Chapter 4
Uncertain Averaptoran Theropods

4.1 Introduction

Several theropods have been briefly described and assigned to the clade Dromaeosauridae. However, some of these taxa may be excluded from such theropod group, based on several osteological features. Regrettably, most of these taxa were only briefly described, or are rather fragmentary, and consequently a complete cladistic analysis is beyond the present article. However, some comments about salient features of each of these taxa are here performed in order to determine their possible phylogenetic positions:

4.2 *Luanchuanraptor henanensis*

This taxon was described by Lu et al. (2007) on the basis of a poorly preserved skeleton from the Late Cretaceous of China. These authors included *Luanchuanraptor* within Dromaeosauridae on the basis of teeth without constriction at base, stalked parapophyses on dorsal vertebrae, and elongate caudal prezygapophyses. However, as previously discussed by Agnolín and Novas (2011), teeth without constrictions at base is a widespread plesiomorphic condition among theropods and is not diagnostic of Dromaeosauridae. Moreover, the presence of stalked parapophyses was also considered by Agnolín and Novas (2011) as diagnostic of Paraves, rather than Dromaeosauridae. Regarding elongate prezygapophyses of caudal vertebrae, Lu et al. (2007) remarked that in *Luanchuanraptor* each prezygapophyses is shorter than in remaining Dromaeosauridae, thus, this theropod shows the typical condition seen in most paravians, in which prezygapophyses span less than half of the preceeding vertebra. In the same way, *Luanchuanraptor* differs from dromaeosaurids and resembles averaptorans in the enlarged deltopectoral crest on humerus, cervical epipophyses shorter than postzygapophyses (see Agnolín and Novas 2011), and ilium without supracetabular crest and reduced antitrochanter (see above; Burnham 2008). This combination of traits allow us to assign *Luanchuanraptor* to Averaptora. Moreover, this genus shows a large fenestra on the coracoid, a synapomorphic condition of Microraptoria (Zheng et al. 2009), suggesting the assignment of *Luanchuanraptor* to that clade.

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4.3 *Hulsanpes perlei*

It was described by Osmólska (1982) on the basis of a single and incomplete foot from the Latest Cretaceous of Mongolia. This taxon was referred with doubts to Dromaeosauridae by Osmólska (1982), a criteria followed by Norell and Makovicky (2004). On the other hand, Currie (2000) indicated that on the basis of the absence of dromaeosaurid apomorphies in the type and only known specimen, *Hulsanpes* may be excluded from Dromaeosauridae, and this author suggested that it may belong to another raptor-like clade. In fact, *Hulsanpes* differs from dromaeosaurids in having poorly excavated distal end of metatarsals II, III, and IV lacking of a ginglymoid articular end (Norell and Makovicky 2004). Moreover, phalanx 2-II lacks the extensive posteroventral heel typical of dromaeosaurids, being craniocaudally shorter, as occurs in basal birds (e.g. *Jeholornis*, *Archaeopteryx*; Paul 2002; Agnolín and Novas 2011). Moreover metatarsal III is proximally pinched, a diagnostic trait of Averaptora (see above), and its metatarsals are extremely gracile, as occurs in most Avialae (Xu and Zhang 2005). In this way, the morphology of the foot of *Hulsanpes* suggests its exclusion from Dromaeosauridae, being here considered as an uncertain Averaptora.

