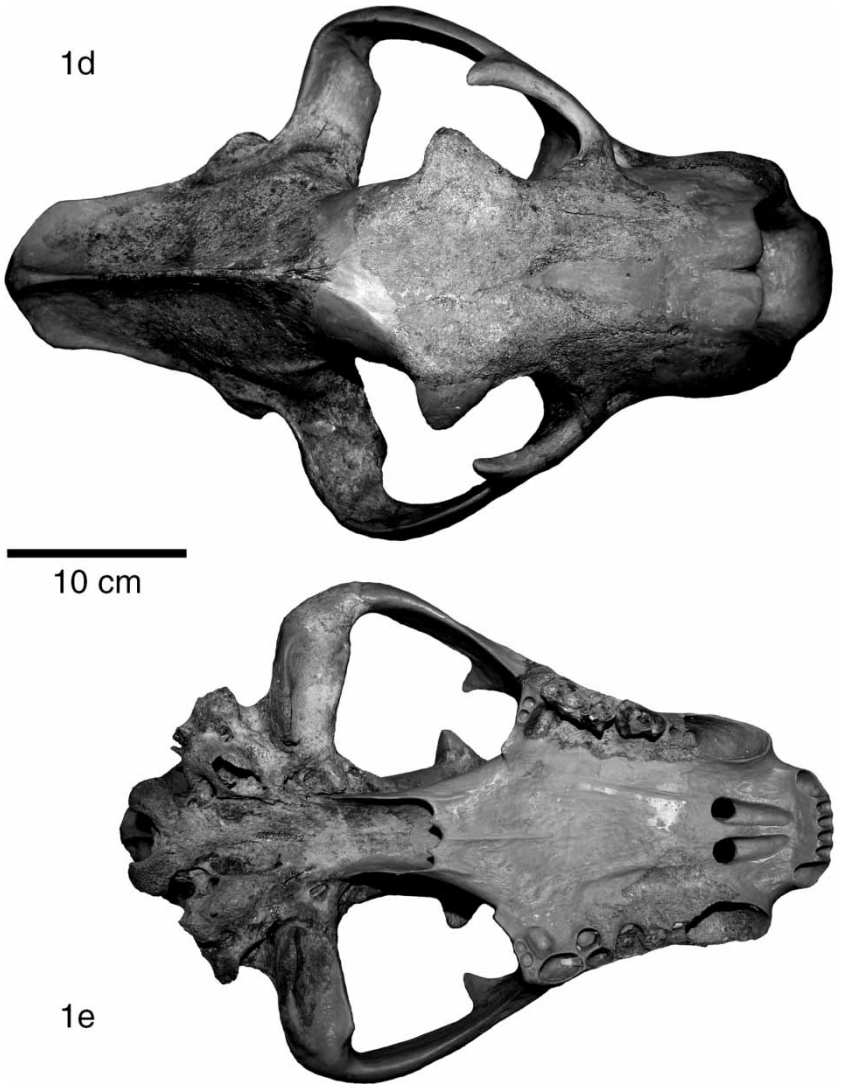

Figure 10. Skull from the adult large lion skeleton of Edingen (Brühl), Edinger Ried (Germany) (SMNS No. 6617.1.9.72.2). (1d) Dorsal and (1e) ventral.

and Žák 2006; Diedrich 2007a,) and by recently new discovered finds from the Urşilor Cave in Romania (Diedrich et al. 2009b–d) or from the Eemian lake deposit Neumark–Nord Lake I in central Germany (Diedrich 2010a,c). The incomplete male lion from the German open-air site Siegsdorf (Bavaria, south Germany) was for long the only known Late Pleistocene lion skeleton of Germany (cf. Gross 1992), at which the close relationship between the African modern lions *P. l.* and the steppe lions *P. l. spelaea* was genetically proven (Barnett et al. 2009).

Sexual dimorphism and lion population

The teeth, skull, lower jaw and long bone material are very useful for the sex identifications of modern and Pleistocene lions (cf. Gross 1992; Diedrich 2009d, 2010b, Turner 1984). Therefore, here, the presented large amount of long bones and the two crania from the Upper Rhine Valley were analysed including other remains from different German and Czech caves (Bohemian Karst caves, Czech Republic: Srbsko Chlum-Komin Cave; Moravian Karst caves, Czech Republic: Výpustek Cave, Sloup Caves; Sauerland Karst Caves, Germany: Perick Caves, Bilstein Caves, Keppler Cave, Balve Cave; Frankonian Karst caves, Germany: Zoolithen Cave; Heller (1953), Diedrich (2007b, 2008a,b, 2009a–2009d, 2010d, 2011a,b). They were compared with the published data from Italian caves (Bona 2006), Spanish caves (Altuna 1981), English caves (Dawkins and Sanford 1900), French caves (Argant 1988), Austrian caves (Tichy 1985), Croatian caves (Guzvica 1998) and Russian caves (Baryshnikov and Boeskorov 2001). Additionally, the open-air site material from northern Germany

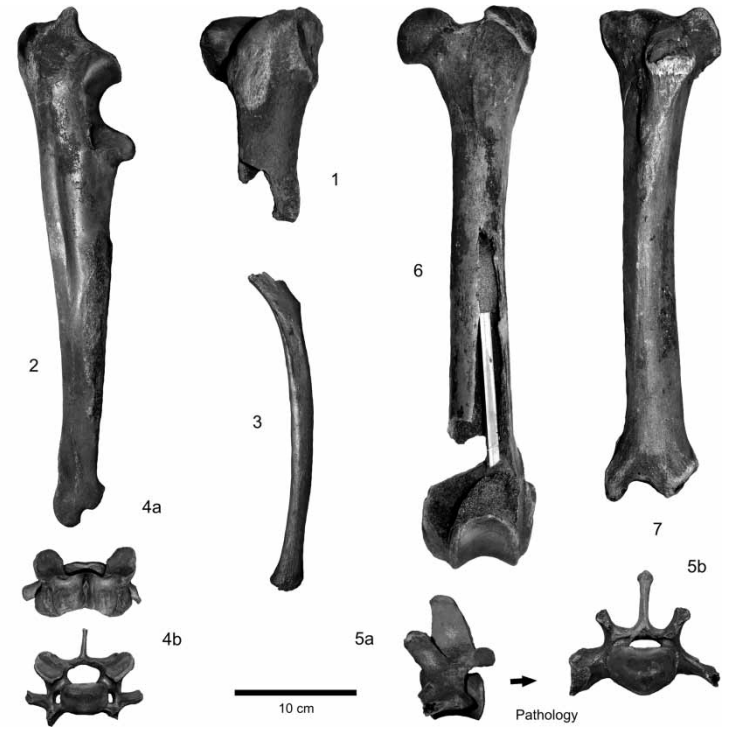

Figure 11. Postcranial bones from the adult large lion skeleton of Edingen (Brühl), Edinger Ried (Germany). (1) Left humerus fragment (SMNS No. 6617.1.7.89.3), cranial. (2) Right ulna (SMNS No. 6617.1.7.89.4), lateral. (3) Middle left costa (SMNS No. 6617.1.7.89.2), lateral. (4) Cervical vertebra 5 (SMNS No. 6617.1.10.89.1), (a) dorsal and (b) cranial. (5) Lumbar vertebra 7 – abnormal in its processus transversi – beginning of sacral fusion (SMNS No. 6617.1.7.89.1), (a) lateral and (b) cranial. (6) Left femur (SMNS No. 6617.1.7.89.5), cranial. (7) Left tibia (SMNS No. 6617.1.7.89.6), cranial.

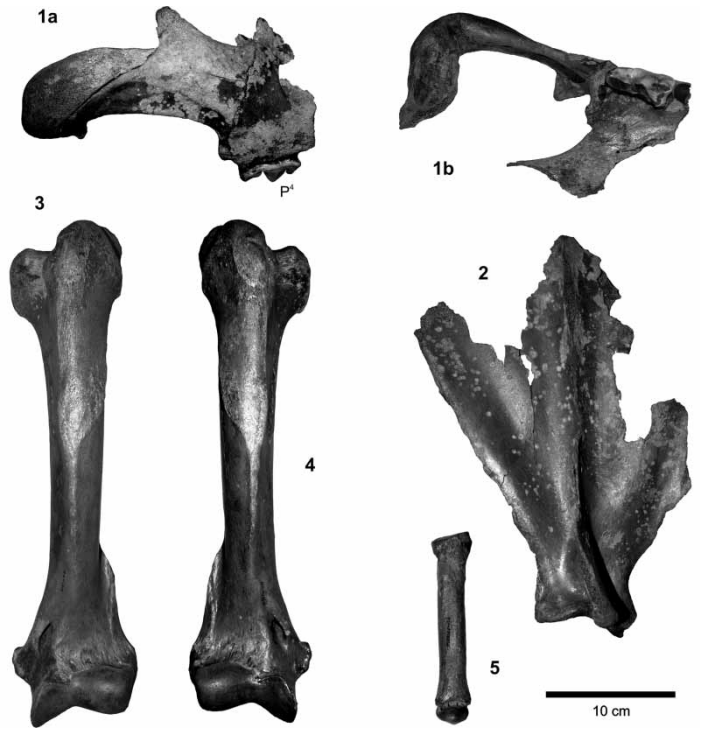

Figure 12. Cranial and limb bones from the adult lion skeleton of Brühl (Koller), Schlangenwinkel (Germany). (1) Right skull fragment (SMNS No. 6616.17.3.82.9.3 and 4) (a) lateral and (b) ventral. (2) Right scapula (SMNS No. 6616.17.3.82.8), lateral. (3) Left humerus (SMNS No. 6616.17.3.82.9), cranial. (4) Right humerus (SMNS No. 6616.17.3.82.10), cranial. (5) Left metatarsal III (SMNS No. 6616.17.7.81.2), cranial.