4.4 *Shanag agile*

It comes from the Lower Cretaceous of Mongolia based on a single specimen that includes an incomplete maxilla and dentary corresponding to of a very small theropod. Turner et al. (2007b) considered *Shanag* as a very basal dromaeosaurid, at a basal polytomy together with microraptorans and velociraptorines, and they noted some features reminiscent to Unenlagiidae. *Shanag* was not included in most ulterior phylogenetic analyses due to its incomplete and poorly informative nature. Nevertheless, the morphology of the putative maxillary fenestra in *Shanag* is clearly different from that of other dromaeosaurids. In *Shanag* this opening differs from that of dromaeosaurids (e.g. *Velociraptor*, *Deinonychus*; Ostrom 1969; Barsbold and Osmolska 1999) in being very reduced and anteroposteriorly short, and being located anteriorly (Fig. 4.1). Moreover, Turner et al. (2007b) indicate that the absence of a promaxillary fenestra was an autapomorphy of *Shanag*, a condition that is considered as diagnostic of Neotheropoda (see Rauhut 2003). In this way, there is some evidence that allow proposing a different interpretation of *Shanag* anatomy. In most paravians the promaxillary fenestra is a slit-like anteriorly located opening (Witmer 1997; Senter et al. 2010), being very similar in shape and position to the structure interpreted by Turner et al. (2007b) as the maxillary fenestra. Moreover, the interpretation of Turner et al. (2007b) of the putatively reduced cranial portion of the antorbital fossa is clearly more reminiscent to the anterior rim of the large maxillary fenestra exhibited by basal Avialae and related taxa (e.g. *Archaeopteryx, Anchiornis, Xiaotingia*; Mayr et al. 2007; Hu et al. 2009; Xu

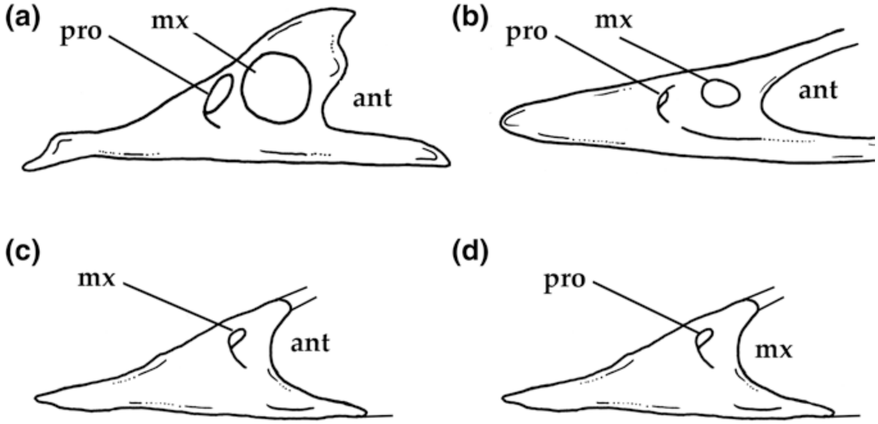

Fig. 4.1 Left maxillae of selected paravians. **a** *Archaeopteryx lithographica*; **b** *Velociraptor mongoliensis*; **c** *Shanag agile* as interpreted by Turner et al. (2007); **d** *Shanag agile* as interpreted here. **a–b** Modified from Senter et al. (2010); **c–d** modified from Turner et al. (2007). Not to scale

et al. 2011). In this way, we reinterpret the antorbital fossa and maxillary fenestra of Turner et al. (2007b) as the anterior rim of the maxillary fenestra and the promaxillary fenestra respectively (Fig. 4.1). *Shanag* was referred to Dromaeosauridae by Turner et al. (2007b) on the basis of large maxillary and dentary teeth, a straight, parallel-sided dentary, and a dorsally displaced maxillary fenestra recessed in a caudodorsally directed depression. However, teeth size of *Shanag* is not different from basal Aves (e.g. *Archaepteryx*; Mayr et al. 2007), troodontids (Sues and Averianov 2008), and microraptorans (Xu 2002), and the morphology of the dentary is clearly more widespread among theropods than previously thought, being widely distributed among basal birds (Zhou et al. 2009; Hu et al. 2010; Agnolín and Novas 2011). Turner et al. (2007b) indicate that *Shanag* resembles Unenlagiidae on the basis of nutrient foramina on external surface of the dentary lying within a deep groove (character 71-1 of Turner et al. 2007b). Regrettably, the presence of such foramina is clearly widespread among paravians, being present in troodontids, basal averaptorans, *Anchiornis*, and *Archaeopteryx* (Agnolín and Novas 2011). On the other hand, *Shanag* shows some features that suggest that this genus may be included within Averaptora, and even among Avialae. *Shanag* exhibits an anteriorly tapering and triangular maxilla, a feature also present in the basalmost avialan *Archaeopteryx* (Turner et al. 2007b) and *Anchiornis* (Hu et al. 2009) and *Xiaotingia* (Xu et al. 2011). In addition, the maxilla of *Shanag* contributes to the narial border and the caudal margin of the narial opening overlaps the rostral border of the antorbital fossa, both features present also in *Archaeopteryx*, but absent in dromaeosaurids (Turner et al. 2007b). Moreover, maxillary teeth show labial longitudinal sulci, a condition seen in microraptorans and unenlagiids (Gianechini et al. 2009; Gianechini and Apesteguía 2011), and anterior maxillary teeth are devoid of serrations, a condition present in microraptorans, unenlagiids, and basal birds (Xu 2002; Agnolín and Novas 2011). Finally, if correctly reinterpreted, the enlarged and rounded maxillary fenestra is a condition which *Shanag* shares with *Anchiornis* and *Archaeopteryx* (Mayr et al. 2007; Hu et al. 2009). In sum, available information suggest *Shanag* as a basal member of Averaptora.