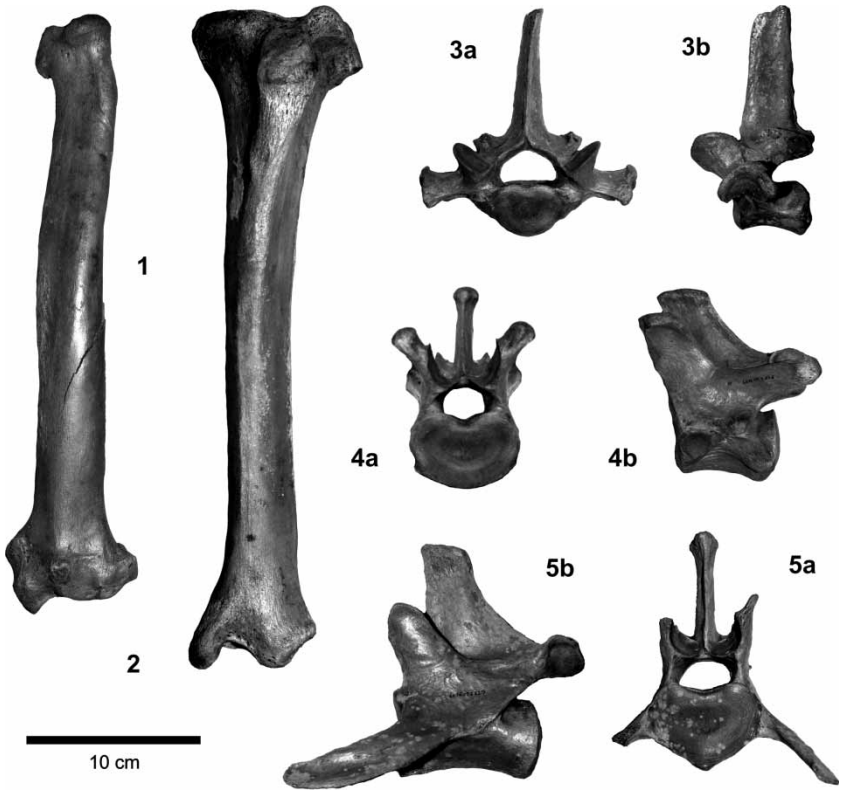

Figure 13. Vertebrae and limb bones from the adult lion skeleton of Brühl (Koller), Schlangenwinkel (Germany). (1) Left radius (SMNS No. 6616.17.3.82.11), lateral. (2) Left tibia (SMNS No. 6616.17.3.82.12), cranial. (3) Thoracic vertebra 1 (SMNS No. 6616.17.3.82.5), (a) cranial and (b) lateral. (4) Last thoracic vertebra 14 (SMNS No. 6616.17.3.82.6), (a) cranial and (b) lateral. (5) Lumbar vertebra 3 (SMNS No. 6616.17.3.82.7) (a) cranial and (b) lateral.

(Diedrich 2011b), Czech Republic (Diedrich 2007b) was important to include with the large amount of bones from the Upper Rhine Valley. The result is an enlarged database about Late Pleistocene Eurasian steppe lions' sexual dimorphism, in which two clusters separate mostly well smaller lionesses from larger male lions, whereas small lion and large lionesses overlap (Figure 23). The problem of the Upper Rhine Valley material is the probable mixing of well-known smaller interglacial and larger glacial-sized lions (Gross 1992; Diedrich 2010b). Especially, not fully grown-up individuals (lioness of Srbsko Cave: Diedrich and Žák (2006); lioness of Ursilor Cave: Diedrich et al. (2009a–2009d)) are not well for use in such statistics, which can compare recently only fully grown-up individuals.

The proportions of the steppe lion skeleton from Huttenheim, Huttenheimer Kammer with preserved skull (Figure 3(A)) indicate a smaller male individual with its medium-sized bone proportions (Figure 23), which is close in its size to the male lion skeleton of Siegsdorf (cf. Gross 1992). The second fragmentary skeleton from Edingen (Brühl), Edinger Ried (Figure 3(B)) also comprises a male whose skull and postcranial long bones are much larger in their proportions to the above-mentioned one. The long bone metrics fall into the larger male bone clusters (cf. Figure 23) and are closer to proportions of the male lion skeleton of Arrikrutz (cf. Altuna 1981). The lion skeleton remain of Brühl (Koller), Schlangenwinkel is mostly incomplete, but the available long bones allow a secure determination as another male individual (Figure 23), which falls into the larger male sizes compared with the material of Arrikrutz (cf. Altuna 1981). However, from SW Germany, skeletons of one smaller and two larger male lions can be reported from the Upper Rhine Valley. Isolated long bones metrics obtained (Figure 23) support the sex identifications of the above-discussed skeletons and single bone remains in most cases. In the statistics for the sex ratio of all material from the Upper Rhine Valley, the skeletons were counted in the individual numbers (MNI, three males), whereas the single bones were counted as bone numbers (NISP). From this, the ratio of 15 females (50%) to 15 males (50%) can be estimated. The right humeri allow a minimum individual number of 11 lion individuals from the Upper Rhine Valley. By the age determination (cf. Smuts et al. 1978), only three bones are from older cubs, most are from adult to high adult animals, whereas

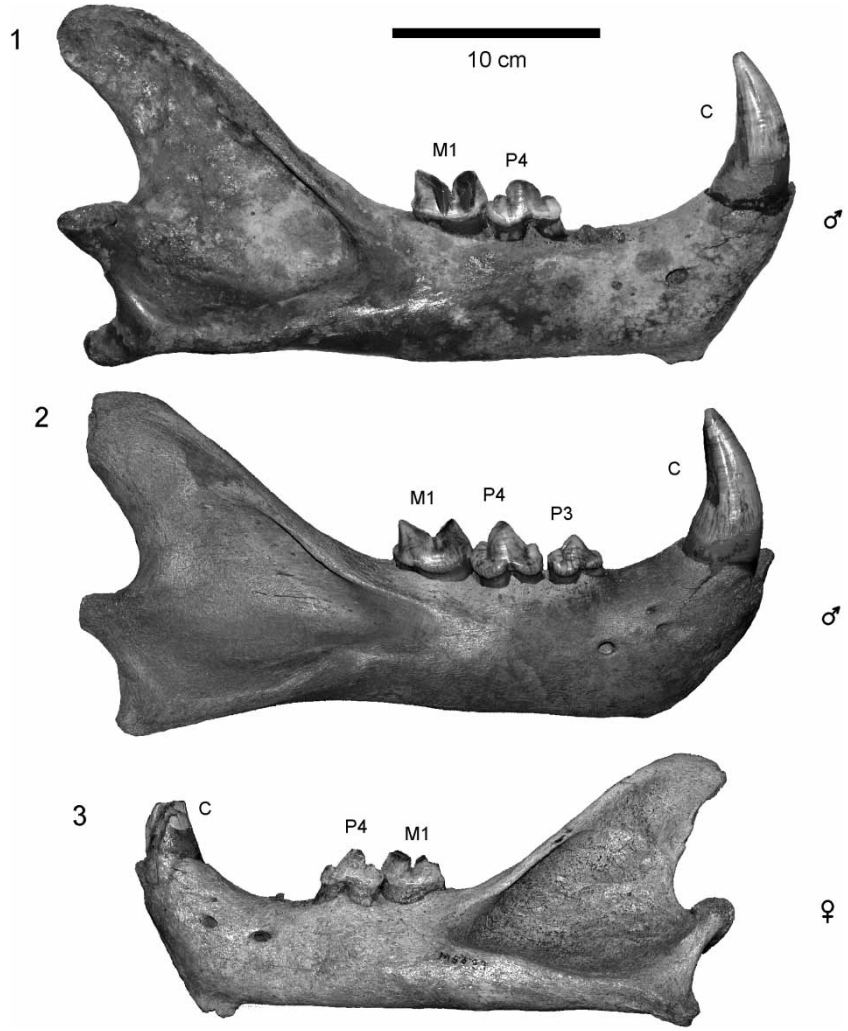

Figure 14. Mandibles from different open-air sites in the Upper Rhine Valley (Germany). (1) Right lower jaw of the adult small male skeleton from Brühl (Koller), Schlangenwinkel (SMNS No. 6616.17.7.81.1), lateral. (2) Right lower jaw of a lion from Lampertheim, In der Tanne (SMNS No. 6316.2.5.84.1), lateral. (3) Left lower jaw of an old lioness from an unknown site in the Upper Rhine Valley (SMF No. M5533), lateral.

several bones and even jaws can be referred to older lions.

Lion bone taphonomy at cave sites

Recently, cave and open-air sites of lion and hyena bone taphonomy studies, especially at newly identified hyena dens (Diedrich 2004–2009, 2010d), indicate lions never to have lived in caves, nor to have protect themselves, nor to have given birth or to have raised cubs there (Diedrich 2007a, 2007b, 2008a, 2008b). Those caves were more or less inhabited by the cave bears (hibernation, cub raising) and Ice Age spotted hyenas (commuting and food storage sites, cub raising). Therefore, lion remains in caves can be explained by two reasons. The first results from the well-known hyena and lion antagonism (Schaller 1972; Joubert and Joubert 2003), where lion carcasses seem to have been imported by hyenas such as other prey remains to their commuting sites, as described for the Perick Caves (Diedrich 2008a, 2008b) and the other from the Sauerland Karst cave sites in NW Germany (Diedrich 2010d). This bone material sometimes is fragmented, shows cracking, chewing or nibbling, and was found in the entrances of caves which were hyena dens.

Lion bone taphonomy in the open environment and the lion–hyena antagonism

The lion remains from the Upper Rhine Valley are only from gravel pits and without good taphonomic context. Therefore, it remains unclear, if bones from those pits were autochthonous or transported and accumulated by hyenas. For the northwestern German Emscher River

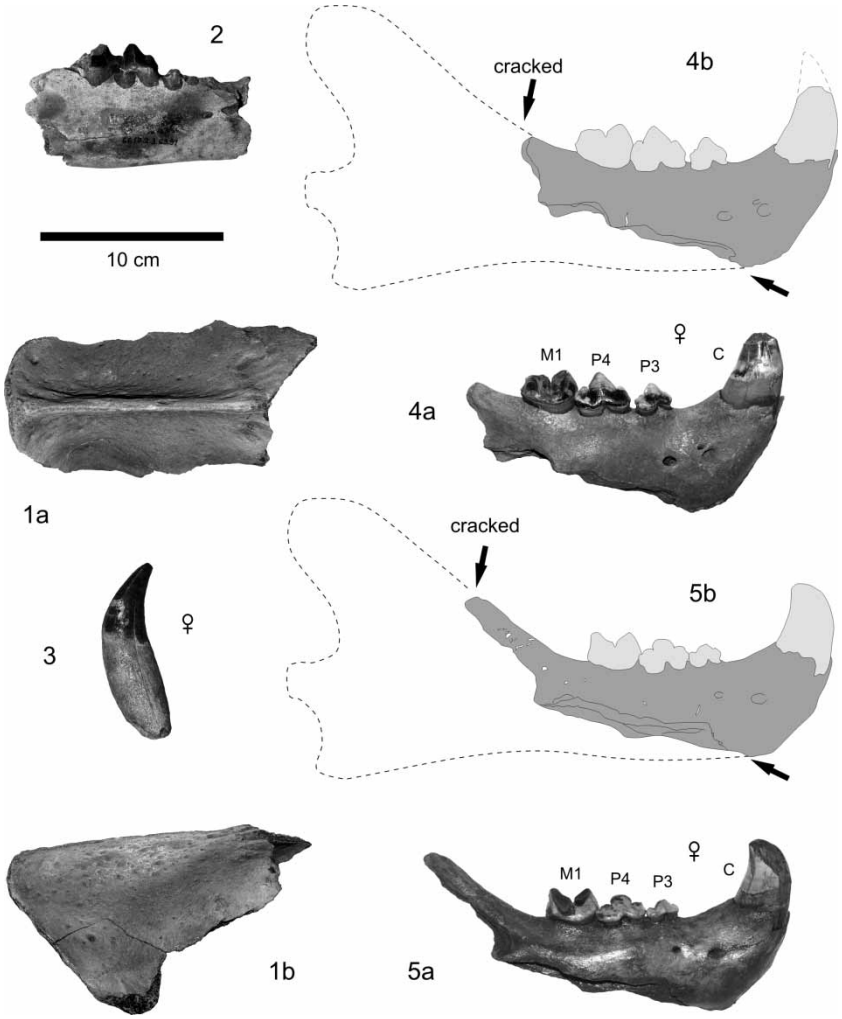

Figure 15. Cranial bones, jaws and teeth from different open-air sites in the Upper Rhine Valley (Germany). (1) Skull fragment from Brühl, Spieswiesen-Ost (SMNS No. 6617.3.1.67.18), (a) dorsal and (b) lateral. (2) Right mandible of a lioness from Brühl, Spieswiesen-West (SMNS No. 6617.2.3.69.91), lateral. (3) Left lower jaw canine of a female from Huttenheim, Huttenheimer Kammer (SMNS No. 6816.5.8.70.1), lateral. (4) Right, by carnivores (hyenas) cracked mandible of a lioness from Heddesheim, Neuwiesen (SMNS No. 6417.1.12.76.1), lateral. (5) Right, by carnivores (hyenas) cracked mandible of a senile lioness from Otterstadt, Altrhein-Süd (SMNS No. 6616.4.9.85.1), lateral.

sites, large amounts of bones also found in gravel pits were attributed recently mainly due to hyena bone accumulations, which were indicated by the hyena bone damages, the best to prove on incomplete woolly rhinoceros bones (Diedrich 2011c). A similar situation seems to be present along the Upper Rhine Valley, but intensive bone taphonomy studies on the herbivorous bones are future projects. Anyway, the presence of hyena skulls and postcranial bones at the lion overlapping sites (Diedrich 2008b) indicates hyena den bone sites, including lion remains. Such bone dumps caused by hyenas on rivers or lakes are also reported from modern African spotted hyenas (e.g. Kruuk 1972; Avery et al. 1984; Estes 1999). From African hyena dens, there are records of lion remains found in between the bone accumulations at hyena communal den sites (Lam 1992; Pokines et al. 2007). Coincidently, similar to the open-air hyena dens of the Upper Rhine River Valley (SW Germany) and the Emscher River (NW Germany), at many of the lion sites, hyena remains also occur (Diedrich 2011d). Especially, in most cases, hyena skulls indicate hyena den sites, which are also proven in Baden-Württemberg at the Upper Rhine River Valley lion sites (Diedrich 2008b). From the Upper Rhine Valley, a few bones are incomplete, similar to that described for different cave sites in Germany (Diedrich 2010b,d), resulting after comparisons with incomplete lion bones from hyena den caves of carnivore and mainly hyena scavenging (Figures 15.4, 15.5, 20.3, 21.1). Very typical for hyena activities are crushed lower jaws of lions, which were figured with several specimens from the Perick Caves hyena den (Diedrich 2009a). Exactly similar