4.5 *Tianyuraptor ostromi*

It was described by Zheng et al. (2009) on the basis of a nearly complete skeleton from the Lower Cretaceous of Liaoning, China. In the strict consensus of the phylogenetic analysis conducted by Zheng et al. (2009) *Tianyuraptor* appears within a polytomy at the base of Dromaeosauridae. Its referral to Dromaeosaridae was based on two features actually present in a wide array of paravians (i.e. dorsal arch of manual ungual I and elongate caudal prezygapophyses and chevrons; Agnolín and Novas 2011). *Tianyuraptor* was considered by Zheng et al. (2009) as a Microraptoria, on the basis of three shared features with members of that clade: laterally sculpted maxilla, shortened manual phalanx III-2, and spatulate pubic symphysis. A sculpted maxilla may constitute a synapomorphy uniting *Tianyuraptor* and Microraptoria, but the remaining features deserve the following comments: the shortened proportions of phalanx III-2 is a condition seen in a wide array of basal avians, including *Archaeopteryx, Jeholornis, Confuciusornis,* and *Anchiornis* (Campbell 2008; Zhou and Zhang 2002; Chiappe et al. 1999; Hu et al. 2009), thus it appears to be more widespread than suggested by Zheng et al. (2009). In regards with the presence of a spatulated pubic boot, it is a condition not only present in microraptorians, but also in basal birds, such as *Anchiornis, Archaeopteryx, Rahonavis, Jeholornis,* and *Confuciusornis* (Forster et al. 1998; Zhou and Zhang 2002, 2003b; Paul 2002; Mayr et al. 2007; Hu et al. 2009). In addition, *Tianyuraptor* lacks several microraptorian apomorphies (see Xu and Wang, 2004), suggesting that this taxon is outside Microraptoria (Zheng et al. 2009). Moreover, as recognized by Zheng et al. (2009) *Tianyuraptor* shows some traits more derived than microraptorans, that are present in unenlagiids and avialans, including an elongate preacetabular process of ilium and strongly concave posterior ischial margin. In sum, we interpret *Tianyuraptor* as an averaptoran of uncertain position.