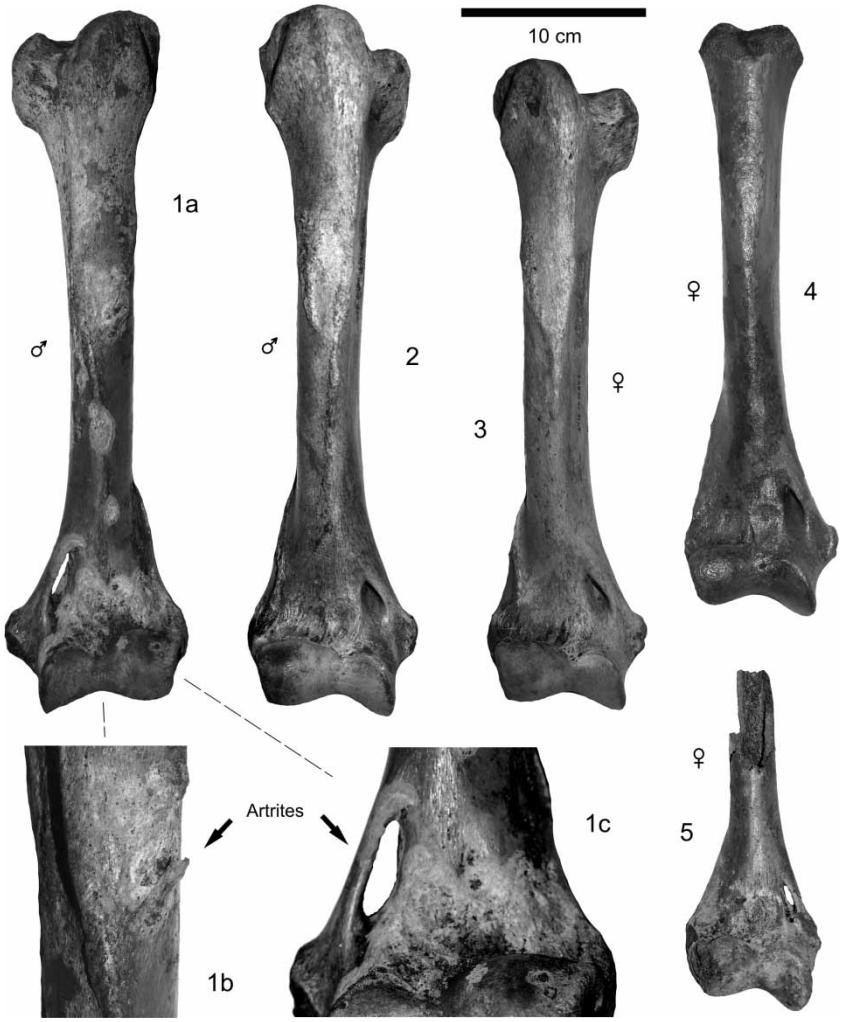

Figure 16. Forelimb bones from different open-air sites in the Upper Rhine Valley (Germany). (1) Left humerus of an adult to senile male from Brühl (Koller), Rheingewann with arthritic ossifications and a very long foramen entepicondylicum (SMNS No. 6616.2.6.89.1), cranial. (2) Right humerus of an adult to senile male from Otterstadt, Waldwiesen (SMNS No. 6616.7.2.87.1), cranial. (3) Left humerus of an adult to senile female from Huttenheim, Sandfeld (SMNS No. 6716.14.11.87.1), cranial. (4) Left humerus of an early adult female from Speyer, Deutschhof (SMNS No. 6616.14.12.83.1), cranial. (5) Right humerus of a late juvenile female from Ketsch, Kreuzwiese (SMNS No. 6617.7.9.62.20), cranial.

cracked mandibles are present from the two Upper Rhine Valley of open-air localities Heddesheim, Neuwiesen (Figure 15.4) and Otterstadt, Altrhein-Süd (Figure 15.5). The incomplete femora from Wiesental, Allmendweg (Figure 20.3) and from Brühl (Koller), Rheingewann (Figure 21.1) were chewed in their joints and have bite scratch marks, but those might have not been caused exclusively by hyenas. Similar bite damages are figured for lion material from the Keppler Cave of the Sauerland Karst (Diedrich 2010d).

The skeleton remains indeed prove, in contrast, that complete carcasses were present at several sites; therefore, *in situ* fossilisation can be proven for some cases. Possibly, such skeletons became fossilised as complete carcasses in similar environmental situations such as the lion of Siegsdorf (Gross 1992) and the lioness of Neumark–Nord (Diedrich 2010c), in which both latter were found in lake or river side branches. The water seems to have protected those carcasses for their destruction, especially from scavenging by hyenas and other predators.

Lion carcass presence at different sites seems to be the result of conflicts at the den itself, when lions, especially ill and weak ones, had to try to steal hyena prey from their commuting site, which was quite dangerous. In such conflicts, lions could have been killed easily. Such examples seem to be the lioness and another young lion from the Srbsko Chlum-Komin hyena den cave (Diedrich 2007a).

Figure 17. Forelimb bones from different open-air sites in the Upper Rhine Valley (Germany). (1) Left humerus of an adult to senile male from Altlussheim, Eichelgarten (SMNS No. 6717.4.7.67.1), cranial. (2) Right humerus of an adult to senile male from Altlussheim, Allmendwiesen (SMNS No. 6717.2.7.65.1), cranial. (3) Right humerus of an adult to senile male from Karlsruhe-Neureut, Kirchfeld-Nord (SMNS No. 6916.3.7.64.1), cranial. (4) Right humerus of an early adult male from Edingen (Brühl), Edinger Ried (SMNS No. 6617.1.4.81.1), cranial. (5) Left ulna of a male from Altlussheim, Silzwiesen (SMNS No. 6616.15.7.73.1), lateral. (6) Right radius from Brühl, Spieswiesen-West (SMNS No. 6617.2.9.67.30), lateral. (7) Right radius from Wörth, Rheinanlagen (SMNS No. 6915.2.12.69.1), lateral. (8) Phalanx 1 from Brühl, Spieswiesen-West (SMNS No. 6617.2.9.67.63), dorsal.

Lion diseases: pathologies

Parietal pathologies on the fossil Pleistocene *P. l. spelaea*, which cannot be observed on the material from the Upper Rhine Valley, were described from different German and Czech localities with the interpretation as the results of fight damages between lions or between lions and hyenas or even with cave bears (Diedrich and Žák 2006; Diedrich 2008a, 2010b).

Postcranial pathologies are described for Pleistocene felids like a tibia that was found in the Upper Rhine Valley (Koenigswald and Schmitt 1987). The pathological tibia presented from another site of the Upper Rhine Valley (Figure 22.3) is strongly deformed and was, therefore, difficult first to define as a lion tibia. This tibia has strong osteoporosis.

A very similar pathological thickening of the processus transverses of a last lumbar vertebra of the lion skeleton of Edingen (Brühl), Edinger Ried (Figure 11.5) was described on a Pleistocene sabre-toothed cat skeleton which was found in the Hurricane Cave, North America (Norman and Youngsteadt 1980). In both felids, nearly a fusion of the processus with the sacrum took place, which happens in older animals.

Comparable pathologies of arthritis and other diseases have been recently studied on the lioness skeleton from Neumark–Nord Lake I, which was about 5–8 years of individual age, and had a broken right hind

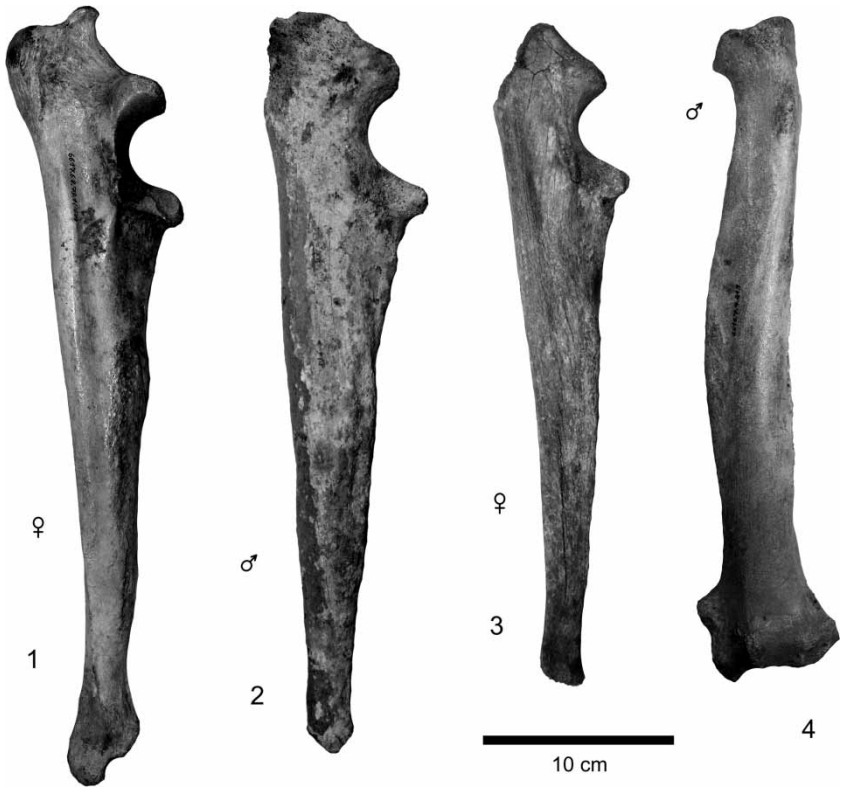

Figure 18. Forelimb bones from different open-air sites in the Upper Rhine Valley (Germany). (1) Right ulna of an adult to senile female from Ketsch, Hohwiesen (SMNS No. 6617.6.8.79.1), lateral. (2) Right ulna of an adult to senile male from Lampertheim, In der Tanne (SMNS No. 6316.2.12.75.1), lateral. (3) Right ulna of an early adult female from Otterstadt, Altrhein-Nord (SMNS No. 6616.16.12.92.1), lateral. (4) Left radius of an adult to senile male from Otterstadt, Waldwiesen (SMNS No. 6616.7.4.81.1), lateral.

leg in healing stage, arthritis or, at least, bone growths on different bones of the right fore limb, and had lost its right canine by a strong maxillary and root inflammation that caused bone deformation and dissolution (Diedrich 2010c).

The lion habitus and fur

In the discussion about the habitus and fur of the subspecies *P. l. spelaea* was speculated on. Selected figurations of Palaeolithic art were not correct in the interpretations (cf. Nagel et al. 2003) of the most important paintings and engravings (Figs. 24A-B). After arguments of Nagel et al. (2003), the lion figurations in Chauvet Cave (see Figure 24(B)) were thought to be 'males'. There is no proof for this because of the lack of the male genitalia drawings, in contrast, the high amount and repeating overlapping figurations (cf. Wehrberger 1994; Chauvet et al. 1995) and even female genitalia fit well to a situation of a lioness pride. Anyway, those are the most important figurations of the last lions of Europe which were more recently argued to prove a steppe lion in Europe by the presence of the tassel (Diedrich 2004) rather than an 'Ice Age tiger'. This 'tiger' which was formerly discussed (Groiss 1996) was finally revised to be of adolescent *P. l. spelaea* individuals of the large Zoolithen Cave lion population (Diedrich 2010b). Also, the most important seems to be the Pal.lithic engraving of the lion in '*en face*' view (cf. Begouen and Clottes 1987; Diedrich 2004). Perfectly showing the typical round felid ears in detail, this lion seems to be a male with a mane, which was artistically made by many small scratches (Figure 24(A)). Therefore, the Late Pleistocene steppe lion *P. l. spelaea* must have been similar in shape and the fur such as the African *P. l. leo*. Both were, respectively, open environment inhabitants, and did not use caves. The Upper Pleistocene lions were present in the open mammoth steppe and also in the boreal forest mountain landscapes of Europe (Diedrich 2010b). Therefore, from the paleobiological point of view, the Late Pleistocene steppe lion seems to have also been a social pride living animal, which was well present in the Upper Rhine Valley during the Upper Pleistocene glacials and interglacials with the mentioned megafaunas, but got extinct from north to south somehow in the latest Upper Pleistocene with the drastic climatic and megafauna change and megafauna prey disappearance (Diedrich 2010e; Stuart and Lister 2010).

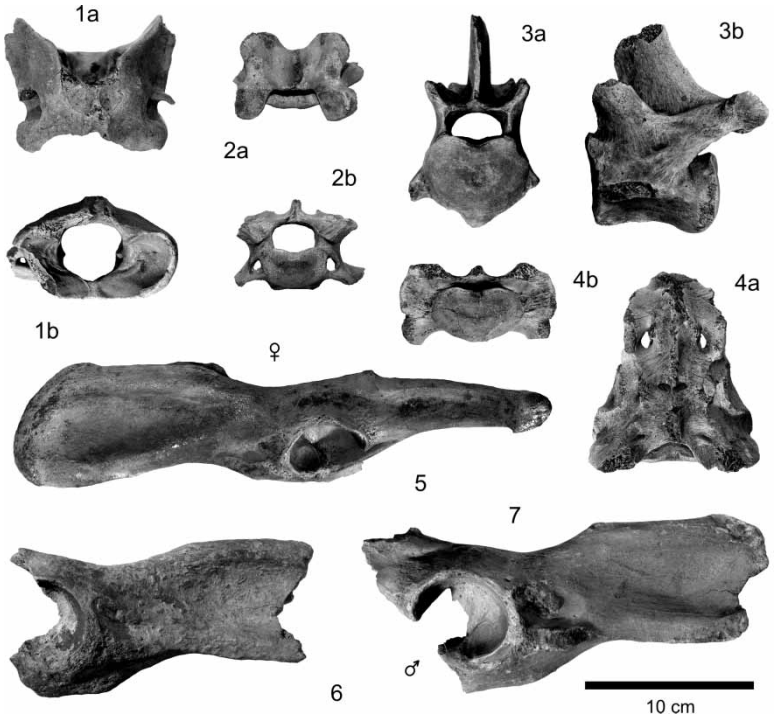

Figure 19. Pelvic bones and vertebrae from different open-air sites in the Upper Rhine Valley (Germany). (1) Atlas of a grown-up animal from Otterstadt, Altrhein-Nord (SMNS No. 6616.16.4.81.1), (a) dorsal and (b) cranial. (2) Cervical vertebra No. 5 of a grown-up animal from Otterstadt, Altrhein-Süd (SMNS No. 6616.4.1.87.3), (a) dorsal and (b) cranial. (3) Lumbar vertebra No. 5 of a grown-up animal from Huttenheim, Huttenheimer Kammer (SMNS No. 6616.5.5.74.7), (a) cranial and (b) lateral. (4) Sacrum of a grown-up animal from Lampertheim, Lüderitzbucht (SMNS No. 6316.3.3.80.1), (a) dorsal and (b) cranial. (5) Left pelvic remain from Otterstadt, Altrhein-Nord (SMNS No. 6616.16.4.81.2), lateral/dorsal. (6) Right pelvic remain from Brühl, Spieswiesen-West (SMNS No. 6617.2.8.83.1), lateral. (7) Right pelvic remain from Otterstadt, Waldwiesen (SMNS No. 6616.8.9.78.1), lateral.

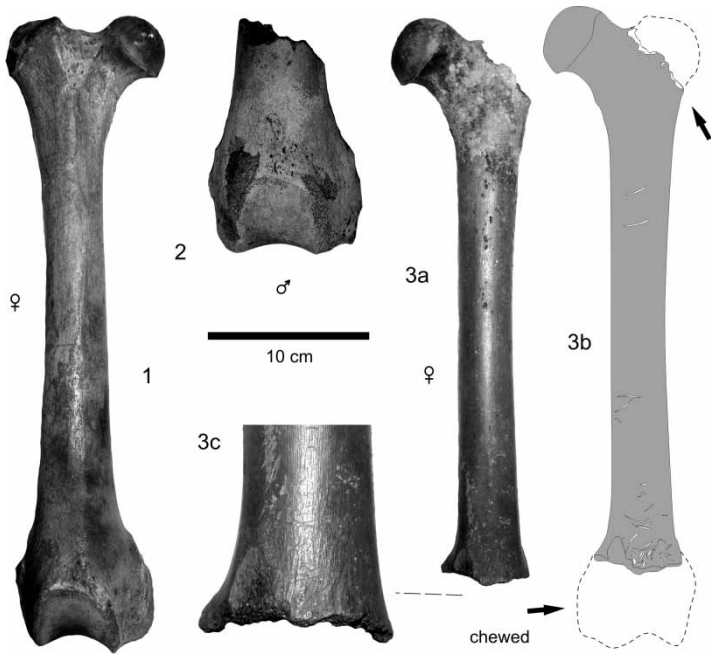

Figure 20. Hindlimb bones from different open-air sites in the Upper Rhine Valley (Germany). (1) Right femur of a lioness from Heddesheim, Neuwiesen (SMNS No. 6417.1.10.76.1), cranial. (2) Right femur of a male from Lichtenau, Hasenkopf (SMNS No. 7213.3.7.76.1), cranial. (3) Left femur of a lioness from Wiesental, Allmendweg (SMNS No. 6717.13.8.83.1), (a) cranial, (b) redrawing with bite marks (white) and (c) detail of the distal part with bite scratches.