4.6 *Mahakala omnogova*

It is a small paravian described by Turner et al. (2007a) on the basis of an incomplete skeleton collected in Campanian beds from Mongolia. This minute theropod was summarily described, and in most analyses appears occpying a basal position within Dromaeosauridae, either forming a polytomy with Microraptoria, Unenlagiidae, and with the remaining dromaeosaurids or Eudromaeosauria (Xu et al. 2008; Longrich and Currie 2008), or as the basalmost Dromaeosauridae (Turner et al. 2007a, 2011). Although *Mahakala* is not included in the present analysis, the phylogenetic position inferred by all those authors implies averaptoran affinities for this taxon. Turner et al. (2007a) recognized many features from which *Mahakala* differed from other dromaeosaurids, including a broad ulna, reduced cuppedicus fossa on ilium, vaulted braincase, fibula not contacting distal tarsals, and minute size. Among these traits, a broad ulna, reduced cuppedicus fossa on ilium, and vaulted braincase are features usually regarded as avialan synapomorphies (Senter et al. 2004; Novas 2004), and a broad ulna is also present in microraptorans (Paul 2002). In addition, a distally reduced fibula, lacking contact with distal tarsals is synapomorphic of birds more derived than *Confuciusornis* (i.e. Ornithothoraces). Moreover, *Mahakala* lacks several dromaeosaurid synapomorphies, including elongate prezygapophyses and chevrons on caudal vertebrae (Turner et al. 2007a). In the same way, *Mahakala* resembles derived averaptoran taxa, such as *Buitreraptor* and *Rahonavis* in having a longitudinal groove or ridge near the neurocentral suture of the lateral surface of middle caudal vertebrae, non opisthopubic pelvis, and pubis shorter than femur (Xu et al. 2010). In addition, Turner et al. (2011) reported several features that *Mahakala* shares with averaptorans and avialans, different from the condition seen in dromaeosaurids. Among these features are the presence of small and numerous teeth devoid of carinae and serrations, weakly curved anterior margin of supratemporal fossa, double squamosal articulation for the quadrate, very large foramen magnum, cervical ribs fused to cervical vertebrae, scapula strongly tapering distally, reduced calcaneum, very short and distally located metatarsal I, and elongate pedal phalanges. All these features are present in more derived taxa, including basal birds, such as *Archaeopteryx* and *Rahonavis*, as recognized by Turner et al. (2011). Moreover, *Mahakala* also shows some features that are present in some basal averaptorans and birds, but are absent in dromaeosaurids. As for example, *Mahakala* resembles *Rahonavis* in having caudal prezygapophyses transversely expanded, posterior caudals with a longitudinal lateral ridge (a condition also reported in *Buitreraptor* and *Microraptor*; Hwang et al. 2002; Makovicky et al. 2005), mound-like trochanteric shelf on femur (also present in *Microraptor* and *Buitreraptor*; Hwang et al. 2002; Makovicky et al. 2005), proximally unconstricted metatarsal III, and distal end of metatarsal II without distal flexor pits (see Turner et al. 2011). Moreover, *Mahakala* shares with *Buitreraptor* the everted dorsal margin of the postacetabular blade of ilium, a condition previously thought to be unique of *Buitreraptor* (Gianechini and Apesteguía 2011). In this way, there is an extensive list of features suggesting that *Mahakala* is more nearly related to averaptorans and birds than previously thought.

Mahakala was referred to Dromaeosauridae by Turner et al. (2007a) on the basis of an accessory tympanic recess dorsal to the crista interfenestralis on the braincase, elongate paroccipital processeses with parallel dorsal and ventral margins that twist rostrolaterally distally, and the presence of a ginglymoid distal metatarsal II. However, as detailed by Paul (2002) the morphology of paraoccipital processes in *Archaeopteryx* and dromaeosaurids show a nearly identical morphology (see also Martin 1991). Moreover, the absence of an accessory dorsal tympanic recess is also seen in a wide variety of taxa, including carnosaurs, *Tyrannosaurus,* ornithomimids and troodontids (Turner et al. 2011). Moreover, in most basal averaptorans and birds (with the exception of *Archaeopteryx*, in which this recess is certainly present; Walker 1985; Xu 2002) the absence or presence of such recess cannot be observed due to deficient preservation of specimens. The morphology of disal metatarsal II is more widespread than previously thought, and its distribution is equivocal among Paraves (Agnolín and Novas 2011). More recently, Turner et al. (2011) added new characters that prompted the inclusion of *Mahakala* within Dromaeosauridae: anterior cervical centrum extends beyond the posterior limit of the neural arch, stalk-like parapophyses on dorsal vertebrae, and anterior tympanic recess anteriorly located. However, the extension of the cervical centrum with respect to the neural arch is a feature that appears to be very variable along the cervical vertebrae of paravians, and was dismissed as a dromaeosaurid synapomorphy by Agnolín and Novas (2011). In *Mahakala* the stalk-like parapophyses of dorsal vertebrae differs from that of dromaeosaurids on the extremely short pedicel (Turner et al. 2011), resembling in this way, *Confuciusornis* and more derived birds (Agnolín and Novas 2011). Moreover, pedunculated parapophyses were considered by Agnolín and Novas (2011) as diagnostic of more inclusive clades, probably Maniraptora. In this way, the only feature that stands as a probable synapomorphy uniting *Mahakala* with dromaeosaurids is the anteriorly placed anterior tympanic recess (Turner et al. 2011). However, it must be noted that tympanic information is not available for several basal averaptorans, including Microraptoria, Unenlagiidae, *Anchiornis* and *Xiaotingia*, as well as, most basal birds. This tends to blur the synapomorphic condition of such anatomical trait.