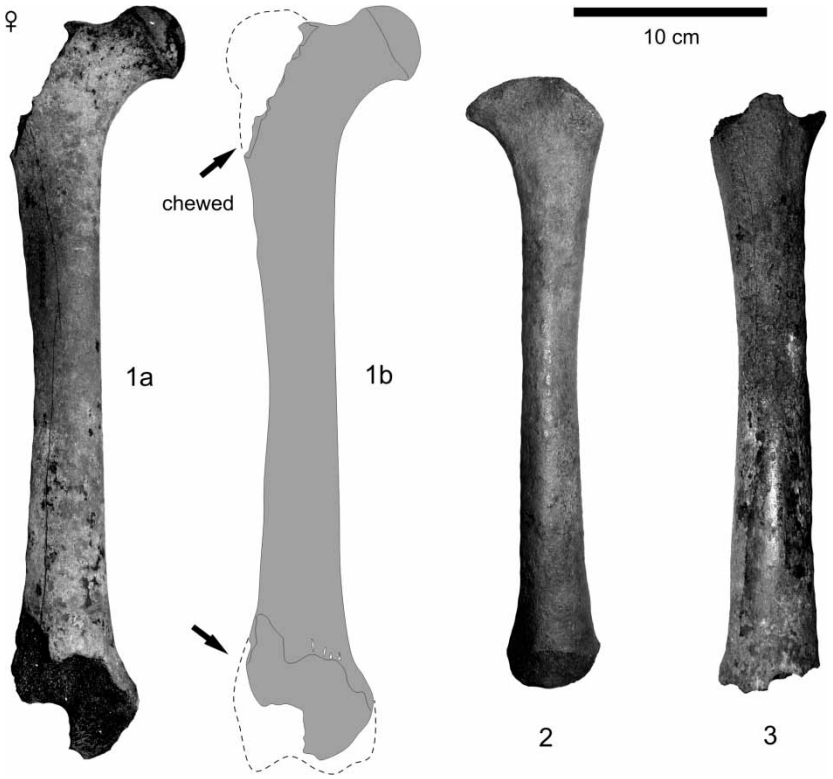

Figure 21. Hindlimb bones from different open-air sites in the Upper Rhine Valley (Germany). (1) Right humerus of a lioness from Brühl (Koller), Rheingewann (SMNS No. 6616.2.6.89.2), cranial. (2) Left femur of a late juvenile animal from Ketsch, Hohwiesen (SMNS No. 6617.6.9.62.7), cranial. (3) Right femur of a grown-up animal from Altrip, Neuhofener Altrhein (SMNS No. 6516.6.5.75.1), cranial.

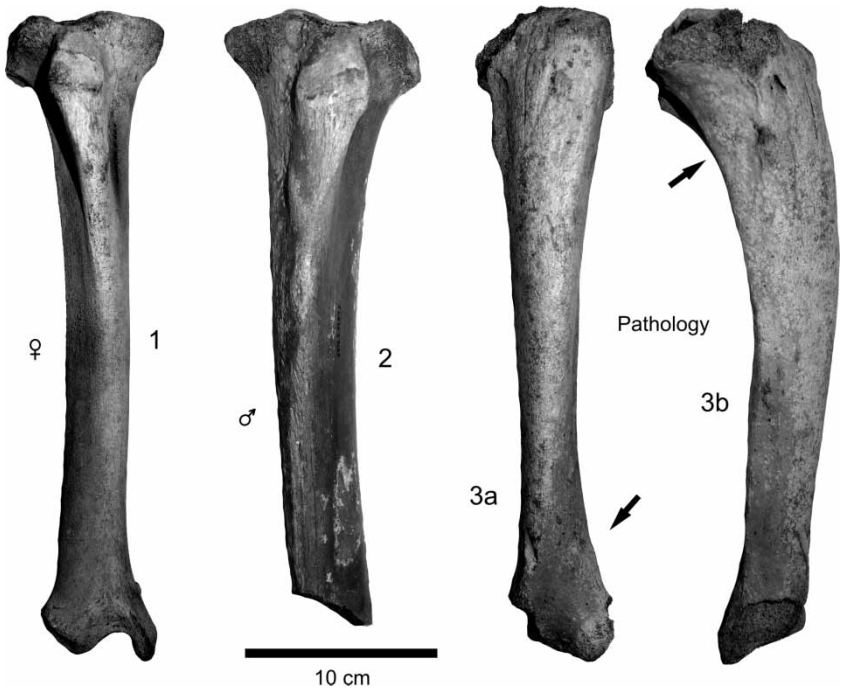

Figure 22. Hindlimb bones from different open-air sites in the Upper Rhine Valley. (1) Right tibia of a grown-up lioness from Speyer, Binsfeld-Südost (SMNS No. 6616.12.6.66.1), cranial. (2) Left tibia of a grown-up lion from Huttenheim, Huttenheimer Kammer (SMNS No. 6816.5.11.87.5), cranial. (3) Pathological (strong osteoporosis) left tibia of a grown-up animal, perhaps a lioness from Wiesental, Viehweg (SMNS No. 6717.12.8.83.1), (a) cranial and (b) lateral.

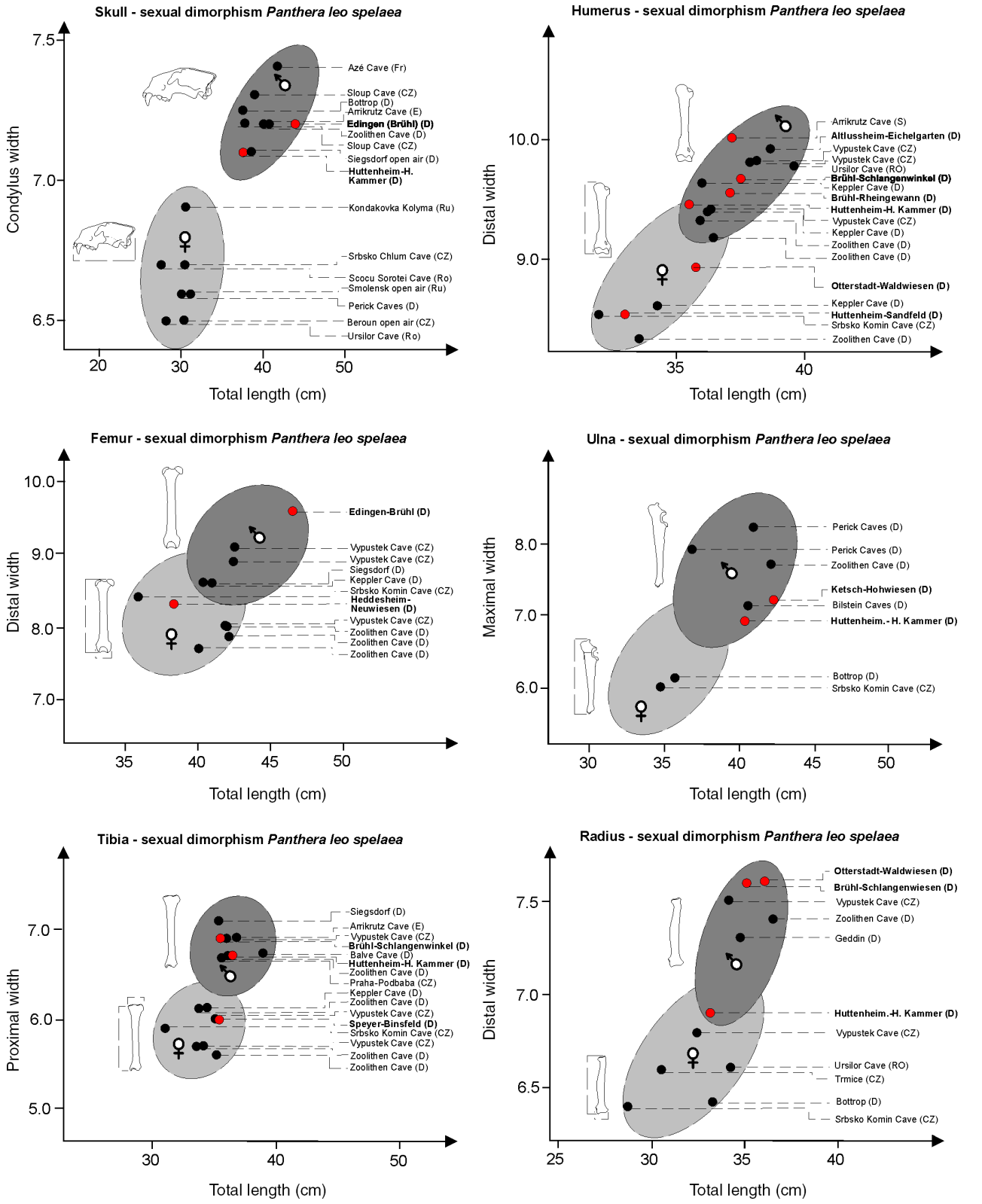

Figure 23. Sexual dimorphism in Upper Pleistocene *P. l. spelaea* from the Upper Rhine Valley (Germany) compared with glacial Late Pleistocene lion remains from Europe (compiled from Diedrich 2010d, 2011b).