Concluding, the absence of clear dromaeosaurid synapomorphies in join with the presence of derived averaptoran and avialan traits (e.g. reduced cuppedicus fossa on ilium, distally reduced fibula) support averaptoran, and even avialan affinities for *Mahakala*.

4.7 *Jinfengopteryx elegans*

This taxon was described on the basis of a nearly complete specimen from the Lower Cretaceous of China (Ji et al. 2005). *Jinfengopteryx* was interpreted as a basal avialan, probably related with *Archaeopteryx* (Ji et al. 2007; Yuan 2008), as coming from the Lower Cretaceous of China. This theropod was lately considered by Xu and Norell (2004) as belonging to the Troodontidae, based mainly on skeletal proportions and tooth morphology. More recently, Turner et al. (2007a) reinforced the troodontid affiliation of *Jinfengopteryx* on the basis of an extensive phylogenetic analysis. These authors, in an Adam′s consensus tree obtained from 1296 MPTs resulted in a single tree with a nearly fully resolved topology that nested *Jinfengopteryx* within Troodontidae. However, if a Strict Consensus is applied on the analysis of Turner et al. (2007a) *Jinfengopteryx* s excluded from

Troodontidae, but results part of a large polytomy within Paraves. In spite of such methodological incongruences, we will analyze the putative troodontid synapomorphies shared by *Jinfengopteryx* with in remaining troodontids. Turner et al. (2007a) indicated several traits (their characters 21-1, 48-1, 51-1, 70-1, 71-1, 85-1, 89-1, 127-1, 203-1, 208-1, 224-1, 225-1, 229-1) as diagnostic of Troodontidae. But, characters 48-1, 51-1, 85-1, 127-1, 224-1, 225-1 and 229-1 are not observable in the holotype of *Jinfengopteryx*. Character 21-1 of Turner et al. (2007a) consists in the presence of a flat internarial bar. This condition, however is not only present in troodontids, but also in *Anchiornis* and *Archaeopteryx*, being unknown in unenlagiid specimens. Thus, its phylogenetic significance is up to now uncertain. The presence of a subtriangular dentary (character 70-1), a row of nutrient foramina that lie within a deep groove at lateral face of dentary (character 71-1), and anterior dentary teeth closely appressed (character 89-1) were considered as widespread among paravians, and were not recovered as diagnostic of any paravian clade (Agnolín and Novas, 2011). The presence of a subarctometatarsalian pes (character 203-1) is currently considered diagnostic of the node Paraves (Agnolín and Novas 2011). Finally, another trait considered by Turner et al. (2007a) as a diagnostic trait of Troodontidae not shared with *Jinfengopteryx* is the asymmetrical foot (character 208-1). However, the foot of *Jinfengopteryx* is very poorly preserved, and only the proximal end of metatarsals has been preserved, being thus the condition of the foot in *Jinfengopteryx* remains uncertain. Besides *Jinfengopteryx* shows derived averaptoran traits, including minute body size, elongate forelimbs (Turner et al. 2011), very elongate metacarpal I, short and unspecialized pedal digit II, short ischial peduncle of ischium, and thin ischial shaft (Ji et al. 2005; Ji and Ji 2007; Yuan 2008; see above). However, *Jinfengopteryx* shows some plesiomorphic traits when compared with other averaptorans, including a distally expanded scapula and short forelimbs. In this way, due to the equivocal skeletal features exhibited by *Jinfengopteryx*, this theropod is here excluded from Troodontidae and it is interpreted as Averaptora *incertae sedis*.

4.8 *Unquillosaurus ceiballi*

It was described by Powell (1979) on the basis of a large pubis of an indeterminate carnosaurian theropod coming from the Late Cretaceous of NW Argentina. Latter, *Unquillosaurus* was considered as a derived paravian by Novas and Agnolín (2004), and as a dromaeosaurid (Norell and Makovicky 2004). However, *Unquillosaurus* lacks any apomorphic feature that may allow its referral to Dromaeosauridae. Recently, Carrano et al. (2012) considered that *Unquillosaurus* belongs to Carcharodontosauridae. They indicated that the distal end of the pubis is strongly abraded, and when complete may have an anteroposteriorly extended distal pubic boot. However, although abraded, the anterior margin of the pubis of Unquillosaurus clearly indicates that the pubis lacks its anterior projection. Moreover, the distally thin pubic boot is a condition that allows inclusion of

Unquillosaurus within Coelurosauria, clearly differing from the morphology seen in Carcharodontosauridae (Benson et al. 2010). On the contrary, *Unquillosaurus* resembles averaptorans in having a reduced pubic symphysis and an anteroposteriorly short pubic boot, without well developed anterior projection, a condition shared with microraptorans and basal birds as *Archaeopteryx* and *Jeholornis*. Moreover, *Unquillosaurus* shows a reduced ischial process of pubis, a condition reminiscent of Unenlagiidae and Avialae (see above). In this way, it is probable that *Unquillosaurus* may represents a very large member of the Averaptora.

4.9 *Pamparaptor micros*

This minute theropod was described as an unenlagiid by Porfiri and collaborators (2011). The specimen consist on an incomplete foot of a small theropod dinosaur. Porfiri et al. (2011) interpreted *Pamparaptor* as an unenlagiid because it shares several common features with *Neuquenraptor* (considered here as a junior synonym of *Unenlagia*), including subarctometatarsal metatarsus, metatarsal IV with a posterolateral flange, proximal half of metatarsal III with an extensor sulcus, and metatarsal II with a lateral expansion over the caudal surface of metatarsal III. However, as pointed out by Agnolín and Novas (2011; see above) all these features are probably more widespread than previously thought, and their status as unenlagiid or dromaeosaurid synapomorphies are discussable. In this way, we consider *Pamparaptor* as an Averaptora *incertae sedis*, until more complete and detailed analysis of the specimen became available.

4.10 European Dromaeosaurids

Makovicky et al. (2005; SI) suggested that some European dromaeosaurids may be included within Unenlagiidae. However, the scanty material belonging to European dromaeosaurids does not particularly resemble those of derived averaptorans, including unenlagiids. For example, *Pyroraptor olympus* Allain and Taquet (2000), from the Latest Cretaceous of France retains a plesiomorphically short ulna, and the phalanx 2-II lacks the weak heel seen in unenlagiids and basal birds, exhibiting a well developed and symmetrical structure comparable to that seen in typical dromaeosaurids (Longrich and Currie 2008; Agnolín and Novas 2011). The genus *Variraptor mechinorum* Le Loeuff and Buffetaut (1998) from the Upper Cretaceous of France, shows a plesiomorphic sacrum with only five coosified vertebrae, cervical vertebrae with very large epipophyses and a robust and stout humerus with a cranially oriented deltopectoral crest, a combination of plesiomorphic traits not seen in any known averaptoran. Moreover, all known dromaeosaurid-like teeth recovered from several fossil localities of Jurassic and Cretaceous ages in Europe (e.g. Buffetaut et al. 1986; Canudo et al. 1997; Zinke 1998; Rauhut

2002) lack the synapomorphic traits seen in unenlagiids, such as absence of serrations in anterior and posterior carinae, and presence of longitudinal sulci along the teeth crowns (Ezcurra 2008; Gianechini et al. 2009; Gianechini and Apesteguía 2011). Concluding, most (if not all) remains of European dromaeosaurid-like specimens lack derived traits that may unite them with Unenlagiidae among averaptoran theropods.

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