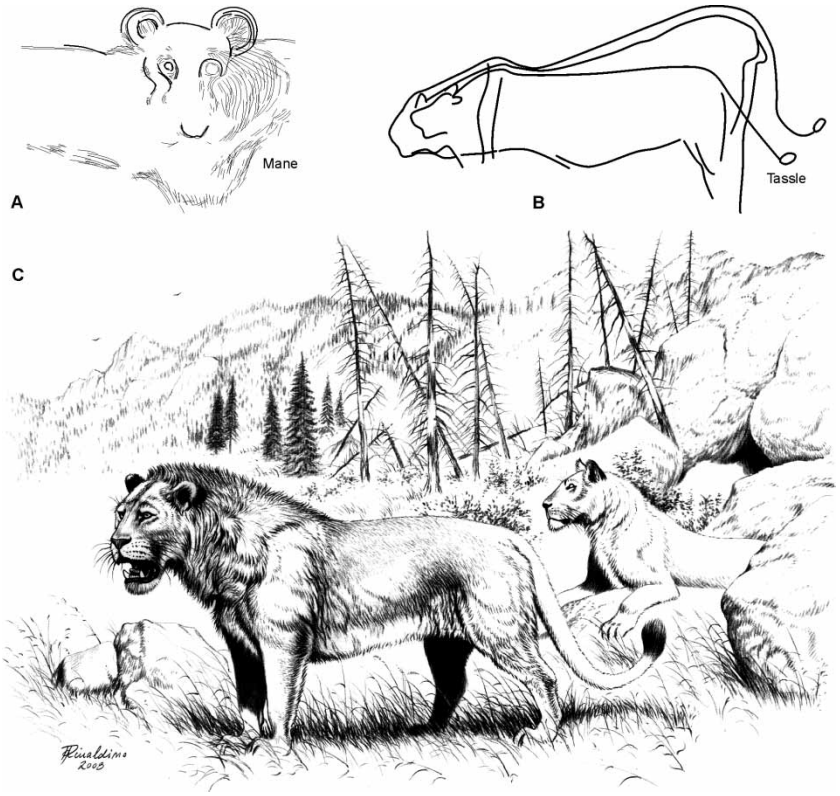

Figure 24. Paleolithic cave art engravings and paintings of *P. l. spelaea* with anatomical details and life reconstruction. (A) *En face* portrait of a male lion with a mane. Engraving in the Trois-Frère cave (France, redrawn from Begouen and Clottes 1987). (B) Outline of the Aurignacien/Gravettien paintings in Chauvet cave of lionesses (France) with presence of the tail tassle typical for lions (redrawn from Chauvet et al. 1995). (C) Illustration of a male and a female steppe lion *P. l. spelaea* on the slope of Black Forest near Baden–Baden looking out into the Rhine River Valley (illustration by G. 'Rinaldino' Teichmann 2008).

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References

Adam KD. 1966. Quartärforschung am Staatlichen Museum für Naturkunde in Stuttgart. Stuttgarter Beiträge zur Naturkunde. 167: 1–14.

Altuna J. 1981. Fund eines Skelettes des Höhlenlöwen (*Panthera leo spelaea* Goldfuss) in Arrikrutz, Baskenland. Bonner zoologische Beiträge. 32(1–2):31–46.

Argant A. 1988. Étude de l′exemplaire de *Panthera spelaea* (Goldfuss, 1810) (Mammalia, Carnivora, Felidae) du gisement Pleistocène moyen recent de la Grotte d′Azé (Saône-et-Loire). Revue de Paléobiologie. 7(2):449–466.

Avery G, Avery DM, Braine S, Loutit R. 1984. Bone accumulation by hyenas and jackals – a taphonomic study. S Afr J Sci. 80:186–187.

Barnett R, Shapiro B, Barnes I, Simon Y, Ho W, Burger J, Yamaguchi N, Thomas F, Higham G, Wheeler HT et al., 2009. Phylogeography of lions (*Panthera leo* ssp.) reveals three distinct taxa and a Late Pleistocene reduction in genetic diversity. Mol Ecol. 18:1668–1677.

Bartz J. 1982. Quartär und Jungtertiär II im Oberrheingraben im Großraum Karlsruhe. Geologisches Jahrbuch A. 63:3–237.

Baryshnikov GF, Boeskorov G. 2001. The Pleistocene cave lion *Panthera spelaea* (Carnivora, Felidae) from Yakutia, Russia. Cranium. 18: 7–4.

Begouen R, Clottes J. 1987. Les Trois Frères after Breuil. Antiquity. 61:180–187.

Berckhemer F. 1927. Neue Funde von Resten eiszeitlicher Löwen aus Württemberg. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg. 83:75–76.

Berckhemer F, Peters E. 1935. Die Irpfelhöhle bei Giengen and der Brenz. Fundberichte aus Schwaben Neue Folge. 8:10–15.

Bona F. 2006. Systematic position of a complete lion-like cat skull from the Eemian ossiferous rubble near Zandobbio (Bergamo, North Italy). Rivista Italiana di Paleontologia e Stratigrafia. 112:157–166.

Böttcher R, Cep B, Kind C-J, Mörike D, Pawlik A, Rähle W, Steppan K-H, Torke R, Torke W, Ziegler R. 2000. Kogelstein – eine paläolithische Fundstelle bei Schelklingen–Schmiechen. Fundberichte aus Baden-Württemberg. 24:1–176.

Chauvet J-M, Deschamps BE, Hillaire C. 1995. Grotte Chauvet. In: Altsteinzeitliche Höhlenkunst im Tal der Ardèche [Palaeolithic cave

art in the valley of the Ardeche]. Thorbecke Speläo 1, Sigmaringen, Germany: Thorbecke-Verlag, p. 120.
Dawkins WB, Sanford WA. 1900. A monograph of the British Pleistocene Mammalia, Vol. I. The British Pleistocene Felidae. Palaeontographical Society Monographs. 1866–1872:1–194.
Diedrich C. 2004. Freilandfunde des oberpleistozänen Löwen *Panthera leo spelaea* (Goldfuss, 1810) in Westfalen (Norddeutschland) [TT]. Philippia. 11(3):219–226.
Diedrich C. 2007a. The fairy tale about the 'cave lions' *Panthera leo spelaea* (Goldfuss, 1810) of Europe – Late Ice Age spotted hyenas and Ice Age steppe lions in conflicts – lion killers and scavengers around Prague (Central Bohemia). Scripta Facultatis Scientiarum Universitatis Masarykianae Geology. 35:107–112.
Diedrich C. 2007b. Upper Pleistocene *Panthera leo spelaea* (Goldfuss, 1810) skeleton remains from Praha–Podbaba and contribution to other lion finds from loess and river terrace sites in Central Bohemia (Czech Republic). Bull Geosci. 82(2):99–117.
Diedrich C. 2008. Upper Pleistocene *Panthera leo spelaea* (Goldfuss 1810) remains from an open air loess bone accumulation and human camp site in Freyburg a. d. U. (Saxony-Anhalt) Jahresschr Mitteldt Vorgesch. 92:9–24
Diedrich C. 2008a. The rediscovered holotypes of the Upper Pleistocene spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) and the steppe lion *Panthera leo spelaea* (Goldfuss, 1810) and taphonomic discussion to the Zoolithen Cave hyena den at Geilenreuth (Bavaria, South-Germany). Zool J Linn Soc Lond. 154:822–831.
Diedrich C. 2008b. Late Pleistocene hyenas *Crocuta crocuta spelaea* (Goldfuss, 1823) from Upper Rhine valley open air sites and the contribution to skull shape variability. Cranium. 25(2):31–42.
Diedrich C. 2009a. Steppe lion remains imported by Ice Age spotted hyenas into the Late Pleistocene Perick Caves hyena den in Northern Germany. Quat Res. 71(3):361–374.
Diedrich C. 2009d. Upper Pleistocene *Panthera leo spelaea* (Goldfuss 1810) remains from the Bilstein Caves (Sauerland Karst) and contribution to the steppe lion taphonomy, palaeobiology and sexual dimorphism. Annales de Paléontologie. 95:117–138.
Diedrich C. 2009e. Cave bear predation by steppe lions in central Europe – and another reason why cave bears hibernated deeply in caves. Abstract, 15th International Cave Bear Symposium, Bratislava, Slovakia. p. 10.
Diedrich C. 2010a. Das Skelett einer kranken Löwin *Panthera leo spelaea* (Goldfuss 1810) und andere männliche Löwenreste aus Neumark–Nord. In: Meller H, editor. Elefantenreich – eine Fossilwelt in Europa [Elephant kingdom – a world in Europe Fossil]. Landesamt für Archäologie Sachsen-Anhalt, Halle-Saale. p. 437–444.
Diedrich C. 2010b. The largest European lion *Panthera leo spelaea* (Goldfuss) population from the Zoolithen Cave, Germany – specialized cave bear predators of Europe. Historical Biology 23(2–3):271–311.
Diedrich C. 2010c. A diseased *Panthera leo spelaea* (Goldfuss 1810) lioness from a forest elephant graveyard in the Late Pleistocene (Eemian) interglacial lake at Neumark–Nord, central Germany. Historical Biology. 2010(4):1–23.
Diedrich C. 2010e. Disappearance of the last hyenas and lions of Europe in the Late Quaternary – a chain reaction of large mammal mammoth and woolly rhino prey extinction. Abstract European Geoscience Union General Assembly, Vienna, Austria.
Diedrich C. 2011a. A Late Pleistocene lion *Panthera leo spelaea* (Goldfuss 1810) skull and other postcranial remains from the Sloup Cave in the Moravian Karst, Czech Republic. Acta Archaeol. 2011, 19–28.
Diedrich C. 2011b. Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss 1810) footprints and bone remains from open air sites in northern Germany – evidence of hyena–lion antagonism in Europe. Quat Sci Rev. 30(2011):1883–1906.
Diedrich C. 2011c. The Late Pleistocene *Crocuta crocuta spelaea* (Goldfuss 1823) population from the Emscher River terrace hyena open air den Bottrop and other sites in NW-Germany – woolly rhinoceros scavengers and their bone accumulations along rivers in lowland mammoth steppe environments. Quat Int (accepted).
Diedrich C. 2011d. Pleistocene *Panthera leo spelaea* (Goldfuss 1810) remains from the Balver Cave (NW Germany) – a cave bear, hyena den and Middle Palaeolithic human cave, and review of the Sauerland Karst lion cave sites. Quaternaire. 22(2):105–127.
Diedrich C, Robu M, Dragusin V, Constantin S, Moldovan O. 2010. New Upper Pleistocene steppe lion skeleton finds between the cave bear hibernation plateaus of the Ursilor Cave bear den, Romania. Abstract 15th International Cave Bear Symposium, Spisska Nova Ves, Slovakia. p. 8–9
Diedrich C, Žák K. 2006. Upper Pleistocene hyena *Crocuta crocuta spelaea* (Goldfuss 1823) prey deposit and den sites in horizontal and vertical caves of the Bohemian Karst (Czech Republic). Bull Geosci. 81(4):237–276.
Estes R. 1999. The safari companion: a guide to watching African Mammals. Vermont: Chelsea Green Publishing Company. p. 459.
Fischer K. 1994. Neufunde von jungpleistozänen Höhlenlöwen *Panthera leo spelaea* (Goldfuss 1810) in Rübeland (Harz). Braunschweiger Naturkundliche Schriften. 4(3):455–471.
Geissert F, Gregor HJ, Rathgeber T. 1986. Molluskenfaunen und Nadelholzfloren aus quartären Ablagerungen des Elsaß und die Säugetierfauna sowie die Nadelholzflora von Huttenheim/Baden nebst Bemerkungen zur Ökologie der Fundstellen. Mitteilungen des Vereins für Naturwissenschaften und Mathematik Ulm/Donau. 34(1985):118–141.
Goldfuss GA. 1810. Die Umgebungen von Muggendorf. Ein Taschenbuch für Freunde der Natur und Altertumskunde [A paperback book for friends of nature and archeology]. Erlangen: JJ. Palm, p. 351.
Groiss T. 1996. Der Höhlentiger *Panthera tigris spelaea* (Goldfuss). Neues Jahrbuch für Geologie und Paläontologie Monatshefte. 1996(7):399–414.
Gross C. 1992. Das Skelett des Höhlenlöwen (*Panthera leo spelaea* Goldfuss 1810) aus Siegsdorf/Ldkr. Traunstein im Vergleich mit anderen Funden aus Deutschland und den Niederlanden, Unpublished Dissertation, Tierärztliche Fakultät der Ludwig-Maximilians-Universität, München, p. 129.
Guzvica G. 1998. *Panthera spelaea* (Goldfuss 1810) from North–Western Croatia. Geologica Croatica. 51(1):7–14.
Harrington CR. 1969. Pleistocene remains of the lion-like cat (*Panthera atrox*) from the Yukon territory and northern Alaska. Can J Earth Sci. 6:1277–1288.
Heller F. 1953. Ein Schädel von *Felis spelaea* Goldfuss aus der Frankenalb. Erlanger geologische Abhandlungen. 7:1–24.
Jäger GF. 1839. Über die Fossilen Säugethiere, welche in Würtemberg in verschiedenen Formationen aufgefunden worden sind, nebst geognostischen Bemerkungen über diese Formationen [About the mammalian fossil animals which have been found in Wurtemberg in various formations, together with geological observations about these formations]. Zweite Abtheilung, Carl Erhard, Stuttgart. p. 4 + 71–214.
Joubert D, Joubert B. 2003. Eternal enemies: lions & hyenas [DVD]. Wildlife Films Botswana for National Geographic, 56 min.
Klähn H. 1922. Ein Fund von *Felis leo* im Löß von Heitersheim i. B., nebst einer variationsstatistischen Untersuchung bezüglich der Stellung des Fossils zu anderen Fossilien. Mitteilungen der Badischen Geologischen Landesanstalt. 9(4):253–366.
Kley A. 1966. Die Höhle bei Aufhausen, Kreis Göppingen. Jahreshefte für Karst- und Höhlenkunde. 6(1965):115–138.
Koenigswald W, von Schmitt E. 1987. Eine pathologisch veränderte Löwentibia aus dem Jungpleistozän der nördlichen Oberrheinebene. Natur und Museum. 117:272–277.
Kruuk H. 1972. The spotted hyena. A story of predation and social behavior. Chicago: Univesity Chicago Press, p. 335.
Lam YM. 1992. Variability in the behavior of spotted hyaenas as taphonomic agents. J Archaeol Sci. 19:389–406.
Nagel D, Hilsberg S, Benesh A, Scholz J. 2003. Functional morphology and fur patterns in recent and fossil *Panthera* species. Scr Geol. 126:227–239.
Norman W, Youngsteadt O. 1980. Prehistoric bear signs and black bear (*Ursus americanus*) utilization of Hurricane River Cave, Arkansas. NSS Bull. 42:3–7.
Pokines JT, Kerbis J, Peterhans CK. 2007. Spotted hyena (*Crocuta crocuta*) den use and taphonomy in the Masai Mara National Reserve, Kenya. J Archaeol Sci. 34:1914–1931.
Rathgeber T. 1982. Neue jungpleistozäne Säugetier-Reste aus der Aufhauser Höhle (Kat.-Nr. 7424/13) bei Geislingen an der Steige

(Schwäbische Alb). Mitteilungen des Verbandes der deutschen Höhlen- und Karstforscher. 28(1):9–12.

Rathgeber T. 1994. Nachweise des pleistozänen Moschusochsen (*Ovibos moschatus*) in Baden-Württemberg. Stuttgarter Beiträge zur Naturkunde Serie B Geologie und Paläontologie. 214:1–36.

Rathgeber T, Ziegler R. 2003. Die Säugetiere im Quartär von Baden–Württemberg [The mammals Baden–Wurttemberg]. Die Säugetiere Baden–Württembergs, 1: Allgemeiner Teil, Ulmer-Verlag, Stuttgart. p. 97–139.

Schaller G. 1972. The Serengeti Lion. A study of predator–Prey relations. Chicago (IL): University of Chicago Press. p. 494.

Smuts GL, Anderson JL, Austin JL. 1978. Age determination of the African lion (*Panthera leo*). J Zool. 185:115–148.

Stuart AJ, Lister AM. 2010. Extinction chronology of the cave lion *Panthera spelaea*. Quat Sci Rev (in press).

Tichy G. 1985. Über den Fund eines Höhlenlöwen (*Panthera felis spelaea* Goldfuss) aus dem Tennengebirge bei Salzburg. Mitteilungen der Gesellschaft für Salzburger Landeskunde. 125:845–864.

Turner A. 1984. Dental sex dimorphism in European lions (*Panthera leo* L.) of the Upper pleistocene: palaeoecological and palaeoethological implications. Ann Zool Fenn. 21:1–8.

Wehrberger K. 1994. Raubkatzen in der Kunst des Jungpaläolithikums. In: M. Ulmer, editor. Der Löwenmensch. Sigmaringen, Germany: Thorbecke Verlag. p. 53–76.

Ziegler R. 1994. Löwen aus dem Eiszeitalter Süddeutschlands. In: M. Ulmer, editor. Der Löwenmensch. Sigmaringen, Germany: Thorbecke Verlag. p. 47–52.

Ziegler R. 1996. Die Großsäuger aus der Frühwürm-zeitlichen Fauna von der Villa Seckendorff in Stuttgart-Bad Cannstatt. Stuttgarter Beiträge zur Naturkunde Serie B Geologie und Paläontologie. 237:1–67.

Ziegler R, Dean D. 1998. Mammalian fauna and biostratigraphy of the pre-Neandertal site of Reilingen, Germany. J Hum Evol. 34(5): 469–484.